Unlocking the hidden diversity of organic-walled microfossils from the early Cambrian of North Greenland

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Abstract

The early Cambrian Buen Formation of North Greenland is celebrated for hosting one of the oldest Cambrian Burgess Shale-type deposits known to date – the Sirius Passet *Lagerstätte*. Further south in a shallower shelf facies belt, the Buen Formation yielded organic-walled microfossils (OWMs) that were originally described with a focus on acritarchs. Later sampling revealed a diversity of small carbonaceous fossils (SCFs) of metazoan origin. This PhD thesis investigates the diversity of OWMs from the Buen Formation using a novel combination of approaches. First, new samples are processed using a gentle acid maceration protocol designed for the recovery of large, delicate elements. Second, a population-based analysis of disparity is conducted to evaluate acritarch diversity, and illuminate the poorly known palaeobiology of these microfossils. New sampling revealed a remarkable diversity of metazoan fragments, including the oldest-known crustacean feeding apparatus, almost complete bradoriid valves preserved in three dimensions, new types of scalidophoran teeth and scalids, and a wide range of cuticular elements of uncertain affinity. Further, an abundance of large and/or asymmetrical acritarchs and filamentous microfossils was recovered, contributing to a rare but expanding record of benthic Proterozoic-like forms among Cambrian OWMs. The recovered diversity of acritarchs and filamentous microfossils totals 50 form taxa, of which 19 are described for the first time in the region. Quantitative and semi-quantitative analyses of acritarch disparity suggest a substantial proportion of these form taxa represent taphomorphs and/or arbitrary portions of abundance peaks. Placing form species in the context of their wider morphological variations allows the recorded diversity to be pared down to 30 morphotypes. On this basis, the presumed life history of *Skiagia*-plexus acritarchs is updated following quantitative analysis of openings, inner bodies, and clustering patterns in the recovered population. Three additional morphotypes are interpreted as bloom-forming and/or colonial species. Collectively, the results of this PhD project demonstrate that a fundamentally different picture of Cambrian diversity emerges when the full spectrum of OWM size ranges and disparity is considered. Applying these methods to the wider Cambrian record clearly shows potential to refine our understanding of macroevolution and palaeoecology as modern ecosystems were being established.

Keywords: Cambrian, acritarchs, organic-walled microfossils, small carbonaceous fossils, Greenland, diversity, disparity, taxonomy, taphonomy, Crustacea, plankton

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To my parents

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I. Wallet, E., Slater, B. J., Willman, S. & Peel, J. S. (2021) Small Carbonaceous Fossils (SCFs) from North Greenland: new light on metazoan diversity in early Cambrian shelf environments. *Papers in Palaeontology*, 7(3):1403–1433.

II. Wallet, E., Willman, S. & Slater, B. J. (2022) Morphometric analysis of *Skiagia*-plexus acritarchs from the early Cambrian of North Greenland: toward a meaningful evaluation of phenotypic plasticity. *Paleobiology*, 48(4):576–600.

III. Wallet, E., Slater, B. J. & Willman, S. Organic-walled microfossils from the early Cambrian of North Greenland: a reappraisal of diversity. *Submitted to Palynology.*

IV. Wallet, E., Slater, B. J. & Willman, S. The palaeobiological significance of clustering in acritarchs: a case study from the early Cambrian of North Greenland. *Submitted to Palaeontology.*

Front cover: *Skiagia* cf. *compressa* from the early Cambrian Buen Formation of North Greenland (**Papers II, III**).

Statement of authorship

Paper I: J. S. P. collected the material, E. W., B. J. S. and S. W. dissolved samples in acid, E. W. hand-picked microfossils, imaged and figured the specimens, conducted analyses and wrote the manuscript with inputs from B. J. S., S. W. and J. S. P.

Paper II: J. S. P. collected the material, E. W. designed and conducted statistical analyses, imaged and figured the specimens, and wrote the manuscript with inputs from S. W. and B. J. S.

Papers III, IV: J. S. P. collected the material, E. W., B. J. S. and S. W. dissolved samples in acid, E. W. hand-picked microfossils, imaged and figured the specimens, conducted analyses and wrote the manuscript with inputs from B. J. S. and S. W.

Additionally, I contributed to the following papers during my PhD:

Botting, J. P., Muir, L. A., Pates, S., McCobb, L. M. E., Wallet, E., Willman, S., Zhang, Y. & Ma, J. (2023). A Middle Ordovician Burgess Shale-type fauna from Castle Bank, Wales (UK). *Nature Ecology & Evolution*, doi:10.1038/s41559-023-02038-4

Peel, J.S., Skovsted, C.B. & Wallet, E. (2021). Morphology and ecology of the bradoriid arthropods *Spinospitella* and *Nikolarites* from the Cambrian (Series 2, Stage 4) of North Greenland (Laurentia). *PalZ*, 95: 413–427.

Wallet, E., Padel, M., Devaere, L., Clausen, S., Álvaro, J. J., & Laumonier, B. (2022). Cambrian Age 3 small shelly fossils from the Terrades inlier, southern Pyrenees, Spain: Biostratigraphic and paleobiogeographic implications. *Journal of Paleontology*, 96(3), 552–582.

Contents

Abbreviations

BST	Burgess shale-type
Ga	Giga-annum, billion years
Ma	Mega-annum, million years
OWM	Organic-walled microfossil
SCF	Small carbonaceous fossil
SSF	Small shelly fossil

Introduction

The early Cambrian Buen Formation of North Greenland is most famously known from the Sirius Passet *Lagerstätte* – one of the three major Burgess Shale-type (BST) deposits alongside Chengjiang and the Burgess Shale (Fig. 1). The 1 km long locality yielded one of the earliest tiered metazoan communities known to date, providing crucial insights into the Ediacaran–Cambrian transition between matground-supported and metazoan-dominated ecosystems (Harper et al. 2019). The Sirius Passet biota is unique both in terms of faunal composition (Holmes et al. 2018) and taphonomy (Strang et al. 2016; Topper et al. 2018; Harper et al. 2019), with many body fossils preserving some of their original three-dimensionality and labile tissues such as digestive tracks, muscle fibres, eyes and nervous systems (Budd 2011; Peel 2017; Young and Vinther 2017; Park et al. 2018; Fig. 1C, F). For these reasons, the Sirius Passet *Lagerstätte* has been the focus of much scrutiny despite its remote location.

Whilst the spectacular macrofossil record of the Buen Formation has been extensively studied, little attention has been drawn to its organic-walled microfossil (OWM) component. This is in part due to the thermal history of the region, which has undergone chloritoid-grade metamorphism during the Ellesmerian Orogeny (Devonian–Early Carboniferous; Ineson and Peel 2011; Topper et al. 2018). Carbonaceous material from the Sirius Passet area has largely been volatilised as a consequence (Slater et al. 2018), yet more southern, shallower-water deposits yielded abundant and diverse OWMs (Vidal and Peel 1993). These OWMs were originally extracted using a standard palynological protocol (Vidal 1988) designed for the recovery of small acritarchs; i.e., vesicular microfossils of uncertain affinity that, in Cambrian successions, are widely used as a proxy for phytoplankton (e.g., Nowak et al. 2015; Zacaï et al. 2021; Kroeck et al. 2022). Recently, a gentler acid-maceration procedure was applied to fossiliferous horizons, and revealed an unexpected diversity of metazoan fragments (Slater et al. 2018). These so-called 'small carbonaceous fossils' (SCFs; Butterfield and Harvey 2012) substantially expand the known coverage of soft tissue preservation in North Greenland, providing a new window into the shallower-water counterpart of the Sirius Passet biota.
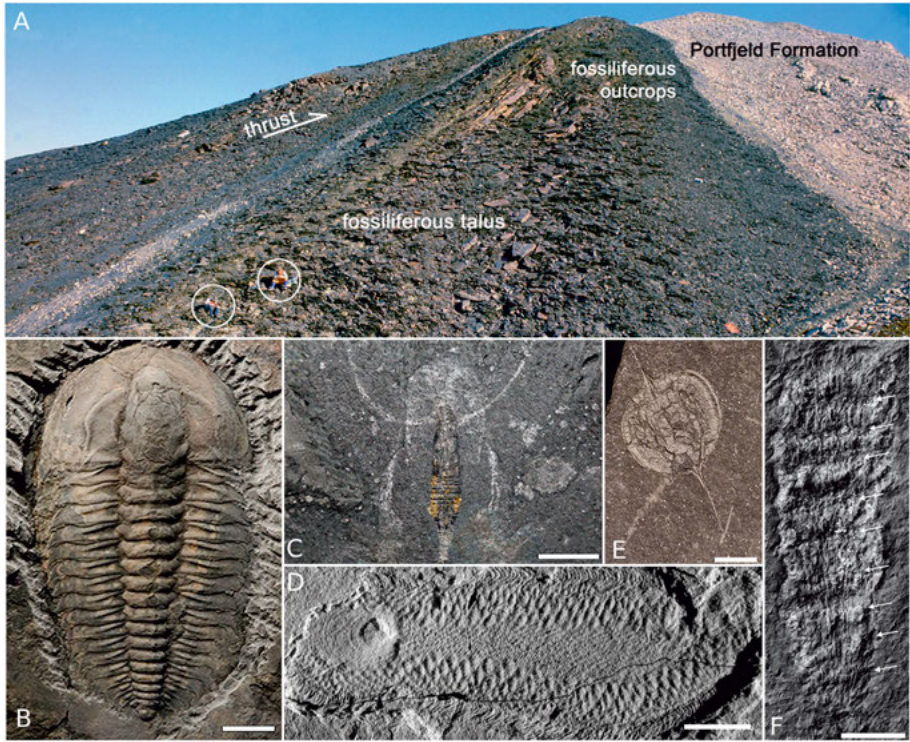
Figure 1. Overview of the Sirius Passet *Lagerstätte*. A, main outcrop area at Locality 1 (Ineson and Peel 2011, fig. 2B), with circled figures for scale. B, *Buenellus higginsi* (Harper et al. 2019, fig. 8a), scale bar 3 cm. C, head of *Kerygmachela kierkegaardi* showing eyes and nervous tracks (Park et al. 2018, fig. 1c), scale bar 5 mm. D, *Halkieria evangelista* (Conway Morris and Peel 1995; fig. 16a), scale bar 1 cm. E, *Isoxys volucris* (Harper et al. 2019, fig. 8f), scale bar 5 mm. F, trunk musculature of *Kiisortoqia soperi* (Young and Vinther 2017; fig. 17A), scale bar 3 mm.

The co-occurrence of OWMs of phytoplanktonic and metazoan origin in the Buen Formation offers a promising pathway to study the unique ecosystems overhanging the Sirius Passet biota. Nevertheless, this prospect is hampered by the poorly known palaeobiology of acritarchs, which stems from a limited array of characters in these problematic microfossils. Further, the continuous morphological variability seen within and among acritarch assemblages has been a consistent obstacle to acritarch classification (Servais 1996) – a problem that has only been exacerbated by the creation of numerous form taxa during the development of acritarch-based biostratigraphy (Servais and Paris 2000). Altogether, these issues generated a noticeable degree of taxonomic confusion that needs to be addressed by careful analyses of large acritarch populations (e.g., Stricanne and Servais 2002; Vanguestaine 2002; Servais et al. 2004; Fatka and Brocke 2008).

Previous investigations of OWMs from the Buen Formation are limited to just two studies; one consists of conventional taxonomic descriptions of acritarchs (Vidal and Peel 1993) and the other reports metazoan SCFs (Slater et al. 2018). This thesis expands upon these studies by applying a novel combination of approaches to the OWM record of the Brillesø locality (southern Peary Land, North Greenland). First, new samples are processed for SCF recovery in order to prospect for previously undetected elements of diversity. Second, a semi-quantitative analysis of acritarchs and filamentous microfossils is conducted to uncover the disparity surrounding the recorded form taxa, and refine our understanding of acritarch diversity and palaeobiology in the early Cambrian of North Greenland.

Aims

The ultimate goal of this thesis is to evaluate the diversity and palaeobiology of OWMs from the early Cambrian of North Greenland, focussing on a richly fossiliferous assemblage from the Brillesø site (Buen Formation, Cambrian Stages 3–4, Peary Land, North Greenland). More specifically, this project is aimed to:

- Describe the metazoan SCFs present at Brillesø **(Paper I)**, building upon the findings of Slater et al. (2018a);
- Contrast metazoan assemblages from across the spectrum of preservation styles seen in North Greenland, shedding light on any potential palaeoecological and/or taphonomic control on fossil distributions **(Paper I)**;
- Reappraise the diversity of non-metazoan organic-walled microfossils at Brillesø **(Papers II, III)**, building upon the findings of Vidal and Peel (1993);
- Analyse patterns of acritarch disparity to reveal aspects of acritarch palaeobiology, including phytoplankton life cycles **(Papers II and IV)** and aggregation strategies **(Paper IV)**;
- Assess the extent of procedural, sampling and taxonomic biases on our perception of Cambrian diversity **(Papers I, II and III)**.

Background: the protracted record of organic-walled microfossils

Organic-walled microfossils (OWMs) are recorded throughout the last ca. 3.2 billion years of the Earth's history (Javaux et al. 2010), and represent a primary source of information for tracking the development of early eukaryotic life (Knoll et al. 2006; Butterfield 2015; Cohen and Kodner 2022). OWMs can be classified into two broad categories on the basis of their size, method of study, and/or presumed affinity. The first category consists of OWMs retrieved through standard acid maceration of rock samples, which typically yields small (< 50 µm) acritarchs and filamentous microfossils. The second category of OWMs is extracted using a gentler processing technique that typically yields larger, more delicate OWMs. In Cambrian palaeontology, these microfossils tend to be known as SCFs; i.e., delicate metazoan fragments reminiscent of microscopic BST compression fossils (Butterfield and Harvey 2012). Although some overlap exists between these two microfossil categories, acritarchs and SCFs are here introduced in separate sections for clarity, following a brief account of their respective extraction protocols. Patterns of OWM diversity and evolution throughout the Proterozoic–Phanerozoic transition are then outlined.

