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Late Ediacaran occurrences of the organic-walled microfossils *Granomarginata* and flask-shaped *Lagoenaforma collaris* gen. et sp. nov.

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Abstract

New occurrences of flask-shaped and envelope-bearing microfossils, including the predominantly Cambrian taxon *Granomarginata*, are reported from new localities, as well as from earlier in time (Ediacaran) than previously known. The stratigraphic range of *Granomarginata* extends into the Cambrian System, where it had a cosmopolitan distribution. This newly reported Ediacaran record includes areas from Norway (Baltica), Newfoundland (Avalonia) and Namibia (adjacent to the Kalahari Craton), and puts the oldest global occurrence of *Granomarginata* in the Indreelva Member (< 563 Ma) of the Stáhpogieddi Formation on the Digermulen Peninsula, Arctic Norway. Although *Granomarginata* is rare within the assemblage, these new occurrences together with previously reported occurrences from India and Poland, suggest a potentially widespread palaeogeographic distribution of *Granomarginata* through the middle–late Ediacaran interval. A new flask-shaped microfossil *Lagoenaforma collaris* gen. et sp. nov. is also reported in horizons containing *Granomarginata* from the Stáhpogieddi Formation in Norway and the Dabis Formation in Namibia, and flask-shaped fossils are also found in the Gibbett Hill Formation in Newfoundland. The *Granomarginata*–*Lagoenaforma* association, in addition to a low-diversity organic-walled microfossil assemblage, occurs in the strata postdating the Shuram carbon isotope excursion, and may eventually be of use in terminal Ediacaran biostratigraphy. These older occurrences of *Granomarginata* add to a growing record of body fossil taxa spanning the Ediacaran–Cambrian boundary.

1. Introduction

The Ediacaran Period (635–538.8 Ma) is the most recently defined and longest geological period (Knoll *et al.* 2006; Xiao *et al.* 2016), and it encompasses a time of significant environmental and biotic changes (Droser *et al.* 2017; Darroch *et al.* 2018; Wood *et al.* 2019). Efforts to subdivide and better constrain timing of these events include carbon isotope chemostratigraphy and biostratigraphy based on faunas of Ediacara-type macrofossils, microfossils (acanthomorphic acritarchs) and trace fossils (Grey, 2005; Jensen *et al.* 2006; Willman & Moczydłowska, 2011; Narbonne *et al.* 2012; Macdonald *et al.* 2013; Xiao *et al.* 2016; Rooney *et al.* 2020; Darroch *et al.* 2021), although much work remains. These efforts face challenges compared with Palaeozoic or younger strata due to taphonomic bias, a relatively low diversity of fossil organisms and a high degree of endemism (cf. Droser *et al.* 2017; Muscente *et al.* 2019). Use of trace fossils and biomineralizing taxa as biostratigraphic indicators is mostly applied to upper Ediacaran strata (e.g. Jensen *et al.* 2006; Tarhan *et al.* 2020; Darroch *et al.* 2021; Chai *et al.* 2021). However, through integration of diverse types of palaeontological and palaeoenvironmental records, a better understanding of the event timeline is emerging, and the community is moving towards a subdivision of the Ediacaran Period at stage level and a better understanding of the sequence of evolutionary events (Xiao *et al.* 2016; Shahkarami *et al.* 2020).

Organic-walled microfossils (OWM; including acritarchs) are used as a proxy for diversity of eukaryotic microbiota and are also one of the biostratigraphic tools for constraining the age of Ediacaran successions (e.g. Grey, 2005; Xiao *et al.* 2016). Acritarchs are a polyphyletic group of mostly single-celled organisms, likely representing a variety of microscopic eukaryotes. They are composed of acid-insoluble organic matter and commonly preserved as compressed carbonaceous vesicles in fine-grained siliciclastics, or by permineralization in cherts or phosphorites. Historically, three assemblages of OWM have been identified during the Ediacaran Period (Grey *et al.* 2003; Grey, 2005): Ediacaran leiosphere palynoflora (ELP); Ediacaran complex acanthomorph palynoflora (ECAP, also referred to as Doushantuo–Pertatataka acritarchs (DPA)) dominated by large process-bearing forms; and late Ediacaran leiosphere palynoflora (LELP), composed mainly of sphaeromorphic OWM. Eukaryotic microfossils were especially diverse during early Ediacaran time as exemplified by taxonomically rich assemblages from Australia (Zang & Walter, 1992; Grey, 2005; Willman & Moczydłowska, 2011), China (Xiao *et al.* 2014; Liu & Moczydłowska, 2019), the East European Platform (Vorob'eva *et al.* 2009), Siberia (Sergeev *et al.* 2011; Moczydłowska & Nagovitsin, 2012), India (Prasad *et al.* 2010; Joshi & Tiwari, 2016) and Laurentia (Willman *et al.* 2020). They have been used in biostratigraphic endeavours to correlate Ediacaran strata (e.g. Grey, 2005; Xiao *et al.* 2016), usually antedating the widespread occurrence of the macroscopic Ediacara-type biota (see Xiao *et al.* 2016). In contrast, the ELP and LELP assemblages are generally depauperate, mostly consisting of simple leiosphaerid acritarchs that possess few distinguishing characters, or other non-diagnostic taxa with very long stratigraphic ranges (e.g. Grey, 2005; Chiglino *et al.* 2015; Kolesnikov *et al.* 2015; Lehn *et al.* 2019). Exceptions were discovered recently; some acanthomorphic (process-bearing) OWM persisted to the latest Ediacaran of Mongolia (Anderson *et al.* 2019) and Russia (Grazhdankin *et al.* 2020). Such assemblages remain rare towards the end of the Ediacaran Period and could have been restricted to specific environments where acanthomorphs thrived or were able to be preserved. More upper Ediacaran strata need to be examined for microfossils in detail, and their utility in a more refined stratigraphic subdivision of the later Ediacaran Period (the upper series) is in progress.

Only a handful of body-fossil taxa span the Ediacaran–Cambrian boundary (Slater *et al.* 2020). Recent studies have shown that several fossil groups persisted through this interval, including skeletal metazoan taxa (cloudinids), small carbonaceous fossils (SCF) and organic problematica (Moczydłowska *et al.* 2015; Yang *et al.* 2016; Zhu *et al.* 2017; Slater *et al.* 2020). Microfossils in this study show a similar trend; we found the predominantly Cambrian taxon *Granomarginata* Naumova (1960) deeper in time, within Ediacaran strata representing a shallow-water to distal shelf-marine environment in Arctic Norway, and nearshore shallow-water setting in Namibia and Newfoundland, Canada (Figs 1–4). In addition to *Granomarginata* previously reported from India (Kumar & Maithy, 2008; Prasad *et al.* 2010) and Poland (Jachowicz-Zdanowska, 2011), our new records suggest a geographically widespread distribution of *Granomarginata* by late Ediacaran time. We further report additional diagnostic OWM co-occurring with *Granomarginata*, including the new flask-shaped taxon *Lagoenaforma collaris* gen. et sp. nov.

2. Methods

Microfossils were isolated from the rock matrix utilizing a palynological acid extraction procedure (Grey, 1999) that includes maceration in 40% hydrofluoric acid (HF) to dissolve silicates, and boiling of the residue in 30% hydrochloric acid (HCl) to remove fluorides. Calcareous fine sandstone samples were first macerated in HCl for > 24 hours to remove carbonates. Residue was filtered through 10 μm mesh and used to prepare strew mounts for a light microscopy overview. Microfossils were observed and imaged with a Zeiss Axioskop 40 transmitted light microscope with Q Imaging camera. All illustrated specimens from the Digermulen Peninsula will be deposited in the palaeontological collections (TSGf) of the Arctic University Museum of Norway, Tromsø, and specimens from Nambia at the Geological Survey of Namibia, Windhoek. To evaluate abundance and diversity, all microfossils were counted on one slide per sample.

Fossiliferous samples were collected from middle–upper Ediacaran strata in three distinct areas: Arctic Norway, Namibia and Newfoundland. *Granomarginata* was recovered from a new locality as well as in strata older than previously reported, which prompted a comparison of the OWM assemblages between these areas.

3. Geological setting

3.a. Arctic Norway

Samples from Arctic Norway were collected during the 2016 and 2018 field expeditions of the Digermulen Early Life Research Group (DELRG). The Digermulen Peninsula in the Finnmark region of mainland Arctic Norway hosts an approximately 3-km-thick succession of mainly siliciclastic sedimentary rocks of Cryogenian–Ordovician age (e.g. Högström *et al.* 2013; Figs 1a, b, 2a, 3a). The base of the Vestertana Group contains glaciogenic diamictites of the Smalfjorden and Mortensnes formations that have been linked to the Marinoan and Gaskiers glacial intervals, respectively (Halverson *et al.* 2005). These sequences bracket the siliciclastic shallow-marine to basinal, non-glacial Nyborg Formation. Organic-walled microfossil taxa characteristic of the early Ediacaran Period (ECAP/DPA), as well as organically preserved remnants of multicellular tissue, have been documented in the upper part of the Nyborg Formation (Agić *et al.* 2018, 2019). Overlying the Mortensnes diamictite is the Stáhpogieddi Formation, which starts with sandstones and shales of the Lillevannet Member, representing a transgressive interval (Banks *et al.* 1971; Jensen *et al.* 2018*b*). Above lies the Indreelva Member composed of mudstones, siltstones and sandstones, which hosts an assemblage of Ediacara-type macrofossils dominated by discoidal taxa (Farmer *et al.* 1992; Högström *et al.* 2013, 2017; Jensen *et al.* 2018*b*). The overlying Manndrapselva Member consists of a basal sandstone unit, followed by two upwards-coarsening cycles of red and grey mudstone and sandstone alterations and, in the second cycle, carbonate concretions and calcareous siliciclastic beds (Meinhold *et al.* 2019*a*). The stratigraphically highest occurrence of macrofossils *Palaeopascichnus* and *Harlaniella* is *c.* 15 m above the carbonates, and the Ediacaran–Cambrian boundary lies close to the base of the third cycle, indicated by the occurrence of the trace fossil *Treptichnus pedum* (Fig. 2a; McIlroy & Brasier, 2017; Jensen *et al.* 2018*a*, *b*).

Fossiliferous samples discussed here were collected from shales and siltstones in the basal part of Indreelva Member from Árasulluokta Cove (Fig. 1a, b). Samples D16-HA-80 (70° 34.165' N, 28° 07.224' E) and D18-HA-20 (70° 34.174' N, 28° 07.204' E, just above a bed with discoidal fossils), were collected 3 m and *c.* 10 m above the lowest occurrence of palaeopascichnids (cf. Jensen *et al.* 2018*b*). Sample D16-HA-53 was recovered 2 m below the earliest aspidellomorphs in the Stáhpogieddi section, 6 m above the Lillevannet–Indreelva transitional beds (70° 32.534' N, 28° 00.929' E). The sample from the Manndrapselva Member third

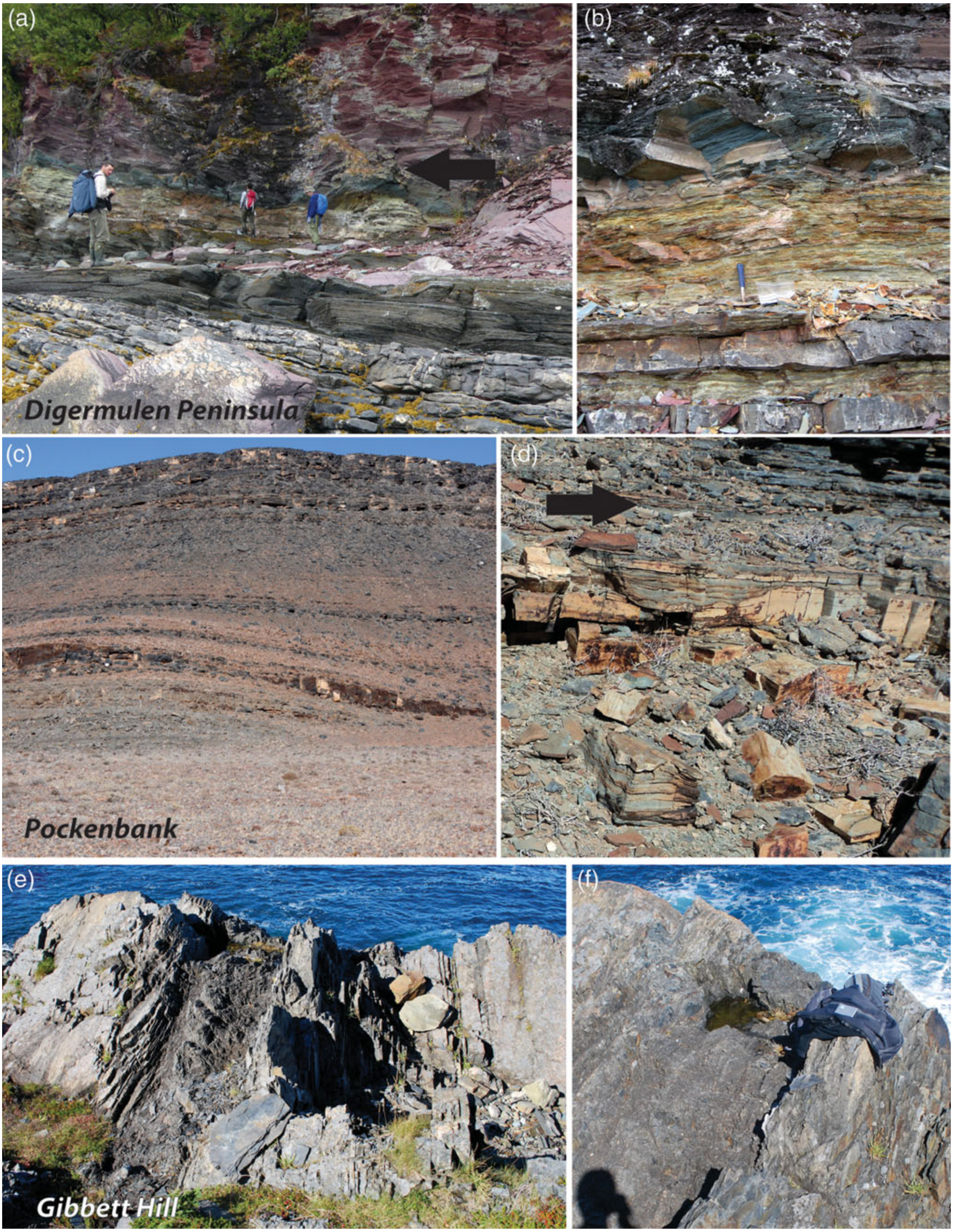

Fig. 1. (Colour online) Localities of sample collections and outcrops with occurrences of *Granomarginata* and *Lagoenaforma* gen. nov. (a) Basal part of the Indreelva Member of the Stáhpogieddi Formation, Vestertana Group in coastal outcrops in northern portion of Árasulluokta Cove, southeastern shore of the Digermulen Peninsula in Norway. (b) Shales and siltstones of the Indreelva Member above the occurrence of macrofossil *Palaeopascichnus*. (c) Basal Nama Group strata on Farm Pockenbank in the Witputs sub-basin in Namibia. (d) Fine arenite of the Mara Member, Dabis Formation, Nama Group exposed on Farm Pockenbank. (e) Gibbett Hill Formation, exposed at the 'Brasier Shale' outcrop on the northern shore of Ferryland Head, eastern coast of the Avalon Peninsula, Newfoundland. This locality was named in honour of Professor Martin Brasier who spent many field excursions studying this outcrop. (f) Enhanced view of the Brasier Shale in the upper Gibbet Hill Formation.

