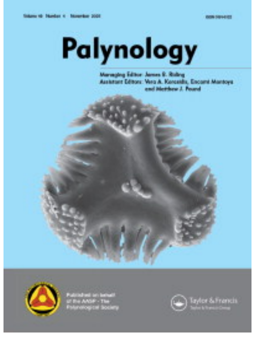
Taylor & Francis
Taylor & Francis Group



Palynology

ISSN: 0191-6122 (Print) 1558-9188 (Online) Journal homepage: www.tandfonline.com/journals/tpal20

Corollasphaeridium: a cryptic record of Cambrian loricate protists

Tom Green, Brian E. Pedder, Mark Williams, Thomas W. Wong Hearing, Pascal Olschewski, Daniel J. Lunt, Thomas Servais & Thomas H. P. Harvey

To cite this article: Tom Green, Brian E. Pedder, Mark Williams, Thomas W. Wong Hearing, Pascal Olschewski, Daniel J. Lunt, Thomas Servais & Thomas H. P. Harvey (2025) *Corollasphaeridium*: a cryptic record of Cambrian loricate protists, Palynology, 49:4, 2494808, DOI: 10.1080/01916122.2025.2494808

To link to this article: https://doi.org/10.1080/01916122.2025.2494808

PALYNOLOGY
2025, VOL. 49, NO. 4, 2494808
https://doi.org/10.1080/01916122.2025.2494808

Corollasphaeridium: a cryptic record of Cambrian loricate protists

Tom Green[a], Brian E. Pedder[b,c], Mark Williams[a], Thomas W. Wong Hearing[a], Pascal Olschewski[d], Daniel J. Lunt[e], Thomas Servais[f], and Thomas H. P. Harvey[a]

[a]Centre for Palaeobiology and Biosphere Evolution, School of Geography, Geology and the Environment, University of Leicester, Leicester, UK; [b]Department of Earth Sciences, University College London, London, UK; [c]Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK; [d]Department of Earth Sciences, Faculty of Science, Memorial University of Newfoundland, St. John's, Canada; [e]School of Geographical Sciences, University of Bristol, Bristol, UK; [f]CNRS, Université de Lille, Lille, France

ABSTRACT

Cambrian palynomorphs include conventional acritarchs (organic-walled microfossils of unknown affinity, often interpretable as phytoplankton cysts) but also spine-shaped forms sometimes interpreted as animal body parts. Here, we examine new specimens of the problematic spine-shaped palynomorph *Corollasphaeridium* Martin and reassess its taxonomic composition and biological affinities. The type species *C. wilcoxianum*, known previously from Cambrian–Ordovician boundary intervals in western Canada and north China, is reported here from the Nolichucky Shale Formation of the USA and the Deadwood Formation of Canada and the USA, extending its biostratigraphical range back to the lower upper Cambrian (Furongian) or middle Cambrian (Miaolingian). The new specimens of *C. wilcoxianum* exhibit the diagnostic form of a trumpet-shaped conical body with 5–12 apical spines, a flaring and infolded aperture rim, and an ornamentation of branched ridges. In contrast, specimens from the lower Cambrian (Series 2, Stage 4) Forteau Formation of Canada are assigned to *C. lissum* sp. nov. In common with lower Cambrian species from Australia and Siberia, *C. lissum* lacks the ridged ornamentation of the type species, but shares a distinctive infolded aperture rim and is intermediate in shape, supporting the reunification of all species under *Corollasphaeridium*. The morphology and size distribution of *Corollasphaeridium* are difficult to reconcile with a phytoplanktic cyst or animal identity and instead support comparisons with the protective cases of protists such as amoebozoan tests and tintinnid ciliate loricae. Therefore, we interpret *Corollasphaeridium* as a loricate protist, albeit without clear synapomorphies with any extant group. The palaeoenvironmental and palaeogeographical distribution of *Corollasphaeridium* suggests localisation in near-shore habitats, possibly limited to warm-water environments (palaeo-tropics to subtropics). Our results further emphasise the hidden high-level taxonomic diversity among 'acritarchs'.

KEYWORDS
Corollasphaeridium; acritarch; tintinnid; lorica; protist; planktic

1. Introduction

The Ediacaran-Cambrian transition represents a pivotal interval in Earth's history marked by the establishment of Phanerozoic-type animal-rich ecosystems. Some of the earliest proposed animal body fossils are spine-shaped and spine-bearing (spinose) organic microfossils recovered as palynomorphs and small carbonaceous fossils (SCFs) (Butterfield and Harvey 2012; Slater and Bohlin 2022). Cambrian examples include the form-genus *Ceratophyton* which encompasses mainly simple, unornamented spines and is widespread in assemblages of early Cambrian age (Fatka and Konzalová 1995; Zang et al. 2007; Palacios et al. 2011). Rare examples of unnamed forms have been reported from the late Ediacaran (Moczydłowska et al. 2015; Willman and Slater 2021). However, accurately ascribing phylogenetic affinity to these microfossils is a major challenge because of the potential for convergent morphologies among animals, algae and protists, and the difficulty of identifying disarticulated fragments in the absence of the larger organismal context.

By definition, acritarchs are vesicular organic-walled microfossils of unknown affinity (Evitt 1963). Although they represent an artificial, polyphyletic grouping of organisms with diverse morphologies from disparate biological origins, perhaps spanning much of the tree of life, the concept is of substantial practical value in the study of palynomorphs (Servais et al. 1997). Many studies focus on the potential insights into pre-Mesozoic phytoplankton: the acritarch record is widely considered to contain a component signal of the planktic primary producers in Palaeozoic seas (Butterfield 1997; Servais et al. 2008; Moczydłowska 2010; Martin and Servais 2020; Harvey 2023). In particular, many of the 'conventional' acritarchs (i.e. rounded vesicles with more or less complex spines) from the Ordovician to Devonian have morphologies and also palaeoecological and palaeogeographical distributions that

CONTACT Tom Green tg210@leicester.ac.uk; Thomas H. P. Harvey thph2@leicester.ac.uk Centre for Palaeobiology and Biosphere Evolution, School of Geography, Geology and the Environment, University of Leicester, Leicester, UK

are broadly comparable to those of dinoflagellate cysts (Martin 1993; Servais et al. 2004; Dale 2023).

However, continued scrutiny of individual acritarch taxa is the only way to confidently ascribe phylogenetic affinities and ecological roles, and in this way, several former acritarchs have been formally transferred to other taxonomic groups. Colbath and Grenfell (1995) identified certain acritarchs as belonging to particular groups of green algae, including the families Prasinophyceae, Botryococcaceae, Hydrodictyaceae, and Zygnemataceae. For example, the identification of distinctive morphological characters of the wall, both external and internal (ultrastructural), has allowed *Tasmanites* to be assigned to the prasinophycean green algae (Tappan 1980; Guy-Ohlson 1996), further supported by organic geochemical comparisons with living forms (Talyzina et al. 2000). Some other former acritarchs have been reattributed to ciliate protists, based on morphological comparison, molecular sequencing and cyst wall composition (Gurdebeke et al. 2018). In another case, the former acritarch *Moyeria* has been assigned to the euglenids based on ultrastructural details of wall ornamentation (Euglenozoa; Gray and Boucot 1989; Strother et al. 2020).

In contrast to these examples of reattribution among groups of essentially vesicular unicellular protists, some acritarchs have been recognised as fragments of metazoan (animal) cuticle in light of more extensive remains recovered *via* gentle acid processing. In this way, the candidate Silurian dinoflagellate *Apylorus* was recognised to be an ornamentation structure from the cuticle of a eurypterid arthropod (Le Herisse et al. 2012), and the former Cambrian acritarch *Goniomorpha* as the disarticulated pharyngeal teeth of a priapulid worm (Shan et al. 2023).

Corollasphaeridium Martin (*in* Dean and Martin 1982) is a Cambrian spinose organic-walled microfossil of disputed affinity that has been classified amongst acritarchs. The genus was first erected for material from the Cambrian–Ordovician boundary interval in the Survey Peak Formation, Wilcox Pass, Alberta, Canada, from five specimens assigned to a single species, *C. wilcoxianum* Martin (*in* Dean and Martin 1982). The limited available material appeared to show a vesicular form with hollow processes, leading to comparisons with co-occurring acritarchs including *Goniosphaeridium*, from which *C. wilcoxianum* is distinguished by an ornamentation on the processes (Martin *in* Dean and Martin 1982). The discovery of material from coeval strata from northern China (Xiaoyangqiao section, Jilin Province; Yin *in* Chen et al. 1988) revealed specimens with an elongate cylindrical form, open at one end and with processes at the other, which were described as a separate species, *C. normalisum* Yin 1986. Through reference to the Chinese material and an expanded sample from Wilcox Pass, Martin (1992) recognised the two proposed species to be the same form preserved in different aspects (lateral view and compressed in transverse view), and therefore synonymised *C. normalisum* with *C. wilcoxianum*. With a main focus on the biostratigraphical significance of the acritarch assemblages, Martin (1992) emended the diagnosis of the species *C. wilcoxianum* (and by implication, the monotypic genus), but did not discuss its possible biological affinities.

Even once the true shape of *Corollasphaeridium* had emerged, Martin (1992) maintained a classification in the Acritarcha, which is a useful label for many palynomorphs of uncertain affinity but should be reserved for vesicular forms if the original concept of Evitt (1963) is to be followed (Servais et al. 1997). Certainly, *Corollasphaeridium* sits uneasily among forms that are widely taken to represent the resting cysts of unicellular phytoplankton (e.g. Nowak et al. 2015), and several workers have mooted alternative biological affinities. Servais et al. (1997) noted similarities to a sub-recent tintinnomorph lorica, i.e. the casing of a particular marine protist. Others have made cursory comparisons to disarticulated animal body parts such as the cuticular spines and teeth of priapulid worms (e.g. Butterfield and Harvey 2012; Grazhdankin et al. 2020), reminiscent of arguments more recently made (on good grounds) for *Goniomorpha* (Shan et al. 2023).

Aside from the type species *C. wilcoxianum*, two rather older species have been reported from lower Cambrian strata (Series 2, Stages 3 and 4) of the Stansbury and Arrowie basins of South Australia (*C. opimolumum* and *C. aliquolumum*; Gravestock et al. 2001; Zang et al. 2007). These differ from *C. wilcoxianum* in lacking a longitudinal ornamentation and a centrally positioned apical process, a distinction shared with recently reported forms from the lower Cambrian Tommotian (Terreneuvian, Stage 2) of the Chuskuna Formation, Siberian Platform (Dantes et al. 2024). Dantes et al. (2024) proposed the erection of a new genus *Spicaticampaniformis* to encompass the Australian and Siberian material, and argued that both genera represent animals, interpreting them as the intact anterior ends of minute spiny-headed worms, specifically acanthocephalans and priapulids, implying exceptional preservation to a remarkable extent.

In addition to ongoing questions of taxonomic membership and biological affinities, the record of *Corollasphaeridium* in space and time has been notably patchy. It is not clear to what extent this reflects a lack of study, poor preservation potential, or a genuinely restricted distribution. From the reasonably well-sampled Baltic region, Volkova (1989) reported *Corollasphaeridium* sp. but did not figure any specimens, and later considered the genus to be restricted to palaeocontinental Laurentia and North China (Volkova 1993, 43), as it otherwise was at the time of publication. Therefore, the absence of substantiated *Corollasphaeridium* from Baltica is not for a lack of search effort. Elsewhere, the stratigraphic distribution (and perhaps the species diversity) of *Corollasphaeridium* in the upper Cambrian of North China is likely to be more extensive than currently described: Shan (2023) reinvestigated the Xiaoyangqiao section and the additional Muqitougou section and reported greater morphological variability than previously known. A detailed redescription of this assemblage is currently in progress.

Here we report new occurrences of *Corollasphaeridium*, from material obtained from palynological residues from the lower Cambrian Forteau Formation (Series 2, Stage 4; Newfoundland, Canada), the middle to upper Cambrian

Deadwood Formation (Miaolingian, Guzhangian to Furongian, Jiangshanian) of Saskatchewan, Canada and South Dakota, USA, and the middle to upper Cambrian Nolichucky Shale Formation (Miaolingian, Guzhangian to Furongian, Paibian) of Tennessee, USA. The stratigraphic range of *C. wilcoxianum* is older than formerly recognised, extending back through the Furongian and possibly into the Miaolingian. The lower Cambrian material is assigned to a new species and supports the reinstatement of a unified genus-level classification. A comparison with various extinct and extant groups suggests that *Corollasphaeridium* represents loricate protists rather than phytoplankton or the disarticulated remains of animals.

2. Geological setting, material and methods

This paper presents a compendium of results from palynological surveys of four Cambrian successions from Laurentia, with initial sampling undertaken during the PhD and postdoctoral work of Tom Harvey and Brian Pedder and continued through the PhD of Tom Green. The geological setting of each sampled succession is summarised below, along with an indication of relative sampling intensity.

The Forteau Formation of Newfoundland and southern Labrador, Canada, is a mixed carbonate and siliciclastic succession with localised archaeocyathid reefs, and represents marine deposition in nearshore to mid-shelf settings on eastern Laurentia during the late early Cambrian (Knight et al. 2017; Skovsted et al. 2017). On the evidence of trilobite biostratigraphy, the formation lies in the middle part of the *Bonnia-Olenellus* trilobite Biozone within the regional Dyeran/Dyerian Stage of North America, which is considered correlative with Cambrian Stage 4 although the base of this stage is yet to be defined (Knight et al. 2017, Table 1; Geyer 2020; Peng et al. 2020). We examined palynological preparations from eleven samples of dark grey mudstones from the Middle Shale Member from various localities in western Newfoundland and southern Labrador (detailed in Harvey 2023) and two new samples from the Upper Limestone Member from a road cutting (locality label R432-6; 51°00′49″ N 56°36.05′ W; $n = 31$) and a nearby small quarry *c.* 1.3 km away (R432-7; 51°00.59′ N 56°35.13′ W; $n = 46$) along Route 432 between Plum Point and Roddickton, Great Northern Peninsula, Newfoundland (Figures 1 and 2a; locality details in Knight et al. 2017). Sample R432-6 was collected from the middle of a 40 cm thick laminated black mudstone unit located around 1 m above the base of the roadside section (Figure 2b; see Knight et al. 2017, fig. 8), where it is overlain by 1 m of interbedded calcareous, cross-laminated siltstone and shale with *Rusophycus*, and then by 4 m of oolitic limestones containing skeletal grains and *Salterella* (see Knight et al. 2017, fig. 8). Sample R432-7 was collected from a 50 cm thick laminated black mudstone unit in the quarry section where it overlies a bioturbated siltstone and is overlain in turn by an oolitic limestone with *Salterella* (Figure 2b; see Knight et al. 2017, fig. 8). The R432 mudstone units apparently represent two distinct but closely spaced stratigraphic intervals within the Upper Limestone Member, with that in the quarry section being the lower according to Knight et al. (2017). The Upper Limestone Member represents deposition in a prograding barrier shoal complex (Skovsted et al. 2017), with the sampled black mudstones apparently recording quiet-water deposition in a protected environment, distinct from the open-shelf conditions prevailing in the underlying Middle Shale Member characterised instead by grey, macrofossil-bearing mudstones.

The Deadwood Formation encompasses a geographically extensive, largely siliciclastic succession known from the subsurface in the Western Canada Sedimentary Basin and outcrop in contiguous regions of the northern USA; it records deposition in the 'inner detrital belt' of an epicontinental sea on the western Laurentian margin from the middle to late Cambrian (Miaolingian to Furongian) and locally, into the

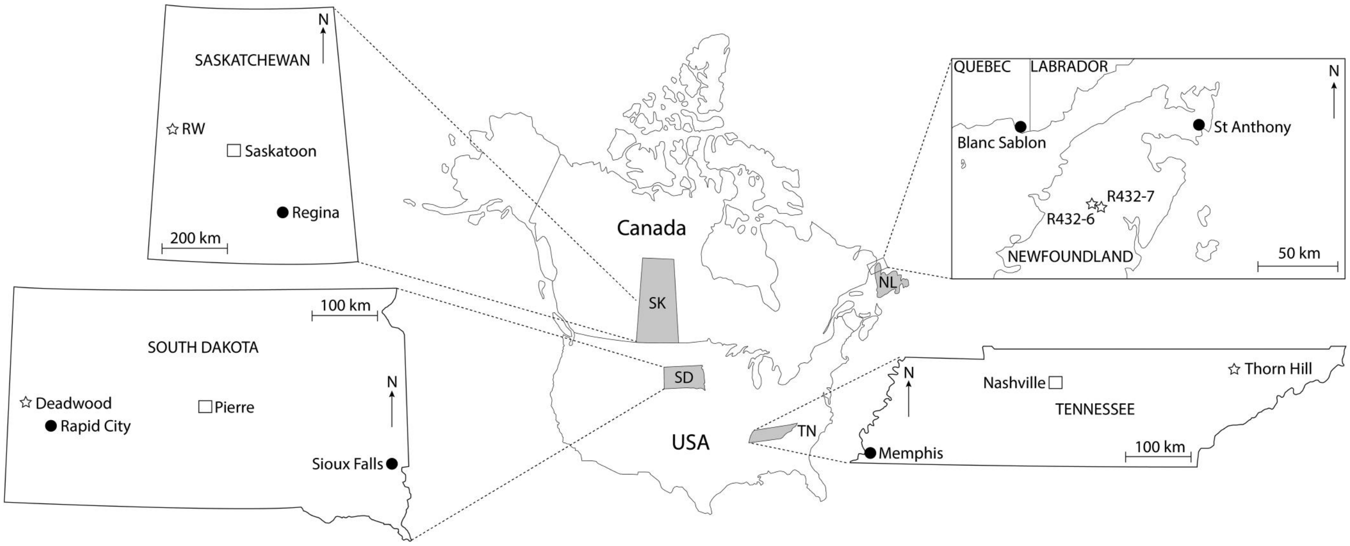


Figure 1. Map of part of North America showing localities which have yielded new specimens of *Corollasphaeridium*. The Deadwood Formation was sampled in the Black Hills, South Dakota and from drill core (RW: Ceepee Reward) in Saskatchewan. The Forteau Formation was sampled at R432-6 and R432-7 in northwestern Newfoundland along Route 432 between Plum Point and Roddickton. The Nolichucky Shale Formation was sampled from Thorn Hill, Tennessee, USA. Source: Map outlines of South Dakota, Newfoundland and Tennessee sourced and redrawn from Google Earth, 2025. Google Earth. 2025. [accessed 2024 Dec]. https://www.google.co.uk/maps/.