OWM extraction methods

A spectrum of standardised acid processing techniques has traditionally been used to retrieve recalcitrant OWMs from their rock matrix (Gray 1965; Evitt 1984; Phipps and Playford 1984; Traverse 1988; Vidal 1988; Traverse 2007). These conventional methods of OWM extraction can be adapted to various sample types and contents (Green 2001; Traverse 2007), but commonly feature the following basic steps (Fig. 2):

1. Preparation of the rock sample, including cleaning and crushing;
2. Sequential maceration of rock sample into hydrochloric acid (to remove carbonates), hydrofluoric acid (to remove silicates) and hydrochloric acid heated to near boiling point (to remove fluoride precipitates);
3. Heavy liquid separation (to remove the remaining inorganic phase);

4. Oxidation in Shulze solution (mixture of chloric and nitric acids, to remove partially decomposed organic matter and mineral encrustations such as pyrite);
5. Alkali treatment and bleaching (to remove oxidized organic matter or unwanted non-palynomorphs);
6. Final cleaning and concentration of residues (e.g., repeat of any previous step if unsuccessful, acetolysis to remove additional unwanted palynomorphs, sieving/filtering to obtain the desired size fraction, deflocculation);
7. Mounting of residues on microscopic slides.

Standard protocol   SCF protocol

Sample preparation → Acid digestion (HCl, HF, HCl ~ 100°C) → Heavy liquid separation → Oxidation → Alkali treatment → Final cleaning and concentration → Slide making

Sample preparation → HF digestion → Sieving → Hand-picking → Slide making
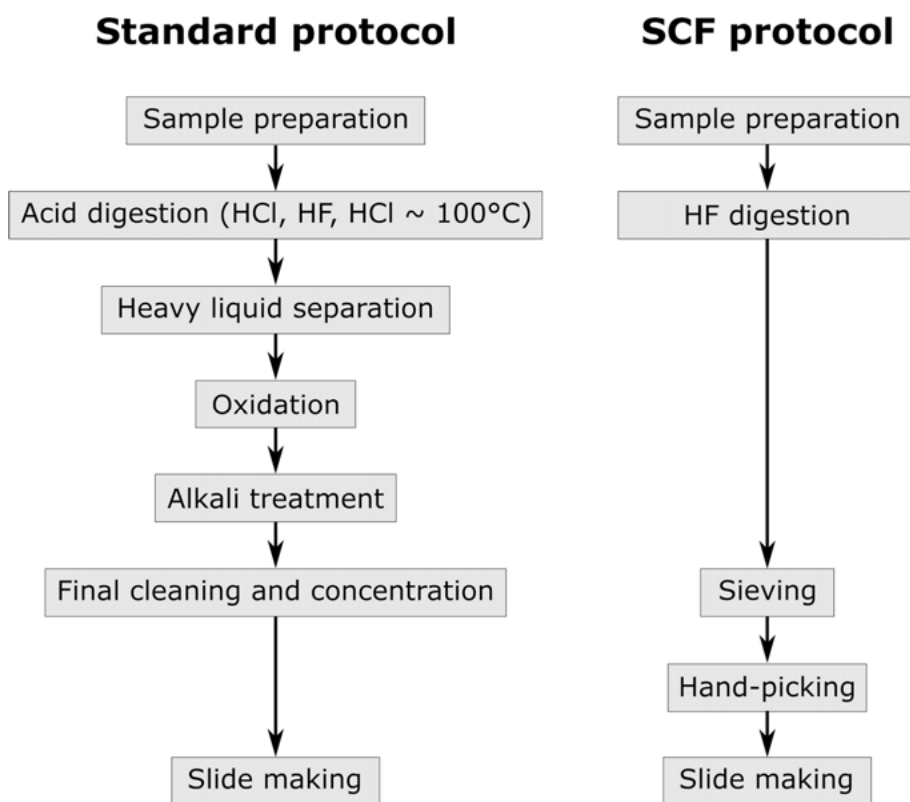
Figure 2. Simplified flowcharts of OWM extraction for recovery of standard palynomorphs (left) and SCFs (right).

Centrifugation is routinely conducted throughout this protocol to separate solid and aqueous phases before decantation. Solutions may also be stirred, heated or placed in an ultrasonic tank to ensure the efficiency of chemical reactions and the removal of unwanted products. Altogether, this speedy extraction process guarantees the cleanness of residues to facilitate subsequent analyses and taxonomic identifications.

A significant drawback of these conventional methods is the selective fragmentation or loss of fragile organic components collectively termed 'non-pollen palynomorphs' (Pound et al. 2021). In the 1990s, a range of alternative preparation protocols was developed to limit mechanical shocks, and revealed a previously unknown diversity of large, delicate OWMs in otherwise unproductive Proterozoic samples (Burzin 1990; Zang and Walter 1989, 1992; Butterfield et al. 1994; Grey 1999). These low-manipulation protocols subsequently became a standard of Proterozoic palynology (Grey 1999), and were later used to recover SCFs in Cambrian successions (Butterfield 1994, 2008; Harvey 2010; Harvey et al. 2011; Butterfield and Harvey 2012; Smith et al. 2015; Slater et al. 2017). SCFs are extracted using a particularly gentle acid extraction protocol, namely:

1. Bedding-plane splitting of samples;
2. Maceration into hydrofluoric acid;
3. Sieving;
4. Hand-picking of individual microfossils from organic residues in solution;
5. Mounting of individual specimens onto microscopic slides.

Hand-picking of microfossils is conducted under a stereomicroscope, which limits the size range of recovered SCFs to the larger palynomorph fraction, commonly > 60 µm (Harvey and Pedder 2013). Phanerozoic OWM assemblages often exhibit a large diversity of forms below this size limit. For this reason, standard acid maceration methods are still widely used in Phanerozoic palynology.

Acritarchs

Definition, morphology and classification

Derived from the Greek *ákritos* meaning 'confused' and *arché* meaning 'origin', the Acritarcha is an informal group created by Evitt (1963) to accommodate OWMs that cannot be unequivocally classified into any known clade. This collection of problematica consists of variably ornamented vesicles (i.e., hollow bodies; Fig. 3) united by a general lack of diagnostic characters.

As *incertae sedis*, acritarchs are classified into artificial categories that are exclusively based on morphology and do not purport to outline phylogenetic relationships. This non-Linnean, hierarchical system consists of species and genera that are named using the International Code of Nomenclature for algae, fungi, and plants (Evitt 1963; Downie et al. 1963). These acritarch species and genera have originally been placed into broader subgroups (Downie et al. 1963; Diver and Peat 1979; Tappan 1980; Strother 1996) that are currently

used informally. The dominant subgroups in Cambrian assemblages are sphaeromorphs, acanthomorphs and pteromorphs (Fig. 3). Sphaeromorphic acritarchs are sphaeroidal vesicles that are either smooth, perforated, or covered in low-relief sculptural elements (Fig. 3A–C); acanthomorphic acritarchs have tubular, hair-like or spine-like projections called 'processes' emerging from the central cavity (Fig. 3F–H); and pteromorphic acritarchs are Saturn-shaped vesicles consisting of a central discoid surrounded by an equatorial rim (Fig. 3D–E).
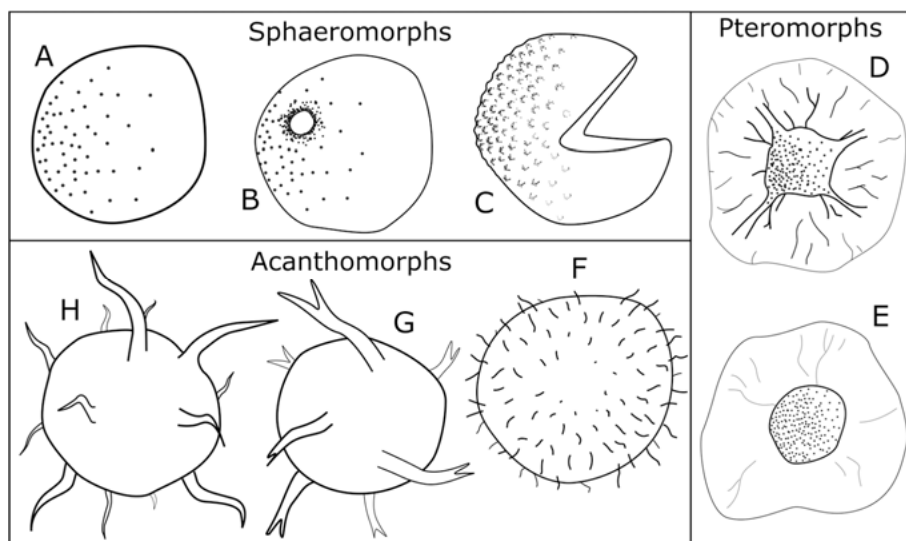
Figure 3. Examples of acritarch morphologies from sphaeromorphic, acanthomorphic and pteromorphic subgroups (modified from Wallet 2018). Note excystment structure by circular pylome in B and partial rupture in C.

Many acritarch morphotypes are sporadically found opened – a tendency that is thought to reflect an excystment process (i.e., the release of offspring cells by rupture of the cyst wall) that is seen in numerous phytoplanktonic groups (Lister 1970; Martin 1993; Strother 1994, 1996). These excystment openings can be classified into different types based on their position and morphology (Tappan 1980; Mendelson 1993; Strother 1996). Acritarch vesicles most commonly show excystment by partial rupture of the cell wall (Fig. 3C), median split (i.e., a partial rupture dividing the vesicle into two equal halves), and pylome (i.e., a circular, oval or polygonal hole; Fig 3B).

The genus- and species-level taxonomy of acritarchs relies on the general outline of the vesicle and its symmetry, the shape of sculptural elements and/or processes, their type (i.e., hollow vs. solid), the presence or absence of separation (e.g., plug, septum) between processes and the central cavity, the type of excystment, and the structure of the wall. The relative importance of these criteria for defining taxonomic boundaries has long been a matter of debate

and varies between authors (for a taxonomic review, see Servais 1996). The core issue encountered by acritarch taxonomists is the high variability seen among acritarch morphologies, which hampers attempts to discretise portions of disparity. These taxonomic puzzles have been exacerbated by the early development of acritarch-based biostratigraphy between the 1960s and the 1980s (Servais and Paris 2000), which witnessed the erection of numerous acritarch taxa singled out from their background populations (Vecoli and Le Hérissé 2004; Fatka and Brocke 2008; Kroeck et al. 2021). This tendency for taxonomic over-splitting led to significant inconsistencies in naming (Stricanne and Servais 2002; Mullins and Servais 2008; Servais et al. 2004) that are currently being assessed on quantitative grounds (Stricanne and Servais 2002; Fatka and Brocke 2008; Yan et al. 2017; Wang et al. 2017; Kroeck et al. 2020, 2021).

What –if anything– are acritarchs?

The classic answer is; 'Nobody knows, by definition' (Mendelson 1993, p. 93). What is certain, however, is that acritarchs represent a polyphyletic group, potentially encompassing remains as diverse as prokaryotes (e.g., Battison and Brasier 2012; Vorob'eva et al. 2015; Beghin et al. 2017), phytoplankton cysts, spores and vegetative cells (e.g., Kaźmierczak and Kremer 2009; Moczydłowska 2010, 2016; Agić et al. 2015), fungi (Butterfield 2005a; Loron et al. 2019; Bonneville et al. 2020), and animal eggs (Yin et al. 2004, 2007; Cohen et al. 2009; Willman 2009) or fragments (e.g., *Ceratophyton*; Butterfield and Harvey 2012; Smith et al. 2015; Slater et al. 2017, 2018b). Despite this, acritarchs are traditionally considered as chiefly phytoplanktonic on the basis of their general morphology, presumed sporopollenin-like wall chemistry, and distribution patterns showing maximal diversity in outer shelf environments (Tappan 1980; Colbath and Grenfell 1995; Vidal and Moczydłowska-Vidal 1997). The recognition of large, asymmetrical benthic forms throughout the Proterozoic record later called this view into question (Butterfield 1997, 2001, 2004, 2005a, b), but the phytoplanktonic origin of the small symmetrical acanthomorphs typifying Palaeozoic assemblages has so far remained largely unchallenged (Butterfield 1997, 2007). More specifically, these small recalcitrant acritarchs are often regarded as cysts produced during the benthic, non-motile resting stage of phytoplanktonic life cycles (Downie et al. 1963; Tappan 1980; Martin 1993; Mendelson 1993; Strother 1994, 1996; Colbath and Grenfell 1995). This assumption is based on the apparent robustness of acritarch walls and the presence of occasional vesicle openings (Fig 3B–C) through which offspring cells are released at the end of the dormancy period (Lister 1970; Martin 1993; Mendelson et al. 1993; Strother 1994, 1996).