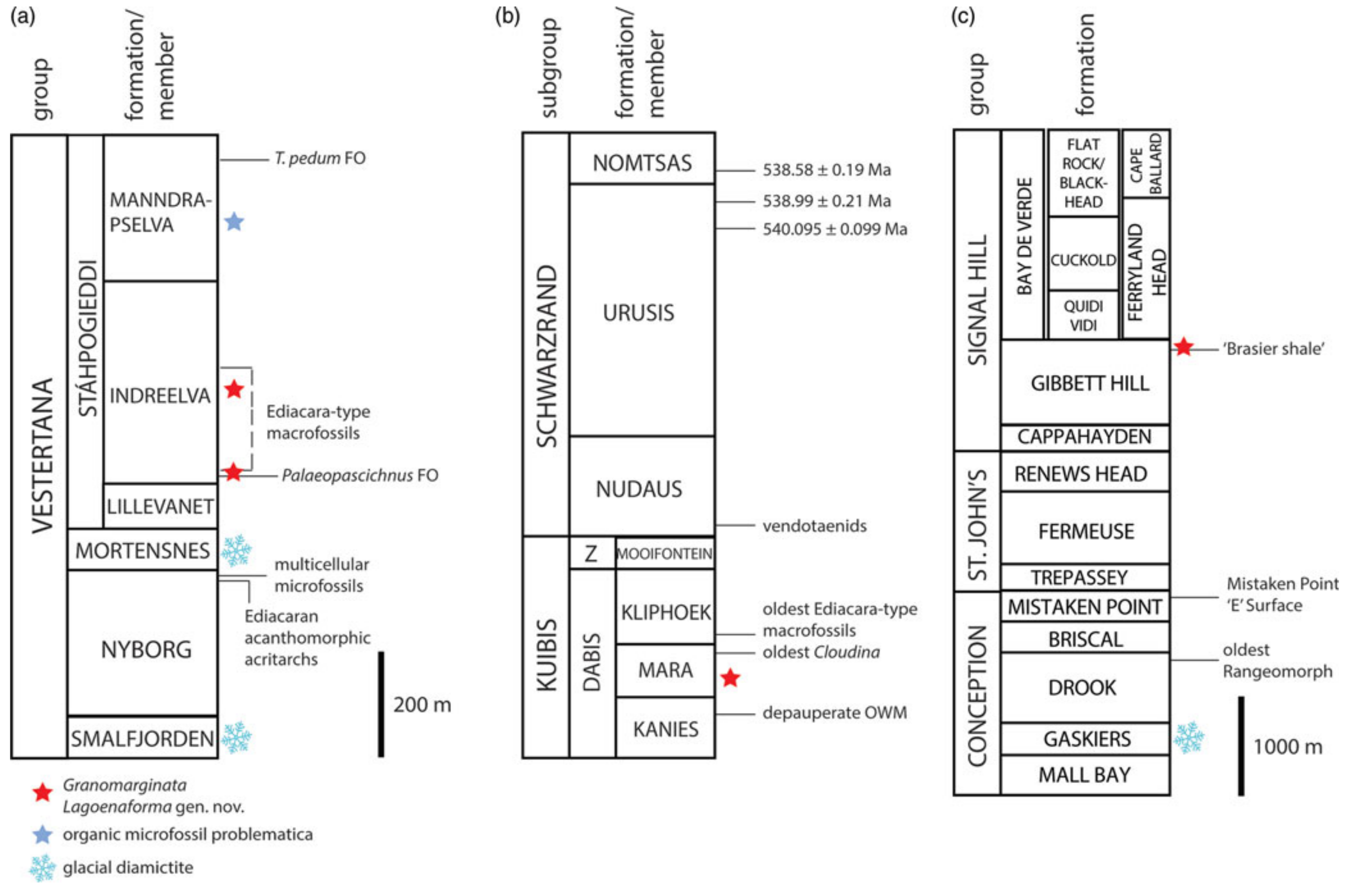

Fig. 2. (Colour online) Simplified schematic regional stratigraphy of the units from which *Granomarginata* and *Lagoenaforma* microfossils were recovered, showing the occurrence of microfossils in relation to the Ediacara-type biota and other stratigraphic markers. Stratigraphic markers from each unit are included to inform about the broad age-rage of *Granomarginata*–*Lagoenaforma*. (a) Ediacaran part of the Vestertana Group exposed on the Digermulen Peninsula in Arctic Norway. The Ediacaran–Cambrian boundary is in the upper part of the Manndrapselva Member, indicated by the first occurrence (FO) of *Treptichnus pedum*. For the distribution of palaeopascichnids and trace fossils in the Vestertana Group see Jensen *et al*. (2018*b*). (b) Stratigraphy of the Nama Group in the Witputs sub-basin, Namibia, modified from Hall *et al*. (2013). Previous record of depauperate microfossils from Germs *et al*. (1986). U–Pb zircon age constraints in the Spitzkop Member, Urusis Formation from Linnemann *et al*. (2019). (c) Stratigraphy of the Conception, St John's and Signal Hill Groups, based on King (1988) and Matthews *et al*. (2021). The stratigraphic position of the 'Brasier Shale' outcrop at Ferryland Head is indicated.

cycle at the Manndrapselva River section (D16-HA-77, 70° 34.575' N, 28° 06.847' E) was collected immediately above the quartzite marking the top of the second cycle.

3.b. Namibia

Fossiliferous samples from Namibia were collected from the Dabis Formation during the field workshop on the Ediacaran Nama Group of southern Namibia, part of the IGCP 587 programme (Xiao *et al.* 2017) on Farm Pockenbank (Figs 1c, d, 2b, 3b). The Nama Group contains *c.* 3 km of fluvial to marine siliciclastics and carbonates, representing a tidal to below-wave-base environment of a foreland basin (Germs *et al.* 1986; Germs & Gresse, 1991). It occurs in a northern Zaris sub-basin and a southern Witputz sub-basin, separated by the Osis Ridge (Germs, 1983). The lower part of the Nama, the Kuibis Subgroup, consists of 200 m of mature siliciclastics and carbonates, and is subdivided into the Dabis and Zaris formations (Germs, 1983; Saylor *et al.* 1995). In the Pockenbank area (Witputz sub-basin), the lowermost Kanies Member of the Dabis Formation contains predominantly arkosic sandstones with ripples and desiccation cracks indicative of shallow, fluvial environments (Germs, 1983; Saylor *et al.* 1995). The Mara Member overlies the transgressively eroded top of the Kanies Member, and contains alternating fine-grained siliciclastics and limestones with microbialites and evaporites within a shallowing-upwards sequence (Germs, 1972*b*, 1983; Saylor *et al.* 1995). Above the Mara Member are the Kliphoek and Aar members that consist of cross-stratified coarse sandstones and carbonates grainstone (Germs, 1983; Saylor *et al.* 1995; Hall *et al.* 2013). Saylor *et al.* (1995) interpreted the Dabis Formation strata as two transgressive sequences. Some of the oldest examples of the youngest Ediacaran evolutionary assemblage – the Nama assemblage – occur in the Kliphoek/Aar members (e.g. Germs, 1983; Narbonne *et al.* 1997; Vickers-Rich *et al.* 2013; Maloney *et al.* 2020). Carbonates (micrite phases) in the Mara Member (Arasab section) preserve a negative δ^{13}C excursion from −6.22‰ to −0.22‰, previously correlated with the recovery from the global Shuram–Wonoka anomaly (Kaufmann *et al.* 1991; Saylor *et al.* 1995, 1998; Grotzinger *et al.* 1995; Hall *et al.* 2013; Wood *et al.* 2015). The excursion is not fully manifested at the locality where the microfossils were collected (cf. Vickers-Rich *et al.* 2016). Sandstones of the overlying Kliphoek and Aar members include fossils in offshore-shoreface settings, characteristic environments inhabited by the late Ediacaran Nama assemblage including such taxa as *Ernietta*, *Pteridinium* and *Rangea*, as well as macroscopic bacterial colonies *Nemiana* (Narbonne *et al.* 1997, 2012;

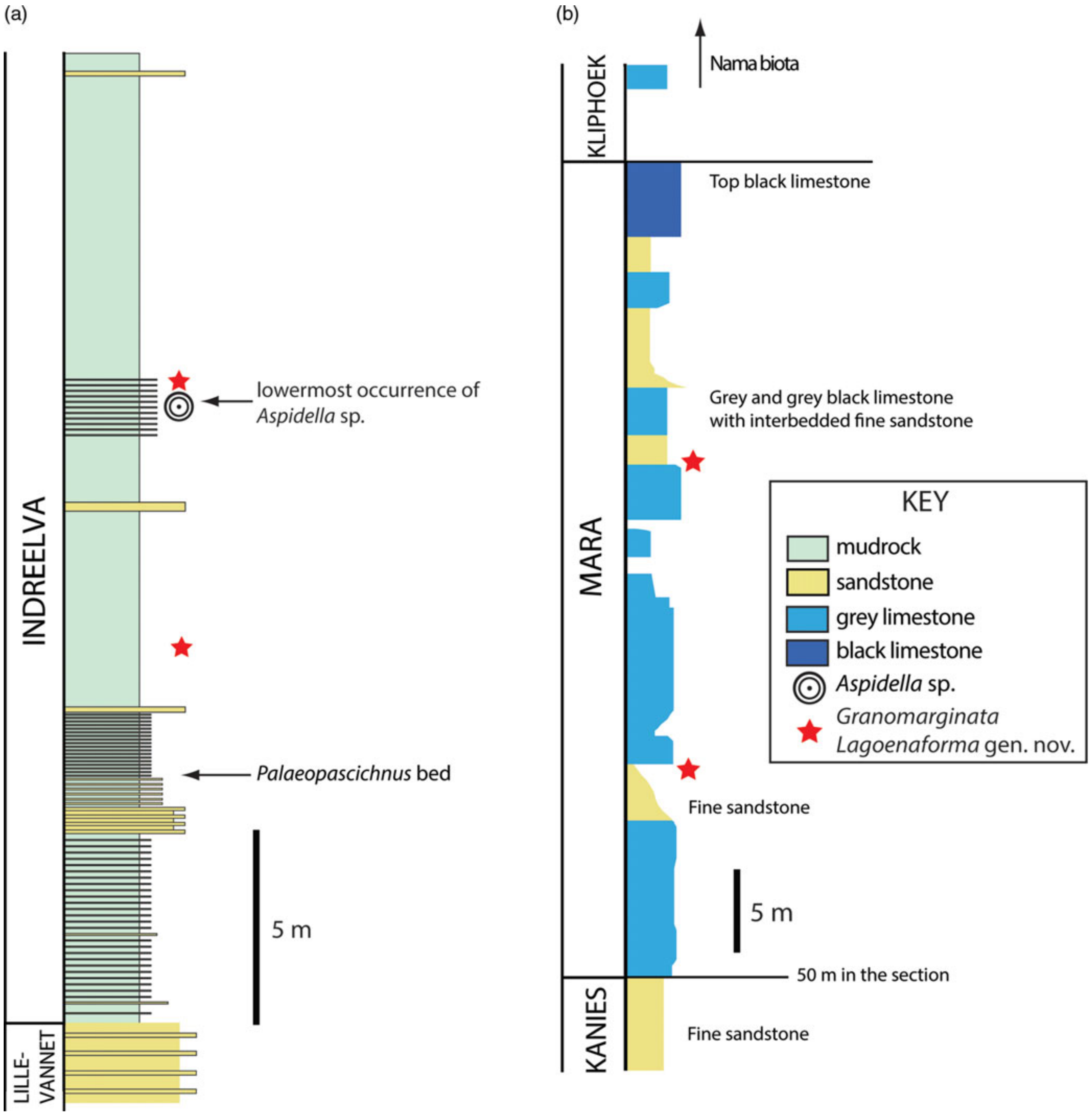

Fig. 3. (Colour online) (a) Microfossil occurrence close to *Palaeopascichnus* and aspidellomorphs in the lower Indreelva Member, Digermulen Peninsula, Norway. (b) Microfossil occurrence in the Mara Member, Farm Pockenbank, Namibia.