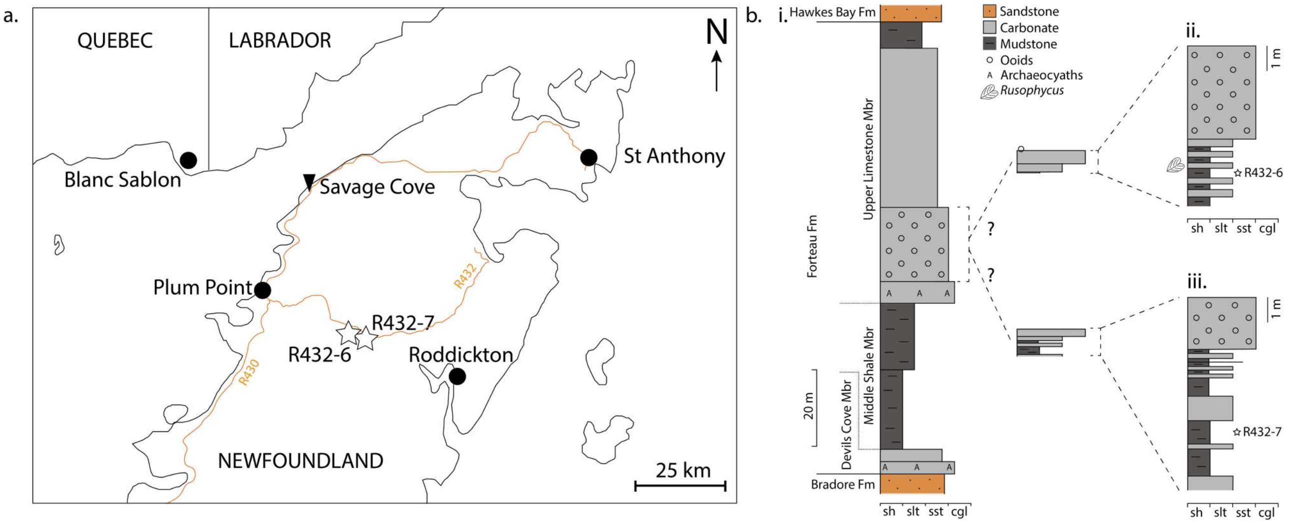


Figure 2. (a) Map of the Great Northern Peninsula of Newfoundland and southern Labrador detailing the sampling locations of R432-6 and R432-7. (b) (i) Simplified stratigraphic log of the Forteau Formation from the DH-NF-1B drillcore at Savage Cove. Modified from Knight et al. (2017, fig. 2, p. 3). Expanded sections show the location of samples (ii) R432-6 and (iii) R432-7. Logs modified from Knight et al. (2017, fig. 8, p. 27). Both samples derive from the Upper Limestone Member and R432-6 overlies R432-7 however the exact relationship is unknown.

Ordovician (Stitt and Straatmann 1997; Hein and Nowlan 1998; Dixon 2008). We examined palynological preparations from ten samples collected from outcrop in the Black Hills region of South Dakota, USA (Figure 1), from a cliff exposure overlooking the city of Deadwood (44°23′3.27″N, 103° 43′26.71″W). In this vicinity, the succession consists of *c.* 130 m of conglomerate, limestone, sandstone and mudstone (Darton and Paige 1925; Steece 1978). The ten samples span a c. 50 m interval from the base of the locally exposed section up to the first thick sandstone unit with prominent *Skolithos* (at around 160 feet in the log of Steece 1978). A productive sample BP09-DW4 was identified in a medium-grey/green shale situated between flat-pebble conglomerates, occurring 44.1 m below the base of the *Skolithos* sandstone. We tentatively assign this sample horizon to the Jiangshanian Stage of the Furongian Series based on reported *Taenicephalus* Zone trilobites and lithology data (green shales interbedded with flat-pebble conglomerates) reported in Stitt and Straatmann (1997), in conjunction with the measured section in Steece (1978) and trilobite zone correlations to the international chronostratigraphy by Geyer (2020).

Further samples processed for palynology from the Deadwood Formation come from petroleum exploration drill cores from Saskatchewan, Canada (Figure 1) that were previously sampled for small carbonaceous fossils (SCFs; see Harvey et al. 2012). From 23 palynological spot samples from across ten wells, a productive horizon was identified at 5401.3 ft/1646.3 m in the Ceepee Reward (RW) borehole in southwest Saskatchewan (locality number 4-28-38-24W3; licence number 58E063: Dixon 2008; Harvey et al. 2012). The succession here records deposition in a wave-dominated lower shoreface to shelf environment (Dixon 2008; Buatois and Mangano 2013). The stratigraphic level of the productive horizon is minimally constrained by upper Cambrian brachiopods some sixty metres higher in the core, which indicates the upper Steptoean to lower Sunwaptan regional stages (Robson et al. 2003), i.e. not higher than the Jiangshanian Stage of the Furongian Series. A maximum constraint is provided by middle Cambrian trilobites in the underlying Earlie Formation representing the upper Wuliuan Stage of the Miaolingian Series (Handkamer et al. 2023). Therefore, the productive horizon most likely belongs to the upper middle Cambrian (Drumian or Guzhangian Stage of the Miaolingian Series) or lower upper Cambrian (Paibian Stage of the Furongian Series).

The Nolichucky Shale Formation, Tennessee, USA (Figure 1), is a succession of grey-green to brown laminated shales interbedded with limestones deposited on the eastern Laurentian margin during the middle to late Cambrian (Byerly et al. 1986; Weber 1988). From a survey of 44 sampled horizons from Thorn Hill, Tennessee (Pedder 2012; Harvey and Pedder 2013), a productive horizon (sample 08BP-33$^{2}/_{3}$) was identified in a moderately dark grey, smooth-textured shale 176.70 m stratigraphically above the base of the formation as locally exposed. Here this upper portion of the formation represents the Upper Shale Member, and records deposition in a shallow marine environment with oolitic, thrombolitic and shelly shoals separated by areas of shale deposition (Weber 1988). The productive horizon at Thorn Hill falls within an interval encompassing the Miaolingian–Furongian boundary according to carbon-isotope stratigraphy and correlations to trilobite-bearing sections nearby (Pedder 2012).

Samples were processed using standard palynological techniques (e.g. Harvey and Pedder 2013). Approximately 30 g of mudstone from each sampled horizon was crushed using a pestle and mortar and pre-treated with hydrochloric acid (HCl at 37 %) to remove carbonates. Treatment with HCl was repeated. Samples were then treated with hydrofluoric acid (HF at 40 %) to remove silicates and then further treated with nitric acid (HNO_3 at 70 %) to remove pyrites and precipitates. Heavy minerals were removed by separating into zinc chloride ($ZnCl_2$). The resultant residue was sieved through a 10 µm mesh, mounted on glass slides using epoxy resin and photographed using transmitted light with differential interference contrast for higher magnifications (×40 and ×100 objective lenses).

In addition to standard palynological processing, lithologically and stratigraphically equivalent samples from the Deadwood Formation of Saskatchewan and the Forteau Formation were subjected to a low-manipulation hydrofluoric acid-extraction technique optimised for recovering small carbonaceous fossils (SCFs; described in Harvey and Butterfield 2008), to test for the presence of larger specimens or articulated arrays.

Specimens from the Forteau Formation and Deadwood Formation (Saskatchewan collection) are reposited at the Geological Survey of Canada, Ottawa, Ontario, Canada, with numbers GSC 144315 to GSC 144357 (see figure captions for details). Specimens from the Nolichucky Shale Formation and Deadwood Formation, South Dakota are reposited in the Centre for Palynology, Department of Animal and Plant Sciences, University of Sheffield, South Yorkshire, UK (Brian Pedder 2012 PhD collection).

3. Results

A total of 92 specimens of *Corollasphaeridium* were recovered from the four sampled successions. All specimens were recovered as isolated individuals on strew slides prepared using standard palynological methods, with none found using the low-manipulation, handpicking technique.

From the Forteau Formation, 77 specimens were recovered from the two samples of notably dark mudstone from the Upper Limestone Member from the R432 localities (Figure 2b), where they co-occur with sphaeromorphic acritarchs, clusters of cells, fragmentary *Wiwaxia* sclerites and priapulid cuticular elements. SCF processing additionally yielded more intact *Wiwaxia* sclerites and more extensive cell clusters. In contrast, no specimens of *Corollasphaeridium* were found in the 11 studied samples from the underlying Middle Shale Member, despite these yielding diverse palynomorphs, notably acanthomorphic acritarchs (reported in Harvey 2023), and various metazoan SCFs (e.g. Harvey 2010). The Forteau specimens of *Corollasphaeridium* exhibit a distinctive array of morphologies, with a cylindrical to an hourglass-shaped body, which flares towards an aperture (Figure 3, particularly d, w and x), an absence of longitudinal ornamentation, and 6 to 12 processes with the apical process often being the longest and widest. The Forteau specimens are assigned to a new species, *C. lissum* (see Systematic Palaeontology).

From the Deadwood Formation, nine specimens were recovered from the Black Hills section of South Dakota, USA (Figure 4a, b, d, g and h) from one of the ten processed samples (BP09-DW4), co-occurring with abundant sphaeromorphic acritarchs, clustered cells, *Granomarginata squamacea* (a pteromorph acritarch) and rare metazoan spines. A further five Deadwood Formation specimens were recovered from southwest Saskatchewan, Canada (Figure 4c, e, f and i), from a single sample at a depth of 5401.3 ft/1646.3 m in the Ceepee Reward borehole, where they co-occur with a sparse assemblage of sphaeromorphic acritarchs, clustered cells, priapulid cuticular elements and reticulate net-like palynomorphs (cf. Harvey et al. 2012). No specimens of *Corollasphaeridium* were noted in palynological preparations from 22 other spot-samples spanning 10 boreholes, nor in any of the >90 SCF preparations from a previous study on the Saskatchewan Cambrian succession (see Harvey et al. 2012). From the Nolichucky Shale Formation at Thorn Hill, Tennessee, USA, a single fragmentary specimen was recovered from sample 08BP-33⅔ (Figure 4j), co-occurring with various sphaeromorphic and acanthomorphic acritarchs; *Corollasphaeridium* was not found in the remaining 43 samples from this section, though palynomorphs were present throughout. Specimens of *Corollasphaeridium* from the Deadwood and Nolichucky Shale formations exhibit considerable morphological variability but are referable to the type species, *C. wilcoxianum*, based on the ornamentation of ridges on both body and processes (see Systematic Palaeontology).

4. Discussion

Our preliminary palynological sampling of the Deadwood Formation of South Dakota and Saskatchewan, and our more systematic surveys of the Nolichucky Shale and Forteau formations, reveal patchily distributed and mostly sparse occurrences of *Corollasphaeridium* that nevertheless contribute significant new information on the stratigraphical range, taxonomy and morphology of this enigmatic Cambrian microfossil.

4.1. Corollasphaeridium wilcoxianum *from the Deadwood and Nolichucky Shale formations: a revised stratigraphical range*

Recovery of *Corollasphaeridium wilcoxianum* from the Deadwood Formation (Saskatchewan and South Dakota) adds to the previous western Laurentian occurrence from the type locality at Wilcox Pass, Alberta, Canada (Martin 1992), while the specimen from the Nolichucky Shale Formation extends the geographical range to eastern Laurentia (Figure 1). Each new occurrence is notable for coming from a substantially lower stratigraphical horizon than previously reported for this species (Figure 5), which has been considered indicative of the Cambrian–Ordovician boundary interval at both Wilcox Pass (Dean and Martin 1982; Martin 1992; Ji and Barnes 1996) and the Xiaoyangqiao section, Jilin Province, north China (Yin *in* Chen et al. 1988; Wang et al. 2019; Shan 2023). At Wilcox Pass, Martin (1992) proposed a succession of acritarch-based units (AU1 to AU6), among which AU2 was designated the *C. wilcoxianum* Zone with the lowest occurrence of this taxon marking the base. A subsequent study of conodonts at Wilcox Pass confirmed that AU2 straddles the Cambrian–Ordovician boundary (Ji and Barnes 1996). Likewise, the range of *C. wilcoxianum* at the Xiaoyangqiao section, where it indexes Microflora Assemblage 3, extends from the uppermost Cambrian


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s
t
u
v
w
x
y
z
aa
ab
ac
ad
ae
af
ag
ah
ai
aj
ak
al
am
20µm

(Furongian Series, uppermost Stage 10) into the Ordovician (Wang et al. 2019). These sections are significant for characterising the base of the Ordovician System; indeed, the Xiaoyangqiao section has been designated an Auxiliary Boundary Stratotype Section and Point (ASSP; Wang et al. 2021). However, the older occurrences of *C. wilcoxianum* in the Deadwood and Nolichucky Shale formations (in each case, upper Miaolingian or lower Furongian series), undermine the utility of this taxon as an index fossil for the Cambrian-Ordovician boundary interval, suggesting instead that *C. wilcoxianum* ranges through more than 10 Myr of Cambrian time (Figure 5).

4.2. A new species of Corollasphaeridium *from the Forteau Formation*

The specimens of *Corollasphaeridium* from the Forteau Formation are the first occurrence from the lower Cambrian of Laurentia. They lack the ornamentation diagnostic of *C. wilcoxianum* (Figure 3), but more closely resemble the other lower Cambrian forms originally described as *C. opimolumum* and *C. aliquolumum* from South Australia (Gravestock et al. 2001) and more recently transferred to a new genus, *Spicaticampaniformis* based on new material from Siberia (Dantes et al. 2024). The Forteau specimens exhibit features in combination that Dantes et al. (2024) considered independently diagnostic of the two genera: the lack of longitudinal structures matches the concept of *Spicaticampaniformis*, but the presence of a pronounced apical process and long, radially arranged processes do not, and are instead shared with *C. wilcoxianum*. This combination of characters undermines the proposed genus-level distinction. Therefore, we assign the new Forteau Formation species to *Corollasphaeridium* rather than *Spicaticampaniformis*, and suggest that *Spicaticampaniformis* should be considered a junior synonym of *Corollasphaeridium* (see Systematic Palaeontology for details). Notably, the stratigraphic position of *C. lissum* sp. nov. in the upper part of the lower Cambrian (Stage 4) is intermediate between the older Australian and Siberian species and the younger *C. wilcoxianum* (Figure 5).

4.3. Biological affinity of Corollasphaeridium

As well as extending the known range of *Corollasphaeridium* in space and time, and clarifying the taxonomic cohesion of the genus, the new occurrences help constrain its possible affinities. Here we assess the various proposed biological interpretations of *Corollasphaeridium* by reference to living and extinct groups, and test for patterns in its palaeoenvironmental range.