Various approaches have been adopted to further clarify the diversity of clades represented among acritarchs. For instance, the reconstruction of ontogenetic sequences based on vesicles enclosing reproductive bodies has helped

to support analogies with chlorophyte life cycles (Moczydłowska 2010, 2016; Shang et al. 2020; Fig. 4). The use of scanning electron microscopy (SEM), transmitted electron microscopy (TEM) and microchemical techniques has also revealed a host of phylogenetically informative characters, including evidence for eukaryotic, green algal and/or dinoflagellate affinities (e.g., Arouri et al. 1999, 2000; Talyzina et al. 2000; Talyzina and Moczydłowska 2000; Willman and Moczydłowska 2007; Gong et al. 2010; Kremer et al. 2012). This new level of analytical study has been used to constrain the timing of appearance of various eukaryotic lineages (Javaux et al. 2004; Javaux and Marshal 2006; Loron et al. 2019), but also brought to light a previously unseen ultrastructural diversity among otherwise similar acritarch morphotypes (Talyzina and Moczydłowska 2000; Javaux et al. 2004; Willman 2009; Moczydłowska et al. 2010) – a possible sign of phylogenetic convergence and/or intraspecific variability.

Despite these advances, Sarjeant's (1970) forecast of the early dismantlement of the Acritarcha has not been achieved. Perhaps the scarcity of taxonomic transfers out of this informal group may be explained by a high potential for phylogenetic convergence in these morphologically simple forms, which limits the scope of any palaeobiological breakthrough to the specimens that were studied, rather than the artificial taxonomic groups they belong to.
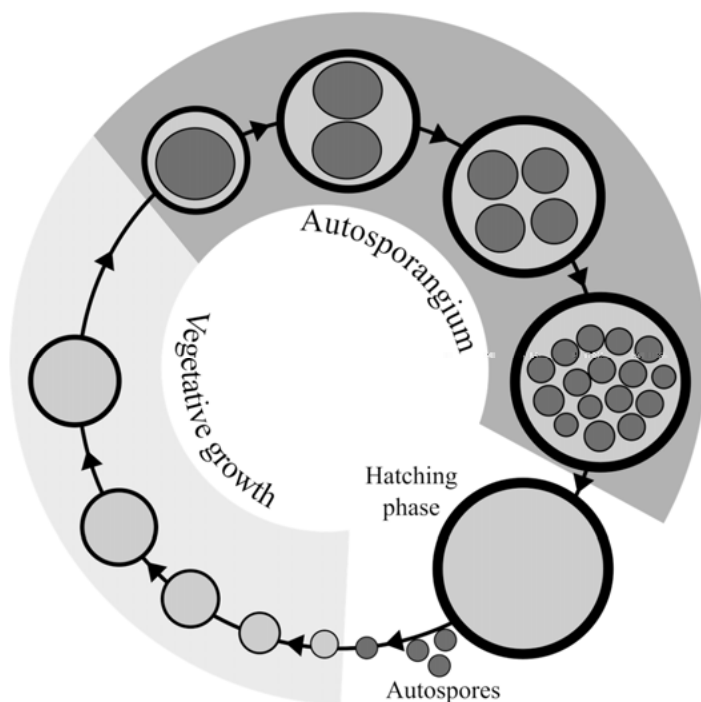

Figure 4. Hypothetical life cycle of the early Cambrian acritarch *Yurtusia uniformis* from South China, reconstructed on the basis of modern chlorophyte analogues (modified from Shang et al. 2020, fig. 8F).

Small carbonaceous fossils

Small carbonaceous fossils (SCFs) are usually defined as OWMs extracted using a low-manipulation acid maceration procedure, being too large and/or fragile to be faithfully captured by conventional palynological preparations, and too small to be seen on bedding plane surfaces (Butterfield and Harvey 2012). Although OWMs of various affinities may be recovered using this protocol (e.g., Butterfield et al. 1994; Harvey et al. 2011; Tang et al. 2017; Slater et al. 2017, 2018a), the term SCF has traditionally been used to refer specifically to metazoan fragments of various origins (Fig. 5). As such, SCFs are comparable to their equally polyphyletic small shelly fossil (SSF) counterparts, but capture both soft-bodied and biomineralizing components of metazoan diversity (Butterfield and Nicholas 1996).

Whilst SCFs and BST body fossils may co-occur (e.g., Butterfield 1990a; Caron et al. 2013; Smith et al. 2015; Botting et al. 2023), the distribution of SCFs clearly extends beyond the off-shelf, low-oxygen settings conducive to BST preservation (Conway Morris 1985, 1986, 1989; Ludvigsen 1989; Butterfield 1990b; Petrovich 2001; Gabbott et al. 2004; Gaines et al. 2012; Schiffbauer et al. 2014). SCF assemblages are commonly recovered from shallow marine, occasionally bioturbated horizons (Butterfield and Harvey 2012; Harvey et al. 2012; Slater et al. 2017; Slater 2023), thereby bringing to light the diversity of soft-bodied metazoans inhabiting shelf environments. Moreover, SCFs predate (Slater et al. 2018a, 2020; Slater and Willman 2019; Slater and Bohlin 2022) and postdate (Shan et al. 2022; Botting et al. 2023) the known Phanerozoic range of BST preservation by ca. 20 and 40 Ma, respectively (Daley et al. 2018). SCF assemblages are therefore more than just 'micro-Burgess Shales' (Butterfield and Harvey 2012), in that the relatively relaxed constraints on their distribution is reminiscent of regular forms of microfossil preservation, such as SSFs or acritarchs (Fig. 6).

Besides their relative commonness, the palaeobiological value of SCFs lies in the exquisite fidelity of their preservation. Despite being largely fragmentary, the unparalleled submicron-level anatomy of these microfossils has proved a vast source of phylogenetic information, offering alternative insights into the affinities of well-known BST body fossils (Butterfield 1990a; Harvey et al. 2011; Butterfield and Harvey 2012; Caron et al. 2013). Metazoan mouthparts preserved as SCFs have also revealed a diversity of specialised feeding styles (Butterfield 1994; Harvey et al. 2012; Harvey and Butterfield 2022; Slater 2023), providing crucial palaeoecological context to Cambrian radiations (Butterfield 1997). More broadly, the quality of SCF preservation allowed the recognition of metazoan clades outside their known stratigraphic range (Butterfield 1994; Slater et al. 2018a, b; Slater and Willman 2019), allowing new constraints to be placed on the timing of early metazoan evolution (Slater and Bohlin 2022).
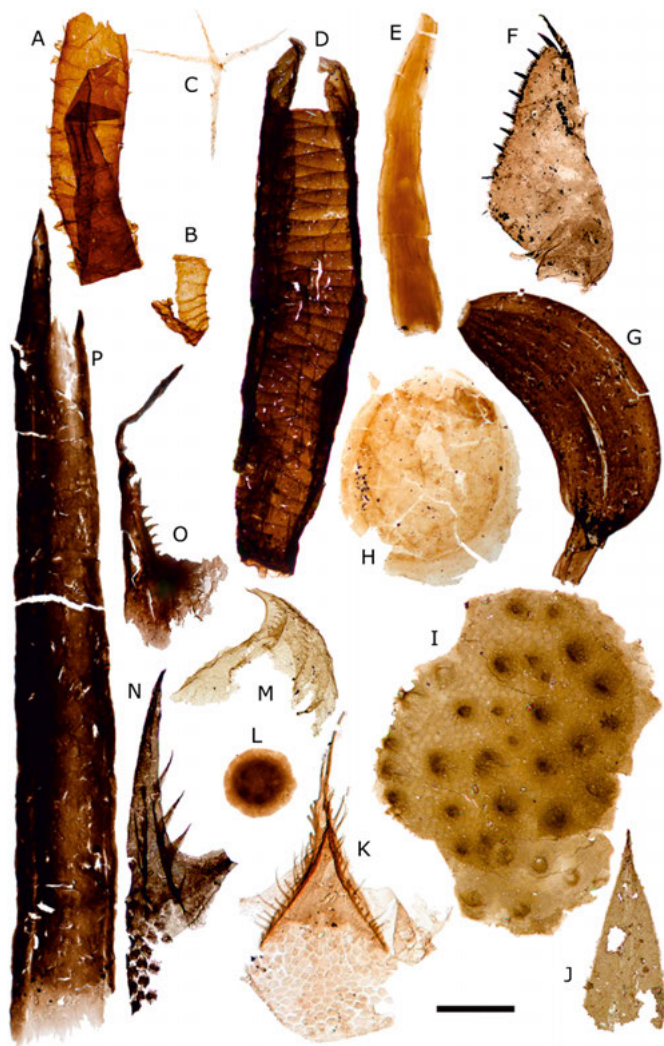
Figure 5. Assortment of metazoan SCFs of various origins (after Slater and Bohlin 2022, fig. 2). A–B, pterobranch *Sokoloviina costata*, Cambrian Fortunian–Stage 2, Estonia (Slater et al. 2018b). C, sponge spicule, Cambrian Stages 3–4, Sweden. D, pterobranch, Cambrian Stages 3–4, Greenland (Slater et al. 2018a). E, lobopodian spine, Cambrian Stage 5/Wuliuan, Sweden (Slater and Bohlin 2022, fig. 2d). F, crustacean tooth blade, Cambrian Stage 4, Canada (Harvey and Butterfield 2022). G, *Wiwaxia* sclerite, Cambrian Stage 3–4, Sweden (Slater et al. 2017). H, brachiopod, Cambrian Stage 5/Wuliuan, Sweden (Slater and Bohlin 2022, fig. 2j). I, bradoriid cuticle, Cambrian Stages 3–4, Greenland (Slater et al. 2018a). J, *Isoxys*-like arthropod spine, Cambrian Stages 3–4, Greenland (Slater et al. 2018a). K, N, sclerites from the priapulid *Ottoia prolifica*, Cambrian Miaolingian, Canada (Smith et al. 2015). L, palaeoscolecid plate, Cambrian Stage 3–4, Sweden (Slater et al. 2017). M, priapulid-like sclerite, Cambrian Stages 3–4, Greenland (Slater et al. 2018a). O, scalidophoran sclerite, Cambrian Stage 2, Canada (Palacios et al. 2018). P, annelid chaeta, Cambrian Stages 3–4, Sweden (Slater et al. 2017). Scale bar represents 200 μm for A–H, J, M; 100 μm for I, L, P; 50 μm for K, N; 40 μm for O.

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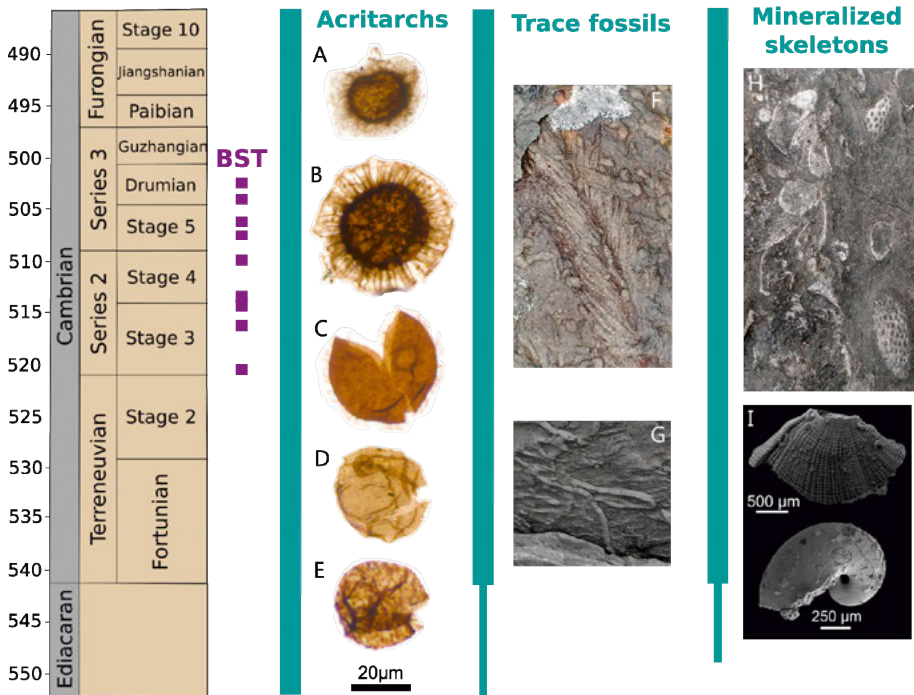Figure 6. Major types of Cambrian fossil records and their stratigraphic ranges (modified from the presentation slides of Wallet [2018]). A–E, organic-walled microfossils from the Buen Formation of North Greenland. F–G, trace fossils from Cwm Graianog (F) and Aberystwyth (G), Wales. H, mineralized skeletons from Marloes, Wales. I, small shelly fossils from the Terrades inlier, Pyrenees (Wallet et al. 2022). BST: Burgess Shale-type preservation.

Patterns of OWM diversity through the Proterozoic–Cambrian transition

OWMs have been used extensively to reconstruct patterns of diversity and macroevolution throughout the Proterozoic–early Palaeozoic transition (Knoll 1994; Vidal and Moczydłowska-Vidal 1997; Huntley et al. 2006; Knoll et al. 2006; Butterfield 2007; Cohen and Macdonald 2015; Agić and Cohen 2021; Cohen and Kodner 2022; Fig. 7). These various compilations of OWM data produced a range of more or less similar chronicles of Proterozoic evolution, pointing to a stepwise increase in cellular complexity, organisation, and differentiation culminating in the advent of multicellularity (Knoll et al. 2006; Butterfield 2009; Agić and Cohen 2021). From a purely morphological perspective, the default trend for many pre-Ediacaran acritarch morphotypes is that of protracted stasis (Butterfield 2007; Riedman and Sadler 2018, fig. 5), despite some visible changes in species richness estimates throughout the Tonian (Knoll et al. 2006; Knoll 2014; Cohen and Macdonald 2015; Riedman

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and Sadler 2018). The first major acritarch diversity spike occurred at the beginning of the Ediacaran period with the appearance of large Doushantuo–Pertatataka-type acanthomorphs (Zang and Walter 1989; Moczydłowska et al. 1993; Zhang et al. 1998; Yuan and Hofmann 1998; Zhou et al. 2001; Grey 2005; Fig. 7). A dominance of small sphaeromorphs typifies the second half of the Ediacaran, although Doushantuo–Pertatataka assemblages persisted until the Ediacaran/Cambrian boundary (Anderson et al. 2017; Grazhdankin et al. 2020). Depauperate sphaeromorphic assemblages prevailed until Cambrian Stage 3, at which point an unprecedented diversity of small acanthomorphic morphotypes is recorded (Knoll et al. 2006; Fig. 7). Subsequent patterns vary between studies and diversity metrics (Vidal and Moczydłowska-Vidal 1997; Nowak et al. 2015; Kroeck et al. 2022), but generally point to high turnover rates relative to the Proterozoic (Knoll 1994).