Vickers-Rich *et al.* 2013). These macrofossiliferous strata span the late Ediacaran Period: an ash bed in the Kuibis Subgroup yielded a U–Pb age of 548.8 ± 1 Ma (Grotzinger *et al.* 1995), and ash beds from the Spitskop Member of the overlying Urusis Formation yielded ages of 538.99 ± 0.21 Ma in the most recent study using U–Pb chemical abrasion – isotope dilution – thermal ionization imaging spectrometry (CA-ID-TIMS) dating technique (Linnemann *et al.* 2019).

Collection for a pilot microfossil survey was carried out from the lower Mara Member, Nama Group on Farm Pockenbank, at the Quiver section (see Vickers-Rich *et al.* 2016): N16-HA-P2 *c.* 9 m above the base of the Mara Member (27° 08.619' S, 16° 26.803' E), and N16-HA-P3 immediately above a grey limestone package. These strata are overlain by grey and pink dolomite, and dark limestone at the top.

3.c. Newfoundland, Canada

The microfossiliferous Gibbett Hill Formation of the Signal Hill Group is exposed on the eastern Avalon Peninsula, Newfoundland, Canada (Sala Toledo, 2004; Hofmann *et al.* 2008). The Signal Hill Group overlies the fossiliferous strata of

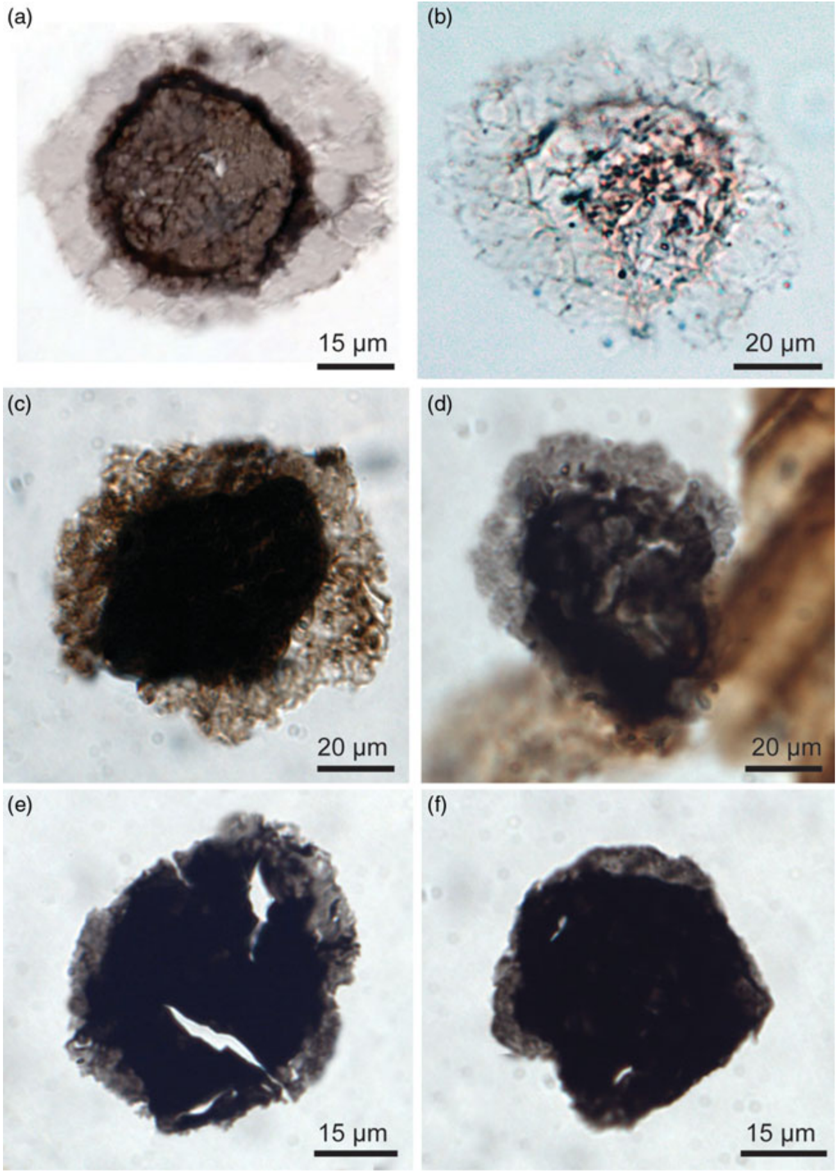

Fig. 4. (Colour online) Transmitted light photomicrographs of the Ediacaran–Cambrian acritarch taxon *Granomarginata* from various Ediacaran units. (a–d) *Granomarginata squamacea*. (a) *G. squamacea* from the Mara Member, Dabis Formation, Nama Group on Farm Pockenbank, Namibia. N16-HA-P2 82×13. (b) N16-HA-P3 81×9, Mara Member. (c) TSGf18448, D18-HA-20 83×16, Indreelva Member, Stáhpogieddi Formation, Vestertana Group on Digermulen Peninsula, Arctic Norway. (d) TSGf18449a, D16-HA-80 87×19, Indreelva Member. (e, f) *Granomarginata prima* from the Indreelva Member in Norway. (e) TSGf18449b, D16-HA-80 84.5×18. (f) TSGf18450a, D16-HA-53 81×14.

the Conception and St John's groups, which contain some of the oldest Ediacara-type macrofossils, that is, the Avalon assemblage (Fig. 2c; Misra, 1969; Narbonne in Fedonkin *et al.* 2007; Liu *et al.* 2015; Matthews *et al.* 2021). Temporal constraints in the upper part of this succession are generally scarce, but the Conception Group contains a glacial diamictite (Gaskiers Formation) dated between 580.90 ± 0.40 and 579.88 ± 0.44 Ma using CA-ID-TIMS U–Pb analyses on zircon grains (Pu *et al.* 2016), and the rangeomorphs from the Fermeuse Formation in the upper St John's Group, have a maximum age of 564.13 ± 0.65 Ma (Matthews *et al.* 2021). A tuffite sample from the lower Fermeuse Formation yielded zircon U–Pb dates from 563.67–569.01 Ma (Matthews *et al.* 2021).

The overlying Signal Hill Group contains *c.* 1500 m of mudstones, fine-grained sandstones and ash beds (Sala Toledo, 2004). Its oldest unit is the Cappahayden Formation, containing laminated grey siltstones. It is overlain by the Gibbett Hill Formation consisting of 760 m of green-grey sandstone, mudstone and black shales (Sala Toledo, 2004) and deposited in a shallow-marine environment.

Rare OWM dominated by sphaeromorphs were previously reported from siliciclastics of the Drook, Mall Bay, Fermeuse and Renews Head formations in the St John's Group (Hofmann *et al.* 1979; O'Brien & King, 2004), and the Cappahayden Formation (underlying the Gibbett Hill Formation) in the Signal Hill Group (Hofmann *et al.* 1979). The microfossils in this study derive from a single sample of the 'Brasier Shale' outcrop in the Gibbett Hill Formation, near Ferryland, Avalon Peninsula, Newfoundland (Fig. 1e–f).

4. Results

A flask-shaped OWM *Lagoenaforma* gen. nov. (Fig. 5) was found in several upper Ediacaran units. This taxon frequently occurs with rare *Granomarginata squamacea* and *G. prima*, which are typically early Cambrian taxa. This new material, along with previous reports (Fig. 4, Table 1), extend the distribution of *Granomarginata* back in time into the late Ediacaran Period. These OWM also co-occur with leiosphaerids and carbonaceous problematica (Fig. 6).

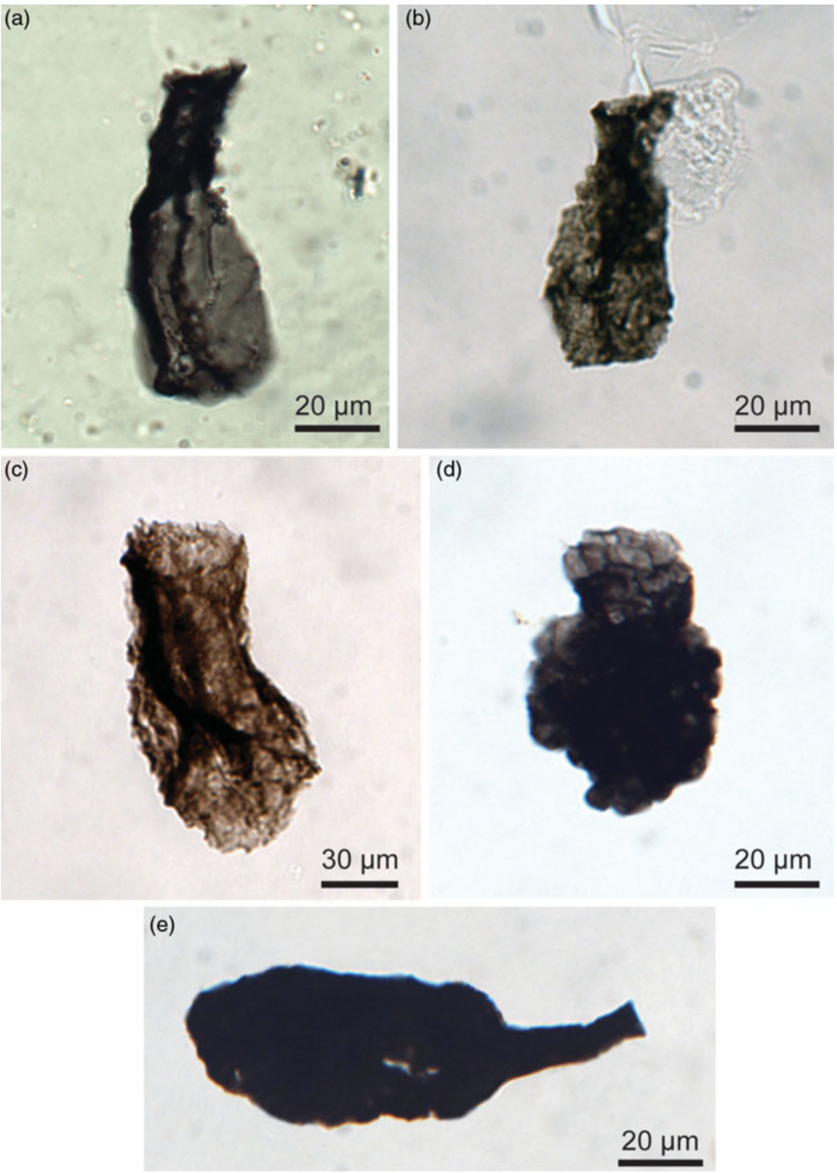

Fig. 5. (Colour online) Transmitted light photomicrographs of the new flask-shaped organic-walled microfossils *Lagoenaforma* gen. nov. from the middle–upper Ediacaran strata. (a) *Lagoenaforma collaris* gen. et sp. nov. from the Indreelva Member, Stáhpogieddi Formation, Vestertana Group on Digermulen Peninsula, Norway. (a) Holotype, TSGf18449c, D16-HA-80 78×15. (b, c) *L. collaris* from the Mara Member, Dabis Formation, Nama Group on Farm Pockenbank in Namibia. (b) N16-HA-P2 76×7. (c) N16-HA-P2 77×5.5. (d) Unnamed Form A, microfossil with a neck-like protrusion from the Manndrapselva Member, Stáhpogieddi Formation, Vestertana Group. TSGf18451a, D16-HA-77 89×23. (e) Opaque neck-bearing microfossil *Lagoenaforma* sp. from the Gibbett Hill Formation, Signal Hill Group, Avalon Peninsula, Newfoundland. Brasier Shale A-1 87×11.

4.a. Ediacaran Indreelva Member, Stáhpogieddi Formation, Digermulen Peninsula, Norway

Out of 13 analysed samples from the Indreelva Member, 10 were barren or had very low organic content, and the rest yielded moderately well preserved OWM. These include: *Granomarginata prima*, *G. squamacea*, *Leiosphaeridia crassa*, *L. jacutica*, a tapering annulated microfossil, a lobate acritarch, fragmented SCF and aggregates of cells *Symplassosphaeridium* sp. A new type of flask-shaped OWM is described: *Lagoenaforma collaris* gen. et sp. nov. (Fig. 5a). Fragmented remains of filamentous prokaryotes and parts of rare larger SCF, as well as often torn membranous extensions of *Granomarginata*, are likely not a result of destructive processing because a low-manipulation acid maceration method was applied; this indicates either degradation within the sediment or transport. Leiosphaerids are the most common component of the Indreelva OWM assemblage (> 80%, Fig. 6a, b, d). There are few *Granomarginata* specimens; it is therefore rarer when compared with its abundance in the Cambrian strata (e.g. 3–10 counts, see Palacios *et al.* 2020). OWM are generally scarce in the strata examined here.

The first record of *G. squamacea* and *L. collaris* in the Indreelva Member occurs in a laminated mudrock 3 m above the level hosting palaeopascichnids, and *c.* 10 m above the transitional beds of the Lillevannet Member (Figs 2a, 3a). Microfossils also occur *c.* 6 m below the first discoidal Ediacara-type macrofossils in the Indreelva Member in the Stáhpogieddi type section. Mudrock samples below the *Palaeopascichnus* horizon in the Árasulluokta Cove were devoid of microfossils apart from rare leiosphaerid fragments. This is likely not preservational bias because at least some OWM (leiosphaerids) are present. *Granomarginata* makes up 4% and *L. collaris* 7.5% of the Indreelva assemblage. Overall filaments and organic problematica represent nearly 10% of the assemblage. Samples from the upper part of the Indreelva Member did not yield any microfossils.