4.3.1. Corollasphaeridium *is distinct from vesicular acritarchs*

Because the genus was first recorded in assemblages investigated for acritarch research, early work on *Corollasphaeridium* logically focussed on comparisons with coeval acritarchs. Evitt (1963) originally intended the term acritarch to be restricted to vesicular microfossils, and indeed the earliest-described specimens of *Corollasphaeridium* are flattened at an angle that conceals their aperture, so they appeared much like the genuinely vesicular *Goniosphaeridium* but with unusually ornamented processes (Martin *in* Dean and Martin 1982). Further comparisons to vesicular acritarchs were entertained even after the aperture was recognised, with Yin (*in* Chen et al. 1988) comparing the broad-based processes of *Corollasphaeridium* to those of *Rhiptoscherma improcera* and noting the differences in process ornamentation from those of *Eliastra* and *Goniosphaeridium*. Several vesicular acritarchs share with *C. wilcoxianum* a lineated ornament, notably certain netromorph acritarchs such as *Deusilites*, *Eupoikilofusa* and *Baiomeniscus* (Manzano et al. 2025; compare e.g. *Eupoikilofusa filifera* in Breuer et al. 2017, pl 9, fig. 1–2, 4). Furthermore, the presence of an aperture does not rule out a vesicular form, because excystment structures or post-mortem breakage can create an opening. For example, several organic-walled microfossil taxa including *Tasmanites* and *Baltisphaeridium* possess a raised rim surrounding a circular opening (cyclopyle), which can be closed by an operculum (Downie 1973). However, no *Corollasphaeridium* specimens have been found with an operculum or operculum attachment structures. *Corollasphaeridium* also bears some resemblance to half of a vesicle of a diacrodian acritarch, which are forms with a bipolar distribution of processes (e.g. Raevskaya and Servais 2009, fig. 1). In particular, the process size, number and surface ornamentation in *Corollasphaeridium* resemble those of upper Cambrian diacrodian acritarchs such as *Ladogella rommelaerei* (e.g. Martin *in* Dean and Martin 1982; Ghavidel-Syooki and Vecoli 2008, pl 2, fig. 1) and the Ordovician species *Arbusculidium filamentosum* (Vavrdova 1965) and *Barakella felix* (Cramer and Díez 1977, pl 5, fig. 1–2, 11). However, *Corollasphaeridium* has never been found as an enclosed vesicle exhibiting a bipolar spinose ornamentation, and ruptured diacrodian acritarchs do not exhibit a

Figure 3. *Corollasphaeridium lissum* sp. nov. from the lower Cambrian (Series 2, Stage 4) Forteau Formation, Newfoundland. (a–o) R432-6 roadcut (51°00.49′ N 56°36.05′ W) and (p-am) R432-7 Quarry (51°00.59′ N 56°35.13′ W) on Route 432 between Plum Point and Roddickton. Specimen labels are in the format: locality name_k(kerogen) or oc(outcrop) (where applicable) _sample number (where applicable)_slide number(where applicable)_England Finder co-ordinates and proceeded by the repository number a. R432-6_01_po1_N28-4 (GSC144315), b. R432-6_01_po1_J25-4 (GSC144316), c. R432-6_01_po2_J24-1(GSC144317), d. R432-6_01_po2_T11 (GSC144318), e. R432-6_01_po1_K33-1 (GSC144319), f. R432-6_01_po2_G22-3 (GSC144320), g. R432-6_01_po2_Y32-1 (GSC144321), h. R432-6_01_po2_T29-1 (GSC144322), i. R432-6_01_po2_K29-2 (GSC144323), j. R432-6_01_po2_C43-4 (GSC144324), k. R432-6_01_po2_V47 (GSC144325), l. R432-6_01_po1_L21-4 (GSC144326), m. R432-6_01_po1_J25-2 (GSC144327), n. R432-6_01_po1_T24-4 (GSC144328), o. R432-6_01_po1_Q50 (GSC144329), p. R432-7_oc_p2_V32-1 (GSC144330), q. R432-7_K_C55-3 (GSC144331), r. R432-7_oc_p1_C51-4 (GSC144332), s. R432-7_oc_p1_H43-3(GSC144333), t. R432-7_oc_p1_D32-4 (GSC144334), u. R432-7_K_P27-2 (GSC144335), v. R432-7_K_U37-4 (GSC144336), w. R432-7_oc_p2_C35-3 (GSC144337), x. R432-7_oc_p1_V49-4 (GSC144338), y. R432-7_oc_p2_T38-2 (GSC144339), z. R432-7_K_W43-3 (GSC144340), aa. R432-7_oc_p2_R49-2 (GSC144341), ab. R432-7_oc_p1_E48-1 (GSC144342), ac. R432-7_oc_p1_N39-2 (GSC144343), ad. R432-7_oc_p2_M43-1 (GSC144344), ae. R432-67_oc_p1_O41-1 (GSC144345), af. R432-7_K_F31-2_1 (GSC144346), ag. R432-7_K_R55-2 (GSC144347), ah. R432-7_K_Q48-4 (GSC144348), ai. R432-7_K_U57-4 (GSC144349), aj. R432-7_K_D31-3 (GSC144350), ak. R432-7_K_S45-1 (GSC144351), al. R432-7_oc_p1_E51-2 (GSC144352), am. R432-7_K_C58-3 (GSC144353).

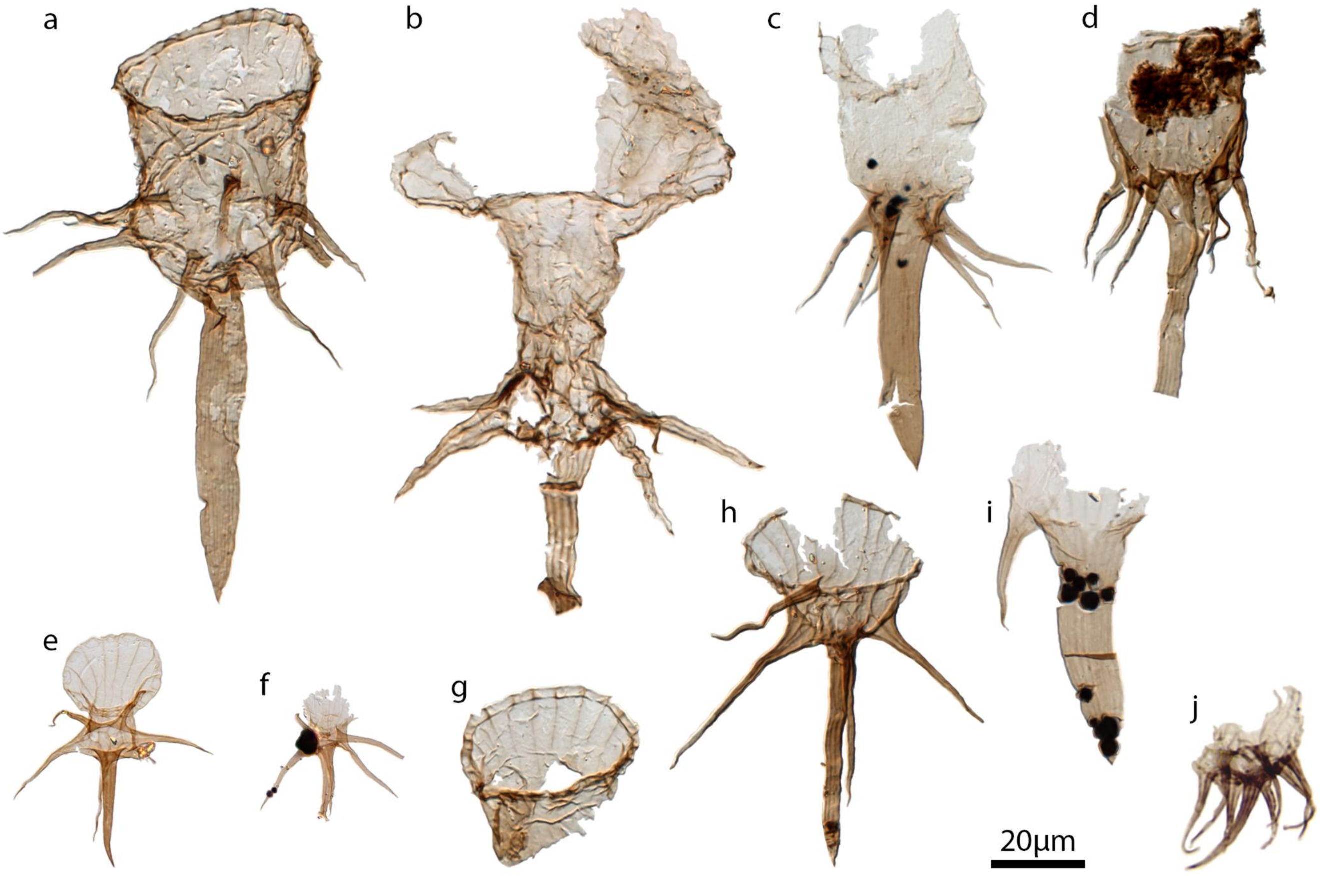


Figure 4. *Corollasphaeridium wilcoxianum* from the Deadwood Formation of South Dakota, USA (a, b, d, g, h), the Deadwood Formation of Saskatchewan, Canada (c, e, f, i) and the Nolichucky Shale Formation of Tennessee, USA (j). For Saskatchewan specimens labels are in the format: locality name + core number_box_depth (cm below boxed top) _slide number_England Finder co-ordinates. For South Dakota specimens labels are in the format: Deadwood + relative distance from stratigraphic base_slide number_slide making episode_England Finder co-ordinates. a. DW4-2-A_L36-2, b. DW4-2-A_S33-2, c. RW13-4-70_po3_H20-3 (GSC144354), d. DW4-2-A_U42-3, e. RW13-4-70-p01-V45-2 (GSC144355), f. RW13-4-70-p01-J39-0 (GSC144356), g. DW4-2-A_O23-2, h. DW4-2-A_N34-1, i. RW13-4-70_po3_O15-1 (GSC144357), j. BEP-0195_K35-0.

comparable thickened collar on the antapical margin, which is a prominent and diagnostic feature of *Corollasphaeridium*. Therefore, although *Corollasphaeridium* might be considered an acritarch in the loose sense of being an organic-walled microfossil of unknown affinity, it is morphologically distinct from vesicular acritarchs that are routinely interpreted as phytoplankton cells or cysts.

4.3.2. Corollasphaeridium *is not a chitinozoan*

The well-defined basal collar in *Corollasphaeridium* is broadly comparable to the characteristic aperture region of another Palaeozoic organic-walled microfossil group, the chitinozoans. Chitinozoans are of unresolved affinity and have been interpreted as metazoan egg sacks, fungi and protozoans (Servais et al. 2013), but recent analyses point to chitinozoans as an ontogenetic series of microorganisms based on quantitative analysis of their variation in comparison to metazoan eggs (Liang et al. 2019). Several chitinozoan taxa have radially arranged processes (e.g. *Ancyrochitina*, Achab et al. 2013, pl 2, fig. 16–17) or a longitudinal ornament (e.g. *Hercochitina*, Achab et al. 2013, pl 1, fig. 1–3, 7–9) which appears superficially similar to the ornamentation of *Corollasphaeridium*. However, no chitinozoan taxa possess an elongated apical process like *Corollasphaeridium*. Instead, chitinozoans possess a flat surface with an aboral mucron or peduncle at their apex (Paris et al. 1999), structures that allow attachment of a series of chitinozoans in a catenary chain (Nõlvak 1993; Miller 1996). The absence of features in *Corollasphaeridium* that are fundamental to chitinozoan aggregation suggests that any similarities between the two groups are superficial.

4.3.3. Corollasphaeridium *is not a metazoan scalid, spine or seta*

The open based, spine-tipped form of *Corollasphaeridium* has led to the suggestion that it represents the disarticulated cuticular ornaments from the body of an ecdysozoan metazoan, the group containing arthropods and other moulting invertebrates (Butterfield and Harvey 2012; Grazhdankin et al. 2020).

In particular, *Corollasphaeridium* has been compared to the cuticular projections which adorn the body and pharynx of priapulid worms (Butterfield and Harvey 2012; Grazhdankin et al. 2020). Priapulid body scalids and

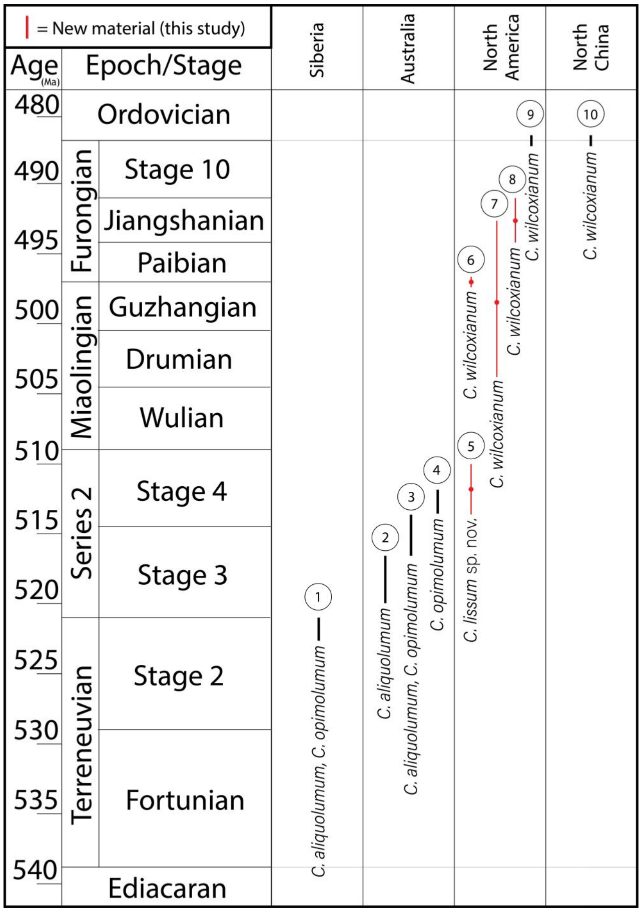


Figure 5. Cambrian timescale showing the occurrences of *Corollasphaeridium* including new occurrences from the (5) Forteau, (6) Nolichucky Shale and Deadwood ((7) Saskatchewan and (8) South Dakota) formations, with error bars (stratigraphic uncertainty), presented herein (this paper), and published records from Siberia: (1) Chuskuna Formation (Dantes et al. 2024), Australia: (2) Wilkawillina Limestone, (3) Parara Limestone and (4) Minalton Formation (Gravestock et al. 2001), Canada: (9) Survey Peak Formation (Wilcox Pass) (Martin *in* Dean and Martin 1982) and North China: (10) Fengshan Formation (Xiaoyangqiao section) (Yin in Chen et al. 1988). Timescale adapted from Peng et al. (2020).

pharyngeal teeth are variously conical or tubular, often with secondary spines and other fine-scale ornamentation related to their roles in sensing, feeding and locomotion (Schmidt-Rhaesa et al. 2012). Being formed of thicker cuticles than the surrounding body wall, priapulid cuticular structures are resistant to decay and readily disarticulate from the body after death (or moulting) (Sansom 2016). Priapulid-derived structures are a prominent component of many Cambrian SCF assemblages, where they can be abundant (Butterfield and Harvey 2012; Harvey et al. 2012; Slater et al. 2017) and morphologically diverse (Wernström et al. 2023), and in some cases are directly comparable to *in situ* remains preserved on Burgess Shale priapulid macrofossils (e.g. *Ottoia* and *Selkirkia*; Smith et al. 2015). In addition to being recoverable *via* hand-picking of gently macerated samples, Cambrian priapulid teeth have also been identified on palynology strew slides, with some having been formerly classified as the acritarch taxon '*Goniomorpha*' (Shan et al. 2023). In light of the emerging priapulid SCF record, an obvious question is whether *Corollasphaeridium* represents a particular morphotype of cuticular structure from a priapulid (or a related type of animal). Indeed, *Corollasphaeridium* co-occurs with known priapulid SCFs in the studied Deadwood and Forteau formations (sometimes in the same sample), and in the *Goniomorpha*-bearing succession at Xiaoyangqiao (Chen et al. 1988). Furthermore, the size range of all specimens of published *Corollasphaeridium*, including those in this study (length 34–179 µm), is broadly encompassed by the size range of priapulid pharyngeal teeth and scalids which range from $<10\,\mu m$ in meiobenthic taxa (e.g. Schmidt-Rhaesa et al. 2013, fig. 2B) to $>500\,\mu m$ in adult macrobenthic individuals (e.g. Smith et al. 2015, fig. 4).

However, although *Corollasphaeridium* appears superficially similar to spinose priapulid cuticular elements, its construction is fundamentally different. Criteria for recognising priapulid teeth among SCFs have been proposed by Smith et al. (2015) and Slater et al. (2018) based on extensive collections from the Saskatchewan Deadwood Formation and elsewhere, and include a robust arch (a thickened ridge supporting the spines) connected to a cuticular pad (a basal extension of cuticle) and associated spur (a thickened strut) which attaches the structure to the body, often with a central prong (lengthened medial spine) and sometimes ancillary denticles extending from the arch. In contrast, *Corollasphaeridium* lacks a bilaterally symmetrical denticulate arch and instead its spinose processes arise coronally from the central cylinder and surround the central process, notably in a radial rather than bilateral arrangement. Modern and fossil priapulid cuticle can also bear a reticulate microtexture representing an imprint of secretory epidermal cells (Wang et al. 2020). This microtexture is commonly preserved on cuticle extending from the base of SCFs of priapulid cuticular structures (e.g. Smith et al. 2015, fig. 9, g, h, k, q), but is not observed in any specimens of *Corollasphaeridium*.

Other cuticular structures in priapulids can be radial in form, notably the flower-like sensory cuticular structures known as flosculi (Moritz and Storch 1971; Storch 1991; Lemberg 1999). Flosculi are known to preserve in phosphatic cuticular plates in palaeoscolecids (extinct priapulid relatives; Harvey et al. 2010). These superficially compare more closely to *Corollasphaeridium* than priapulid pharyngeal teeth and scalids due to their radial symmetry with 'petals' (e.g. Kirsteuer and Rützler 1973, fig 2). However, flosculi lack a central process or raised ridge ornamentation and are significantly smaller, at around 4 µm (e.g. Kirsteuer and Rützler 1973, fig. 2.9), than the known size range of *Corollasphaeridium*.