Whilst it is tempting to interpret these patterns in terms of radiations and extinctions, a direct reading of acritarch species richness estimates is hampered by the artificial basis of acritarch taxa. Indeed, a single biological species may generate multiple acritarch morphotypes (e.g., through the course of its life cycle). Conversely, multiple biological species are likely represented among morphologically simple acritarchs such as *Leiosphaeridia* (Talyzina and Moczydłowska 2000; Javaux et al. 2004; Willman and Moczydłowska 2007; Javaux and Knoll 2017). In this light, a peak of species richness may be regarded as a true radiation event or a more passive, intraspecific exploration of disparity (e.g., driven by ontogenetic or environmental factors). Likewise, a drop of species richness may alternatively represent an extinction event or the phylogenetic convergence of advantageous morphologies.
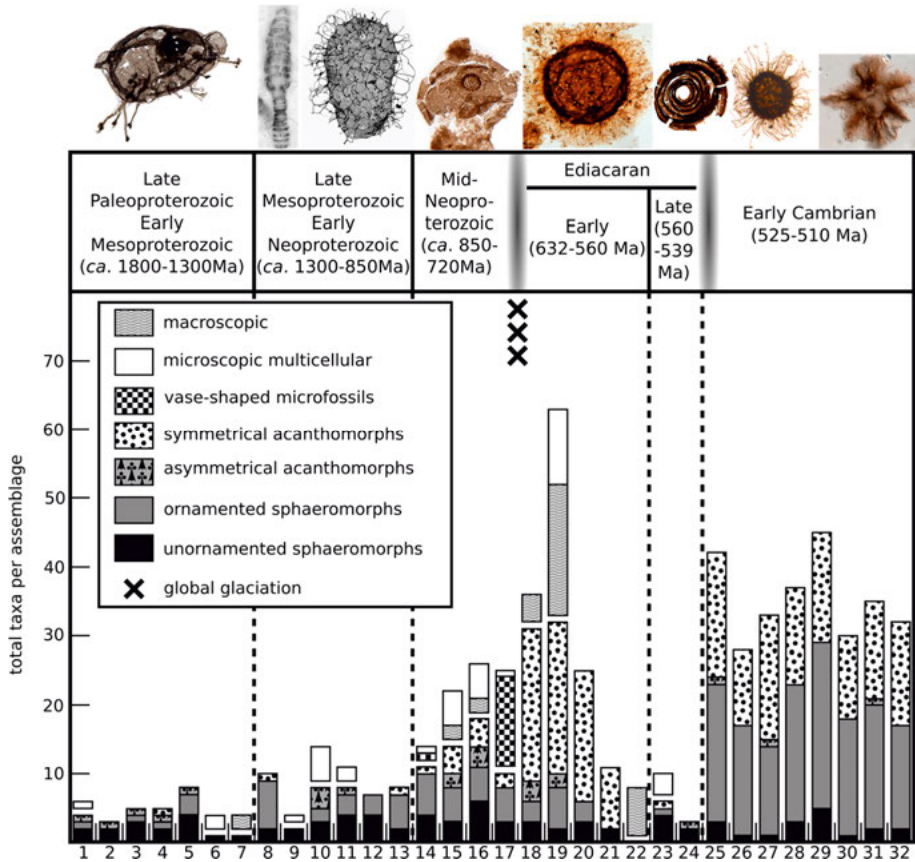
Figure 7. Species richness and composition of acritarch assemblages from the Late Palaeoproterozoic to the early Cambrian (modified from Knoll et al. 2006, fig. 4). Each number on the X axis represents an assemblage. Representative examples of OWM taxa are shown for each time interval; from left to right: *Tappania plana*, early Mesoproterozoic of the USA (Adam et al. 2017, fig. 4b); *Bangiomorpha pubescens*, ca. 1 Ga, arctic Canada (Butterfield 2000, fig. 5B); '*Tappania plana*', Neoproterozoic of arctic Canada (Butterfield 2005a, fig. 2A); *Kaibabia gemmulella*, Tonian of the USA (Porter and Riedman 2016, fig. 7.9); *Appendisphaera tabifica*, Ediacaran of Australia (Willman and Moczydłowska 2008, fig. 6D); *Cochleathina* (Slater et al. 2020, fig. 6C); *Skiagia* cf. *compressa*, Cambrian Stages 3–4, North Greenland (**Papers II, III**); *Liepaina plana*, Cambrian Stage 4, Canada (Palacios et al. 2017, fig. 6j).

This thesis: a reappraisal of OWM diversity in North Greenland

Resampling OWMs from the Buen Formation

This thesis is based on material collected by John S. Peel in 1974 and 1994 from three horizons at the Brillesø site (Buen Formation, Peary Land, North Greenland; Fig. 8). Nine palynological slides were produced by Vidal and Peel (1993) using a standard palynological procedure (Vidal 1988), and additional samples were processed following a gentle protocol as part of this PhD. Altogether, these assemblages yielded a remarkable diversity of OWMs, including exquisitely preserved metazoan SCFs (**Paper I**) and 50 acritarch form taxa (**Paper III**). The range of new OWMs uncovered by this project fills in as much as it reveals important gaps in the Cambrian fossil record. In the following sections, the novel aspects of this assemblage are outlined, and their significance for evaluating the completeness of the Cambrian OWM record is discussed.
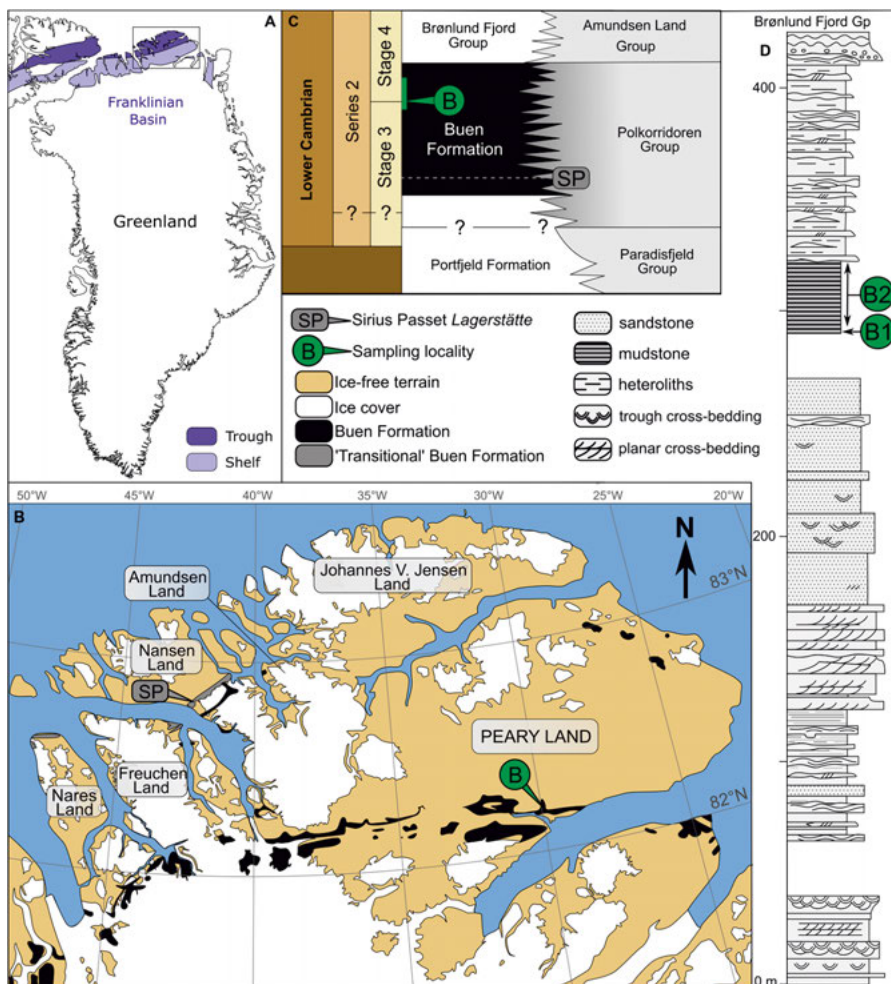
Figure 8. Geological setting of the sampled site (from **Paper I**). A, extent of trough and shelf sediments in North Greenland, with studied area magnified in B. B, exposed extent of the Buen Formation and location of the sampled site (B). C, Neoproterozoic–Cambrian stratigraphy of North Greenland in the southern (left, black/white) and northern (right, grey) outcrop belts. D, sedimentary log of the Buen Formation at its type section.

New elements of OWM diversity

One of the most significant elements brought to light are various crustacean feeding appendages (**Paper I**, Fig. 9L–M). Evidence for pancrustaceans in the Cambrian fossil record is scarce and subject to debate (Strausfeld 2016; Aria and Caron 2017; Vannier et al. 2018; Zhai et al. 2019), but exceptionally rich SCF assemblages from the Cambrian of Canada have offered a promising alternative means of tracking early crustacean evolution (Butterfield 1994; Har-

vey et al. 2012; Harvey and Butterfield 2022). Compared to these diverse crustacean SCFs, the newly recovered assemblage exhibits a moderate degree of sophistication, consisting of two main types of molar surfaces, rare filter plates and potential labra (**Paper I**, fig. 8). The relative simplicity of these grinding and filtering elements could potentially represent the proximal stem of a subsequent radiation of crustacean crown groups. At an approximate age of ca. 515 Ma, the recovered crustacean appendages are effectively the oldest crustacean SCFs recovered to date, and cement other crustacean records from Cambrian Stage 3 (Zhang et al. 2007, 2010; Zhai et al. 2019).

In addition to these rare SCFs, a diversity of three-dimensional spinose cuticles was recovered (Fig. 9G–J). Similar SCFs were recovered in previous investigations and tentatively identified as bradoriid fragments from the SSF taxon *Spinospitella* (Slater et al. 2018a). Newly recovered SCFs include an almost intact bradoriid valve having a *Spinospitella*-type ornamentation and a stiff, three-dimensionally preserved construction (Fig. 9F), thereby uniting a range of spinose cuticle types previously found in isolation (Fig. 9G–I). Further, SEM images of these exquisitely preserved cuticles show the diagnostic corona of third-order spines of *Spinospitella coronata* Skovsted et al., 2006 (**Paper I**; Peel et al. 2021), confirming earlier taxonomic assessments. The recovery of bradoriid OWMs provides additional support for the secondary origin of most of the phosphate contained in bradoriid carapaces, and reveals a potential to capture this important Cambrian fossil group outside the narrow phosphatization windows from which it is largely known (e.g., Siveter and Williams 1997; Hu et al. 2002; Williams et al. 2007; Skovsted et al. 2006; Ivantsov et al. 2005).

A large range of additional metazoan fragments was recovered (**Paper I**), including perforated trilobite cuticles (Fig. 9K) and new types of scalidophoran teeth and scalids (Fig. 9N–O). Numerous SCFs of more problematic origin were also retrieved, including portions of potential hyoliths (Fig. 9A–B), fibrous metazoan fragments of possible Lophotrochozoan origin (Fig. 9Q), and spines with an apparent cone-in-cone construction (Fig. 9P). Altogether, these finds contribute to a rapidly expanding SCF record that will serve as a basis for future comparisons.