Distinct OWM are not commonly found very close to the beds containing Ediacara-type biota (Grey in Fedonkin *et al.* 2007). Although microfossils in the Indreelva Member are rare and occur sporadically, these results from the Digermulen Peninsula represent a rare distribution of acritarchs and Ediacaran macrofossils within a few metres of each other.

4.b. Ediacaran–Cambrian Manndrapselva Member, Stáhpogieddi Formation, Digermulen Peninsula, Norway

Granomarginata was previously documented higher up in the stratigraphy on the Digermulen Peninsula, in association with leiosphaerids in the third cycle of the Manndrapselva Member of the Stáhpogieddi Formation, correlated with the basal Terreneuvian (Högström *et al.* 2013), as well as in the Cambrian Series 2 to Miaolingian Duolbagáisá Formation further up in the stratigraphy (Palacios *et al.* 2020). Only two samples (one fossiliferous) from the Manndrapselva Member below the Ediacaran–Cambrian boundary were analysed here, but no *Granomarginata* was recovered. Instead, these strata contain organic problematica such as a neck-bearing microfossil (Fig. 5d), as well as fragments of leiosphaerids, bacterial filaments and SCF. Palacios *et al.* (2017) observed lobate SCF problematica upsection in the third cycle similar to microfossils from the Gibbett Hill Formation on Newfoundland (Fig. 6c).

4.c. Mara Member assemblage, Dabis Formation, Nama Group, Farm Pockenbank, Namibia

Organic-walled microfossils recovered from the Mara Member of the Nama Group on Farm Pockenbank occur in fine sandstones/silts interbedded with limestones, deposited in a shallow-marine environment. Taxa include: *Granomarginata squamacea*, *Lagoenaforma collaris* gen. et sp. nov., *Leiosphaeridia crassa*, *Simia annulare* (Fig. 6f), *Bavlinella* sp. (Fig. 6h), *Symplassosphaeridium* sp. and vesicle fragments of smooth-walled microfossils or possible SCF (Fig. 6j). Fragments of broad filaments are rare, but similar to material identified as *Vendotaenia* sp. from the Kuibis Subgroup by Germs *et al.* (1986). The newly reported microfossils here occur below strata containing possible first occurrence of cloudinids (following an unillustrated report of *Cloudina* by Germs, 1972*a*; cf. Wood *et al.* 2015), and they are uncomformably overlain by the Kliphoek and Aar members, which contain the Ediacara-type macrofossils *Ernietta* (Pflug, 1966; Elliot *et al.* 2016), *Pteridinium* (Gürich, 1930) and *Rangea* (Narbonne *et al.* 1997; Vickers-Rich *et al.* 2013) characteristic of the late Ediacaran Nama assemblage (Narbonne *et al.* 1997).

OWM from the weathered sediments of the Mara Member are slightly lighter in colour than the specimens from Newfoundland and Arctic Norway (thermal alteration index (TAI) = 3–4 *sensu* Hayes *et al.* 1983), which indicates a lower degree of thermal alteration. Leiosphaerids make up the bulk of the OWM assemblage in the Mara Member (*c.* 80 % of the overall microfossil abundance). Cell aggregates *Symplassosphaeridium* are the next most common component. *Granomarginata* represents 3.5% and *L. collaris* 6% of the assemblage. This preliminary record of Ediacaran OWM from Namibia, despite being of low diversity, is encouraging future explorations of the late Ediacaran microfossil record hosted in the Nama Group.

4.d. Gibbett Hill Formation microfossils, Signal Hill Group, Avalon Peninsula, Newfoundland, Canada

The Gibbett Hill Formation contains rare and poorly to moderately preserved OWM. The most common component are fragments of prokaryotic filaments and leiosphaerids. As a low-manipulation acid maceration method was used, the fragmentation is likely not a result of palynological processing and could instead indicate transport. Additional microfossils include prokaryotic clusters of cells *Symplassosphaeridium* sp., a small carbonaceous problematicum with lateral protrusions (Unnamed Form B, Fig. 6c), a fragment of a single-celled microfossil with a spongy envelope – likely *Granomarginata prima* (Fig. 6l) – and a dark flask-like microfossil with an elongate neck-like structure *Lagoenaforma* sp. (Fig. 5e). The dark colour of the Gibbett Hill OWM indicates high thermal alteration of the organic matter. Only a single specimen of a poorly preserved *Granomarginata* has been recovered. However, due to the presence of the late Ediacaran organic problematica (Fig. 6c) and *L. collaris*, which co-occur with *Granomarginata* in the Ediacaran strata of Norway and Namibia, the identification of envelope-bearing microfossil from Gibbett Hill as *Granomarginata* is plausible. These microfossils occur hundreds of metres above the fossiliferous successions hosting some of the oldest assemblage of Ediacaran macrofossils (cf. Hofmann *et al.* 2008; Liu *et al.* 2015; Matthews *et al.* 2021), consistent with a broadly late Ediacaran age of the Gibbett Hill Formation.

5. Discussion

5.a. Ediacaran Granomarginata

The lower Ediacaran strata accommodate a rich and diverse record of organically preserved microfossils of biostratigraphic importance (e.g. Zang, 1988; Grey, 2005; Vorob'eva *et al.* 2009; Sergeev *et al.* 2011; Willman & Moczydłowska, 2011). On the contrary, however, the strata postdating localized short-lived glaciations, the Shuram negative carbon isotope excursion (CIE) and the first appearance of the macroscopic Ediacara-type biota are generally depauperate of microfossils, with little distinctive morphologies. The strata bearing Ediacaran macrofossils rarely contain acritarchs, mainly leiosphaerids and prokaryotes (cf. Hofmann *et al.* 1979; Grey, 2005; Leonov & Ragozina, 2007) in lower abundance than in older, pre-Gaskiers or pre-Shuram strata. This pattern is observed on the Digermulen Peninsula where the lower Ediacaran Nyborg Formation contains acanthomorphs (Agić *et al.* 2018), whereas the strata above in the Stáhpogieddi Formation are mostly barren and relatively depauperate until Cambrian time. OWM assemblages of low diversity, with few eukaryotic forms, have also been reported from Argentina, Australia, Brazil, East European Platform, Namibia and Siberia (Germs *et al.* 1986; Gaucher *et al.* 2003; Grey, 2005; Leonov & Ragozina, 2007; Chiglino *et al.* 2015; Kolesnikov *et al.* 2015; Ragozina *et al.* 2016; Arrouy *et al.* 2019; Arvestål & Willman, 2020). Late Ediacaran acanthomorphic acritarchs were found in Mongolia (Anderson *et al.* 2019) and in a drillcore from Siberia (Grazhdankin *et al.* 2020), but these occurrences are exceptions among the generally low-diversity late Ediacaran OWM assemblages.

The organic-walled microfossil genus *Granomarginata* is one of the more distinguishable OWM taxa of the Terreneuvian epoch, known from units in Canada, China, the East European Platform, Finland, India, Norway, Siberia, and Spain (Moczydłowska, 1991, 2011; Palacios & Moczydłowska, 1998; Kumar & Maithy, 2008; Yin *et al.* 2009; Palacios *et al.* 2018, 2020; Slater & Willman, 2019), and was also reported from the uppermost Ediacaran strata of India (Prasad *et al.* 2010) and Poland (Gunia, 1990; Jachowicz-Zdanowska, 2011). It is a common component of the *Granomarginata prima* Zone of the East European Platform (EEP) (Jankauskas & Lendzion, 1992), the *Granomarginata* Zone in Newfoundland (Palacios *et al.* 2018), and rare to common in abundance in *Skiagia*-bearing zones (e.g. Palacios *et al.* 2018, 2020) that characterize the latest Terreneuvian and Cambrian

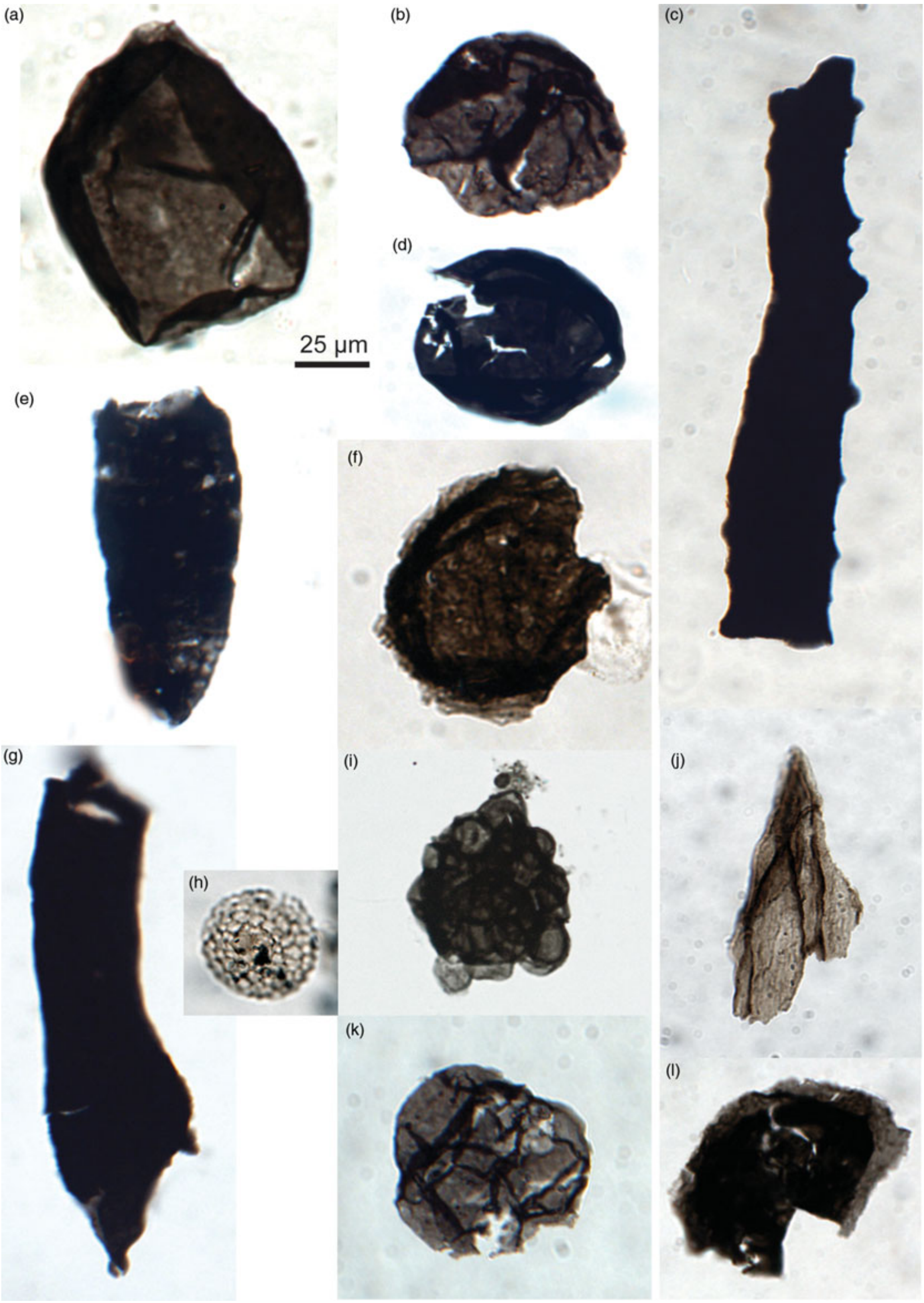

Fig. 6. (Colour online) Other common organic-walled microfossils co-occurring with *Granomarginata* and *Lagoenaforma* gen. nov. in units of middle–late Ediacaran age, common components of the late Ediacaran leiosphaerid palynoflora (LELP, cf. Grey, 2005) as well as older Precambrian assemblages, and small carbonaceous fossils. (a) *Leiosphaeridia jacutica* from the upper Mara Member, Dabis Formation, Nama Group on Farm Pockenbank, Namibia. N16-HA-P2 78×19. (b) *Leiosphaeridia crassa* from the Mara Member, N16-HA-P2 89×11. (c) Unnamed Form B, a small carbonaceous problematicum with lateral protrusions, from the Gibbett Hill Formation, Signal Hill Group, Avalon Peninsula, Newfoundland. Brasier Shale A-1 91×11. (d) *L. crassa* from the Indreelva Member, Stáhpogieddi Formation, Vestertana Group in Norway. TSGf18449d, D16-HA-80 85.5×9. (e) Unnamed Form C, tapering elongated and annulated microfossil from the Indreelva Member. TSGf18450b, D16-HA-53 85×9. (f) *Simia annulare* from the Mara Member, Dabis Formation, Nama Group in Namibia. N16-HA-P2 77×10. (g) SCF from the Manndrapselva Member, Stáhpogieddi Formation. TSGf18451b, D16-HA-77 88×14. (h) *Bavlinella* sp. from the Mara Member. N16-HA-P2 80×11. (i) *Symplassosphaeridium* sp. from the Indreelva Member. TSGf18449e, D16-HA-80 80×18. (j) SCF problematicum from the Mara Member. N16-HA-P2 77×16. (k) Lobate or dividing acritarch, from the Indreelva Member. TSGf18449f, D16-HA-80 81×7. (l) Fragmented microfossil with a spongy envelope, *Granomarginata prima* from the Gibbett Hill Formation, Newfoundland. Brasier Shale A-1 87×5. Scale bar is the same for all images: 25 µm. All images are transmitted light photomicrographs.