Aside from comparisons of overall shape and ornamentation, the presence of a discrete basal rim in *Corollasphaeridium* argues against an identity as a cuticular projection from a priapulid, or indeed any other kind of ecdysozoan. *Corollasphaeridium* exhibits a discrete aperture, which is surrounded by a thickened rim (Yin *in* Chen et al. 1988; Martin 1992), and the new Forteau and Deadwood formation specimens confirm that this rim is infolded for a short distance. Such a feature is unknown amongst ecdysozoan projections, including arthropodan spines and setae, which can sometimes show a basal annulation (for example when mounted in a raised 'socket' – see Garm and Watling 2013, fig. 6.3B) but are fundamentally an extension of the surrounding cuticle, rather than a separate articulating part. Furthermore, no known arthropodan setae possess comparable coronal arrangements of spines or thickened longitudinal ridges, despite the broad range of setal morphotypes documented from modern arthropods (e.g. Garm and Watling 2013) and from disarticulated Cambrian SCFs (e.g. Harvey and Butterfield 2022).

4.3.4. Corollasphaeridium *is not a metazoan introvert or lorica*

Rather than being a disarticulated cuticular fragment, it may be that *Corollasphaeridium* represents a larger part of a smaller-bodied organism. Dantes et al. (2024) argued that *C. wilcoxianum* and *Spicaticampaniformis* (their proposed new name for lower Cambrian species, but not retained here) represent the spine-bearing head and introvert regions of metazoan worms (respectively priapulids and acanthocephalans). They employed a geometric-morphometric principal component analysis to explore similarities to modern taxa. However, the study did not identify any homologous structures shared by *Corollasphaeridium* and the comparison worm taxa; for example, there is no indication of a mouth opening in *Corollasphaeridium*. As such it is likely that any anteriorly spinose organism would plot similarly in the morphospace, based on a superficial similarity in outline. In addition, the presence of a discrete basal rim, commonly observed in *Spicaticampaniformis* (Dantes et al. 2024, fig. 1–2, 9–10) is not consistent with the interpretation of these taxa as the tooth-bearing introvert of a metazoan worm, because the introvert is continuous with the rest of the body cuticle. Furthermore, the orientation of spines in *Spicaticampaniformis* and *Corollasphaeridium* is towards the closed apex of the cone/bulb, in contrast to the posteriorly orientated introvert spines in acanthocephalans (e.g. Brázová et al. 2014, fig. 2A–C) and priapulids (Schmidt-Rhaesa et al. 2022).

Instead, the structurally reinforced open collar and cylindrical shape of *Corollasphaeridium* invites comparison with loricate animals, i.e. those with a cuticular casing around the body, which occurs in two phyla of minute animals, the rotifers and loriciferan ecdysozoans. Loricate rotifers are unlike *Corollasphaeridium* in having both anterior and posterior openings, bilateral rather than radial symmetry and apertural processes rather than posterior coronal processes (e.g. Wallace et al. 2015). Closer comparisons exist amongst loriciferans that have a cuticularised lorica into which the anterior body can be withdrawn (Schmidt-Rhaesa et al. 2012). Loriciferan loricae are represented in the Cambrian fossil record as SCFs from the Deadwood Formation of Saskatchewan, assigned to *Eolorica deadwoodensis* (Harvey and Butterfield 2017). In common with some modern loriciferans, *E. deadwoodensis* has a lorica with an approximately circular cross section constructed from a number of longitudinal strips ('plicae'), 20 in this case (Harvey and Butterfield 2017). The aperture of the lorica in *E. deadwoodensis* is hemmed with an invaginated rim bearing 1.5 μm long fine fimbriae on the inner surface (Harvey and Butterfield 2017). *Corollasphaeridium* therefore resembles certain loriciferan loricae in overall form, symmetry, longitudinal lineations (cf. *C. wilcoxianum*) and in having a strengthened aperture. In size, too, there is a close comparison: the loricae of *E. deadwoodensis* range from 120 to 215 μm in length, and modern loriciferans range in body size (head plus lorica) down to *c.* 50 μm in larval forms (Harvey and Butterfield 2017), encompassing the length range of *C. wilcoxianum* (50–179 μm). However, *Corollasphaeridium* exhibits several structural features not seen in loriciferans, notably the prominent coronal processes. Although certain larval stages of extant loriciferans possess articulated posterior projections ('toes') and fine posterodorsal setae with locomotory and sensory functions respectively (Neves et al. 2016), these are unlike the open-based processes of *Corollasphaeridium*. Furthermore, the observed pattern of taphonomic disarticulation in Cambrian loriciferan SCFs, with lorica plicae detaching from one another longitudinally (see Harvey and Butterfield 2017, fig. 1c), is unlike *Corollasphaeridium* which instead maintains a coherent aperture even in damaged specimens.

4.3.5. Corollasphaeridium *is most likely to be a loricate protist*

Outside metazoans, various protists (i.e. eukaryotes excluding multicellular fungi, plants and animals) construct a protective casing around the cell. In some groups such as unilocular (single-chambered) foraminiferans, the casing lacks a substantial aperture (e.g. Mikhalevich and Debenay 2001) but several groups possess a structurally analogous cup-like casing which characterises various protists, where it is likewise termed a lorica or test. Among extant protists, loricate forms are found among testate amoebae (various orders including Amoebozoa, Cercozoa and stramenopiles), choanoflagellates (Opisthokonta: Choanoflagellata) and tintinnids (Ciliophora: Tintinnida).

Choanoflagellates in the family Salpingoecidae produce a variety of organic theca morphologies from cups to flasks (Leadbeater 1977; Dayel et al. 2011) although none compare closely to the complex spinose morphology of *Corollasphaeridium*. Neither is there evidence in *Corollasphaeridium* for the microfibrillar construction that characterises salpingoecidan thecae (cf. Carr et al. 2008, fig. 1). More comparable are certain testate amoebae, which comprise unilocular shell-forming protists (Charman 2001) and are found in a variety of terrestrial and aquatic (occasionally marine) environments (Chardez 1965; Golemansky and Davidova 2019). In modern species, tests can be siliceous, calcareous, agglutinated or organic-walled (proteinaceous) (Mitchell et al. 2008), and the latter are commonly recovered as 'non-pollen palynomorphs' (NPPs) in modern palynological studies (Andrews et al. 2021). The fossil record of testate amoebae begins in the early Neoproterozoic, represented by organic-walled and mineralised vase-shaped microfossils (VSMs; Porter and Knoll 2000). *Corollasphaeridium* shows similarity to proteinaceous testate amoebae tests in its thin-walled, apertured, smooth, cup-like appearance with an internal space suitable for housing a cell. Several testate amoebae, such as *Centropyxis aculeatea* and *Difflugia corona* (Patterson et al. 2002, figs. 7, 8), exhibit radially arranged conical processes arising from the aboral apex of their test (Figure 6a) equivalent in position to those in *Corollasphaeridium*, although they lack a central aboral

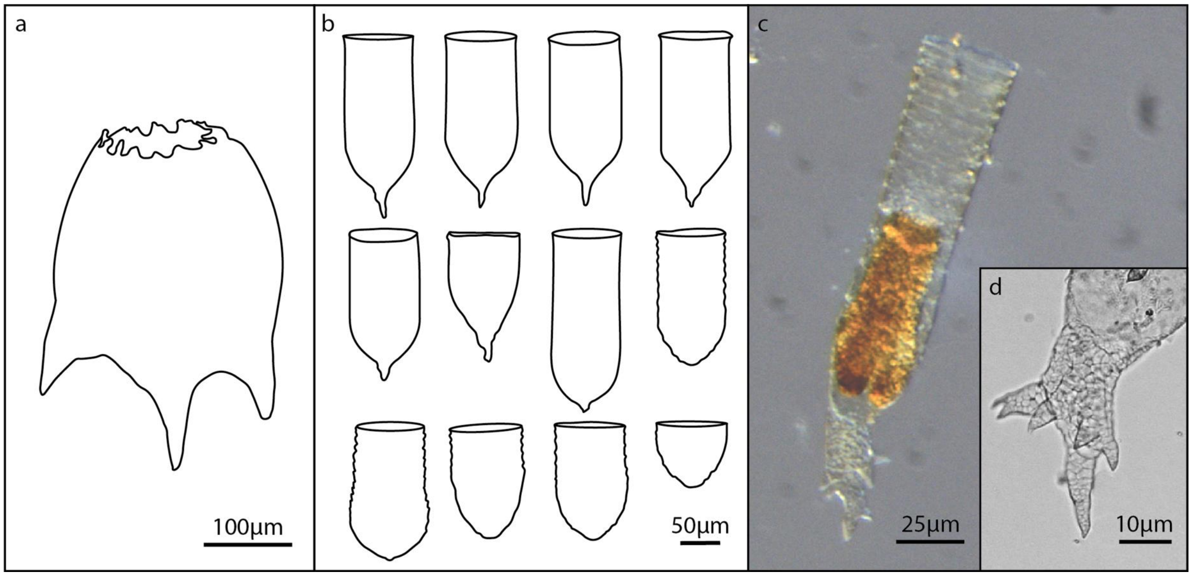


Figure 6. Comparative images of modern loricate protists. (a) spinose test of the testate amoeba *Difflugia corona* redrawn from Silva-Briano et al. (2007, fig. 1, p. 226). (b) Twelve laboratory-cultured loricae from the marine tintinnid *Favella ehrenbergii* demonstrating a large degree of intraspecific variation. Redrawn from Kim et al. (2010, fig. 1–12, p. 462). (c) Lorica of the tintinnid *Rhizodomus tagatzi* with branched aboral horn structure and inhabitant ciliate cell. (d) Details of the branched aboral horn of *Rhizodomus tagatzi*. Images c and d are reproduced with the permission of Alessandro Saccà (Saccà et al. 2012, fig. 2 and 5, p. 220–221).

process. Other species e.g. *Difflugia protaeiformis,* possess a central process but lack coronal processes (Patterson et al. 2002, fig. 8). Overall, modern amoebozoan tests range from 4 to 400 μm (Payne et al. 2012), fully encompassing the 50-179 μm length range of *Corollasphaeridium wilcoxianum*.

One important distinction between amoebozoan tests and *Corollasphaeridium* is the shape and position of the apertural region. Most freshwater amoebozoan tests become constricted towards their aperture (e.g. Andrews et al. 2021, fig. 2), and although several marine species have a trumpet-like flared aperture more similar to that of *Corollasphaeridium* (e.g. *Chardezia caudata*; Golemansky and Davidova 2019, fig. 2) it tends to be angled laterally (Golemansky 2008, fig. 12–13), being adapted for an interstitial lifestyle adhering to sand grains (Golemansky and Davidova 2019).

A further group for comparison among loricate protists is the tintinnids, microscopic planktic ciliates that construct and occupy a vase-shaped lorica (Dolan 2010) composed either of agglutinated particles or secreted hyaline proteinaceous material (Kofoid and Campbell 1929). Certain extant tintinnids share with *Corollasphaeridium* a hollow tapering cylindrical shape with flared aperture and apical extension into a spine, e.g. *Cyttarocylis* (e.g. Williams et al. 1994, fig 1) and *Favella* (e.g. Kim et al. 2010, fig. 27–34). The notably bulbous form of *Corollasphaeridium opimolumum* (Gravestock et al. 2001, plate IV 6: Dantes et al. 2024, fig. 1–2) also finds equivalents among modern tintinnids (e.g. Reid and John 1978, plate I, C–E). Hyaline loricae are highly variable in extant populations because lorica formation is controlled by environmental conditions (Agatha and Strüder-Kypke 2012) and each tintinnid taxon can produce multiple lorica forms over a lifecycle (Laval-Peuto 1981, 1983). This variation in extant forms (Figure 6b) is reminiscent of the wide variation among co-occurring specimens of *Corollasphaeridium* (cf. Figure 2). The combination of a flared apertural opening and invaginated rim exhibited by *Corollasphaeridium* match TEM images of extant tintinnids *Cyttarocylis* sp., showing an inner rim and flaring outer rim on a lorica in cross section (Agatha and Bartel 2022, fig. 1). Some tintinnid taxa show a clear thickening of the lorica towards the aperture e.g. *Xystonella clavata* (Agatha and Bartel 2022, fig. 15). Although previous studies have called into question putative tintinnid fossils where they have an infolded rim (Lipps et al. 2013) detailed studies involving transmission electron microscopy prove an infolded aperture in some extant taxa (Agatha and Bartel 2022, fig. 1). Tintinnid loricae possess a variety of surface ornamentations ranging from folds and spiralled whorls to longitudinal and spiralled thickened ridges, which in some taxa, e.g. *Rhabdonella spiralis* (Agatha and Bartel 2022, fig. 7B), resemble the thickened longitudinal ridges of *C. wilcoxianum*.

A notable distinction between *Corollasphaeridium* and tintinnids is the presence and absence, respectively, of coronal spines. A possible spinose tintinnid represented by a single specimen recovered from Holocene deposits of the Banda Sea, Indonesia, labelled ARABNO-3 and interpreted as a tintinnomorph lorica (Van Waveren 1993, 1994), exhibits a typical tintinnid-type lorica but with five aboral spines (Van Waveren 1994, plate 1, fig. 4). Similarities with *Corollasphaeridium* were noted by Servais et al. (1997). It is unclear whether ARABNO-3 represents a real biological species or a teratological individual since it is known from only a single specimen, or even whether it is a tintinnid. Nevertheless, process-bearing forms do occur among securely identified tintinnids. *Rhizodomus tagatzi* exhibits a ‘branched aboral horn’ where a primary horn on the apex of the test is surrounded by two to five branched horns (Figure 6c; Saccà et al. 2012). Although this morphology differs from the regularly arranged coronal spines in *Corollasphaeridium*, it demonstrates the ability of tintinnids to construct protruding aboral processes.

In addition to these comparisons in outline, *Corollasphaeridium* exhibits comparable size variation to modern tintinnid loricae. Measurements compiled for 42 species of tintinnid by Dolan (2010) indicate a 13 to 120 µm range in lorica oral diameter and 35 to 409 µm range in lorica length. *C. wilcoxianum* (including new Deadwood Formation specimens) ranges from 20 to 100 µm in lorica oral diameter and 50 to 179 µm in lorica length whereas *C. lissum* (Forteau Formation) ranges from 25 to 53 µm in lorica oral diameter and 35 to 92 µm in lorica length. Modern tintinnid size range in lorica oral diameter and lorica length fully encompasses the range exhibited by *Corollasphaeridium*.

Corollasphaeridium satisfies the morphological criteria of Dunthorn et al. (2015) for identifying tintinnids in the fossil record based on lorica morphology, in having a posteriorly tapered cylindrical body, a flared and continuous rim and a wide unconstricted opening. Tintinnid ciliates have a well-accepted fossil record ranging back to the Jurassic (Rust 1885) and they diversified in the Cretaceous (Eicher 1965); possibly they include the calcareous calpionellids (Tappan and Loeblich 1968; Remane 1985; Tappan 1993). By contrast, molecular clock estimates of divergence date (Douzery et al. 2004; Parfrey et al. 2011) and fossil biomarker evidence (Summons et al. 1988) support the origin of ciliates sometime in the Neoproterozoic. The stratigraphically earliest reports of tintinnomorph fossils come from the 1.6 Ga Huangmailing Formation, China (Li and Zhang 2006; Li et al. 2009), but the specimens occur in high-grade metamorphic granulites and leptites (Li and Zhang 2006; Li et al. 2009) and are more parsimoniously interpreted as contaminants or mineral shards (Lipps et al. 2013). Organic flask structures with a rimmed aperture, medial constriction and rounded bowl are also reported from the Tsangan Oloom Formation, Mongolia from 715 to 635 Ma and have been interpreted as tintinnids (Bosak et al. 2011), but their heavily invaginated collar which significantly restricts the test aperture is unknown in modern tintinnids (Lipps et al. 2013). A further candidate Proterozoic record comes from the Weng'an Phosphate Member of the Doushantou Formation, China (Ediacaran) (Li et al. 2007), although an interpretation of these structures as degraded and deformed acritarchs was considered more plausible by Dunthorn et al. (2010). In the Palaeozoic, reported tintinnid-like cup structures ranging from Ordovician to Carboniferous in age have been disputed based either on composition or structure (Lipps et al. 2013).

Because *Corollasphaeridium* is separated in time from the first unambiguous fossil tintinnids by over 300 Myr, any resemblance may well be convergently evolved. Nevertheless, we regard tintinnids as the most useful group for comparison, from among a (polyphyletic) suite of protist groups that produce a cup-like protective casing of one sort or another. Therefore, we support an interpretation of *Corollasphaeridium* as a testate/loricate protist, though not necessarily belonging to any extant group.

4.4. *Autecology of* Corollasphaeridium

Many Palaeozoic acritarchs have been reasonably interpreted to represent phytoplankton cysts unless there is evidence to the contrary (discussed in Servais et al. 1997). Reinterpretation of *Corollasphaeridium* as a likely loricate protist suggests a contrasting, heterotrophic ecology for this particular form, in common with all modern loricate protists. Beyond this, the size and morphology of *Corollasphaeridium* appear consistent with a heterotrophic planktic mode of life. Although the presence of a lorica or test does not imply a particular ecology – modern testate amoebae for instance are generally benthic (Han et al. 2008) – the close resemblance to modern tintinnids is suggestive. Tintinnids are a widely distributed component of the microzooplankton, where they feed on nannoplankton (Dolan 2010). It has been suggested that hyaline organic loricae act as a buoyancy aid for tintinnids (Kofoid 1930), and elongated loricae with a strongly developed posterior spine have been suggested as an adaption to maintain swimming direction (Kofoid and Campbell 1939).