Gentle acid maceration of newly recovered material also revealed a range of large and/or asymmetrical acritarchs and branching filaments (**Paper III;** Fig. 9R, X–Z), most of which were not detected in previous investigations. These include forms showing intriguing similarities with iconic Proterozoic acritarchs such as *Tappania* (Fig. 9X) and Doushantuo–Pertatataka-type acanthomorphs (Fig. 9R). These likely benthic eukaryotes are well-known in Proterozoic OWM assemblages, but are largely missing from Cambrian literature. Diverse acritarch colonies and other monospecific aggregates have also been found in both conventional and hand-picked preparations (Fig. 9S–T, W), revealing important aspects of planktonic life cycles and defence strategies (**Paper IV**).
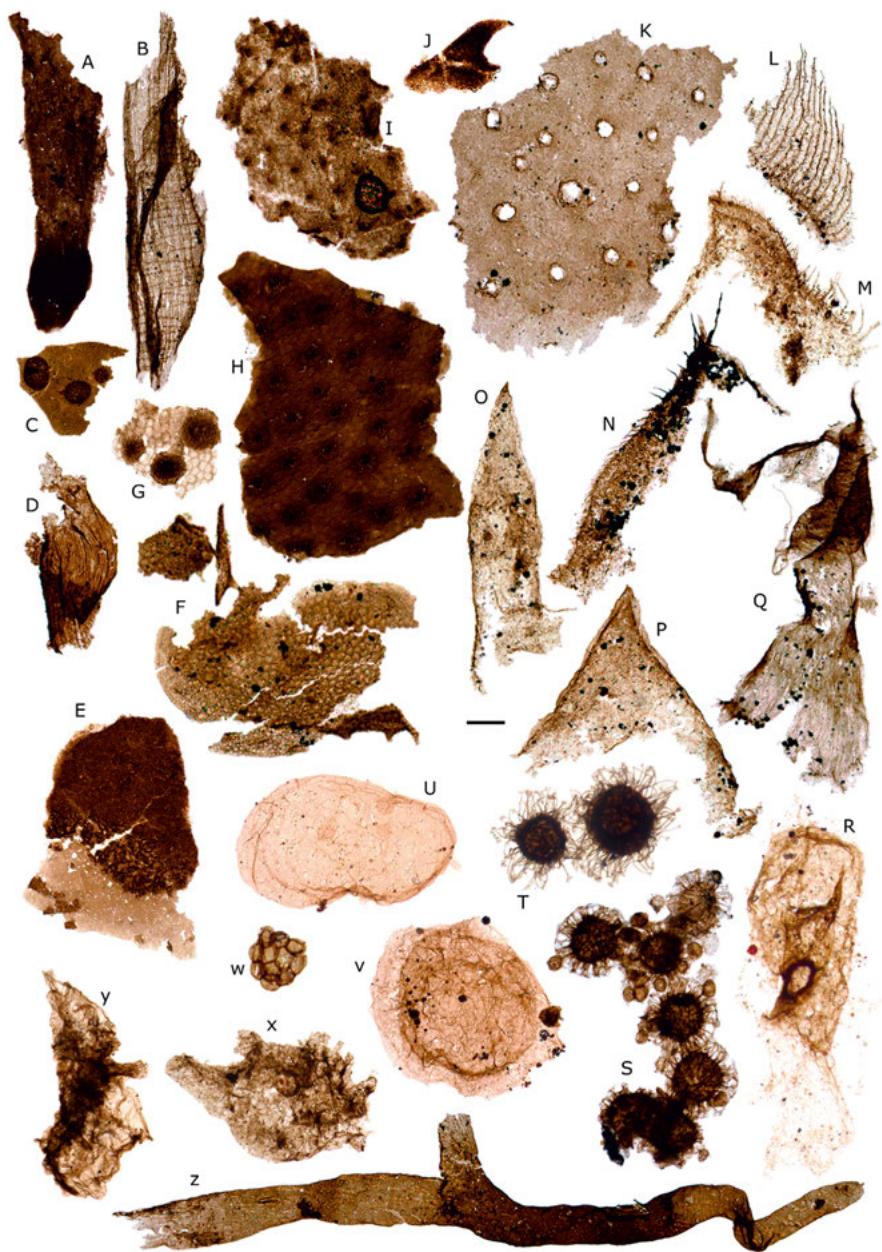
Figure 9. New diversity of hand-picked OWMs from the Buen Formation. A–E, Q, metazoan fragments of uncertain affinity. F–J, fragments of spinose bradoriids likely sourced from *Spinospitella*. K, trilobite cuticle. L–M, crustacean filter plate (L) and mandible (M). N–O, spines of likely scalidophoran origin. P, spine with an apparent cone-in-cone construction. R–Y, acritarchs including *Comasphaeridium*? *brillesensis* (R), *Skiagia* clusters (S–T), *Leiosphaeridia* enclosing spores (U), *Pterospermopsimorpha* sp. (V), *Synsphaeridium* (W), an unknown form similar to *Tappania* (X), and flimsy *Leiosphaeridia* (Y). Z, *Palaeosiphonella* sp. Scale bar represents 100 μm for A–B; 50 μm for C–E, G–K, N–Q, Z; 40 μm for L–M, X–Y; 25 μm for F, R–W.

Significance of palynological extraction methods

The choice of palynological extraction protocol undoubtedly exerts a strong influence on the composition OWM assemblages, yet overlaps do exist between assemblages retrieved using different procedures (Butterfield and Harvey 2012; Harvey and Pedder 2013; Slater and Bohlin 2022; Barr et al. 2022). Rather surprisingly, nearly all hand-picked metazoan components from **Paper I** feature in the standard preparations of Vidal and Peel (1993; Fig. 10A–F), even crustacean filter plates, mandibles and labra (Fig. 10C–E) that are so far only known from relatively exceptional instances of preservation (Butterfield and Harvey 2012; Harvey et al. 2012; Harvey and Butterfield 2022). A significant difference, however, is their relative proportions. Standard palynological slides are consistently dominated by small acritarchs that dilute any other form of OWM preservation (**Paper III**, fig. 2). In this light, the absence of metazoan OWMs and asymmetrical palynomorphs in the original description of the assemblage (Vidal and Peel 1993) reflects the destructive character of standard acid-maceration as much as the general focus of the study, directed towards acritarchs used for biostratigraphy. These routine palynological practices likely concealed a substantial proportion of Cambrian OWM diversity that is only starting to be uncovered by SCF studies (e.g., Harvey et al. 2011; Slater et al. 2017, 2018b).
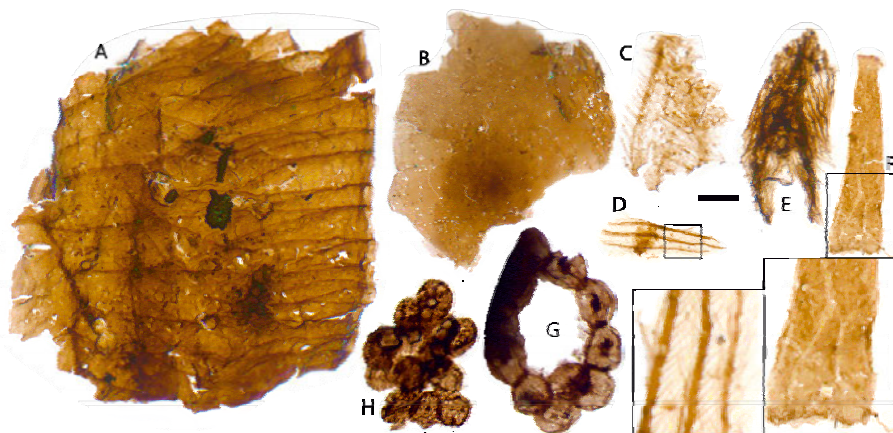
Figure 10. Metazoan fragments and acritarch clusters recovered by standard palynological processing. A, fragment of pterobranch hemichordate. B, fragment of bivalved arthropod. C–E, crustacean fragments including a mandible (C), a setal array (D) and a potential labrum (E). F, spine with internal structure resembling a cone-in-cone construction. G–H, acritarch clusters including *Synsphaeridium* (G) and *Asteridium* (H). Scale bar equals 20 μm for A–F, 10 μm for G–H and enlargement in F, 5 μm for enlargement in D.

Acritarch clusters also rarely feature among descriptions of Phanerozoic palynomorphs (Mullins 2003; Palacios 2015; Wang et al. 2022; Kovář et al.

2023). In this case, the scarcity of information is hardly attributed to extraction procedures, as acritarch aggregates have previously been figured in publications focusing on standard palynomorphs (e.g., Deunff 1968, pl. 1, fig. 15; Downie 1973, pl. 25, fig. 1; Pedder 2012, pl. 4, fig. 6; Jachowicz-Zdanowska 2013, pl. 4, fig. 1). The diversity of aggregates described in **Paper IV** is predominantly derived from the conventional slides of Vidal and Peel (1993; Fig. 10G–H), and represented by several hundred specimens. The prospect of palynomorph clumping during the acid extraction process (Tappan 1980) may have downplayed the relevance of investigating acritarch clusters, a factor that may explain their consistent under-reporting.

A rare record of soft-bodied metazoans from oxygenated shelf environments

Our current understanding of Cambrian ecosystems is heavily reliant on BST *Lagerstätten*, which are likely confined to off-shelf, dysoxic settings (Conway Morris 1985, 1986, 1989; Ludvigsen 1989; Butterfield 1990b; Petrovich 2001; Gaines et al. 2012; Schiffbauer et al. 2014). This has led to legitimate concerns as to whether our picture of the Cambrian Explosion is biased in favour of unusual, slow-evolving deep sea communities (Conway Morris 1989). This view tends to be supported by an emerging SCF record from the shallows, which in recent years has revealed an entirely new diversity of soft-bodied metazoans inhabiting regular, well-oxygenated shelf environments (Butterfield and Harvey 2012; Harvey et al. 2012; Slater et al. 2017; Harvey and Butterfield 2022).

The confluence of facies and preservation styles in North Greenland provides a promising framework on which to evaluate the hypothesis of community partitioning between shelf settings and deeper-water environments (**Paper I**), albeit with two significant caveats. The first is the presence of a thermal alteration gradient between southern (i.e., outer shelf) and northern (i.e., shelf-slope break) outcrops, which has resulted in the almost complete removal of organic matter in the Sirius Passet *Lagerstätte* (Slater et al. 2018a). The second is the slight age difference between the Sirius Passet biota (Cambrian Stage 3) and the section at Brillesø (Cambrian Stages 3–4). Despite these difficulties, the assemblage from Brillesø features animal groups that are otherwise mostly (if not exclusively) known from shelf environments (**Paper I**), namely bradoriids (Williams et al. 2007, 2011, 2015) and small zooplankton-scale crustaceans (Butterfield and Harvey 2012). In particular, the distribution of *Spinospitella coronata* appears to be restricted to outer shelf settings (Peel et al. 2021), while crustacean SCFs have so far only been recovered from relatively proximal epicratonic sequences (Butterfield and Harvey 2012; Harvey and Butterfield 2022). Moreover, sponges are abundant in Sirius Passet (Botting and Peel 2016) and other BST deposits (Caron and Jackson 2008; Zhao

et al. 2009; O'Brien and Caron 2016), but are conspicuously absent from the sampled site despite a potential for SCF preservation (Harvey 2010; Slater and Bohlin 2022) and silica preservation (Peel 2019).

Lateral partitioning may account for the scarcity of overlaps between the Sirius Passet biota and assemblages from Brilleso (**Paper I**, fig. 15), as well as the general paucity of acritarchs from off-shelf environments in the wider Cambrian record (Moczydłowska and Vidal 1992; Shan et al. 2022). Such palaeoecological constraints on metazoan and phytoplankton distributions warrant the consideration of sampling megabiases in our perception of Cambrian diversity.

Decoding the palaeobiological meaning of acritarch populations

Being phylogenetically unresolved by definition, acritarchs have chiefly been used for biostratigraphic purposes (Molyneux et al. 1996; Rushton and Molyneux 2001). Their phenetic classification into numerous discrete categories reflects this practical need to identify short-lived and widespread morphologies able to provide relative time constraints in settings where other index fossils are absent (Moczydłowska 1991, 1998, 1999; Moczydłowska and Zang 2006; Zang et al. 2007; Palacios et al. 2011, 2018, 2020; Ahn and Zhu 2017; Barr et al. 2022). Nevertheless, the artificial character of acritarch form taxa does not necessarily mean attempts to resolve their palaeobiology are doomed to failure. The diverse, abundant and well-preserved acritarch record of the Brillesø site is amenable to statistical analysis, providing a promising new pathway to explore the relationships between acritarch morphology, taxonomy, diversity and palaeobiology.

Population analyses: towards a meaningful measure of phenotypic plasticity and taxonomic diversity

The concept of population analyses introduced by Le Hérissé (1989) advocates the use of a large number of specimens to explore acritarch morphology within and beyond taxonomic boundaries. This approach offers a powerful means to rein in taxonomic inflation by calibrating species diagnoses with distinct abundance peaks. Population analyses have triggered the revision of numerous upper Cambrian and Ordovician acritarch taxa (Fatka and Brocke 2008; Stricanne and Servais 2002; Vanguestaine 2002; Servais et al. 2004; Wang et al. 2017; Yan et al. 2017; Kroeck et al. 2020, 2021); yet lower Cambrian taxa have so far remained exempt from population-based investigations.

The acritarch assemblage of the Buen Formation has been used as a case study to evaluate the taxonomy of lower Cambrian acritarchs on a population

basis. Acritarch populations have been subjected to both quantitative (**Paper II**) and semi-quantitative analyses (**Papers III**) using criteria widely used in form taxonomy. This approach allowed the recorded form taxa to be recognised as parts of broader abundance peaks embedded in continuous morphological variations (Fig. 11). Taphonomic factors are acknowledged as a significant source of this disparity (e.g., breakage or agglutination of processes, alteration of process morphology, flattening and inflation of process bases; **Paper III,** Fig. 11F–J), even though biological factors (e.g., ontogeny, phenotypic variation) likely contribute to intraspecific variability (**Papers II, III;** Fig. 11A–E). Once these potential sources of morphological variation are carefully assessed, the recorded diversity can be pared down from 50 conventional form taxa to a maximum of 30 morphotypes (**Paper III**).
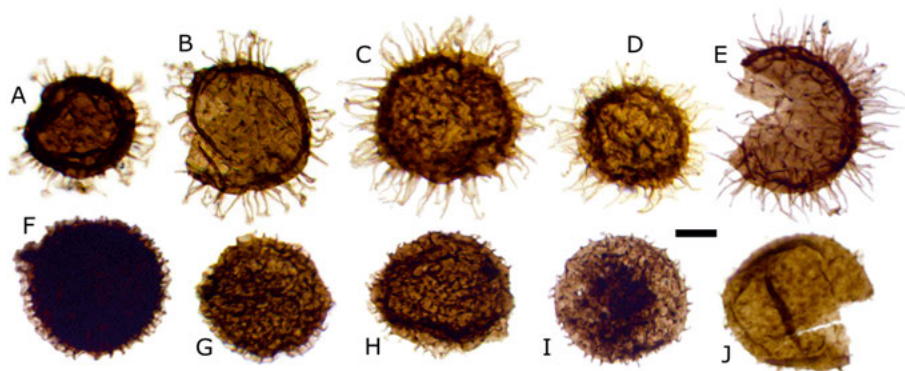
Figure 11. Morphological gradients in *Skiagia*. A–E, *S. orbiculare*, *S. compressa*, *S. ornata* and transitional forms between them. A–B, *S. orbiculare*. C, transitional form between *S. orbiculare*, *S. compressa* and *S. ornata*. D, transitional form between *S. compressa* and *S. ornata*. E, opened *S. ornata* with truncated process tips. F–J, *S. ciliosa* and related taphomorphs exhibiting various degrees of surficial abrasion.