Table 1. A list of Ediacaran units containing the *Granomarginata–Lagoenaforma* association or either of the two taxa, and their approximate ages. Where this information is available, all organic-walled microfossils (OWM) are of low abundance, consistent with characterization of depauperate late Ediacaran leiosphere palynoflora (LELP) assemblage (cf. Volkova *et al.* 1979; Grey, 2005).

Formation and locality	Likely age	Co-occurring taxa	Reference
Upper Schwarzrand Subgroup, Namibia	Late Ediacaran (< 548 Ma)	*Bavlinella faveolata*, "*Comasphaeridium*-like microfossil" similar to *Granomarginata*, leiosphaerids, *Vendotaenia* sp.	Germs *et al.* (1986)
Mara Member, Dabis Formation, Namibia	Late Ediacaran (> 548 Ma)	*Bavlinella* sp., *Granomarginata*, *Lagoenaforma corallis*, *Leiosphaeridia crassa*, *Simia annulare*, *Symplassosphaeridium* sp., filaments (?*Vendotaenia*)	This study
Małopolska Block, Poland	Late Ediacaran (549 ± 3 Ma)	*Eoenthophysalis* sp., *Granomarginata prima*, leiosphaerids, *Obruchevella* sp., filaments (*Siphonophycus*)	Jachowicz-Zdanowska (2011)
Gibbett Hill Formation, Newfoundland	Late Ediacaran (<< 564 Ma)	?*Granomarginata prima*, leiosphaerid fragments, *Lagoenaforma* aff. *corallis*, *Symplassosphaeridium* sp., serrated SCF	This study
Jodhpur Formation, India	Middle–late Ediacaran ("570–542 Ma")	*Bavlinella faveolata*, *Granomarginata prima*, leiosphaerids, *Lophosphaerdium rarum*, filaments (*Siphonophycus*)	Prasad *et al.* (2010)
Kahar Formation, Iran	Late Ediacaran (< 560–550 Ma)	*Cochleatina* sp., Leiosphaerids, flask-shaped microfossils, "*Melanocyrillum* sp.", *Octoedryxium truncatum*, *Pterospermopsimorpha insolita*	Sabouri *et al.* (2003) (age: Etemad-Saeed *et al.* 2016)
Indreelva Member, Stáhpogieddi Formation, Arctic Norway	Middle–late Ediacaran (< 563 Ma, postdating Gaskiers-equivalent glacial interval)	*Granomarginata*, *Lagoenaforma corallis*, *Leiosphaeridia crassa*, *Leiosphaeridia jacutica*, *Symplassosphaeridium* sp., lobate vesicle (?*Archaeophycus*), tapering annulated microfossl	This study
Kotlin Formation, Estonia	Late Ediacaran (Kotlin regional stage)	"Opaque acanthomorphic acritarch" similar to *Granomarginata*, *Coneosphaera arctica*, *Simia annulare* & *Pterospermopsimorpha* sp., leiosphaerids, serrated SCF, *Symplassosphaeridium* sp., prokaryotic filaments and cell aggregates	Arvestål & Willman (2020)

Series 2. The new record documented here extends its distribution deeper in time as well as to a new region: Namibia.

Granomarginata is a single-celled eukaryote consisting of a central body and an uneven equatorial extension with granular surface. Its morphology resembles a phycoma of prasinophyte algae (Moczydłowska, 2011). Because of its widespread palaeogeographic distribution and occurrence in sediments deposited in both shallow and deep waters, it is assumed to have been a cyst of a planktonic organism. Microfossils with distinct morphological elements (e.g. processes and envelopes) provide a useful biostratigraphic tool, and the envelope-bearing *Granomarginata* is one of the few non-leiosphaerid acritarchs present in low-diversity microfossil assemblages of upper Ediacaran strata, in addition to organically preserved problematica (cf. Golubkova & Raevskaya, 2005; Leonov & Ragozina, 2007; Moczydłowska *et al.* 2015; Slater *et al.* 2020). Microfossils of this material differ from more ubiquitous Proterozoic envelope-bearing taxa such as *Simia* (also present in the Nama Group) in their fluffy, granular envelope with an uneven outline, which is likely a result of its less resistant nature compared with the central body (Naumova, 1960; Moczydłowska, 1991). Although the material from Norway and Newfoundland is relatively poorly preserved, it possesses sufficient diagnostic features that fall into the preservational range of *Granomarginata* reported in younger, thermally altered sedimentary successions (e.g. Moczydłowska, 2002).

Until now, *Granomarginata* was considered characteristic of the lower Cambrian Lontovan regional stage of the EEP (Volkova *et al.* 1983; Jankauskas & Lendzion, 1992). Yet similarly to recent observations that the fossil record of some traditionally Cambrian groups such as SCF extends back into the Ediacaran (Slater *et al.* 2020, see also Chiglino *et al.* 2015), *Granomarginata* first occurs in older strata globally, albeit in lower abundance. In the lower Cambrian Chapel Island Formation on Newfoundland, *Granomarginata* precedes the first appearance of small process-bearing acritarchs characteristic of the early Cambrian Period, which was the rationale used for the establishment of the *Granomarginata* Zone (Palacios *et al.* 2018). Considering our findings and previously published data on the Ediacaran *Granomarginata* (Gunia, 1990; Prasad *et al.* 2010; Jachowicz-Zdanowska, 2011), the *Granomarginata* Zone could represent an extension of late Ediacaran OWM assemblages into the Cambrian. *Granomarginata*'s appearance on the Digermulen Peninsula is just above the beds containing the macroscopic fossil *Palaeopascichnus* attributed to the middle–upper Ediacaran (Fig. 2a; Jensen *et al.* 2018*b*) and below and through the horizons bearing discoidal and dickinsoniamorph Ediacara-type macrofossils in Norway (cf. Högström *et al.* 2013, 2017). On Newfoundland, *Granomarginata* occurs in upper Ediacaran strata (Fig. 2c), in units well above formations bearing Avalon assemblage macrofossils (cf. O'Brien & King, 2004; Matthews *et al.* 2021). In Namibia, *Granomarginata* occurs in the unit below strata bearing *Cloudina* (cf. Germs, 1972a, 1983), and in strata overlain by a member containing the late Ediacaran Nama assemblage (Fig. 2; cf. Narbonne *et al.* 1997; Vickers-Rich *et al.* 2013; Elliot *et al.* 2016; Maloney *et al.* 2020). Rocks in these localities are not coeval, and we do not correlate them, but all three sequences represent the post-Shuram late Ediacaran time interval (cf. Xiao *et al.* 2016) and offer insights about the age range of flask-shaped microfossils and *Granomarginata*.

Two *Granomarginata* morphotypes are recognized in the present material. The type with a wider equatorial extension is consistent with the diagnosis of *G. squamacea* (Fig. 4a–d). The morphotype with a narrower extension (Fig. 4e, f) is consistent with *G. prima*. This taxon is also known from the upper Ediacaran strata of Poland (Jachowicz-Zdanowska, 2011), but it is the more pervasive morphotype in younger strata, known from the Terreneuvian deposits of the Digermulen Peninsula (Högström *et al.* 2013; Palacios *et al.* 2020), New Brunswick (Palacios *et al.* 2011) and Newfoundland (Palacios *et al.* 2018) in Canada, from the lower–middle Cambrian of China (Yin *et al.* 2009), as well as from elsewhere on Baltica (Volkova *et al.* 1983; Jankauskas & Lendzion, 1992), the EEP (Jachowicz-Zdanowska, 2013; Szczepanik & Żylińska, 2016) and the eastern Cordillera (Rubinstein *et al.* 2003). In the stratigraphic correlation chart presented by Kumar & Maithy (2008), the Stáhpogieddi Formation in Norway was aligned with the Ediacaran to lowermost Cambrian Kauriyala Formation of the Lesser Himalayas in India, which also contains *G. prima*. It was potentially reported from the Kuibis Subgroup in Namibia by Germs *et al.* (1986, fig. 6i) as a '*Comasphaeridium*-like fossil'.

Granomarginata is a rare component (*c.* ≤ 5 specimens per slide) of the leiosphaerid-dominant palynomorph assemblage (*c.* 50–70 leiosphaerids per sample) in the upper Ediacaran successions studied here, where it co-occurs with rare small carbonaceous problematica. Both *Granomarginata* morphotypes are more common and abundant in the Fortunian Stage, and define the *Granomarginata* Zone. Their higher abundance (> 10 specimens per slide), along with Cambrian-characteristic taxa, can be viewed as more indicative of lower Cambrian strata (e.g. Palacios *et al.* 2018). On the other hand, a low abundance of *Granomarginata* within a leiosphaerid-dominant assemblage, in association with flask-shaped *L. collaris*, is so far found in upper Ediacaran or transitional strata.

5.b. The life and times of the Granomarginata–Lagoenaforma *association*

The new flask-shaped microfossil *Lagoenaforma* (Fig. 5) was observed in the horizons containing Ediacaran *Granomarginata*. Flask-shaped microfossils resembling chitinozoans are common in Ordovician–Devonian strata and some non-chitinozoan flask-shaped problematica are present in Ordovician strata (e.g. Loeblich & McAdam, 1971), but have not been previously described from the Ediacaran. *L. collaris* is a minor component of leiosphaerid-dominated assemblages, but in addition to *Granomarginata* it is one of the few OWM taxa outside of dominant simple sphaeromorphs in the upper Ediacaran (LELP assemblage). As *L. collaris* is currently unknown from Cambrian units, it serves as a better representative of the late Ediacaran microbiota of the two. A low-diversity OWM assemblage with *G. prima* occurs along with 'flask-shaped bodies' in the lower Cambrian Withycombe Formation, UK (Rushton & Molyneux, 1990). No microfossils were illustrated in that publication, so affinities with *Lagoenaforma* could not be determined. However, the presence of other soft-bodied flask-shaped microfossils higher up in the stratigraphy on the Digermulen Peninsula (A. Högström, pers. obs.) and in other upper Ediacaran – Cambrian units worldwide (Table 1; cf. Sabouri *et al.* 2003), as well as agglutinated forms (Gaucher & Sprechmann, 1999), suggests that flask-shaped OWM may be a common component of the microbiota during this transitional interval.

We found these OWM in upper Ediacaran units with a depauperate palynomorph assemblage, but their full stratigraphic range still needs to be determined. We used information on the age of the rocks hosting *Granomarginata*–*Lagoenaforma* to assess their age range. *Granomarginata* and *Lagoenaforma* do not co-occur with the classic acanthomorphic acritarch assemblage (ECAP/DPA) in the underlying lower Ediacaran strata in Norway (H. Agić, pers. obs.), nor have they been recognized so far in the older deposits on Newfoundland (see Hofmann *et al.* 1979) or elsewhere (e.g. Grey, 2005), so we view them as constituents of the late Ediacaran OWM assemblage (LELP *sensu* Grey, 2005). On Newfoundland, a flask-shaped microfossil was found in an assemblage hundreds of metres above the youngest occurrence of rangeomorphs in the St John's Group that have a maximum age of 564.13 ± 0.65 Ma (U–Pb zircon data; Matthews *et al.* 2021). In Namibia *Granomarginata* and *Lagoenaforma* are found in the Mara Member, below all local occurrences of Ediacaran body fossils, and which records a negative δ^{13}C excursion that has been interpreted as correlative with the Shuram–Wonoka CIE (cf. Grotzinger *et al.* 1995; Saylor *et al.* 1995; Narbonne *et al.* 1997). In Arctic Norway, these fossils appear immediately above the first occurrence of palaeopascichnids and below the first Ediacara-type fossils including discs and dickinsoniamorphs (Högström *et al.* 2013, 2017; Jensen *et al.* 2018*b*), suggesting an age of 565–550 Ma based on radioisotopic ages that constrain similar fossils assemblages (cf. Jensen *et al.* 2018*b*; Kolesnikov *et al.* 2018; Soldatenko *et al.* 2019). These examined units are not coeval, but their ages are mostly younger than the Shuram anomaly, the most negative carbon isotope excursion in Earth's history and a global, synchronous event with bounding Re–Os ages of 574.0 ± 4.7 to 567.3 ± 3.0 Ma (Rooney *et al.* 2020). Based on these occurrences, and depending on the age of palaeopascichnids in the Indreelva Member (see Jensen *et al.* 2018*b*), the *Granomarginata*–*Lagoenaforma* association first appeared after, or coincides with, the latest part of the Shuram excursion. It has a relatively long range to the uppermost Ediacaran, and *Granomarginata* becomes more common in the Cambrian strata.