The distinctive coronal spines of *Corollasphaeridium* may also a reflect planktic ecology. Most modern tintinnids lack such processes, and the functional significance of the 'horns' in *Rhizodomus tagatzi* are not known; its neritic, often lagoonal or estuarine habitat is not unique among tintinnids (Saccà et al. 2012; Saccà and Giuffrè 2013). However, long radiating processes in other comparative groups are often inferred to have a role in flotation and/or defence against predators in the planktic realm. In general, the presence of spines increases hydrodynamic resistance to sinking in the water column (Padisák et al. 2003). Spines can be expected to increase drag and enhance prey capture in zooplankton by increasing fluid motion around oral cilia (Emlet and Strathman 1985). Spines can also be developed as a response to predation pressure, including in phytoplankton such as scenedesmacean green algae (e.g. Hessen and Van Donk 1993) and zooplankton such as rotifers (Garza-Mourino et al. 2005), because they increase effective body size. Benthic organisms can also employ spines to deter predators but the radial arrangement in *Corollasphaeridium* is well suited to a three-dimensional planktic setting.

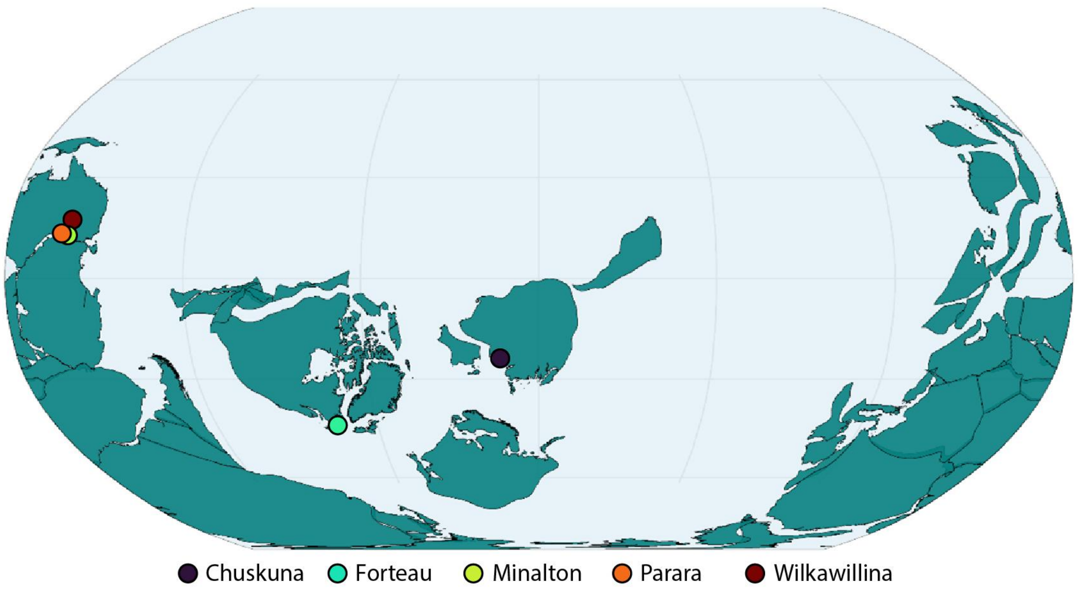
The distribution of processes in *Corollasphaeridium* is most reminiscent of chitinozoans, which offer potential functional comparisons despite their distinct affinities. For spinose chitinozoan taxa, a variety of functions have been suggested including flotation (Wrona 1980) and predation defence (Laufeld 1974). Similarly, despite the lack of precise modern analogues, we suggest that the spinose morphology of *Corollasphaeridium* is likely to reflect adaptations to floating and predation avoidance in a zooplanktic organism. The presence of a lorica in itself suggests a response to predation pressure, as tough outer casings help protect protists from cell-piercing predators (Porter 2011).

4.5. *Palaeoenvironmental and biogeographical distribution of* Corollasphaeridium

Corollasphaeridium occurrences remain rare and species of the genus therefore have a patchy distribution in the fossil record, so far limited to the Cambrian and lowermost Ordovician. However, the new occurrences provide important insights into its palaeoenvironmental and biogeographical range. The type species, *C. wilcoxianum*, occurs in a shallow but markedly offshore palaeo-depositional setting at its type locality at Wilcox Pass, Alberta, Canada coming from the Basal Silty Member of the Survey Peak Formation (Martin 1992; Ji and Barnes 1996). This succession forms part of the carbonate platform belt of the Western Canada Sedimentary Basin, which was deposited hundreds of kilometres from the cratonic shoreline (Slind et al. 1994). The palaeoenvironment in this facies belt was at times very shallow and even emergent, given the epeiric sea setting, although the particular member yielding *Corollasphaeridium* represents a deeper, carbonate-starved environment (Ji and Barnes 1996). This setting contrasts with the new occurrence of *Corollasphaeridium* from the more easterly part of the basin in Saskatchewan (Deadwood Formation), where through much of the middle to late Cambrian deposition was dominated by coarser siliciclastics characterising the 'inner detrital belt' facies (Slind et al. 1994). Here the Deadwood succession records deposition in a wave-dominated setting (Buatois and Mangano 2013), with a diversity of metazoans and other organisms recorded by co-occurring SCFs (Harvey et al. 2012), but a paucity of typical Cambrian marine fossils such as trilobites,

a.

PALAEOMAP reconstruction at 485 Ma



b.

PALAEOMAP reconstruction at 485 Ma

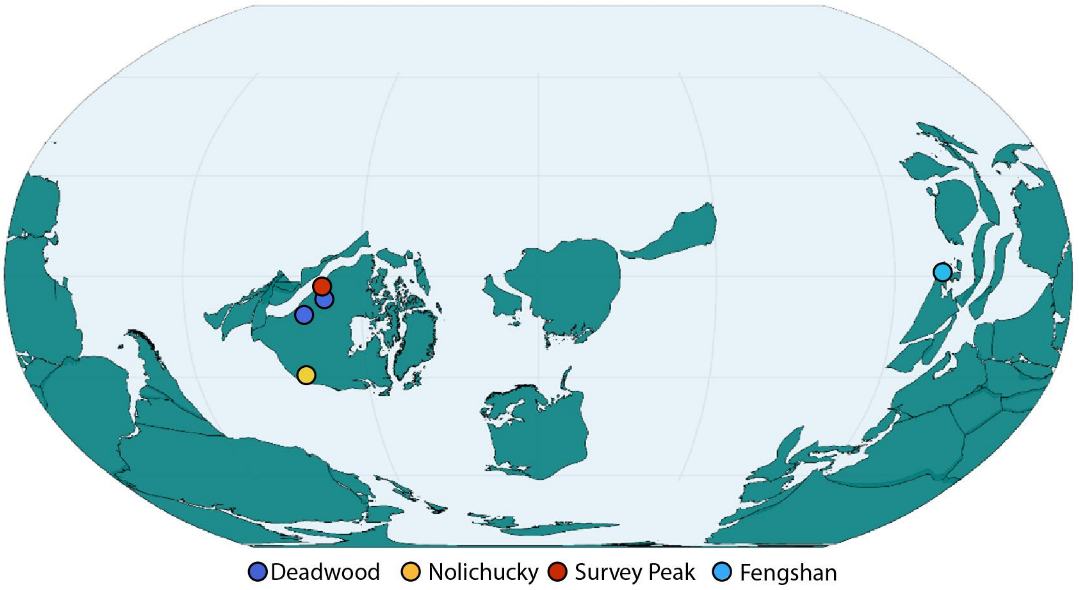


Figure 7. Reconstructions of Cambrian palaeogeography (PALEOMAP, Scotese and Wright 2018) at 524 Ma (a) and 485 Ma (b), showing the distribution of *Corollasphaeridium* bearing formations. (a) Composite plot of early Cambrian localities bearing any *Corollasphaeridium* species. *Corollasphaeridium* is restricted to palaeotropical and palaeosubtropical latitudes in the early Cambrian. (b) *Corollasphaeridium wilcoxianum* is distributed broadly across Laurentia and North China in the middle to late Cambrian but limited to the palaeotropics. Palaeogeographic maps were plotting in R using the rgplates package (Müller et al. 2018; Kocsis and Raja 2023).

echinoderms and hyoliths, implying a somewhat restricted environment. The Deadwood Formation occurrence in South Dakota is also interpreted as representing inner detrital belt facies (Stitt and Straatmann 1997), though the presence of limestones and trilobites suggest a less restricted part of the basin. Overall, the presence of *C. wilcoxianum* from these widely spaced and contrasting settings in the Western Canada Sedimentary Basin is consistent with a planktic ecology and broad ecological tolerance, although a generalist benthic ecology is also possible.

Further afield, the other occurrences of *C. wilcoxianum* exhibit a similar range of environments. In Tennessee, USA, the palaeo-depositional setting is an epicratonic basin, with the Nolichucky Shale Formation at Thorn Hill including ooidal

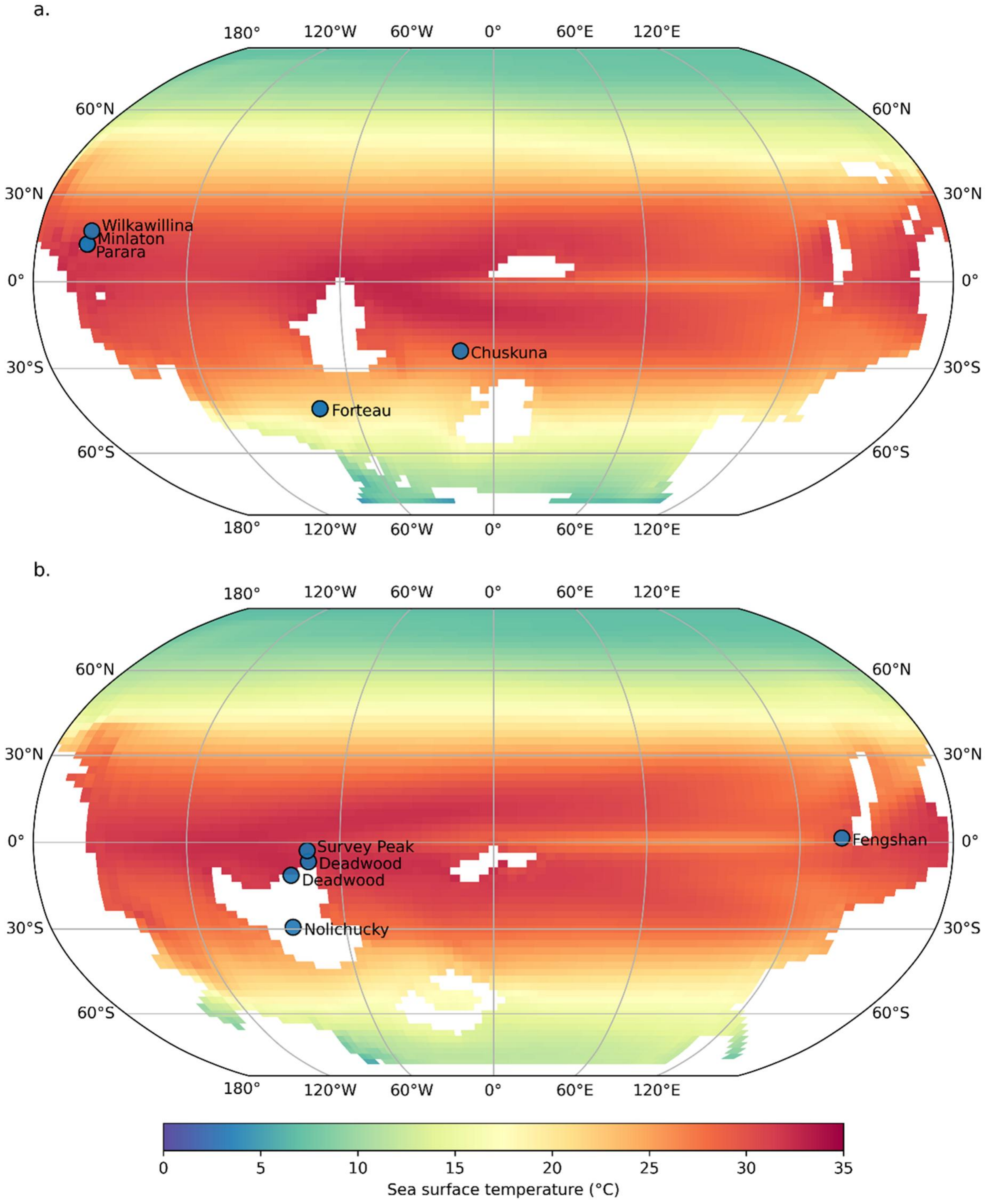


Figure 8. Sea surface temperature estimates for (a) 525 Ma and (b) 485.4 Ma with the palaeo-rotated positions of *Corollasphaeridium* bearing formations. *Corollasphaeridium* is restricted to warm, tropical, surface waters of ~20 to 35 °C in both the early and late Cambrian, according to climate model simulations of sea surface temperature. Climate simulations were performed using the HadCM3L model with pCO_2 values tuned to give similar global mean temperatures to the long-term temperature reconstructions of Scotese et al. (2021). The simulations are identical to the "scotese_08" simulations described in Judd et al. (2024), and are archived as simulation set "tfks" in the Providing Unified Model Access (PUMA) code archive.

grainstones indicating very shallow conditions (Glumac and Walker 1998), whereas in north China, the taxon occurs in a siliciclastic-dominated unit within a trilobite-bearing carbonate platform succession laid down in an epeiric sea, with storm-triggered redistribution of material suggesting a relatively deep-water, downslope position (Wang et al. 2019).

The remaining three species of *Corollasphaeridium* are known from various palaeo-depositional marine settings of the early Cambrian. The stratigraphically lowermost record, from Cambrian Stage 2 of Siberia (Dantes et al. 2024), comes from a mixed carbonate and siliciclastic succession representing upper shoreface to offshore settings; the productive horizons come from a shaley interval in the Chuskuna Formation, associated with wave-rippled sandstone interbeds coarsening upwards into a sandy prodelta deposit (Nagovitsin et al. 2015; Grazhdankin et al. 2020). The South Australian records come from several drillcore intervals in Cambrian Series 2 from the Stansbury and Arrowie basins, from shaley units within mostly carbonate-dominated successions recording shallow to moderately deep-shelf or platform settings (Wilkawilina Limestone; Parara Limestone) and the nearshore, likely somewhat restricted Minlaton Formation (Zang et al. 2007; Jago et al. 2012). In each case, the occurrences will partly reflect the distribution of lithologies best suited to preservation and palynological processing (i.e. mudstones rather than carbonates or sandstones). Notably, the new record from the Forteau Formation (Stage 4 of Newfoundland) provides the opportunity to assess the distribution of *Corollasphaeridium* in a basin with widespread mudstone deposition. From among samples representing nearshore inter-reef muds to offshore deep basin, the productive horizons are limited to comparatively thin (*c.* 40 cm) mudstone units from within a sandstone and ooidal grainstone-dominated part of the succession interpreted as a prograding barrier shoal complex (the Upper Limestone Member; Skovsted et al. 2017). Co-occurring palynomorphs are dominated by sphaeromorphs and clustered cells without the acanthomorphic acritarchs or colonial green algae that occur in the underlying Middle Shale Member (cf. Harvey 2023), which represents open shelf conditions (Skovsted et al. 2017). The presence of trilobite body and trace fossils in the Upper Limestone Member in units that both underlie and overlie the mudstones (Knight et al. 2017) suggest that marine conditions prevailed, but the finely laminated, notably dark mudstones yielding *Corollasphaeridium* but no macrofossils suggest adaptation to a somewhat restricted, potentially ecologically stressed environment between ooid shoals.

The highly localised occurrence of *Corollasphaeridium lissum* in the Forteau Formation contrasts with greater ecological tolerance of *C. wilcoxianum* in the Western Canada Sedimentary Basin, and also with the broader-scale palaeogeographic distributions of *C. wilcoxianum* and the other early Cambrian species (Figure 7). All records of *Corollasphaeridium* are consistent with a sub-tropical (Forteau Formation) and tropical distribution (Figure 7), occupying waters ranging from ∼20 to 35 °C according to climate model simulations of sea surface temperature (Judd et al. 2024) (Figure 8); the lack of substantiated reports from palaeocontinental Baltica, which is well sampled for palynology, and which occupied a mid-latitudinal position, suggests a first-order palaeoclimatic control. A low-latitude distribution for *Corollasphaeridium* was previously noted by Volkova (1993) at a time when confirmed occurrences were limited to Wilcox Pass, Canada, and Xiaoyangqiao, North China. Beyond this, the shared species occurrences in South Australia and Siberia in the lower Cambrian, and the widely distant palaeogeographic occurrences of *C. wilcoxianum* in Laurentia and North China (Figure 7), point to considerable dispersal capabilities in some *Corollasphaeridium* species. Extant tintinnids exhibit distribution patterns ranging from localised in nearshore environments to widely dispersed in the tropical oceanic realm (Dolan and Pierce 2013); the different species of *Corollasphaeridium* in the Cambrian likewise seem to have developed a range of ecological strategies.