This analysis illustrates how conventional taxonomic practice can artificially inflate taxonomic richness in a typical Cambrian OWM assemblage – a finding that questions the reliability of larger-scale diversity records for this period (e.g., Tappan 1980; Vidal and Knoll 1982; Knoll 1994; Strother 1996, 2008; Vidal and Moczydłowska-Vidal 1997; Knoll et al. 2006; Nowak et al. 2015; Zheng et al. 2020; Zacaï et al. 2021; Kroeck et al. 2022). Because acritarch taxonomy is informal and subject to revisions, measures of species richness for any given time interval have often been regarded as preservable portions of disparity (Knoll 1994; Cohen and Macdonald 2015) or coarse approximations of taxonomic diversity (Vidal and Moczydłowska-Vidal 1997; Zheng et al. 2020). A quantitative examination of the genus *Skiagia* from North Greenland suggests that, at least locally, these diversity metrics offer an arbitrary measure of disparity deprived of palaeobiological meaning, and surrounded

by considerable uncertainties resulting from difficulties in taxonomic identification (**Paper II**). A more systematic analysis of acritarch populations from the wider OWM record may help to refine current estimates of within-assemblage diversity, and pave the way for taxonomic revisions.

New perspectives on plankton reproduction and defence strategies

Observed patterns of morphological variation were contrasted against the presence of discrete features in acritarch vesicles, such as excystment structures, inner bodies, outer membranes and clustering habits (**Papers II, IV**). This multifaceted approach shows the prospect of linking population variations to various aspects of plankton ecology and ontogeny.

In the recovered *Skiagia* population, an inverse correlation between excystment rates (i.e., proportion of opened vesicles) and encystment rates (i.e., proportion of inner bodies) was detected along a morphological gradient uniting five species (**Paper II**). The predominance (but overall scarcity) of inner bodies in acritarch morphologies exhibiting low excystment rates suggests these structures were produced during particularly hostile conditions inhibiting germination. These morphotypes showing a low excystment rate vs. high encystment rate also tend to form monospecific clusters (**Paper IV**), which suggests that a capacity for facultative colony formation and/or passive aggregation was acquired to speed up the descent of cysts in the benthos during periods of environmental stress. The hypothesis of an ontogenetic origin for the phenotypic plasticity seen in *Skiagia* (Moczydłowska 2010) is not supported by the monospecific character of recovered *Skiagia* clusters, and the presence of a mature stage (i.e., opened vesicles) in all *Skiagia* morphotypes. Instead, *Skiagia* species are more reliably interpreted as variably sticky (i.e., aggregation-prone) ecophenotypes produced during the life cycle of one or a few phytoplanktonic species.

Comasphaeridium-type acritarchs form a distinct population of small (< 20 μm) cluster-forming acanthomorphs (**Paper III**). These acritarchs lack excystment and encystment structures, but instead show potential evidence for binary fission, which suggests they do not represent cysts but actively growing planktonic cells (**Paper IV**). Their general abundance and occurrence on a diversity of more or less monospecific acritarch cluster types is suggestive of an opportunistic, possibly bloom-forming habit. Careful analysis of acritarch populations also revealed likely colonial species. These include densely packed aggregates consisting of *Asteridium*-type acanthomorphs. The absence of consistent patterns of cellular organisation and morphology between aggregates of various sizes and isolated *Asteridium* vesicles suggests that colony formation was facultative in these acritarchs. Aggregate formation in modern

phytoplankton can be induced by a variety of factors such as predation pressures (e.g., Hessen and Van Donk 1993; Lürling and Beekman 2006; Yang et al. 2008; Xiao et al. 2018), salinity (Khona et al. 2016; Wei et al. 2017), nutrient levels (Wassmann et al. 1990), light intensity and temperature (Li et al. 2013). On the other hand, the highly conserved structure of *Synsphaeridium* clusters is suggestive of a truly colonial habit. The tightly packed and highly ordered cellular arrangement of these aggregates is seen in numerous extent green algae having a colonial lifestyle (e.g., *Coelastrum*, *Astrephomene*, *Edorina*; *Palambages*; Stein 1958; Tappan 1980; Yamashita et al. 2016; Adam and Haryono 2022).

Altogether, this integrative approach on acritarch populations has revealed a range of cellular structures, lifestyles, defence and/or reproduction strategies at a time when novel grazing pressures were rapidly evolving. These promising results demonstrate that a renewed focus on acritarch clusters in the context of their wider population variations can elucidate aspects of phytoplankton palaeobiology that have so far largely been overlooked.
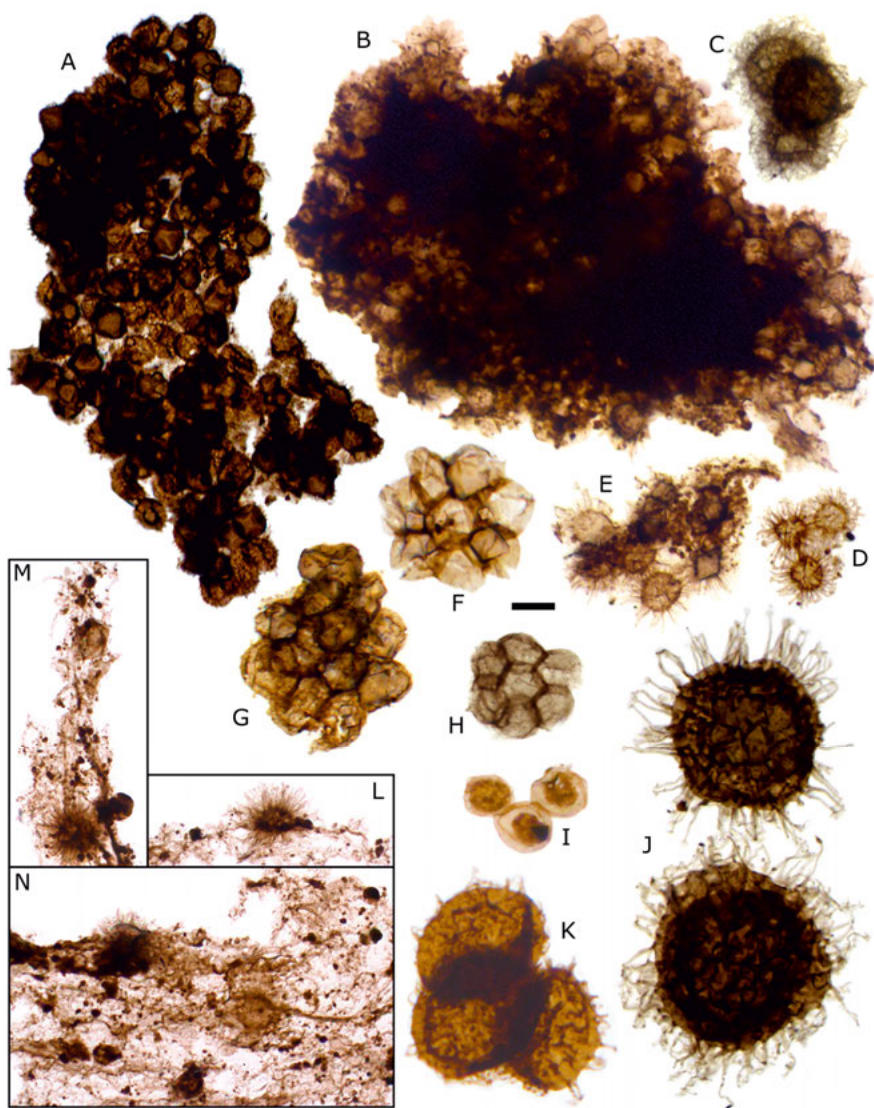
Figure 12. Acritarch clusters from the Buen Formation. A, *Asteridium* aggregate. B–E, *Comasphaeridium*-type aggregates. F–I, *Synsphaeridium*, including clustered vesicles with inner bodies (I). J–K, *Skiagia* clusters, including entangled *S. ornata* and *S.* cf. *compressa* having an inner body (J), and monospecific *S. ciliosa* cluster (K). L–N, enlargements of heterogeneous agglomeration consisting of *Comasphaeridium*-type acritarchs, dark sphaeroids and thin filaments. Scale bar represents 10 μm.

Conclusions, pending questions and perspectives

Thirty years after their original description, OWMs from the Buen Formation were subjected to renewed scrutiny. New sampling techniques enabled a rich diversity of metazoans and primary producers to be uncovered, including crustacean mouthparts and appendages, bivalved arthropods, diverse scalidophoran sclerites, large benthic eukaryotes and a myriad of acritarchs exhibiting complex life histories and clustering habits. On the other hand, a careful inspection of acritarch disparity helped to clarify the taxonomy and palaeobiology of these problematic fossils, while prompting a reconsideration of acritarch diversity. The core findings of this thesis are based on just three horizons at a single locality, but to which extent do they reflect the state of (in)completeness of the wider Cambrian OWM record? Can the approaches and methods used in the Buen Formation be applied successfully in other settings? How much diversity has been overlooked, overestimated, or selectively removed during palynological processing? Future research directions that could provide partial answers to these questions are explored below. The key to success in these areas is widespread OWM sampling – a prospect that is expected to fill in many of the knowledge gaps surrounding OWM preservation and diversity in the years to come.

OWMs: a mosaic of preservation styles?

OWMs consist of a polyphyletic collection of microscopic remains that likely captures a wide spectrum of organic preservation styles. Clarifying the range of cellular structures and tissues that can plausibly be preserved in the OWM record is pivotal to assist identification efforts, and interpret wider patterns of OWM diversity. In particular, the extent to which the OWM record responds to the opening and closure of taphonomic windows is largely unknown. SCFs are traditionally regarded as instances of BST preservation imported from diverse environments (Butterfield and Harvey 2012), but the exact relationships between SCF and BST preservation styles is unclear at present. SCFs themselves consist of a suite of more-or-less decay-resistant tissues, ranging from robust wiwaxiid and priapulid sclerites to exceptionally preserved crustacean

setal arrays (Butterfield and Harvey 2012; Slater and Bohlin 2022). The recovery of bradoriid SCFs as part of this PhD thesis (**Paper I**) has uncovered a new, three-dimensional, apparently silicious type of OWM preservation (Fig. 13). Whether this indicates primary or secondary mineral encrustation is unclear, but the sheer stiffness of the recovered *Spinospitella* fragments and their striking similarity with their SSF counterparts hints at an unexpected overlap between SCF preservation and the more continuous record of skeletal fossils.

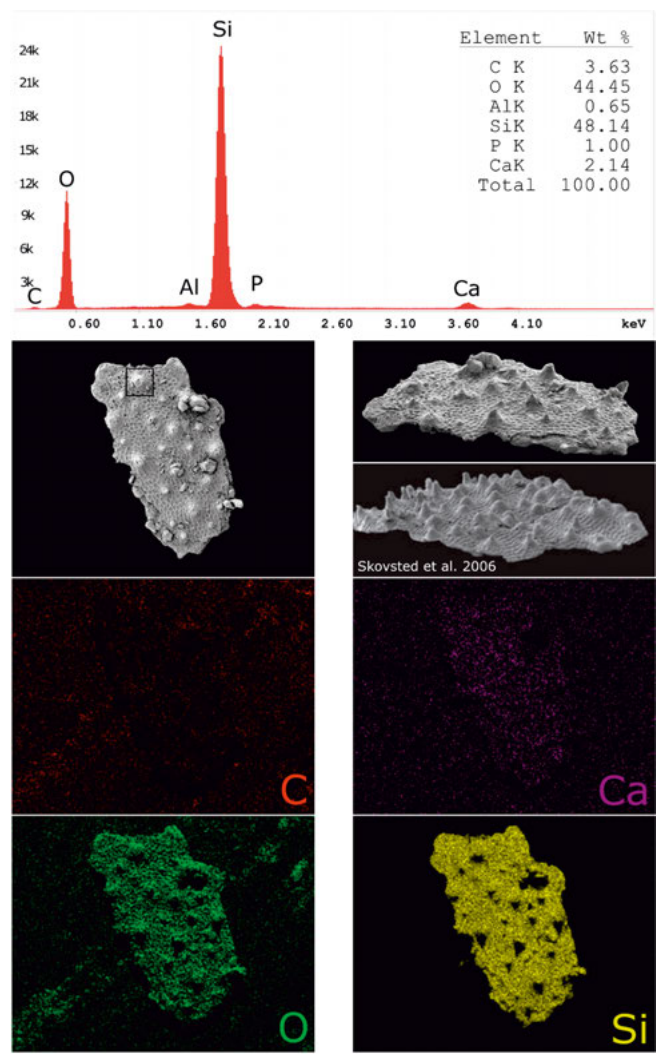Figure 13. Preliminary results of energy dispersive X-ray analysis (EDAX) of bradoriid cuticles from the Buen Formation. The EDAX spectrum and associated elemental composition were obtained from the squared area shown on the left SEM image. An SEM image of *Spinospitella coronata* is shown on the right for comparison (Skovsted et al. 2006). Elemental maps of carbon, calcium, oxygen and silica are given.