The age uncertainty of the Norwegian strata presents two possibilities for the overall age range of the *Granomarginata*–*Lagoenaforma* association (Fig. 7b). The Mortensnes Formation diamictite (separated from the Indreelva Member by the Lillevannet Member, Fig. 2a) is thought to be of Ediacaran age (Halverson *et al.* 2005). A dolomite bed 20 m below the Mortensnes diamictite on the neighbouring Varanger Peninsula contains depleted δ^{13}C values (< −8‰) considered 'a likely correlative of the Shuram–Wonoka anomaly' (Rice *et al.* 2011, p. 598), and it is thought to correlate with the Shuram CIE in the upper Johnnie Formation in Death Valley, USA (Halverson *et al.* 2005). This suggests a younger age of the Mortensnes diamictite than the Marinoan glaciation and it was correlated with the short-lived Ediacaran Gaskiers glaciation expressed in diamictites on Newfoundland. At the time that model was proposed, the Gaskiers was assumed to be near in age to the Wonoka (=Shuram) anomaly (cf. Halverson *et al.* 2005). Subsequently, the age of the Gaskiers glaciation was constrained to *c.* 579 Ma (Pu *et al.* 2016), which is older than the recent age constraints on the Shuram–Wonoka excursion based on Re–Os geochronology of strata in Oman and NW Canada (*c.* 574–567 Ma, Rooney *et al.* 2020) and estimates from astrochronology (*c.* 570–

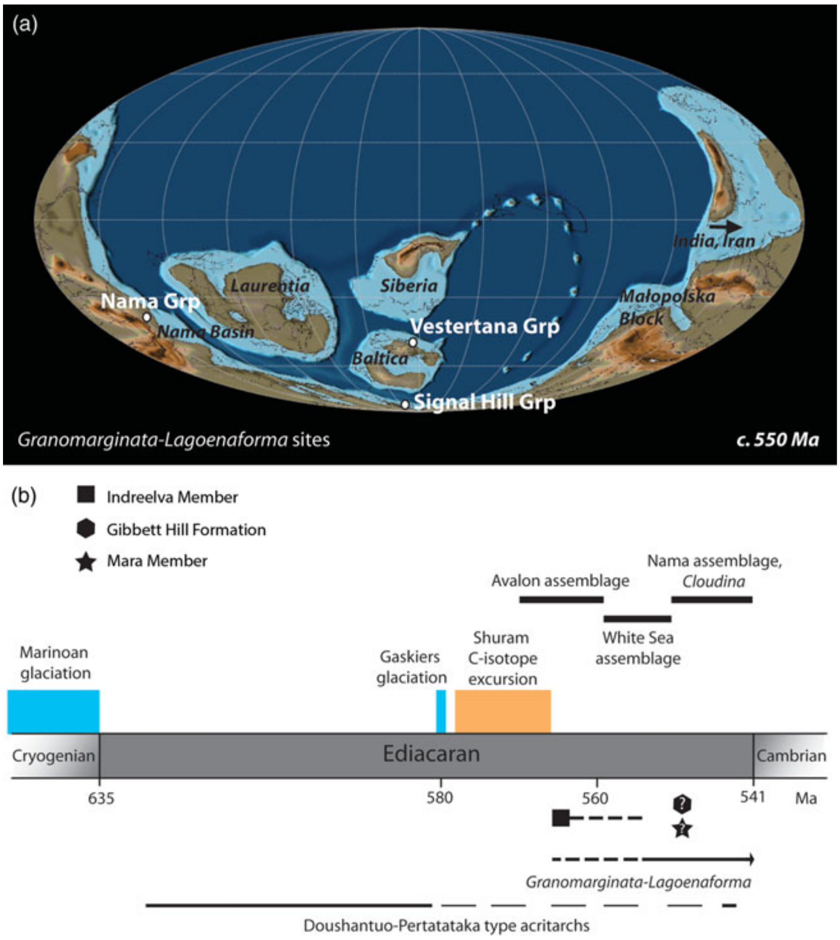

Fig. 7. (Colour online) Distribution and occurrences of documented *Granomarginata–Lagoenaforma* in the Ediacaran Period. (a) Microfossils from the studied units occur in three distinct areas: Baltica (Indreelva Member, Vestertana Group), Avalonia (Gibbett Hill Formation, Signal Hill Group) and Nama Basin (Mara Member, Nama Group), in white. Localities with additional occurrences of Ediacaran *Granomarginata* or flask-shaped organic-walled microfossils are marked in black. Continental reconstruction around 550 Ma was produced using PaleoAtlas for GPlates program (Scotese, 2016). (b) Schematic timeline of the appearance and the stratigraphic range of *Granomarginata–Lagoenaforma* relative to macrofossil assemblages and major environmental events in the Ediacaran Period. The orange box represents the permissible time of the duration of the Shuram negative carbon isotope excursion, following Rooney *et al.* (2020). Fossiliferous localities are marked by black symbols. A dashed line represents the interval of age-uncertainty for each locality (see Discussion for details).

562 Ma, Gong & Li, 2020). This places the Shuram–Wonoka excursion after the Gaskiers glaciation. Accepting the interpretation that the negative $\delta^{13}C$ values in the Nyborg Formation carbonates are representative of the Shuram–Wonoka anomaly, the Mortensnes diamictite could be younger than the Gaskiers and Trinity diamictites on Newfoundland, which suggests an even younger age for the base of the overlying Indreelva Member. This places it closer in age to the studied strata in Newfoundland and Namibia, and implies a narrower stratigraphic range of OWM at the end of the Ediacaran Period.

Alternatively, if the Mortensnes Formation is of Gaskiers age (Halverson *et al.* 2005) and therefore older than the Shuram excursion, the *Granomarginata–Lagoenaforma* association has approximately the same age constraint as *Palaeopascichnus* (Fig. 7b). This is supported by the presence of palaeopascichnids of a type around 565 Ma or younger in age in the Indreelva Member (Jensen *et al.* 2018*b*), just below the occurrence of OWM, which coincides with the later part of the permissible duration of the Shuram excursion. Moreover, the OWM and the palaeopascichnids occur prior to the appearance of dickinsoniamorphs (Högström *et al.* 2017), whose stratigraphic range is around 558–550 Ma (Narbonne *et al.* 2012). The older age of the Mortensnes diamictite, probably coeval with the Gaskiers and Trinity diamictites, is therefore more likely, and indicates a longer age range of *Granomarginata–Lagoenaforma* through late Ediacaran time.

A negative carbon isotope excursion in the Nama Group was correlated to excursions recorded in the upper Nafun (*c.* 550 Ma) and lower Ara groups in Oman, above the Shuram Formation (Grotzinger *et al.* 1995; Halverson *et al.* 2005). However, these depleted $\delta^{13}C$ values in the carbonates of the Dabis Formation, including the Mara Member, have also been interpreted as heralding the end of the Shuram excursion (Hall *et al.* 2013; Wood *et al.* 2015). The excursion recorded in the Mara Member elsewhere (Kaufman *et al.* 1991; Wood *et al.* 2015) is not fully expressed in the sampled section, possibly because the Pockenbank area was on a palaeo-high compared with that of other localities that record the Shuram anomaly in full (see Vickers-Rich *et al.* 2016). Additional micropalaeontological investigation is needed to evaluate the extent of the association's range through the lower Nama Group and in relation to its chemostratigraphy.

Throughout the late Ediacaran interval, both *Granomarginata* and *Lagoenaforma* are rare in comparison to leiosphaerid and filamentous microfossils, but still more morphologically distinct than most other OWM in the upper Ediacaran strata. The association also co-occurs with the coccoid aggregate structure *Bavlinella* sp. (Fig. 6h), which is relatively common in Neoproterozoic strata (cf. Vidal, 1976) and was previously recovered from the Ediacaran strata of Namibia by Germs *et al.* (1986). Smooth-walled OWM (leiosphaerids; Fig. 6a, b, d) are the most abundant component of the examined assemblages, consistent with the idea that the late Ediacaran microbiota was generally of low diversity and dominated by simple leiosphaerids (Moczydłowska, 1991; Grey, 2005). *Lophosphaeridium* is another OWM best known from Cambrian strata that was also reported from the upper Ediacaran Frecheirinha Formation (Chiglino *et al.* 2015) and

Maricá and Bom Jardin groups in Brazil (Lehn *et al.* 2019). This taxon was not found in the present material, so it may not have been distributed globally or it may have been restricted to a specific environment, and more work is needed to assess its distribution at this time. Regardless, both *Lophosphaeridium* and *Granomarginata* first appeared during the rise of macroscopic Ediacara-type biota, and have subsequently diversified and became more prominent components of OWM assemblages in the Cambrian strata (e.g. Moczydłowska, 1991; Palacios *et al.* 2018).

Because of the presence of taxa and fossil groups that 'cross' the Ediacaran–Cambrian boundary, the composition of whole assemblages may also be relevant for the OWM biostratigraphy of the Ediacaran–Cambrian transition. A leiosphaerid-dominant assemblage with *Lagoenaforma* in association with *Granomarginata* is present in multiple palaeogeographic areas and, pending further studies, has potential to be broadly used as one of the indicators of the upper series Ediacaran. However, this association may also reflect a specific environmental control.

5.c. Palaeoenvironmental implications

Our new data show that *Granomarginata* and *Lagoenaforma* are relatively rare components of the late Ediacaran microbiota, but were present on several palaeocontinents (Fig. 7a; Table 1). The studied strata in Norway, Newfoundland and Namibia are not coeval, but can be viewed as part of the upper series Ediacaran (cf. Xiao *et al.* 2016). Considering the palaeogeographic reconstruction for this time, the *Granomarginata*–*Lagoenaforma* association was widely dispersed (Fig. 7a), and possibly an assemblage of cosmopolitan taxa. The association could be representative of taxa occupying a specific type of environment. All strata in which this assemblage occurs (including the upper Ediacaran rocks bearing *Granomarginata* in India, Poland and Baltica; Prasad *et al.* 2010; Jachowicz-Zdanowska, 2011; Arvestål & Willman, 2020), represent a marine shallow-water to marginal shelf environment. Leiosphaerids are usually highly abundant in nearshore, shallow-water environments (e.g. Li *et al.* 2004). They comprise most of the OWM assemblage containing *Granomarginata* and *Lagoenaforma*, so this is further indication of a shallow-water setting.

Acanthomorphic OWM characteristic of ECAP/DPA do not occur in the studied strata, although rare cases of late Ediacaran acanthomorphs are documented in Mongolia (Anderson *et al.* 2017, 2019) and Siberia (Grazhdankin *et al.* 2020). These assemblages are an exception among the depauperate OWM assemblages prevalent at this time (Grey, 2005; Leonov & Ragozina, 2007). While the pre-Shuram ECAP assemblages are generally diverse (e.g. 54 taxa in the Doushantuo Formation; Xiao *et al.* 2014), the LELP assemblages tend to contain fewer taxa (e.g. 16 in the Lyamtsa Formation, White Sea region; Leonov & Ragozina, 2007), many of which are bacterial. The exceptionally preserved microfossils from the Khesen Formation in Mongolia exhibit Doushantuo-style preservation (Anderson *et al.* 2017), similar to ECAP microbiota from phosphorites of the lower Ediacaran Doushantuo Formation in China (e.g. Xiao *et al.* 2014). The Khesen assemblage is preserved in phosphatic grainstones, within a sediment-starved, condensed carbonate succession. The acid-extracted acanthomorphs from the Oppokun Formation in Siberia occur in a thick succession of mudstones (Grazhdankin *et al.* 2020), probably deposited in a low-energy environment. These occurrences in different depositional environments may result in different assemblages: nearshore shallow marine in the case of the *Granomarginata*–*Lagoenaforma* association and depauperate leiosphaerid assemblage (LELP) recognized by Grey (2005), or low-energy environments in the case of ECAP. The overall dearth of microfossils across the Ediacaran–Cambrian transition could also be a result of the lack of sampling for palynological analyses, or a depositional hiatus. Many relevant successions consist of mainly unsuitable lithologies for OWM preservation (especially in Australia; Grey, 2005), although this is not the case on EEP and Baltica. The dearth of OWM could also relate to the Kotlinian Crisis: a drop in diversity of soft-bodied taxa near the increase of bioturbation and expansions of reef-builders (Kolesnikov *et al.* 2015).

Some prasinophyte-like OWM (in addition to *Granomarginata*, e.g. *Tasmanites* and *Pterosperma*-like morphotypes) persisted through the Ediacaran–Cambrian transition, and it was suggested that perhaps these organisms played a role as primary producers in sustaining the metazoan ecosystem during this transitional interval (Moczydłowska, 2011). This is difficult to reconcile with biomarker evidence for bacterially dominated primary production on Baltica and the EEP in the upper Ediacaran strata (Pehr *et al.* 2018). Prasinophytes are generally successful in low diversities of other phytoplankton taxa and in an aftermath of crises, which labels them disaster-taxa (e.g. van de Schootbrugge *et al.* 2007). A community of such disaster-taxa and potential mixotrophs (flask-shaped microfossils) is therefore a likely response of eukaryotic microbiota to ecosystem perturbations (cf. Kolesnikov *et al.* 2015; Wood *et al.* 2019) through the late Ediacaran Period.

6. Conclusions

The organic-walled microfossil *Granomarginata*, otherwise a constituent of lower Cambrian acritarch assemblages, was recovered from middle–upper Ediacaran strata, in addition to a new taxon *Lagoenaforma collaris* gen. et sp. nov. New locations include three palaeocontinents: Avalonia (Newfoundland), Baltica (Norway) and adjacent to the Kalahari Craton (Namibia). While *Granomarginata* survived into and became more prominent in the Cambrian, *Lagoenaforma* is so far known only from the Ediacaran, although other neck-bearing forms occur in the lowermost Cambrian strata in Norway. Problematic microfossils in other Ediacaran units resembling *Granomarginata* are reviewed in this study; the taxon's occurrence was additionally documented elsewhere on Baltica, the Indian palaeocontinent and the Małopolska Block of Poland (Table 1). The stratigraphic range of *Granomarginata* is therefore extended further back in time, which places it into the so-called late Ediacaran leiosphaerid palynoflora (LELP; *sensu* Grey, 2005), a depauperate assemblage of predominantly sphaeromorph and envelope-bearing organic-walled microfossils. Our records from three palaeocontinents and previous reports show that both taxa were geographically widespread by late Ediacaran time. Their occurrence deeper in the stratigraphy suggests a protracted transition into Cambrian-like assemblages.