5. Conclusions

New specimens from the Forteau, Deadwood and Nolichucky Shale formations of North America have expanded the known temporal, spatial and morphological range of the Cambrian-Ordovician organic-walled microfossil *Corollasphaeridium*, more than doubling the occurrences of *C. wilcoxianum* and extending its known range back to the lower Furongian or upper Miaolingian, and revealing a new lower Cambrian species, *C. lissum* sp. nov. Considered together, a survey of the new and published specimens of *Corollasphaeridium* reveals similarities to various testate and loricate protists, particularly the planktic tintinnid ciliates, which can exhibit similarly thickened apertures and aboral/apical spines. However, *Corollasphaeridium* lacks definitive tintinnid synapomorphies and is separated from unambiguous Jurassic fossil tintinnids by more than 300 million years. Previous studies into putative fossil tintinnids have warned against ‘shoehorning’ Palaeozoic cup-shaped microfossils into group Tintinnida which could obfuscate true evolutionary relationships and risk inappropriate calibration of molecular clocks (Dunthorn et al. 2015). Nevertheless, our analysis supports an affinity for *Corollasphaeridium* amongst loricate heterotrophic protists rather than phytoplankton or metazoans. There is no longer a case for considering *Corollasphaeridium* to be a vesicular acritarch, and we feel there is no value in regarding it as an atypical acritarch. Although it does not yet have a precise taxonomic position to be transferred to, we suggest removing it from Acritarcha, and have amended its diagnosis to remove terminology intended for acritarchs. Whatever its biological affinity, the palaeoenvironmental and palaeogeographical distribution of *Corollasphaeridium* indicates localisation in nearshore habitats in the palaeotropics and subtropics, with growing evidence for wide dispersal within and between palaeocontinents for some species, perhaps aided by an open-water planktic ecology.

6. Systematic palaeontology

Specimens from the Forteau Formation and Deadwood Formation, Saskatchewan are reposited at the Geological Survey of Canada, Ottawa, Ontario, Canada. Specimens from the Nolichucky Shale Formation and Deadwood Formation, South Dakota are reposited in the Centre for Palynology, Department of Animal and Plant Sciences, University of Sheffield, South Yorkshire, UK.

Domain **EUKARYOTA**

Genus ***Corollasphaeridium wilcoxianum*** Martin in Dean and Martin 1982, emend. Martin 1992 emend nov.

Junior synonym. *Spicaticampaniformis* Dantes et al. (2024), fig. 1–15, p.388.

Type species. *Corollasphaeridium wilcoxianum* Martin *in* Dean and Martin 1982, emend. Martin 1992 nov. emend.

Species attributed to the genus.

Corollasphaeridium wilcoxianum Martin *in* Dean and Martin 1982, emend. Martin 1992 nov. emend.

Corollasphaeridium opimolumum Zang *in* Gravestock et al. 2001 (referred to as *Spicaticampaniformis* in Dantes et al. 2024)

Corollasphaeridium aliquolumum Zang *in* Gravestock et al. 2001 (referred to as *Spicaticampaniformis* in Dantes et al. 2024)

Corollasphaeridium lissum sp. nov.

Emended diagnosis. A cylindrical to hourglass shaped lorica, which flares towards an aperture. Aperture markedly thickened and infolded. Distally the apex is adorned with multiple processes that are hollow and open into the lorica.

Remarks. Previous diagnoses by Martin (*in* Dean and Martin 1982) and Yin (*in* Chen et al. 1988) were emended by Martin (1992). Martin's (1992) emendations made at the species (*C. wilcoxianum*) level were also applicable at the genus level as the genus was monospecific at the time of emendation:

> Vesicle originally cylindrical, or almost so. Outline originally elongate in lateral view and circular to slightly polygonal in transverse view. One extremity (apical pole) of vesicle progressively prolonged by a collarette that is always open distally, relatively transparent, lacks an operculum, and has a length approximately equal to that of central body. The other extremity (antapical pole) carries six to ten simple, conical, hollow processes whose internal cavity communicates with that of the vesicle. Five to nine (generally five or six) processes arranged more or less regularly around a more developed central process that prolongs the longitudinal axis of the vesicle and may be as long as the latter. The smallest processes carry two to four longitudinal fibrils; the best developed processes carry four to ten. The most strongly marked of these ridge-like thickenings extend into the vesicle as far as the distal extremity of the collarette, the opening of which is bordered by a thickening of similar type. The principal fibrils of the vesicle, including those on the collarette, may be secondarily anastomosed. The membrane, excluding fibrils, is smooth and apparently single layered.

The language of the original genus diagnosis, and more recent emendations, reflects the use of an interpretive framework of vesicular acritarchs. For example, Yin's (*in* Chen et al. 1988) reference to a lack of operculum refers to the cylinder being permanently open.

The new emended diagnosis herein uses language more appropriate to protists (lorica rather than vesicle), and removes the distinction of 'longitudinal fibrils' (herein referred to as ridges) on the cylinder and processes as this feature is currently restricted to *C. wilcoxianum* (see below).

Corollasphaeridium was first erected for material from the uppermost Cambrian and lowermost Ordovician Wilcox Pass, Alberta, Canada with material assigned to *C. wilcoxianum* Martin (*in* Dean and Martin 1982). The limited available specimens showed a vesicular acanthomorphic acritarch distinguished from co-occurring *Goniosphaeridium* by ornamentation of the processes (Martin *in* Dean and Martin 1982). Discovery of coeval specimens in the Xiaoyangqiao section, north China (Yin *in* Chen et al. 1988) revealed specimens with an elongate cylindrical form, open at one end and with processes at the other, which were described as a separate species, *C. normalisum* Yin 1986. Martin (1992) synonymised *C. normalisum* with *C. wilcoxianum* and emended the diagnosis of the species (and by implication, the monotypic genus). Two species were also identified from the lower Cambrian of Australia and added to the genus: *C. opimolumum* and *C. aliquolumum* (Gravestock et al. 2001).

Dantes et al. (2024) published new lower Cambrian specimens from Siberia which they identified to be congeneric with Australian lower Cambrian species described as *Corollasphaeridium opimolumum* and *C. aliquolumum* (Gravestock et al. 2001). They assigned all of these taxa to their new genus *Spicaticampaniformis* and suggested that the absence of a central apical outgrowth (spine), lack of longitudinal ridge ornamentation and smaller spines distinguished *Spicaticampaniformis* from *Corollasphaeridium*. We note that the open, bulb-cone shaped form, discrete basal rim and multi-spinose ornamentation of *Spicaticampaniformis* are shared with other species of *Corollasphaeridium*. However, we note that *C. lissum* sp. nov. (see below) shares the absence of a longitudinal ornamentation with species moved to *Spicaticampaniformis,* whereas its radial arrangement of processes and central apical process are shared with *C. wilcoxianum*. Because *C. lissum* sp. nov. represents a morphological intermediate between early Cambrian forms and later Cambrian *C. wilcoxianum*, as well as lying stratigraphically between the two sets of occurrences, it weakens support for a genus-level distinction. We therefore consider *Spicaticampaniformis* to be a junior synonym of *Corollasphaeridium.*

Corollasphaeridium wilcoxianum. Martin *in* Dean and Martin 1982, emend. Martin 1992 nov. emend.

Figure 4a–j

Synonymy.

1982 *Corollasphaeridium wilcoxianum* gen. et sp. nov. Martin *in* Dean and Martin 1982 (p. 136, Pl. 1, figs. 15, 16.)

1986 *Corollasphaeridium normalisum* sp. nov. Yin *in* Chen et al. 1988 (p. 337, Pl. 88, figs. 1, 2, 4, 6, 9, 15; Textfig. 123.)

1986 *Corollasphaeridium wilcoxianum* Yin *in* Chen et al. 1988 (p. 338, Pl. 88, figs. 12, 14.)

1992 *Corollasphaeridium wilcoxianum* Martin 1992 (p. 25, Pl. 6, figs. 2–4, 8, 10–16.)

2019 *Corollasphaeridium wilcoxianum* Wang et al. 2019 (fig. 8, a–c)

Original diagnosis. Martin *in* Dean and Martin 1982, emend. Martin 1992. As for the genus and reproduced above.

Emended diagnosis. *Corollasphaeridium* in which the lorica exhibits an ornamentation of thickened longitudinal ridges which extend from the collar to the tip of the processes. Branching of the ridges to form a polygonal network at the base of the processes. Strongly developed central process surrounded by elongate radially arranged processes which are typically smaller than the central process.

Description. The most complete specimens in our new collections preserve a narrow cylindrical body with a pronounced trumpet-like flared shape towards the aperture (Figure 4b and e). The aperture is rimmed with a thickened collar (Figure 4a, e and h). The edge of the rim is infolded into the cylinder by 2.0 to 4.7 µm ($n = 8$). An enlarged spine projects from the apex of the cylinder surrounded by 4 to 9 regularly arranged smaller spines. Thickened ridges ornament the spines and branch to form a polygonal network at the base of the processes, then continue onto the cylinder down to the collar (Figure 4e). The cylinder wall is relatively thin whereas the spines appear darker and thickened.

New material. Fourteen specimens from the Deadwood Formation (five from Saskatchewan and nine from South Dakota) (Figure 4). Specimens from Saskatchewan come from drillcore sample RW13-4-70 from Ceepee Reward (well site 101/4-28-38-24W3, licence number: 58E063), core number 13, box number 4, 70 cm from boxed core top (5401.3 ft/1646.3 m), constrained to the Drumian to Paibian interval (upper middle to lower upper Cambrian). Specimens from the Deadwood Formation of South Dakota come from outcrop sample BP09-DW4 from the section above Deadwood town, 44.1 m below the base of the sandstone marker, likely in the *Taenicephalus* trilobite Zone, Jiangshanian Stage of the Furongian Series. One specimen from the Upper Shale Member of the Nolichucky Shale Formation, Tennessee, USA (sample 08BP-33⅔, 176.70 m stratigraphically above the base of the formation as exposed at Thorn Hill), in an interval containing the Miaolingian to Furongian boundary (see section Geological setting, materials and methods for full locality details).

Dimensions (minimum (mean) maximum). In specimens complete enough to be measured:

Overall aperture diameter of 7 specimens: 21 (54.6) 101 µm (Standard deviation: 22.8).

Overall length of 4 specimens: 50 (128.6) 179 µm (Standard deviation: 53.1).

Remarks. Material from the Deadwood and Nolichucky Shale formations reveals further morphological details of the characteristic collar structure of *Corollasphaeridium*. New specimens show that the collar structure is infolded a short distance (Figure 3a, e and g). The longitudinal ridge ornament continues onto the infolded collar.

Corollasphaeridium lissum sp. nov.

Figure 3a–am and w.

Holotype. R432-7_oc_p2_C35-3, GSC144337, Forteau Formation, Newfoundland. Figure 2w.

Diagnosis. A species of *Corollasphaeridium* with a smooth lorica wall. Radially arranged short triangular processes (<¼ of the total length) with a broad base surrounding a larger central process.

Description. The most complete specimens consist of a cylindrical to hourglass body which flares towards its aperture. The aperture is markedly thickened in well preserved specimens and may be invaginated inside the cylinder by a distance of 0.6 to 4.9 µm (Figure 3a, e, and u–x). The apex is adorned by a central process which is often the largest and widest process. The central process is surrounded by 5–12, coronally arranged, additional processes. Wall thickness appears variable as some specimens are a dark brown colour whilst others from the same sample are translucent yellow.

New material. Seventy-seven specimens from the lower Cambrian (Stage 4) Forteau Formation (Upper Limestone Member), Newfoundland, Canada (31 from R432-6 and 46 from R423-7) (Figure 3). *Corollasphaeridium*-bearing samples were collected from the middle of a 40 cm thick laminated black mudstone unit located around 1 m above the base of a roadside section (Knight et al. 2017, fig. 8) (R432-6: 51°00.49′ N 56°36.05′ W) and a 50 cm thick laminated black mudstone unit, 4 m from the base of the section in a small quarry (Knight et al. 2017, fig. 8) (R432-7: 51°00.59′ N 56°35.13′ W) along Route 432 between Plum Point and Roddickton, Great Northern Peninsula, Newfoundland (Figure 1).

Dimensions (minimum (mean) maximum). In specimens complete enough to be measured:

Overall aperture diameter of 13 specimens: 21 (37.9) 53 µm (Standard deviation: 8.2). Overall length of 21 specimens: 34 (62.1) 92 µm (Standard deviation: 16.2).

Remarks. *Corollasphaeridium lissum* is distinguished from *C. wilcoxianum* by a lack of ornamentation of longitudinal ridges and by its shorter, stout processes, and from *C. opimolumum* and *C. aliquolumum* by the regular arrangement of processes around a central process. The processes in *C. lissum* are proportionately shorter and broader than those of *C. aliquolumum*. The lorica shape of *C. opimolumum* is markedly expanded in the apical portion in comparison to *C. lissum*. *C. normalisum* of Yin (*in* Chen et al. 1988) is recognised as a junior synonym of *C. wilcoxianum* preserved in lateral view (see Martin 1992).

A thickened collar structure is a significant feature in the best-preserved specimens of *C. lissum* sp. nov. (Figure 3u–x). The collar is markedly thickened in relation to the cylindrical body and folded in a short distance inside the cavity, a character shared with *C. wilcoxianum*. The hourglass proportions of the body are also distinctive in the new specimens (Figure 3c–d and t–z) and differ from the generally cylindrical to flaring shape of *C. wilcoxianum*.

Corollasphaeridium lissum in the Forteau Formation exhibits high interspecific variability. This is particularly significant when considering its relatively limited stratigraphic and geographic distribution. Some specimens are short and wide whilst others are elongate. Aspect ratio (width/length) in specimens complete enough for measurements to be made ranges from 0.37 to 1.07.

Derivation of name. Derived from the Latin *lisso* for smooth, alluding to its smooth lorica surface and lack of ornamentation and the gender-neutral suffix *um*.

Acknowledgements

We thank David Bodman of MB Stratigraphy for palynological preparation of the R432-7 Forteau samples. We are grateful to Fran Haidl, Gavin Jensen and Melinda Yurkowski at the Subsurface Geological Laboratory, Regina, Canada for facilitating access to the Deadwood drillcore from Saskatchewan and to Nicholas Butterfield (University of Cambridge) for granting permission to publish material extracted from Saskatchewan samples obtained by him as part of NERC standard grant NE/H009914/1. Parks Canada gave permission to examine sections and collect samples in Gros Morne National Park, Newfoundland (permit number GMNP-2023-45613). We also thank Nathalie Djan-Chékar and Doug Boyce of The Rooms, St John's, Newfoundland, Canada for access to additional material from the Forteau Formation. BP would like to thank John Beck, Elizabeth La Padula, and Noel Schaff, for their invaluable help in the field, and Charles Wellman and Paul Strother for their unending support and encouragement.

Author contributions statement

Fieldwork and sample collection: Tom Green, Tom Harvey, Brain Pedder, Pascal Olschewski. Palynological sample processing: Brian Pedder. Gentle acid maceration for SCFs: Tom Green and Tom Harvey. Microscopy: Tom Green, Tom Harvey, Brian Pedder. Analysis: Tom Green. Systematic palaeontology: Tom Green, Mark Williams and Thomas Servais. Palaeobiogeographic analysis: Tom Green and Thomas Wong Hearing. Climate modelling: Dan Lunt and Thomas Wong Hearing. Manuscript preparation: Tom Green supported by Tom Harvey, Mark Williams and Thomas Servais.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Ethics statement

Microfossil specimens were obtained from field localities outside of National Parks and other areas of special regulation. Samples processed for microfossils from Gros Morne National Park, Newfoundland were collected under Parks Canada permit number GMNP-2023-45613. Specimens from the Forteau Formation and Deadwood Formation, Saskatchewan are reposited at the Geological Survey of Canada, Ottawa, Ontario, Canada. Specimens from the Nolichucky Shale Formation and Deadwood Formation, South Dakota are reposited in the Centre for Palynology, Department of Animal and Plant Sciences, University of Sheffield, South Yorkshire, UK under the title 'Pedder 2012'.

Funding

This work was supported by the Natural Environment Research Council (NERC) CENTA DTP Studentship Grant NE/S007350/1 to T. Green and NERC Open CASE award NE/F013833/1 to B. Pedder. Sampling of the Deadwood Formation in Saskatchewan was supported by NERC Standard Grant NE/H009914/1 to N. Butterfield and T. Harvey. The work on palaeogeographical and climate reconstructions is supported by The Leverhulme Trust grant RPG-2022-233 to M. Williams and T. Harvey.

ORCID

Tom Green http://orcid.org/0009-0002-4019-6338
Brian E. Pedder http://orcid.org/0009-0008-6021-2685
Mark Williams http://orcid.org/0000-0002-7987-6069
Thomas W. Wong Hearing http://orcid.org/0000-0002-6770-6433
Pascal Olschewski http://orcid.org/0000-0002-2472-7138
Daniel J. Lunt http://orcid.org/0000-0003-3585-6928
Thomas Servais http://orcid.org/0000-0002-4089-7874
Thomas H. P. Harvey http://orcid.org/0000-0002-2717-7004

Data availability statement

All data are published in the paper.

References

Achab A, Asselin E, Desrochers A, Riva JF. 2013. The end-Ordovician chitinozoan zones of Anticosti Island, Québec: definition and stratigraphic position. Review of Palaeobotany and Palynology. 198:92–109.

Agatha S, Bartel H. 2022. A comparative ultrastructural study of tintinnid loricae (Alveolata, Ciliophora, Spirotricha) and a hypothesis on their evolution. Journal of Eukaryotic Microbiology. 69(2):e12877.