In common with skeletal fossils, acritarchs are widely assumed to lie at the recalcitrant end of the taphonomic spectrum owing to their presumed sporopollenin-like wall composition (Colbath and Grenfell 1995; Butterfield 2003). Nevertheless, the chemical characterization of recalcitrant macromolecules in both extant and fossil taxa is hampered by technical difficulties (De Leeuw et al. 2006). The known ultrastructural and chemical diversity of acritarch walls (e.g., Talyzina and Moczydłowska 2000; Willman and Moczydłowska 2007) presumably illustrates a range of decay resistance, a property that is also reflected by their various susceptibilities to acid maceration protocols (Grey 1999; **Paper III**). The diversity of clades that can be preserved in this taphonomic spectrum is unclear, but it seems likely that a variety of cellular structures is represented in the acritarch record, including phytoplankton cysts, vegetative cells and coenobia (**Paper IV**) – all of which likely have their own set of requirements for preservation.

Altogether, the diversity of remains represented among acritarchs and SCFs suggest patterns of OWM preservation are subject to significant taphonomic filters. The distribution of various types of OWMs in time and space is likely controlled by a range of parameters, meaning that the gentle sampling method used as part of this PhD project may not be as productive in settings that do not meet the full set of criteria conducive to OWM preservation. A more widespread use of geochemical proxies should help elucidate the taphonomic pathways leading to specific types of OWM preservation (e.g., Guilbaud et al. 2018). More specifically, clarifying the taphonomic relationships between acritarch, SCF and BST preservation offers the prospect of assessing the relative continuity of the soft-bodied metazoan fossil record in the Cambrian, and assist with SCF sampling efforts.

State of SCF sampling and future prospects

The large majority SCFs known to date have been sampled from Cambrian successions, covering a stratigraphic range similar to that of BST preservation. Even so, SCFs have only rarely been retrieved from BST *Lagerstätten*, which hampers attempts to correlate these two important records. The diversity of SCFs of uncertain origins recovered in **Paper I** (figs. 9–14) clearly demonstrates a need for taxonomic bridges between fragmentary and more complete instances of organic preservation (Harvey and Pedder 2013), a prospect that can be achieved by SCF sampling around *Lagerstätten* sites.

The relatively recent development of SCF research means that current SCF sampling is patchy in time and space (Fig. 14). SCFs are so far chiefly known from the northern hemisphere, particularly in Baltica and Laurentia. In contrast, a much more continuous acritarch record has been built through decades of research to develop a robust acritarch-based biostratigraphy. Careful examination of existing palynological collections should be conducted to detect

fragments of metazoan origin and focus SCF sampling efforts (Slater and Bohlin 2022). However, the conventional OWM record itself has been unevenly sampled, with regions such as Africa, Antarctica and South America being represented by just a few studies (Slater and Bohlin 2022). Moreover, a distinct decrease in reports of metazoan OWMs is clearly visible towards the later part of the Cambrian (Stage 4 and Wuliuan; Slater and Bohlin 2022). Filling these Cambrian gaps using SCFs should help to provide more accurate constraints on the timing of appearance of otherwise poorly known metazoan clades, and track their evolutionary development as modern ecosystems were being established.
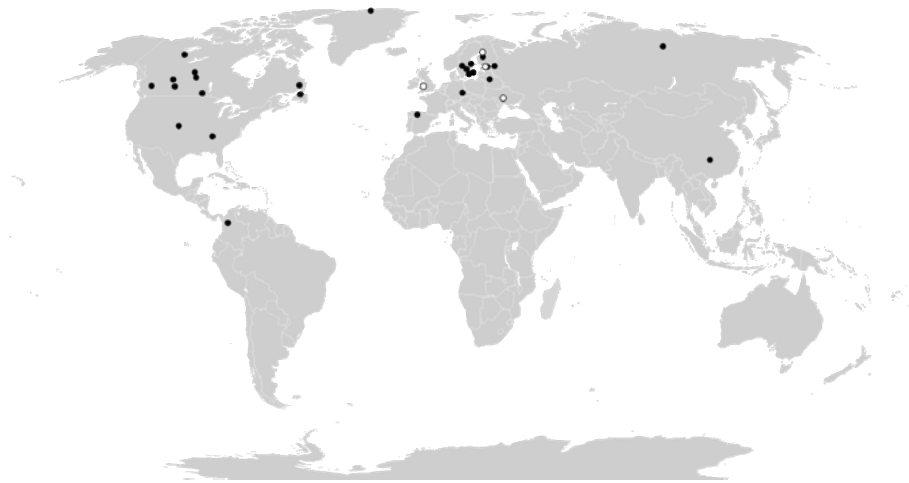
Figure 14. Distribution of hand-picked OWMs from the Proterozoic–Phanerozoic transition. Black dots represent Cambrian OWMs; white dots represent OWMs from Ediacaran and Ordovician periods.

Only few reports of hand-picked SCFs are known from around the stratigraphic boundaries of the Cambrian period (Slater et al. 2020; Slater and Bohlin 2022; Botting et al. 2023). SCF-style extraction methods have proved successful in numerous later Phanerozoic successions (e.g., Batten 1998; Selden et al. 1991; Slater et al. 2015; McLoughlin et al. 2016), demonstrating a clear potential for SCF preservation well beyond the BST taphonomic window. While additional sampling of SCFs from the Ediacaran period should help to consolidate the timing of bilaterian evolution (Willman and Slater 2021), pushing the upper bounds of the SCF record to the Ordovician period shows the promising prospect of elucidating the macroevolutionary relationships between Cambrian and Palaeozoic faunas (Sepkoski 1981). The discovery of miniaturized animal groups from upper Cambrian (Harvey and Butterfield 2017) and Ordovician (Botting et al. 2023) strata indeed suggests a hidden diversity of metazoan SCFs has yet to be uncovered from these intervals.

Scaling up population analyses of acritarchs

The 30 acritarch morphotypes identified in the Buen Formation were defined on the basis of local acritarch populations and singletons (**Paper III**), but whether these populations can be recognised more widely remains to be determined. The community structure and morphology of modern phytoplankton vary considerably depending on regional parameters (e.g., temperature, salinity) and their intra-annual and inter-annual dynamics (e.g., Hays et al. 2005; Zingone et al. 2010; Mertens et al. 2011; Ellegaard et al. 2017; Bedford et al. 2020). When imparted to the fossil record, these temporal and spatial sources of variation may generate site-specific disparity patterns. Scrutinising acritarch populations from a range of depositional settings is therefore pivotal to clarify the factors that impinge on acritarch morphology, a prospect that may be aided by correlating observed morphological variations with a geochemical record.

Important aspects of phytoplankton life cycles and palaeobiology can be revealed by integrating continuous (e.g., process length, vesicle size) and discrete (e.g., excystment structures, inner bodies, clustering habits) characters into morphometric analyses of acritarch populations. These approaches could be used as powerful tools to detect novel adaptations to grazing pressures (**Papers II**, **IV**), and may also help in designing objective diversity and/or disparity metrics (**Paper II**). Further, conducting morphometric analyses of acritarch populations across successive biozones offers the prospect of clarifying the disparity of index taxa, and identifying biostratigraphically significant portions of acritarch morphospace (**Paper II**). More broadly, applying quantitative approaches to acritarch populations worldwide should help to ground acritarch taxonomy into statistically robust aspects of morphology.

The abundance of acanthomorphic acritarch clusters from the Buen Formation suggests that an important source of palaeobiological information has been neglected in previous acritarch studies (**Paper IV**). Taken in the context of their wider populations, acritarch clusters can be used to detect colonial and bloom-forming habits (Mullins 2003; Kovář et al. 2023), but also assess the origin(s) and extent of coagulation processes in the planktonic realm. The 'sticky' morphologies of early Cambrian acanthomorphs undoubtedly favoured aggregation, sinking and burial (Butterfield 1997) – processes that are central to the functioning of the modern biological pump (Iversen 2023). Whilst the significance of metazoan grazers in driving vertical carbon fluxes is being increasingly recognised (Butterfield 1997; Lerosey-Aubril and Pates 2018; Pates et al. 2021), the contribution of bloom-forming, aggregation-prone phytoplankton remains poorly documented in the Cambrian OWM record. A worldwide compilation of acritarch aggregates throughout the Ediacaran–Cambrian transition would be needed to check coagulation theory against factual evidence, and clarify the role of phytoplankton in the establishment of a modern-style biological pump.

Svensk sammanfattning

De evolutionära händelser som ägde rum under den kambriska perioden (för 539–485 miljoner år sedan) var starten på det som sedan blev till den dynamiska och livliga planet som vi ser och tar del av idag. Under denna period diversifierades djuren snabbt och de näringsvävar som fortfarande finns i haven började utvecklas. Vår kunskap om denna viktiga period i livets historia bygger framförallt på tolkning av olika fossila källor, där en av de viktigaste komponenterna består av mikroskopiska organismer med bevarade organiska höljen, ofta benämnda som OWM, från engelskans "organic-walled microfossils".

Organiska mikrofossil extraheras från berggrunden med hjälp av kemiska metoder och följer normalt sett ett standardprotokoll som framförallt är utformat för att extrahera små (<50 μm) svårförklarliga mikrofossil som ofta tar formen av en ihålig sfär – så kallade akritarker. De flesta akritarker betraktas som primärproducerande växtplankton och ger som sådana viktiga inblickar i hur de kambriska näringsvävarna var uppbyggda. På grund av akritarkernas tämligen enkla uppbyggnad så är vår kunskap om deras levnadsförhållanden relativt begränsad, vilket i sin tur gör att vi inte med säkerhet kan klassificera akritarker till några specifika växtplanktongrupper. För att ytterligare komplicera bilden så producerar nutida växtplankton en rad olika former under sin livstid, exempelvis beroende på miljö eller livsstadie. Detta innebär att motsvarande fossil kan tolkas som separata "arter" trots att de inte nödvändigtvis är det. Av dessa skäl är biologiska tolkningar av fossila akritarker problematiska, och primärproducenternas roll i utvecklingen av kambriska näringsvävar är för närvarande fortfarande oklar.

För att extrahera mikrofossil som är särskilt ömtåliga eller något större än 50 μm så används istället en mer skonsam metod. Med denna metod kan man dokumentera fragment av djur som normalt saknas från studier av kambriska bergarter. Dessa mikrofossil (kallade SCF från engelskans "small carbonaceous fossils") bidrar till att fylla viktiga luckor i djurens utveckling, men är fortfarande till stor del förbisedda.

I den här avhandlingen studerar jag tidig-kambriska bergarter från norra Grönland för att undersöka bland annat just klassificering av akritarker och hur vi kan använda SCF för att tolka och förstå tidiga ekosystem. Fokus på avhandlingen är därför att studera, dokumentera och utvärdera mångfalden av både

SCF och akritarker från Brillesø-området (södra Peary Land, norra Grönland) genom att använda en kombination av strategier. För att komplettera tidigare studier av organiska mikrofossil från området har nya bergartsprover analyserats. Dessutom använder jag statistiska metoder för att förfina vår uppfattning av akritarkerna från Brillesø, och därmed också mångfalden hos primärproducenterna.

De nya proverna avslöjar en anmärkningsvärd, och hittills odokumenterad mångfald av SCF, inklusive ett av de äldsta kända kräftdjuren, vackert utsmyckade leddjurskal och ett stort antal taggar från marina maskar. Den mer skonsamma metoden för extrahering av organiska mikrofossil avslöjar också nya typer av akritarker, inklusive stora former som endast undantagsvis har hittats i kambriska bergarter. Resultaten visar att genom att använda en kombination av extraktionsmetoder så kan man måla en bättre och mer fullständig bild av mångfalden. Vidare jämförs de djurgrupper som hittas vid Brillesø med de fossila djurgrupper som hittas från Sirius Passet - ett exceptionellt bevarat fossilt djursamhälle som ligger norr om mitt primära studieområde. Skillnaden mellan dessa två områden visar bland annat hur olika marina djursamhällen anpassat sig till att leva på olika vattendjup, förmodligen för att undvika konkurrens. Denna typ av fördelning av faunan skedde därmed tidigt i livets historia. Mina resultat visar vikten av att studera olika miljöer för att få en fullständig bild av djurens utveckling under kambrium, i detta fall från grundare vatten (Brillesø) till djupare vatten (Sirius Passet).

Totalt identifieras 50 olika "arter" av akritarker och trådliknande mikrofossil, varav 19 beskrivs för första gången från Brillesø. En noggrann undersökning av fossilen visar att vissa tidigare beskrivna "arter" i själva verket är deformerade fragment av redan kända arter. Andra "arter" verkar i själva verket representera olika stadier i en annan arts livscykel. Med denna kunskap i åtanke kan man istället bara urskilja högst 30 olika typer av akritarker. Denna analys illustrerar vikten av att ta hänsyn till naturliga och onaturliga variationer av akritarkernas form när vi tolkar dess mångfald.