Co-occurring taxa include prokaryotic OWM and organic problematica (Table 1). *Granomarginata* and flask-shaped microfossils occur in strata that mostly postdate the Shuram–Wonoka excursion and so far have not been recovered from lower Ediacaran assemblages (cf. Hofmann *et al.* 1979; Grey, 2005; Agić *et al.* 2019). Based on these occurrences in post-Gaskiers and post-Shuram rocks, the age range of the *Granomarginata*–*Lagoenaforma* association is broadly late Ediacaran.

Together, the record presented here along with other reports on late Ediacaran microfossils support the conclusion that some OWM and SCF survived into the Phanerozoic Eon with their abundance increasing during the Cambrian Period. The LELP assemblage is indeed dominated by leiosphaerids, but contains more taxa than previously recorded, even outside the few Doushantuo–Pertatataka acritarch assemblages that persisted into the upper Ediacaran. Although this record is rather limited, it calls for a more thorough palynological investigation of middle–upper Ediacaran strata. Globally, few units have been examined in detail (with the exception of Russia and Ukraine), so perhaps the diversity of late Ediacaran protistan microfossils is underestimated. Additional OWM records in such little-studied deposits could not only aid in biostratigraphic endeavours, but also help constrain the timing of the turnover of late Neoproterozoic microscopic eukaryotes, and the onset of the microbiota characteristic of the early Phanerozoic Eon.

7. Systematic palaeontology

Genus *Granomarginata* Naumova (1960)

Type species. Granomarginata prima Naumova (1960, p. 114) described from the lower Cambrian 'Blue Clay' (=Lontova Formation) of Estonia.

Remarks. Specimens of *Granomarginata* in the present material resemble *Ostiumsphaeridium complitum* (Vorob'eva *et al.* 2009, figs. 14.1, 14.2) from the upper Neoproterozoic strata on the East European Platform, found in association with large spinose OWM (DPA/ECAP). Both taxa have a darker central body with a fluffy extension, yet the vesicle of *Ostiumsphaeridium* additionally possesses a large, oval slit-like excystment opening. No openings are observed in present or previously described *Granomarginata*.

Granomarginata can be distinguished from more common and long-ranging Proterozoic envelope-bearing OWM such as *Simia annulare* Timofeev (1969) emend. Mikhailova in Jankauskas *et al.* (1989), in its texture and shape of its outer envelope. Both taxa have a central body surrounded by an extension in the equatorial plane that forms a rim of varying width between species. Whereas the extension in *Simia* is sharply outlined and crisp, with occasional concentric folding caused by compression (e.g. Vorob'eva *et al.* 2009, fig. 14.7; Agić *et al.* 2017, fig. 14h–i), the extension of *G. prima* is fluffy and filmy (e.g. Moczydłowska, 1991). Jankauskas *et al.* (1989, p. 66) noted that *Simia* has a 'less-rough surface'. *Simia* co-occurring in the same sample as *Granomarginata* in the Nama Group (Fig. 6f) has a well outlined and thick-walled central body as characteristic for the taxon, and its extension shows different properties: faint concentric folding from compression that is not observed in *Granomarginata*. Furthermore, the outline between the central body and the extension in *Simia* is sharp and well-defined (Jankauskas *et al.* 1989), whereas Moczydłowska (1991, p. 57) observed that the spongy nature of the *Granomarginata* wall may 'appear as irregular filaments on the outline of the equatorial zone'. The extension in *Granomarginata* often appears fragmented or uneven (e.g. Volkova, 1968), and is likely less resistant than the central body (Moczydłowska, 2011). Material presented here supports this. Many documented *Simia* specimens also have a fragmentary extension (e.g. Agić *et al.* 2017, fig. 10g, h), but the breakage there is sharper than seen in *Granomarginata*, indicating a more brittle nature of the envelope in *Simia*. *Granomarginata* also differs from envelope-bearing *Pterospermopsimorpha*. A disphaeromorph, *Pterospermopsimorpha* is a sphere-within-sphere with a well outlined inner vesicle and a robust outer envelope (e.g. Jankauskas *et al.* 1989, pl. 3, figs 3–8; Agić *et al.* 2017, fig. 10a–c). The inner vesicle is not always centrally located within the envelope, as is the case in *Simia* or *Granomarginata*. *Pterospermopsimorpha* is quite rare in Ediacaran strata relative to other OWM taxa (Grey, 2005), as well as compared with its abundance in pre-Cryogenian fossiliferous units (H. Agić, pers. obs.).

Granomarginata prima Naumova (1960)
Figure 4e, f

Synonymy. cf. 1986 '*Comasphaeridium*-like fossil'; Germs *et al.*, p. 56, fig. 5i.
1990 *Granomarginata* sp.; Gunia, p. 109, pl. 1, figs 10, 11.
2010 *Granomarginata prima*; Prasad *et al.*, p. 420, pl. 1, fig. 6.
2011 *Granomarginata prima*; Jachowicz-Zdanowska, p. 91, fig. 4I.
See additional synonymy of Cambrian specimens by Palacios *et al.* (2018).

Material. Two specimens (D16-HA-80 84.5×18 and D16-HA-53 81×14) from the Indreelva Member, Stáhpogieddi Formation, Vestertana Group in Norway. One complete specimen and one hemisphere fragment (N16-HA-P3 79×16) from the Mara Member, Dabis Formation, Nama Group, Pockenbank in Namibia. A fragment of a vesicle with a spongy envelope from the Gibbett Hill Formation, Signal Hill Group on Avalon Peninsula in Newfoundland (Brasier Shale A-1 87×5).

Description. Round to oval, discoid vesicles with central body that is surrounded by a narrow, membrane-like, spongy extension. The extension rim on our specimens is uniform in width, but it seems less resistant than the central body, so it is occasionally fragmentary or appears etched and uneven.

Dimensions. Vesicle diameter range observed in *G. prima* is 24–40 µm (cf. Moczydłowska, 1991). In the present material, the overall diameter of the microfossil ranges over 31–39 µm, $n = 4$, mean ($\bar{x}$) = 35.5 µm, standard deviation (σ) = 4.8 µm.

Remarks. G. prima differs from *G. squamacea* in a narrower rim. There is no prior known occurrence of *Granomarginata* from Namibia. However, Germs *et al.* (1986) have documented an acritarch specimen strongly resembling *G. prima*, identified as '*Comasphaerdium*-like fossil' (Germs *et al.* 1986, fig. 6i) from the upper Kuibis subgroup. Although the specimen is poorly preserved, and its features are difficult to discern in the black-and-white photomicrograph, it appears to bear a narrow spongy rim characteristic of *G. prima*. Poorly preserved specimens of *Granomarginata* may superficially resemble acanthomorphic acritarchs with thin processes (cf. Spina *et al.* 2020, pl. 1 figs 6–8). Specimens of *G. prima* from upper Ediacaran strata represent this species' oldest known occurrence to date, but they are very rare in Ediacaran units, in comparison to the taxon's ubiquity in the Cambrian strata. It is a more common component of the *Granomarginata* Zone and *Asteridium tornatum–Comasphaeridium velvetum* Zone in the Terreneuvian Series (Fortunian) of lower Cambrian strata, as well as in the *Volkovia dentifera–Liepaina plana* and *Skiagia ornata–Fimbriaglomerella membranacea* zones in Cambrian Series 2 (Palacios *et al.* 2018, 2020). Examples of *Granomarginata* with a darker central body are common in the thermally altered rocks, for example in the Såvvovare/Grammajukku formations in Sweden (Moczydłowska, 2002) and higher up in the stratigraphy on the Digermulen Peninsula (Manndrapselva Member; Högström *et al.* 2013, fig. 6C), as well as in some strata with lower thermal alteration such as the File Haidar Formation in Sweden (Eklund, 1990).

Occurrence. In Ediacaran-age deposits, *Granomarginata prima* occurs in the following units: Indreelva Member, Stáhpogieddi Formation, Vestertana Group, Norway; Dabis Formation, Nama Group, Namibia; Jodhpur Formation, Marwar Supergroup, India (Prasad *et al.* 2010); boreholes from the Małopolska block adjacent to East European Platform, Poland (Jachowicz-Zdanowska, 2011); and potentially Gibbett Hill Formation, Signal Hill Group, Newfoundland. For a list of Cambrian occurrences of *G. prima*, see work by Moczydłowska (1991, 2011) and Palacios *et al.* (2018). *G. prima* and organic problematica are found also in the Cambrian strata on the Digermulen Peninsula, in the third cycle of the Manndrapselva Member, Stáhpogieddi Formation (Fig. 2a; Högström *et al.* 2013), and in the Duolbagáisá Formation, Digermulen Group correlated to Cambrian Stage 3–4 (Palacios *et al.* 2020), which overlies the Vestertana Group.

Stratigraphic range. The first appearance of *G. prima* is in the upper Ediacaran strata above the first appearance of *Palaeopascichnus* and discoidal macrofossils in Norway, and below the strata containing upper Ediacaran macrofossils in Namibia. The taxon ranges to the Miaolingian Series (Moczydłowska, 1991).

Granomarginata squamacea Volkova (1968)
Figure 4a–d

Synonymy. cf. 2020 ‘unknown c’; Arvestål & Willman, fig. 12d.

See additional synonymy of Cambrian occurrences by Moczydłowska (2011).

Material. Three specimens and three fragments (D18-HA-20 81×6, D16-HA-80 87×19, D16-HA-80 85×21) from near the base of the Indreelva Member, Stáhpogieddi Formation (Vestertana Group), exposed on the Digermulen Peninsula, Norway. Two specimens and three fragments (N16-HA-P2 82×13, N16-HA-P3 81×9) from the Mara Member, Dabis Formation, Nama Group, from Farm Pockenbank, southern Namibia.

Description. Circular to oval vesicles consisting of a central body surrounded by a wide, spongy, membranous extension in the equatorial part. The extension is thin and of varying breadth; it often appears uneven in outline or etched.

Dimensions. Vesicle diameter of *G. squamacea* in the material reported here ranges over 32–58 µm, $n = 9$, $\bar{x} = 45.7$ µm, $\sigma = 8.2$ µm, marginally larger than the reported size range for this taxon of 20–55 µm by Moczydłowska (2011). Central body diameter is 25–32 µm.

Remarks. Unlike *G. prima*, the extension in *G. squamacea* is often creased. Moczydłowska (1991, p. 57) noted that the spongy part of *G. squamacea* “appears as irregular ‘filaments’ on the outline of the equatorial zone”. In a few poorly preserved specimens this may lead to their erroneous identification as an acanthomorph taxon with dense thin processes, for example, *Comasphaeridium*. This filamentous appearance of the extension was probably obtained as the vesicle underwent post-depositional compression. Specimens of *G. squamacea* in this material differ from other Proterozoic envelope-bearing taxa such as *Simia* and *Pterospermopsimorpha* in a membranous, spongy extension and fluffy wall (Moczydłowska, 1991), as mentioned above. The distinction between the two taxa was also illustrated by Moczydłowska (2002, fig. 9.3, 9.4). *G. squamacea* with an opaque central body is also known from the thermally altered Cambrian strata of the Swedish Caledonides (Moczydłowska, 2002, fig. 9.4). Such an appearance is then not unexpected within the Indreelva Member, where the sediments have experienced tectono-metamorphic deformation related to the late Scandian Orogeny, and have a postmature overprint of 200–250 °C (Meinhold *et al.* 2019*b*). Some Neoproterozoic specimens of *G. squamacea* (Pyatiletov, 1988) were subsequently dismissed as globular kerogen particles (Vidal *et al.* 1995). *G. squamacea* is rare compared with leiosphaerids or filamentous organic-walled microfossils from the same samples.

Occurrence. The first appearance of *Granomarginata squamacea* to date is in the Ediacaran Stáhpogieddi Formation, Vestertana Group (Arctic Norway), above the first occurrence of *Palaeopascichnus delicatus* estimated at < 565 Ma (cf. Jensen *et al.* 2018*b*). Other Ediacaran occurrences include an additional record from Baltica – *Granomarginata*-like acritarch from the Kotlin Formation in Estonia (Arvestål & Willman, 2020) – as well as the material documented here from the Dabis Formation, Nama Group in Namibia. For a compilation of global Cambrian occurrences, we refer to Moczydłowska (1991, 2011).

Stratigraphic range. The range of *G. squamacea* is hereby extended lower in the stratigraphy, from above the deposits of the Ediacaran glaciation and the first appearance of palaeopascichnids in Norway, and below the unit containing macrofossils of the Nama assemblage in Namibia.

Genus *Lagoenaforma* gen. nov.

Type species. *Lagoenaforma collaris* gen. et sp. nov.

Etymology. From the Latin *lagoena*, - ae, f. (loaned from the Greek λαγηνος) meaning pitcher or flask, and *forma*, - ae, f., meaning shape, describing the microfossil’s resemblance to a wine pitcher. Pliny the Younger (Mynors, 1963) refers to his hunting flask as lagena/laguncula.

Description. As for type species.

Lagoenaforma collaris gen. et sp. nov.
Figure 5a–c

Synonymy.

cf. 1988 ‘chitinozoan-like microfossil, Form II’; Zang, pl. 16, figs A, B.

1989 *Germinosphaera guttaformis*; Jankauskas *et al.*, pl. 47, fig. 7.

2003 ‘Chitinozoa-like microfossils’; Sabouri *et al.*, pl. 3, fig. 10.

Etymology. From Latin *collum*, -i, m. meaning neck, in reference to the neck-like protrusion from the elongate vesicle.

Holotype. TSGf18449c 78×15, sample D16-HA-80 (Fig. 5a) from the Ediacaran Indreelva Member, Stáhpogieddi Formation, Vestertana Group in Norway.