Agatha S, Strüder-Kypke MC. 2012. Systematics and evolution of tintinnid ciliates. In: Dolan JR, David JSM, Agatha S, Wayne DC, Diane KS, editors. The biology and ecology of tintinnid ciliates: models for marine plankton. Oxford (UK): Wiley; p. 42–84.

Andrews LO, Payne RJ, Swindles GT. 2021. Testate amoebae as non-pollen palynomorphs in pollen slides: usefulness and application in palaeoenvironmental reconstruction. Geological Society, London, Special Publications. 511:1–16.

Bosak T, Macdonald F, Lahr D, Matys E. 2011. Putative Cryogenian ciliates from Mongolia. Geology. 39(12):1123–1126.

Brázová T, Poddubnaya LG, Miss NR, Hanzelová V. 2014. Ultrastructure and chemical composition of the proboscis hooks of *Acanthocephalus lucii* (Müller, 1776) (Acanthocephala: Palaeacanthocephala) using X-ray elemental analysis. Folia Parasitologica. 61(6):549–557.

Breuer P, Al-Hajri S, Le Hérissé A, Paris F, Steemans P, Verniers J, Wellman CH. 2017. A distinctive marginal marine palynological assemblage from the Přídolí of northwestern Saudi Arabia. Revue de Micropaleontologie. 60(3):371–402.

Buatois L, Mangano MG. 2013. Paleoenvironmental variability of the lower Paleozoic Earlie and Deadwood formations in subsurface Saskatchewan: a preliminary bassessment. In: Summary of Investigations 2013, Saskatchewan Geological Survey, Saskatchewan Ministry of the Economy, Miscellaneous, Rep 2013-4.1 A-3, Vol. 1; p. 1–8.

Butterfield NJ. 1997. Plankton ecology and the Proterozoic-Phanerozoic transition. Paleobiology. 23(2):247–262.

Butterfield NJ, Harvey THP. 2012. Small carbonaceous fossils (SCFs): a new measure of early Paleozoic paleobiology. Geology. 40(1):71–74.

Byerly DW, Walker KR, Diehl WW, Ghazizadeh DM, Johnson RE, Lutz CT, Schoner AAK. 1986. Thorn Hill: a classic Paleozoic stratigraphic section in Tennessee. In: Neathery TL, editor. Centennial field guide volume 6: southeastern section. Boulder (CO): Geological Society of America; p. 131–136.

Carr M, Leadbeater BS, Hassan R, Nelson M, Baldauf SL. 2008. Molecular phylogeny of choanoflagellates, the sister group to Metazoa. Proceedings of the National Academy of Sciences of the United States of America. 105(43):16641–16646.

Chardez D. 1965. Ecologie generale des thecamoebiens [General ecology of thecamoebians]. Bulletin de l'Institut Agronomique et des Stations de Recherche de Gembloux. 33:307–341. French.

Charman DJ. 2001. Biostratigraphic and palaeoenvironmental applications of testate amoebae. Quaternary Science Reviews. 20(16-17): 1753–1764.

Chen JY, Qian YY, Zhang JM, Lin YK, Yin LM, Wang ZH, Wang ZH, Yang JD, Wang YX. 1988. The recommended Cambrian–Ordovician global Boundary stratotype of the Xiaoyangqiao section (Dayangcha, Jilin Province), China. Geological Magazine. 125(4):415–444.

Colbath GK, Grenfell HR. 1995. Review of biological affinities of Paleozoic acid-resistant, organic-walled eukaryotic algal microfossils (including "acritarchs"). Review of Palaeobotany and Palynology. 86(3-4):287–314.

Cramer FH, Díez MdCR. 1977. Late Arenigian (Ordovician) acritarchs from Cis-Saharan Morocco. Micropaleontology. 23(3):339–360.

Dale B. 2023. Paleontological evidence for dinoflagellates and ciliates as early eukaryotes. Journal of Marine Science and Engineering. 11(3):533.

Dantes OV, Nagovitsin KE, Raevskaya EG. 2024. Cambrian microfossils of the genus *Corollasphaeridium*: new interpretation and revision of systematics. Paleontological Journal. 58(4):385–397.

Darton NH, Paige S. 1925. Description of the Central Black Hills. US Geological Survey Geologic Atlas, Central Black Hills Folio No. 219.

Dayel MJ, Alegado RA, Fairclough SR, Levin TC, Nichols SA, McDonald K, King N. 2011. Cell differentiation and morphogenesis in the colony-forming choanoflagellate *Salpingoeca rosetta*. Developmental Biology. 357(1):73–82.

Dean WT, Martin F. 1982. The sequence of trilobite faunas and acritarch microfloras at the Cambrian–Ordovician boundary, Wilcox Pass, Alberta, Canada. In: Bassett MG, Dean WT, editors. The Cambrian–Ordovician boundary: sections, fossil distributions, and correlations. Geological Series 3. Cardiff (UK): National Museum of Wales; p. 131–140.

Dixon J. 2008. Stratigraphy and facies of Cambrian to Lower Ordovician strata in Saskatchewan. Bulletin of Canadian Petroleum Geology. 56(2):93–117.

Dolan J. 2010. Morphology and ecology in tintinnid ciliates of the marine plankton: correlates of lorica dimensions. Acta Protozoologica. 49: 235–244.

Dolan JR, Pierce RW. 2013. Diversity and distributions of tintinnids. In: Dolan JR, Montagnes DJS, Agatha S, Coats DW, Stoecker DK, editors. The biology and ecology of tintinnid ciliates, models for marine plankton. Oxford (UK): Wiley; p. 214–243.

Douzery EJ, Snell EA, Bapteste E, Delsuc F, Philippe H. 2004. The timing of eukaryotic evolution: does a relaxed molecular clock reconcile proteins and fossils? Proceedings of the National Academy of Sciences of the United States of America. 101(43):15386–15391.

Downie C. 1973. Observations on the nature of the acritarchs. Palaeontology. 16(2):239–259.

Dunthorn M, Lipps JH, Dolan JR, Saab MA-A, Aescht E, Bachy C, de Cao MSB, Berger H, Bourland WA, Choi JK, et al. 2015. Ciliates—protists with complex morphologies and ambiguous early fossil record. Marine Micropaleontology. 119:1–6.

Dunthorn M, Lipps JH, Stoeck T. 2010. Reassessment of the putative ciliate fossils *Eotintinnopsis*, *Wujiangella*, and *Yonyangella* from the Neoproterozoic Doushantuo Formation in China. Acta Protozoologica. 49(2):139–144.

Eicher DL. 1965. Cretaceous tintinnids from the western interior of the United States. Micropaleontology. 11(4):449–456.

Emlet RB, Strathman RR. 1985. Gravity, drag, and feeding currents of small zooplankton. Science. 228(4702):1016–1017.

Evitt WR. 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres and acritarchs. II. Proceedings of the National Academy of Sciences of the United States of America. 49(3):298–302.

Fatka O, Konzalová OFM. 1995. Microfossils of the Paseky Shale (Lower Cambrian, Czech Republic). Journal of the Czech Geological Society. 40(4):55–66.

Garm A, Watling L. 2013. The crustacean integument: setae, setules, and other ornamentation. Functional Morphology Diversity. 1:167–198.

Garza-Mourino G, Silva-Briano M, Nandini S, Sarma SSS, Castellanos-Paez ME. 2005. Morphological and morphometrical variations of selected rotifer species in response to predation: a seasonal study of selected brachionid species from Lake Xochimilco (Mexico). Hydrobiologia. 546:169–179.

Geyer G. 2020. A comprehensive Cambrian correlation chart. Episodes. 42:321–332.

Ghavidel-Syooki M, Vecoli M. 2008. Palynostratigraphy of Middle Cambrian to lowermost Ordovician stratal sequences in the High Zagros Mountains, southern Iran: regional stratigraphic implications, and palaeobiogeographic significance. Review of Palaeobotany and Palynology. 150(1-4):97–114.

Glumac B, Walker KR. 1998. A Late Cambrian positive carbon-isotope excursion in the Southern Appalachians; relation to biostratigraphy, sequence stratigraphy, environments of deposition, and diagenesis. Journal of Sedimentary Research. 68(6):1212–1222.

Golemansky V. 2008. Origin, phylogenetic relations, and adaptations of the marine interstitial testate ameobae (Rhizopoda: Lobosea, Filosea, and Granuloreticulsea). Advances in Arachnology and Developmental Biology. 12:87–100.

Golemansky V, Davidova R. 2019. Biodiversity, distribution and ecology of testate amoebae (Arcellinida and Euglyphida) from the Bulgarian Black Sea Coast and the related brackish lakes. A synthesis. Acta Scientifica Naturalis. 6(2):14–39.

Gravestock DI, Alexander EM, Demidenko YE, Esakova NB, Holmer LE, Jago JB, Lin TR, Melnikova N, Parkhaev PY, Rozanov AY, et al. 2001. The Cambrian biostratigraphy of the Stansbury Basin, South Australia. Transactions of the Paleontological Insitute Russian Academy of Sciences. 282:1–341.

Gray J, Boucot AJ. 1989. Is *Moyeria* a euglenoid? Lethaia. 22(4):447–456.

Grazhdankin DV, Marusin VV, Izokh OP, Karlova GA, Kochnev BB, Markov GE, Nagovitsin KE, Sarsembaev Z, Peek S, Cui H, et al. 2020. Quo vadis, Tommotian? Geological Magazine. 157(1):22–34.

Gurdebeke P, Mertens KN, Takano Y, Yamaguchi A, Bogus K, Dunthorn M, Matsuoka K, Vrielinck H, Louwye S. 2018. The affiliation of *Hexasterias problematica* and *Halodinium verrucatum* sp. nov. to ciliate cysts based on molecular phylogeny and cyst wall composition. European Journal of Protistology. 66:115–135.

Guy-Ohlson D. 1996. Green and blue-green algae, 7B-Prasinophycean algae. In: Jansonius J, McGregor DC, editors. Palynology: principles and applications. Vol. 1, Chapter 7. Salt Lake City (UT): American Association of Stratigraphic Palynologists Foundation; p. 181–189.

Han BP, Wang T, Lin QQ, Dumont HJ. 2008. Carnivory and active hunting by the planktonic testate amoeba *Difflugia tuberspinifera*. Hydrobiologia. 596(1):197–201.

Handkamer NM, Ichaso A, Pratt BR, Mángano MG, Buatois LA. 2023. Systematics and biostratigraphy of a new trilobite fauna collected from the subsurface Earlie Formation (Wuliuan Stage, Miaolingian Series, Cambrian) in southwestern Saskatchewan. Canadian Journal of Earth Sciences. 60(9):1307–1326.

Harvey THP. 2010. Carbonaceous preservation of Cambrian hexactinellid sponge spicules. Biology Letters. 6(6):834–837.

Harvey THP. 2023. Colonial green algae in the Cambrian plankton. Proceedings. Biological Sciences. 290(2009):20231882.

Harvey THP, Butterfield NJ. 2008. Sophisticated particle-feeding in a large Early Cambrian crustacean. Nature. 452(7189):868–871.

Harvey THP, Butterfield NJ. 2017. Exceptionally preserved Cambrian loriciferans and the early animal invasion of the meiobenthos. Nature Ecology & Evolution. 1(3):22.

Harvey THP, Butterfield NJ. 2022. A new species of early Cambrian arthropod reconstructed from exceptionally preserved mandibles and associated small carbonaceous fossils (SCFs). Papers in Palaeontology. 8(4):e1458.

Harvey THP, Dong X, Donoghue PC. 2010. Are palaeoscolecids ancestral ecdysozoans? Evolution & Development. 12(2):177–200.

Harvey THP, Pedder BE. 2013. Copepod mandible palynomorphs from the Nolichucky Shale (Cambrian, Tennessee): implications for the taphonomy and recovery of small carbonaceous fossils. Palaios. 28(5): 278–284.

Harvey THP, Vélez MI, Butterfield NJ. 2012. Small carbonaceous fossils from the Earlie and Deadwood formations (middle Cambrian to lower Ordovician) of southern Saskatchewan. Summary of Investigations 2012, Volume 1, Saskatchewan Geological Survey, Saskatchewan Ministry of the Economy, Miscellaneous, Rep. 2012-4.1, Paper A-1. 1:8.

Hein FJ, Nowlan GS. 1998. Regional sedimentology, conodont biostratigraphy and correlation of Middle Cambrian-Lower Ordovician(?) strata of the "Finnegan" and Deadwood formations, Alberta subsurface, Western Canada Sedimentary Basin. Bulletin of Canadian Petroleum Geology. 46:166–188.

Hessen DO, Van Donk E. 1993. Morphological changes in *Scenedesmus* induced by substances released from *Daphnia*. Archiv für Hydrobiologie. 127(2):129–140.

Jago JB, Gehling JG, Paterson JR, Brock GA, Zang W. 2012. Cambrian stratigraphy and biostratigraphy of the Flinders Ranges and the north coast of Kangaroo Island, South Australia. Episodes. 35(1):247–255.

Ji Z, Barnes CR. 1996. Uppermost Cambrian and lower Ordovician conodont biostratigraphy of the survey peak formation (Ibexian/Tremadoc), Wilcox Pass, Alberta, Canada. Journal of Paleontology. 70(5):871–890.

Judd EJ, Tierney JE, Lunt DJ, Montañez IP, Huber BT, Wing SL, Valdes PJ. 2024. A 485-million-year history of Earth's surface temperature. Science. 385(6715):eadk3705.

Kim SY, Yang EJ, Gong JUN, Choi JK. 2010. Redescription of *Favella ehrenbergii* (Claparède and Lachmann, 1858) Jörgensen, 1924 (Ciliophora: Choreotrichia), with phylogenetic analyses based on small subunit rRNA gene sequences. The Journal of Eukaryotic Microbiology. 57(6):460–467.

Kirsteuer E, Rützler K. 1973. Additional notes on *Tubiluchus corallicola* (Priapulida), based on scanning electron microscope observations. Marine Biology. 20(1):78–87.

Knight I, Boyce WD, Skovsted CB, Balthasar U. 2017. The Lower Cambrian Forteau Formation, southern Labrador and Great Northern Peninsula, western Newfoundland: lithostratigraphy, trilobites, and depositional setting. Government of Newfoundland and Labrador, Department of Natural Resources, Geological Survey, St. John's (Canada). Occasional Paper 1; p. 1–72.

Kocsis AT, Raja NB. 2023. rgplates: R interface for the GPlates Web Service and desktop application. Ver. 0.5.0. [accessed 2024 Jan 01].

Kofoid CA. 1930. Factors in the evolution of the Tintinnoinea. In: Contributions to marine biology, lectures and symposia given at the Hopkins Marine Station, December 20–21, 1929, at the mid-winter meeting of the Western Society of Naturalists. Stanford (CA): Stanford University Press; p. 1–39.

Kofoid CA, Campbell AS. 1929. A conspectus of the marine and freshwater Ciliata belonging to the suborder Tintinnoinea, with descriptions of new species principally from the Agassiz expedition to the Eastern Tropical Pacific 1904–1905. University of California Publications in Zoology. 34:1–403.

Kofoid CA, Campbell AS. 1939. The Ciliata: the Tintinnoinea. Bulletin of the Museum of Comparative Zoology. 84:1–473.

Laufeld S. 1974. Silurian Chitinozoa from Gotland. Foss Strata. 5:1–130.

Laval-Peuto M. 1981. Construction of the lorica in Ciliata Tintinnina. In vivo study of *Favella ehrenbergii*: variability of the phenotypes during the cycle, biology, statistics, biometry. Protistologica. 17:249–272.

Laval-Peuto M. 1983. Sexual reproduction in *Favella ehrenbergii* (Ciliophora, Tintinnina) taxonomical implications. Protistologica. 19(4): 503–512.

Le Herisse A, Masure E, Javaux EJ, Marshall CP. 2012. The end of a myth: *Arpylorus antiquus* Paleozoic dinoflagellate cyst. PALAIOS. 27(6):414–423.

Leadbeater BS. 1977. Observations on the life-history and ultrastructure of the marine choanoflagellate *Choanoeca perplexa* Ellis. Journal of the Marine Biological Association of the United Kingdom. 57(2):285–301.

Lemburg C. 1999. Ultrastrukturelle untersuchungen an den larven von *Halicryptus spinulosus* und *Priapulus caudatus*. Hypothesen zur phylogenie der Priapulida und deren bedeutung für die evolution der nemathelminthes. [Ultrastructural studies on the larvae of *Halicryptus spinulosus* and *Priapulus caudatus*. Hypotheses on the phylogeny of the Priapulida and their significance for the evolution of the Nemathelminthes] cuvillier. Göttingen, German; p. 393.

Li CW, Chen JY, Lipps JH, Gao F, Chi HM, Wu HJ. 2007. Ciliated protozoans from the Precambrian Doushantuo Formation, Wengen, South China. Geological Society Special Publication. 286:151–156.

Li YX, Zhang SX. 2006. New material of microfossils from Middle Proterozoic in Hubei Province. Acta Palaeontogica Sinica. 45:102–107.

Li YX, Zhang SX, Zhang J. 2009. Mesoproterozoic Calymmian tintinnids from central China. Open Paleontology Journal. 2:10–13.