För att utforska fördelarna med att studera akritarkernas form granskades fem "arter" från släktet *Skiagia* med hjälp av statistiska metoder. Tio formparametrar, alltså variationer av utseendet, mättes och analyserades tillsammans med diskreta funktioner som rör bland annat livsstil och reproduktionsstrategier hos växtplankton. Trots förekomsten av många mellanformer av *Skiagia*-"arter" visar den kvantitativa analysen att en viss form (*Skiagia ornata*/*compressa*) skiljer sig från de andra "arterna" genom att den har en tendens att bilda anhopningar, eller kluster, och att den ibland omsluter en inre mörkare struktur som kallas endocyst. Den sistnämnda anses innesluta avkomma, vilken i sin tur frigörs när den yttre cellväggen bryts ned. Denna typ av akritark hittas dock sällan öppnad, vilket innebär att fortplantningscykeln avbrutits, förmodligen på grund av ogynnsamma förhållanden (t.ex. låg syrehalt eller hög predation). Moderna växtplankton har en förmåga att bilda vilostadier (eller cystor) på havsbotten vid just perioder av ogynnsamma förhållanden. En

tolkning är följaktligen att akritarker från släktet *Skiagia* representerar just sådana vilostadier, men som också utvecklat en förmåga att bilda kluster som ett sätt att påskynda sin nedstigning till havsbotten när deras överlevnad stod på spel.

Slutligen beskrivs ytterligare tre typer av akritarkkluster från Brillesø. Kluster av *Comasphaeridium*-typ består av oregelbundna sammanslutningar av nästan identiska akritarker som ibland är fästa vid andra organiska rester, ett mönster som kan ha uppstått under växtplanktonblomningar. Kluster av *Asteridium*-typ är mer kompakta och deras organiserade struktur tyder på att de skulle kunna representera kolonier. Å andra sidan tyder det konsekventa och kompakta arrangemanget av celler i *Synsphaeridium*-kluster starkt på att dessa kluster representerar kolonier av växande växtplankton.

Genom att undersöka kambriska organiska mikrofossil från norra Grönland med hjälp av flera olika extraktionsmetoder, och studera deras form och utseende ger mina resultat en ny bild av mångfalden hos denna viktiga grupp. Resultaten ger oss också insyn i hur näringsvävarna var strukturerade, vilket förbättrar vår förståelse för livets tidiga utveckling avsevärt.

Translated by Sebastian Willman, with inputs from Madeleine Bohlin.

Summary

The evolutionary events that took place during the Cambrian Period (539 to 485 million years ago) were arguably the origins of the dynamic and lively planet that we see today. This period saw the diversification of animals and the development of modern ocean food webs. Our understanding of this major transition relies on various fossil sources, of which one of the most significant is the organic-walled microfossil (OWM) record.

OWMs are normally extracted using a standardized protocol designed for the recovery of microscopic (< 50 µm) 'acritarchs' – enigmatic microfossils that usually take the form of tiny hollow spheres. Most acritarchs are thought to be the fossil remains of phytoplankton, and therefore could provide insights into the base of Cambrian food webs. Nevertheless, our knowledge of acritarchs is limited by their relatively simple shapes that make them difficult to classify into known phytoplankton groups. To complicate matters further, phytoplanktonic species living in the ocean today produce a range of forms throughout their lifespan, which in the fossil record could be recognised as distinct acritarch 'species'. For these reasons, interpreting acritarch diversity is problematic, and the role of primary producers in the development of Cambrian food webs remains obscure at present.

Recently, a gentler extraction protocol has been developed for the recovery of large and/or fragile OWMs. When applied to Cambrian rocks, this method occasionally yields fragments of animals that are otherwise absent or rarely preserved in the wider Cambrian record. These 'small carbonaceous fossils' (SCFs) have helped to fill important gaps in our understanding of animal evolution, but remain largely overlooked.

This thesis uses an early Cambrian OWM assemblage from North Greenland as a case study to address the problems of acritarch classification and SCF sampling. The central aim of this project is to re-evaluate the diversity of SCFs and acritarchs from the Brillesø locality (southern Peary Land, North Greenland) by using a novel combination of approaches. First, new samples are processed to recover SCFs and supplement the diversity of OWMs extracted using standard protocols. Second, the acritarch record of Brillesø is inspected using statistical methods to refine our understanding of diversity among primary producers.

New sampling revealed a remarkable diversity of SCFs, including one of the oldest crustaceans known to date, beautifully ornamented arthropod shells,

and a wide range of spines from marine worms. Gentle OWM extraction also revealed new types of acritarchs, including large forms that have only rarely been found in Cambrian rocks. These results demonstrate the value of using a combination of extraction methods to obtain a more complete picture of diversity. Further, animal groups recorded at Brillesø are compared to the Sirius Passet fossil biota – an exceptionally preserved animal community located north of the sampled site. The difference between these two assemblages could represent an early example of faunal partitioning, where certain marine animal communities are confined to specific water depths. This finding suggests that sampling fossils from shallow (Brillesø) to deeper-water (Sirius Passet) depositional environments is necessary to obtain a more complete picture of animal diversity in the Cambrian.

In total, 50 'species' of acritarchs and filamentous microfossils are identified, of which 19 are described for the first time in Brillesø. A careful examination of these fossils revealed that some previously described 'species' are actually the result of fragmentation and deformation of known species. Other 'species' seem to represent different stages in the life cycle of another species. When these sources of variation are considered, a maximum of 30 types of acritarchs can be distinguished. This analysis illustrates the importance of considering shape variations in our estimations of acritarch diversity.

To further explore the benefits of acritarch shape analyses, five 'species' from the genus *Skiagia* are evaluated using statistical methods. Ten shape parameters are measured and analysed alongside discrete features pertaining to algal lifestyles and reproduction strategies. Despite the presence of many intermediate forms between *Skiagia* 'species', this quantitative analysis showed that one particular form (*Skiagia ornata/compressa*) differs from other 'species' in showing a tendency to form clusters, and in occasionally enclosing a dark internal structure called an endocyst. The latter is thought to represent a sac of offspring cells that would be released upon rupture of the outer cell wall. However, this type of acritarch was only rarely found opened, meaning that the reproduction cycle had been interrupted, presumably under hostile conditions (e.g., low oxygen concentrations, or high predation). Many algal species today spend part of their lifespan in the form of 'cysts' resting on the seafloor, where they stay protected during periods of environmental stress. By comparison, acritarchs from the genus *Skiagia* may represent cysts that developed an ability to form clusters as a way of speeding up their descent to the seafloor when their survival was at stake.

Finally, three additional types of acritarch clusters are described from the Buen Formation. *Comasphaeridium*-type clusters consist of irregular associations of nearly identical acritarchs sometimes attached to other organic debris, a pattern that might have been generated during phytoplankton blooms. *Asteridium*-type clusters are similar, but their more compact and organised structure suggests they could represent colonies. On the other hand, the very consistent

and compact arrangement of cells in *Synsphaeridium* clusters strongly suggests these aggregates represent colonies of growing phytoplankton.

Altogether, these results demonstrate that a fresh picture of Cambrian diversity emerges when (1) OWMs are sampled using a combination of extraction protocols, and (2) OWMs are considered in the context of their background shape variations. If applied more widely, these approaches could help to expand our understanding of diversity across all levels of Cambrian food webs.

Résumé

La diversification des animaux marins durant la période du Cambrien (il y a 539 à 485 millions d'années) a entrainé le développement des premières chaines alimentaires à grande échelle. Ces événements évolutifs sont à l'origine de la Terre foisonnante de vie que nous connaissons aujourd'hui. Nos connaissances sur cette transition majeure reposent sur des sources fossiles variées, dont l'une des plus importantes est celle des microfossiles à parois organiques (MPO).

Les MPO sont normalement extraits par le biais d'un protocole standard conçu pour récupérer de petites sphères organiques connues sous le nom d'acritarches. La plupart des acritarches sont considérés comme des restes fossilisés d'algues microscopiques, et donnent donc un aperçu de la productivité primaire à la base des chaines alimentaires cambriennes. Cependant, ces microfossiles possèdent trop peu de caractères morphologiques pour être classés parmi les groupes d'algues connus aujourd'hui. De plus, les espèces d'algues marines qui vivent dans l'océan de nos jours produisent un éventail de formes qui, une fois fossilisées, pourraient être considérées comme des 'espèces' d'acritarches distinctes. Par conséquent, il est difficile d'estimer la diversité des algues cambriennes à partir de leurs restes fossilisés, ce qui complique leur étude dans le cadre des chaines alimentaires cambriennes.

Récemment, un nouveau protocole d'extraction a été développé pour obtenir des MPO plus larges et/ou fragiles. Lorsqu'elle est appliquée à des roches cambriennes, cette méthode permet parfois de récupérer des fragments d'animaux qui ne sont que rarement fossilisés en temps normal. Ces 'small carbonaceous fossils' (SCFs) ont permis de combler d'importantes lacunes dans le registre fossile des animaux, mais sont à ce jour peu étudiés.

Cette thèse porte sur les MPO du Cambrien inférieur de la localité de Brillesø (Peary Land, Groenland), et a pour but central de réévaluer leur diversité tout en abordant les problèmes de classification des acritarches sous la forme d'une étude de cas. Pour ce faire, une double stratégie est adoptée. Premièrement, de nouveaux échantillons sont dissous pour extraire des SCFs, et complémenter la diversité de MPO récupérés lors d'extractions standards. Secondement, les acritarches de la localité de Brillesø sont soumis à des analyses statistiques pour clarifier leur biologie et diversité.

Les échantillons nouvellement dissous ont révélé une diversité remarquable de SCFs, dont les crustacés les plus anciens connus à ce jour, des carapaces d'arthropodes finement ornées, et une large gamme d'épines provenant de vers marins. La technique d'extraction des SCFs a aussi permis de récupérer des acritarches de grande taille qui ne sont que rarement documentés dans le registre fossile cambrien. Ces résultats démontrent l'intérêt d'utiliser plusieurs méthodes d'extraction pour obtenir une gamme plus complète de fossiles, et donc améliorer nos mesures de diversité au Cambrien. Par ailleurs, les groupes d'animaux découverts à Brillesø ont été comparés à ceux de Sirius Passet. Cette localité, située à 180 km au nord-ouest de Brillesø, est un site de conservation exceptionnelle où toute une communauté d'animaux vivant dans des eaux profondes a été fossilisée. La différence marquée entre ces deux sites suggère que certaines communautés d'animaux sont spécifiques à certains environnements. Cette observation montre qu'il est important d'échantillonner des conditions de dépôt sédimentaire multiples (c'est-à-dire des sédiments déposés à plusieurs profondeurs d'eau) pour maximiser la diversité d'animaux recueillis, et déterminer au mieux leur évolution dans le temps.

Au total, 50 'espèces' d'acritarches et de microfossiles filamenteux ont été identifiées, dont 19 sont décrites pour la première fois à Brillesø. Un examen approfondi de ces microfossiles permet de démontrer que certaines 'espèces' décrites initialement ne sont qu'en fait le résultat de la fragmentation et/ou déformation d'autres espèces connues. En outre, certaines 'espèces' semblent représenter différentes étapes dans le cycle de vie d'une seule et même espèce. Quand ces facteurs sont pris en compte, 30 groupes d'acritarches distincts peuvent être identifiés. Cette analyse illustre à quel point il est important d'analyser l'éventail complet des formes d'acritarches pour pouvoir estimer leur diversité plus précisément.

L'éventail de formes adopté par les acritarches du genre *Skiagia* a été analysé statistiquement pour essayer de clarifier leur mode de vie. Dix paramètres de forme ont été mesurés et analysés en parallèle avec des caractères liés au cycle de vie des algues marines. Malgré la présence de nombreuses formes intermédiaires entre les 'espèces' du genre *Skiagia*, cette analyse statistique a montré qu'une forme particulière (*Skiagia ornata/compressa*) se distingue des autres par sa propension à s'agglomérer à d'autres formes du même type. De plus, cette forme a tendance à posséder une sphère interne de couleur sombre. On pense que cette structure interne représente un sac de cellules filles (progéniture) qui devaient être libérées par le biais d'une ouverture dans la cellule mère. Cependant, de telles ouvertures n'ont été observées que rarement dans ce type d'acritarches, ce qui signifie que le cycle de reproduction a été interrompu, vraisemblablement par des conditions hostiles à la germination (par exemple, de faibles concentrations en oxygène ou des prédateurs trop nombreux). Beaucoup d'espèces d'algues modernes passent une partie de leur vie sous forme de 'kystes' en état de repos temporaire dans les fonds marins, où elles restent protégées pendant les périodes de stress environnemental. Par

analogie, les acritarches du genre *Skiagia* pourraient représenter des kystes ayant la capacité de se regrouper sous forme d'agrégations, de manière à couler plus facilement vers les fonds marins quand leur survie est menacée.

Trois autres types d'agrégations sont présentes à Brillesø. Les agrégations de type *Comasphaeridium* se composent de groupements irréguliers d'acritarches presque identiques parfois attachés à d'autres débris organiques. Ces caractéristiques rappellent les agrégations formées au cours d'efflorescences algales (ou 'blooms'), pendant lesquelles une espèce particulière d'algues prend le dessus sur les autres en augmentant rapidement le nombre d'individus dans sa population. Les agrégations de type *Asteridium* sont similaires, mais sont plus compactes et ont une structure plus organisée, ce qui indique plutôt un style de vie colonial. En outre, l'organisation très compacte et cohérente des cellules dans les agrégations de type *Synsphaeridium* suggère que ces acritarches représentent des colonies en cours de développement.

En définitive, ce projet propose une façon nouvelle d'aborder le registre des MPO. L'utilisation de plusieurs méthodes d'extraction permet de récupérer une gamme plus large de MPO, qui peut ensuite être analysée de manière à identifier des populations d'acritarches distinctes. L'adoption de ces méthodes dans des contextes géologiques plus variés pourrait permettre d'affiner nos connaissances sur la diversité cambrienne à tous les niveaux de la chaine alimentaire.

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