Material. Ten specimens in total. Four specimens (D16-HA-80 78×15, D16-HA-80 83×4, D16-HA-53 85×9, D16-HA-53 79×18) well to moderately well preserved from the Indreelva Member, Stáhpogieddi Formation (Vestertana Group) on Digermulen Peninsula, Arctic Norway. Three specimens (N16-HA-P2 76×7, N16-HA-P2 77×5.5, N16-HA-P2 79×11) from the Mara Member, Dabis Formation, Nama Group, on Farm Pockenbank, southern Namibia.

Diagnosis. Oval to elongate vesicle with a neck-like protrusion. The neck is open distally and terminates by widening outwards; it never tapers. The neck is up to one third of the overall vesicle length. Wall texture smooth to chagrinate.

Dimensions. The length of the vesicle including the 'neck' is 67–94 µm ($\bar{x} = 78$ µm, $\sigma = 10.7$ µm, $n = 9$). The opening of the 'neck' ranges over 15–32 µm. The neck width is 12–30 µm, except the outlier specimen from the Gibbett Hill Formation which possesses a 4-µm-wide 'neck'.

Remarks. *L. collaris* exhibits no ornamentation or sculpture, but its wall texture can be smooth (Fig. 5a) or 'fluffy' (Fig. 5b, c), which is likely a preservational feature. The Newfoundland specimen is opaque akin to other microfossils from the Gibbett Hill Formation (e.g. Fig. 6c). This is common in OWM from units that have undergone a higher degree of thermal alteration (Spina *et al.* 2018), but it can also result from accelerated degradation in oxygenated environments (Schiffbauer *et al.* 2012). The Newfoundland specimen has a narrower 'neck' compared with other specimens of *L. collaris* (4 µm in width), but the widening-outwards at the tip indicates that the 'neck' structure is not a process, but likely an open-ended protrusion.

Jankauskas *et al.* (1989) erected a new species of a long-ranging Precambrian taxon *Germinosphaera* that includes one flask-shaped morphotype: *G. guttaformis* from the upper Riphean (=Tonian–Cryogenian) of Siberia. Only one specimen in their material has an elongate, flask-shaped main vesicle and a thick single process, truncated at the tip, whereas the rest possess a thick, circular vesicle 80–60 µm in diameter (Jankauskas *et al.* pl. 47, figs 7, 8). *G. guttaformis* specimen on plate 47, figure 8 has a narrow process, more similar to the narrow 'neck' in the Gibbett Hill specimen described here, but its vesicle is still bigger and more rounded than that of *L. collaris*. Although the rest of *G. guttaformis* material described by Jankauskas *et al.* (1989) is relatively consistent, a single elongate specimen (pl. 47, fig. 7) is unlike other members of this genus; both the original and emended diagnoses for *Germinosphaera* imply a circular vesicle (Mikhailova, 1986; Butterfield *et al.* 1994). That morphotype therefore does not belong to *Germinosphaera*, and we do not include our similar specimens into this genus. Willman & Moczydłowska (2011, pl. 7, fig. 7) illustrated a flask-like microfossil interpreted as a fragmented cyanobacterial sheet from the upper Dey Dey Mudstone in the Officer Basin, Australia, *Tanarium*-bearing beds. That morphotype differs from *L. collaris* in its longer and straighter 'neck'.

Some chitinozoan-like microfossils from several sections of the upper Ediacaran Kahar Formation in northern Iran (Sabouri *et al.* 2003, pl. 3, fig. 10) are comparable to *L. collaris*. Similar 'chitinozoan-like microfossils' were also reported from the Liulaobei Formation, Huainan Group in China (Zang, 1988), now understood to be Tonian in age (see Tang *et al.* 2013). An outlier among those microfossils, called 'Form II' (pl. 16, figs a, b), resembles *L. collaris* in shape and size. Zang (1988) noted that distribution of 'chitinozoan-like' microfossils declined from deep to shallow water, which is in contrast to present material where *L. collaris* occurs in shallow-water environments. The relationship of *L. collaris* to these Tonian OWM is unclear. Additional soft-bodied forms similar to *L. collaris* from the Proterozoic Vindhyan Supergroup of India (Maithy & Babu, 1989, pl. 1) were attributed to chitinozoans, including *Melanocyrillium*. However, those microfossils lack diagnostic characteristics of *Melanocyrillium* like a well-defined aperture and a curved neck (Bloeser, 1985). Superficially similar morphology to *L. collaris* is seen in mineralized vase-shaped microfossils (VSM) with long necks from the Neoproterozoic Urucum Formation in Brazil (Morais *et al.* 2017, figs 6.7–6.9), interpreted as testate amoebae. VSMs with a mineralized or organic wall coated by minerals are mostly found in upper Tonian organic-rich shales (Porter *et al.* 2003). Chai *et al.* (2020) reported an uncharacteristically young occurrence of VSM from the late Ediacaran Dengying Formation in China. In contrast to *Lagoenaforma*, those are permineralized in three dimensions, and differ in that they have a shorter and narrower 'neck'.

The flask-shaped morphology mostly resembles chitinozoans, organic-walled marine microfossils common in Ordovician–Devonian strata. Few flask-shaped, neck-bearing, organic taxa are known from the Proterozoic and Cambrian strata (e.g. Yin, 1980), and there is a rare Cambrian Stage 5 occurrence of chitinozoans (Shen *et al.* 2013); however, due to the simple morphology of *L. collaris*, further comparisons are impractical. *Lagoenaforma* is also similar to Ordovician flask-like OWM *Aremoricanium* (Deunff, 1955). They differ in size and shape of the neck structure, which is wider and shorter in *L. collaris*, and the texture of its organic wall, which is thinner and smoother among *Aremoricanium* species. The difference in the vesicle wall could potentially be attributed to preservation as the Ediacaran fossils studied here are not as exquisitely preserved as the Ordovician material. Nevertheless, *Aremoricanium* has a well defined stratigraphic range (Loeblich & MacAdam, 1971) and lacks a Cambrian record, so such a significant time gap makes it less likely that these fossils represent the same or a related organism. *L. collaris* also differs from the Cambrian acanthomorphic acritarch *Volkovia dentifera* (Downie, 1982) by its overall larger size, and a shorter and wider protrusion instead of the narrow, single process of *Volkovia*. The distal tip of the process in *Volkovia* is pointed and closed (cf. Moczydłowska, 1991), whereas the neck in *L. collaris* is open-ended and slightly widens outwards. The possibility that the protrusion in *L. collaris* is truncated and could therefore represent a *Volkovia* with a broken-off process (or another single-processed OWM such as *Aliumella baltica* Umnova & Vanderflit, 1971) is dismissed because the *L. collaris* 'neck' terminates with a widening end (Fig. 5).

A single microfossil from the Manndrapselva Member (Fig. 5d) possesses a neck-like structure akin to *L. collaris*, but its main vesicle is rounded and its 'neck' is shorter, which is more similar to *Sinianella uniplicata* (Yin, 1980). The Manndrapselva Member includes additional neck-bearing OWM but with a more rounded vesicle and much longer neck structures (Palacios *et al.* 2017; A. Högström, pers. obs.).

L. collaris shares the morphology of a flask-shaped body plan with a variety of living non-testate protists. A neck-like opening is commonly an indicator of a mixotrophic lifestyle. Some prostomateid ciliates possess a variety of oral bulges used in feeding (e.g. *Enchelyodon longikineta*, Şenler & Yịldịz, 2003, fig. 2), similar to the 'neck' of *L. collaris*. *Vasicola ciliata* (Taylor & Sanders, 2010; fig. 3.22.O) has a soft-bodied, chitinous lorica (protective outer covering) in the shape of a pitcher, and the chitinous composition would increase its preservation potential. However, apart from these morphological similarities, the affinity of *L. collaris* is unclear.

Occurrence. The taxon appears in the Ediacaran shales and siltstones of the Indreelva Member, Stáhpogieddi Formation, Vestertana Group in Norway; Mara Member, Dabis Formation, Nama Group in Namibia; and the Gibbett Hill Formation, Signal Hill Group in Newfoundland.

Stratigraphic range. Upper Ediacaran.

?*Lagoenaforma* sp.
Figure 5e

Material. One specimen and one fragment ('Brasier Shale A'-1 89×7, 91×11,) from the Gibbett Hill Formation, Signal Hill Group on Avalon Peninsula, Newfoundland.

Description. Oval to elongate vesicles with a neck-like protrusion. The base of the neck is slightly wider. The necks are open distally and terminate by widening outwards; they never taper. The necks are up to one third of the overall vesicle length. Wall texture smooth to chagrinate.

Dimensions. The length of the vesicle including the 'neck' is 87 µm. The 'neck' is 5 µm wide and 7 µm wide at the tip.

Remarks. This flask-shaped OWM differs from *Lagoenaforma collaris* in a longer and narrower 'neck' structure. It is similar to, but half the size of, some rare, enigmatic, flask-shape structures from the Wallara 1 drill hole, lower Ediacaran Pertatataka Formation in Australia (Grey, 2005, fig. 274c).

Unnamed Form A
Figure 5d

Material. One specimen (TSGf18451a 89×23, sample D16-HA-77) from the Manndrapselva Member, Stáhpogieddi Formation, Vestertana Group on the Digermulen peninsula, Arctic Norway.

Description. Rounded vesicle with short and wide neck-like protrusions, flaring outwards. The vesicle wall has bulbous sculpture.

Remarks. This specimen resembles *Sinianella uniplicata* (Yin, 1980), but it differs from it in having a bulbous wall sculpture. It is unclear from observing a single specimen if the body is composed of smaller cells or if those are a part of the wall sculpture. A similar microfossil with an opaque wall and a wide-based, neck-like protrusion from the middle–upper Santa Bárbara Group, Camaquã Basin in Brazil was assigned to *Germinosphaera* sp. (Lehn *et al.* 2019, fig. 3j). The Brazilian specimen bears a strong similarity to a truncated *Germinosphaera*, but also possesses a wider process base compared with members of this genus (cf. Butterfield *et al.* 1994), and appears as a 'neck' structure terminating in an opening. Unnamed Form A differs only slightly from the Camaquã Basin specimen in a widening-outwards 'neck'. Further micropalaeontological examination of middle–upper Ediacaran strata worldwide will show the frequency of this morphotype. OWM with short, neck-like protrusions are not uncommon in the Precambrian though; such morphologies were also reported from the Mesoproterozoic strata of northern China (Agić *et al.* 2017, fig. 13d, e), and the genus *Sinianella* from Tonian–lower Cambrian strata (Zang, 1988).

Similar OWM occur in the Ediacaran Kahar Formation in Iran as '*Melanocyrillum*' (=*Melanocyrillium*), alongside late Ediacaran SCF *Cochleatina* (Sabouri *et al.* 2003, pl. 3, figs 7–9). However, *Melanocyrillium* is a Tonian VSM taxon that differs from these chitinozoan-like microfossils with a curved neck and well defined aperture, as well as in the mode of preservation (cf. Bloeser, 1985).

Unnamed Form B
Figure 6c

Material. Two specimens ('Brasier Shale A'-1 91×11, 'Brasier Shale A'-1 90×13) in the Gibbett Hill Formation, Signal Hill Group, Ferryland on the Avalon Peninsula, Newfoundland.

Description. Elongate and straight, organically preserved microfossil with short lateral protrusions. Both specimens are truncated, up to 160 µm in length and 32 µm in width. Individual protrusions are broken distally, and up to 7 µm wide.

Remarks. Problematic SCF are common in uppermost Ediacaran and lower Cambrian units worldwide (Moczydłowska *et al.* 2015; Slater *et al.* 2020). Previously, the youngest occurrence of SCF in Newfoundland was documented from the Random Formation (Cambrian Stage 2) on Burin Peninsula (Palacios *et al.* 2018).

This form co-occurs with leiosphaerids and fragments of *Granomarginata prima* in the Gibbett Hill Formation. Similar forms have been observed in the Ediacaran–Cambrian transition strata on the Digermulen Peninsula in Norway (A. Högström, pers. obs.). Arvestål & Willman (2020, fig. 12K, p. 26) documented a hooked microfossil with lateral serrations from the Ediacaran of Estonia, 'possibly related to *Ceratophyton*'. In contrast, the Gibbett Hill microfossils are straight and have more defined and spread out lateral protrusions.

A high degree of coalification is evident in the dark colour of Gibbett Hill Formation microfossils (including leiosphaerids), corresponding to TAI = 4.

Unnamed Form C
Figure 6e

Material. One specimen (TSGf18450b 85×9, D16-HA-53) in the Indreelva Member, Stáhpogieddi Formation, Digermulen Peninsula, Norway.

Description. Elongate and conical vesicle. One end is tapering outwards, closed and blunt. The other end is nearly twice as wide and terminates in a wide opening. The vesicle appears creased, almost annulated.

Remarks. This microfossil shares an ovoidal shape and a similar polar opening to the Ediacaran–Cambrian taxon *Teophipolia lacerata* Kirjanov in Volkova *et al.* 1979 (e.g. Jankauskas *et al.* 1989, pl. 54, fig. 5); however, Unnamed Form C is smaller and narrower, with a faintly annulated vesicle. Similar microfossils also occur in the Cambrian Breidvika Formation, upper Vestertana Group on the Digermulen Peninsula (A. Högström, pers. obs.). This form is also strongly similar to *Navifusa crassa* (Sin & Liu, 1978), a rod-like vesicle with rounded ends and occasionally a distal opening on one end (cf. Zang, 1988, pl. 40, fig. H). However, even though specimens of *N. crassa* with a crumpled or faintly annulated wall have been documented (Zang, 1988), the original description of this taxon implies a smooth surface texture and a spongy wall. This contrasts with the delicate annulation in Unnamed Form C, so we consider it a separate entity.

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