Liang Y, Bernardo J, Goldman D, Nõlvak J, Tang P, Wang W, Hints O. 2019. Morphological variation suggests that chitinozoans may be fossils of individual microorganisms rather than metazoan eggs. Proceedings. Biological Sciences. 286(1908):20191270.

Lipps JH, Stoeck T, Dunthorn M. 2013. Fossil tintinnids. In: Dolan JR, David JSM, Agatha S, Wayne DC, Diane KS, editors. The biology and ecology of tintinnid ciliates: models for marine plankton. Oxford (UK): John Wiley & Sons; p. 186–197.

Manzano EG, Monnet C, Mertens KN, Servais T. 2025. Netromorph acritarchs and related morphotypes in the middle Paleozoic: a proposal for classification. Palynology. doi:10.1080/01916122.2024.2446470

Martin F. 1992. The uppermost Cambrian and lower Ordovician acritarchs and lower Ordovician chitinozoans from Wilcox Pass, Alberta. Geological Survey of Canada Bulletin. 420:1–65.

Martin F. 1993. Acritarchs: a review. Biological Reviews. 68:475–538.

Martin RE, Servais T. 2020. Did the evolution of the phytoplankton fuel the diversification of the marine biosphere? Lethaia. 53(1):5–31.

Mikhalevich V, Debenay JP. 2001. The main morphological trends in the development of the foraminiferal aperture and their taxonomic significance. Journal of Micropalaeontology. 20(1):13–28.

Miller MA. 1996. Chitinozoa. In: Jansonius J, McGregor DC, editors. Palynology: principles and applications. Salt Lake City (UT): American Association of Stratigraphic Palynologists Foundation; p. 307–337.

Mitchell EA, Payne RJ, Lamentowicz M. 2008. Potential implications of differential preservation of testate amoeba shells for paleoenvironmental reconstruction in peatlands. Journal of Paleolimnology. 40(2):603–618.

Moczydłowska M. 2010. Life cycle of early Cambrian microalgae from the *Skiagia*-plexus acritarchs. Journal of Paleontology. 84(2):216–230.

Moczydłowska M, Budd GE, Agić H. 2015. Ecdysozoan-like sclerites among Ediacaran microfossils. Geological Magazine. 152(6):1145–1148.

Moritz K, Storch V. 1971. Elektronenmikroskopische untersuchung eines mechanorezeptors von evertebraten. (Priapuliden, Oligochaeten.). [Electron microscopic study of a mechanoreceptor from invertebrates. (Priapulids, Oligochaetes.)]. Zeitschrift für Zellforschung und mikroskopische Anatomie. 117:226–234. German.

Müller RD, Cannon J, Qin X, Watson RJ, Gurnis M, Williams S, Pfaffelmoser T, Seton M, Russell SH, Zahirovic S. 2018. GPlates: building a virtual Earth through deep time. Geochemistry, Geophysics, Geosystems. 19(7):2243–2261.

Nagovitsin KE, Rogov VI, Marusin VV, Karlova GA, Kolesnikov AV, Bykova NV, Grazhdankin DV. 2015. Revised Neoproterozoic and Terreneuvian stratigraphy of the Lena-Anabar Basin and north-western slope of the Olenek Uplift, Siberian Platform. Precambrian Research. 270:226–245.

Neves RC, Reichert H, Sørensen MV, Kristensen RM. 2016. Systematics of phylum Loricifera: identification keys of families, genera and species. Zoologischer Anzeiger – A Journal of Comparative Zoology. 265:141–170.

Nõlvak J. 1993. Salapärased mikrokivistised. Horis. 8:32–35.

Nowak H, Servais T, Monnet C, Molyneux SG, Vandenbroucke TR. 2015. Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: a review of Cambrian acritarch diversity. Earth-Science Reviews. 151:117–131.

Padisák J, Soróczki-Pintér É, Rezner Z. 2003. Sinking properties of some phytoplankton shapes and the relation of form resistance to morphological diversity of plankton – an experimental study. Hydrobiologia. 500(1):243–257.

Palacios T, Jensen S, Barr SM, White CE, Miller RF. 2011. New biostratigraphical constraints on the lower Cambrian Ratcliffe Brook Formation, southern New Brunswick, Canada, from organic-walled microfossils. Stratigraphy. 8(1):45–60.

Parfrey LW, Lahr DJ, Knoll AH, Katz LA. 2011. Estimating the timing of early eukaryotic diversification with multigene molecular clocks. Proceedings of the National Academy of Sciences of the United States of America. 108(33):13624–13629.

Paris F, Grahn Y, Nestor V, Lakova I. 1999. A revised chitinozoan classification. Journal of Paleontology. 73(4):549–570.

Patterson RT, Dalby A, Kumar A, Henderson LA, Boudreau RE. 2002. Arcellaceans (thecamoebians) as indicators of land-use change: settlement history of the Swan Lake area, Ontario as a case study. Journal of Paleolimnology. 28:297–316.

Payne RJ, Lamentowicz M, van der Knaap WO, van Leeuwen JF, Mitchell EA, Mazei Y. 2012. Testate amoebae in pollen slides. Review of Palaeobotany and Palynology. 173:68–79.

Pedder BE. 2012. The palynology and stratigraphy of the Cambrian Nolichucky Shale and associated formations at Thorn Hill, Tennessee, USA [dissertation]. Sheffield (UK): University of Sheffield.

Peng S, Babcock LE, Cooper RA. 2020. The Cambrian Period. In: Gradstein FM, Ogg JG, Schmitz MD, Ogg GM, editors. The geologic time scale 2020. Vol. 2. Amsterdam (Netherlands): Elsevier; p. 565–629.

Porter S. 2011. The rise of predators. Geology. 39(6):607–608.

Porter SM, Knoll AH. 2000. Testate amoebae in the Neoproterozoic Era: evidence from vase-shaped microfossils in the Chuar Group, Grand Canyon. Paleobiology. 26(3):360–385.

Raevskaya EG, Servais T. 2009. *Ninadiacrodium*: a new late Cambrian acritarch genus and index fossil. Palynology. 33(1):219–239.

Reid PPC, John AW. 1978. Tintinnid cysts. Journal of the Marine Biological Association of the United Kingdom. 58(3):551–557.

Remane J. 1985. Calpionellids. In: Bolli HM, Saunders JB, Persh-Nielsen K, editors. Plankton stratigraphy vol. 1. Planktic foraminifera, calcareous nannofossils and calpionellids. Cambridge (UK): Cambridge University Press; p. 555–572.

Robson SP, Nowlan GS, Pratt BR. 2003. Middle to Upper Cambrian linguliformean brachiopods from the Deadwood Formation of subsurface Alberta and Saskatchewan, Canada. Journal of Paleontology. 77(2): 201–211.

Rüst D. 1885. Beiträge zur Kenntniss der fossilen Radiolarien aus Gesteinen des Jura. [Contributions to the knowledge of fossil radiolarians from Jurassic rocks]. Palaeontogr. 31:273–321.

Saccà A, Giuffrè G. 2013. Biogeography and ecology of *Rhizodomus tagatzi*, a presumptive invasive tintinnid ciliate. Journal of Plankton Research. 35(4):894–906.

Saccà A, Strüder-Kypke MC, Lynn DH. 2012. Redescription of *Rhizodomus tagatzi* (Ciliophora: Spirotrichea: Tintinnida), Based on morphology and small subunit ribosomal RNA gene sequence. The Journal of Eukaryotic Microbiology. 59(3):218–231.

Sansom RS. 2016. Preservation and phylogeny of Cambrian ecdysozoans tested by experimental decay of *Priapulus*. Scientific Reports. 6(1): 32817.

Schmidt-Rhaesa A, Bang-Berthelsen IH, Kristensen R, Maas A, Neuhaus B, editors. 2012. Nematomorpha, Priapulida, Kinorhyncha, Loricifera. Vol. 1. Berlin (Germany): Walter de Gruyter; p. 381.

Schmidt-Rhaesa A, Cañete JI, Mutschke E. 2022. New record and first description including SEM and µCT of the rare priapulid *Acanthopriapulus horridus* (Priapulida, Scalidophora). Zoologischer Anzeiger. 298:1–9.

Schmidt-Rhaesa A, Rothe BH, Martínez AG. 2013. *Tubiluchus lemburgi*, a new species of meiobenthic Priapulida. Zoologischer Anzeiger – A Journal of Comparative Zoology. 253(2):158–163.

Scotese CR, Song H, Mills BJW, van der Meer DG. 2021. Phanerozoic paleotemperatures: the earth's changing climate during the last 540 million years. Earth-Science Reviews. 215:103503.

Scotese CR, Wright N. 2018. PALEOMAP paleodigital elevation models (PaleoDEMS) for the Phanerozoic. PALEOMAP Project. https://www.earthbyte.org/paleodem-resource- scotese-and- wright-2018/

Servais T, Achab A, Asselin E. 2013. Eighty years of chitinozoan research: from Alfred Eisenack to Florentin Paris. Review of Palaeobotany and Palynology. 197:205–217.

Servais T, Brocke R, Fatka O, Al LH, Molyneux S. 1997. Value and meaning of the term acritarch. Acta Universitatis Carolinae – Geologica. 40(3):631–643.

Servais T, Lehnert O, Li J, Mullins GL, Munnecke A, Nützel A, Vecoli M. 2008. The Ordovician biodiversification: revolution in the oceanic trophic chain. Lethaia. 41(2):99–109.

Servais T, Stricanne L, Montenari M, Pross J. 2004. Population dynamics of galeate acritarchs at the Cambrian-Ordovician transition in the Algerian Sahara. Palaeontology. 47(2):395–414.

Shan L. 2023. Miaolingian (Cambrian)–Early Ordovician acritarchs and Small Carbonaceous Fossils of the Baishan area, Jilin Province [unpublished PhD thesis]. Nanjing, China: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS).

Shan L, Harvey TH, Yan K, Li J, Zhang Y, Servais T. 2023. Palynological recovery of small carbonaceous fossils (SCFs) indicates that the late Cambrian acritarch *Goniomorpha* Yin 1986 represents the teeth of a priapulid worm. Palynology. 47(3):2103757.

Silva-Briano M, Martínez-Hernández SL, Adabache-Ortíz A, Ventura-Juárez J, Salinas E, Quintanar JL. 2007. Ultrastructural analysis and identification of membrane proteins in the free-living amoeba *Difflugia corona*. Biocell. 31(2):225–228.

Skovsted CB, Knight I, Balthasar U, Boyce WD. 2017. Depth related brachiopod faunas from the lower Cambrian Forteau Formation of southern Labrador and western Newfoundland, Canada. Palaeontologia Electronica. 20(3):1–52.

Slater BJ, Bohlin MS. 2022. Animal origins: the record from organic microfossils. Earth-Science Reviews. 232:104107.

Slater BJ, Harvey TH, Butterfield NJ. 2018. Small carbonaceous fossils (SCFs) from the Terreneuvian (lower Cambrian) of Baltica. Palaeontology. 61(3):417–439.

Slater BJ, Harvey TH, Guilbaud R, Butterfield NJ. 2017. A cryptic record of Burgess Shale-type diversity from the early Cambrian of Baltica. Palaeontology. 60(1):117–140.

Slind OL, Andrews GD, Murray DL, Norford BS, Paterson DF, Salas CJ, Tawadros EE, Aitken JD. 1994. Middle Cambrian to Lower Ordovician strata of the Western Canada Sedimentary Basin. In: Mossop GD, Shetsen I, editors. Geological atlas of Western Canada. Vol. 4. Calgary (AB): Canadian Society of Petroleum Geologists; Alberta Research Council; p. 87–108.

Smith MR, Harvey TH, Butterfield NJ. 2015. The macro-and microfossil record of the Cambrian priapulid *Ottoia*. Palaeontology. 58(4):705–721.

Steece FV. 1978. Deadwood Formation in the Williston Basin, South Dakota. Montana Geological Society, 24th Annual Conference: 1978 Williston Basin Symposium. Montana (MT): The Economic Geology of Williston Basin, p. 63–69.

Stitt JH, Straatmann WM. 1997. Trilobites from the upper part of the Deadwood Formation (upper Franconian and Trempealeauan stages, upper Cambrian), Black Hills, South Dakota. Journal of Paleontology. 71(1):86–102.

Storch V. 1991. Priapulida. In: Harrison FW, Ruppert EE, editors. Microscopic anatomy of invertebrates. New York (NY): Wiley-Liss. p. 333–350.

Strother PK, Taylor WA, Van De Schootbrugge B, Leander BS, Wellman CH. 2020. Pellicle ultrastructure demonstrates that *Moyeria* is a fossil euglenid. Palynology. 44(3):461–471.

Summons RE, Brassell SC, Eglinton G, Evans E, Horodyski RJ, Robinson N, Ward DM. 1988. Distinctive hydrocarbon biomarkers from fossiliferous sediment of the Late Proterozoic Walcott Member, Chuar Group, Grand Canyon, Arizona. Geochimica et Cosmochimica Acta. 52(11): 2625–2637.

Talyzina NM, Moldowan JM, Johannisson A, Fago FJ. 2000. Affinities of Early Cambrian acritarchs studied by using microscopy, fluorescence flow cytometry and biomarkers. Review of Palaeobotany and Palynology. 108(1-2):37–53.

Tappan H. 1980. The paleobiology of plant protists. San Francisco (CA): Freeman and Co.

Tappan H. 1993. Tintinnids. In: Lipps JH, editor. Fossil prokaryotes and protists. Boston (MA): Blackwell; p. 285–303.

Tappan H, Loeblich ARJ. 1968. Lorica composition of modern and fossil Tintinnida (ciliate Protozoa), systematics, geological distribution, and some new Tertiary taxa. Journal of Paleontology. 42:1378–1394.

Van Waveren IM. 1993. Planktonic organic matter in surficial sediments of the Banda Sea (Indonesia) – a palynological approach. Geologica Ultraiectina. 104:1–237.

Van Waveren IM. 1994. Tintinnomorphs from deep-sea sediments of the Banda Sea (Indonesia). Scripta Geologica. 105:27–51.

Vavrdova M. 1965. Ordovician acritarchs from central Bohemia. Věstník Ústředního Ústavu Geologického. 40:351–357.

Volkova NA. 1989. Acritarchs of the upper part of the Pakerort horizon of the north of Estonia and Leningrad region. In: Akhmetyev MA, editor. Paleofloristics and stratigraphy of the Phanerozoic. Moscow (Russia): Geological Institute of the USSR Academy of Sciences; p. 213. Russian.

Volkova NA. 1993. Akritarkhi pogranichnikh otlozhenij kembriya i ordovika priglintovoj polosy estonii (skvazhina M-56) [Acritarchs from the Cambrian–Ordovician boundary beds (boring core M-56) of the

Estonian near-clint area]. Proceedings of the Estonian Academy of Sciences. Geology. 42:15–22. Russian.

Wallace RL, Snell TW, Smith HA. 2015. Phylum Rotifera. In: Thorp JH, Rogers DH, editors. Thorp and Covich's freshwater invertebrates. London (UK). Elsevier. p. 225–271.

Wang D, Vannier J, Yang XG, Sun J, Sun YF, Hao WJ, Tang QQ, Liu P, Han J. 2020. Cuticular reticulation replicates the pattern of epidermal cells in lowermost Cambrian scalidophoran worms. Proceedings of the Royal Society. 287:20200470.

Wang XF, Stouge S, Maletz J, Bagnoli G, Qi YP, Raevskaya EG, Wang CS, Yan CB. 2019. Correlating the global Cambrian–Ordovician boundary: precise comparison of the Xiaoyangqiao section, Dayangcha, North China with the Green Point GSSP section, Newfoundland, Canada. Palaeoworld. 28(3):243–275.

Wang XF, Stouge S, Maletz J, Bagnoli G, Qi YP, Raevskaya EG, Wang CS, Yan CB. 2021. The Xiaoyangqiao section, Dayangcha, North China: the new global Auxiliary Boundary Stratotype Section and Point (ASSP) for the base of the Ordovician System. Episodes. 44(4):359–383.

Weber LJ, Jr. 1988. Paleoenvironmental analysis and test of stratigraphic cyclicity in the Nolichucky Shale and Maynardville Limestone (Upper Cambrian) in central east Tennessee [dissertation]. Knoxville (TN): The University of Tennessee.

Wernström JV, Slater BJ, Sørensen MV, Crampton D, Altenburger A. 2023. Geometric morphometrics of macro-and meiofaunal priapulid pharyngeal teeth provides a proxy for studying Cambrian "tooth taxa". Zoomorphology. 142(4):411–421.

Williams R, McCall H, Pierce RW, Turner JT. 1994. Speciation of the tintinnid genus *Cymatocylis* by morphometric analysis of the loricae. Marine Ecology Progress Series. 107(3):263–272.

Willman S, Slater BJ. 2021. Late Ediacaran organic microfossils from Finland. Geological Magazine. 158(12):2231–2244.

Wrona R. 1980. Microarchitecture of the chitinozoan vesicles and its paleobiological significance. Acta Palaeontologica Polonica. 25(1): 123–184.

Yin LM. 1986. Acritarchs. In: Chen JY, editor. Aspects of Cambrian-Ordovician boundary in Dayangcha, China. Beijing: China Prospect Publishing House; p. 314–373.

Zang WL, Moczydłowska M, Jago JB. 2007. Early Cambrian acritarch assemblage zones in South Australia and global correlation. Memoirs of the Association of Australasian Palaeontologists. 33:141–177.