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Coccolithophores in Polar Waters: *Papposphaera sarion* HET and HOL revisited

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ABSTRACT: *Papposphaera sarion* was first described from West Greenland waters and has not since then been reported from other sites. We present here additional material of *P. sarion* from the type locality, transmission electron images of *P. sarion* from the NEW polynya (NE Greenland) and scanning electron images from Svalbard. Study of a vastly extended source of images provides new morphological data, particularly on the variability of coccolith central area calcification in this species. Combination coccospheres involving a *Turrisphaera* sp. were frequently observed in samples from the NEW polynya as was also the holococcolithophore *Turrisphaera* phase of this species. *Papposphaera sarion* has in its life-cycle previously been associated with *Turrisphaera arctica*. However, a careful re-examination of the micrographs accompanying the description of *T. arctica* and unpublished material available to us clearly reveals that *T. arctica* combines with a different, but as yet undescribed species of *Papposphaera*. A striking similarity is pointed out between *P. sarion* HET and species of *Stradnerlithus*, e.g. *Stradnerlithus fragilis* from the middle Jurassic.

Keywords: coccolithophore, *Papposphaera sarion*, *Turrisphaera*, polar regions, *Stradnerlithus*

INTRODUCTION

A contingent of weakly calcified high latitude coccolithophores was described almost four decades ago mostly from Arctic sites (see e.g. Manton and Oates 1975; Manton and Sutherland 1975; Manton et al. 1976a,b; Manton et al. 1977; Thomsen 1980a,b,c,d; 1981; Thomsen et al. 1988). From a recent analysis of a large hitherto unpublished source of material from both Polar Regions it has become clear that some of the original descriptions of genera and species are in need of revision. In some cases there is an obvious lack of detail in the original description due to fully understandable limitations at the time in the availability of material, i.e. the number of cells examined and the overall quality of the material analyzed in terms of clearly exposing diagnostic features. In order to remedy this we are in the process of revisiting all genera and species described during the early phase of the exploration of polar coccolithophores (Thomsen et al. 2013; Thomsen and Østergaard 2014a,b; 2015a,b). We are in this process fortunate enough to also be able to draw upon Svalbard material being currently processed for scanning electron microscopical examination.

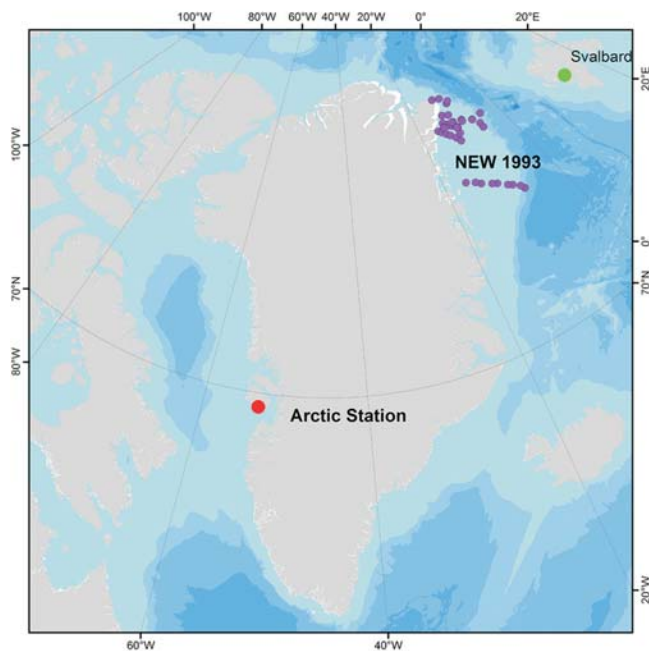
While the unravelling of the generic concept within coccolithophores to form part of life-cycles that involve an environmentally triggered phase shift between a diploid heterococcolithophore and a haploid holococcolithophore has revolutionized our understanding of basic biological principles within these organisms, it has also seriously impacted on biological nomenclature. A single formal name should thus be applied to organisms recognized to be part of a shared life-cycle (see e.g. Thomsen et al. 1991). In order to achieve precision the use of 'HET' and 'HOL' added to the species name has been suggested as an informal

way of indicating the life-cycle state observed or referred to (see e.g. Young et al. 2003). A formal nomenclatural change with respect to *Papposphaera sarion* Thomsen 1988, the target organism of this contribution, was introduced by Thomsen et al. (1991). Based on the finding of combination coccospheres involving *P. sarion* and what the authors at that time identified as *Turrisphaera arctica* Manton, Sutherland and Oates 1976, the combination *P. arctica* (Manton, Sutherland and Oates 1976) Thomsen, Østergaard and Hansen 1991, was formally erected. However, access to much more diverse Arctic material and a careful re-examination of the micrographs accompanying the description of *T. arctica* has unambiguously revealed that *T. arctica* sensu Manton et al. (1976b) is not identical to the *Turrisphaera* counterpart of *P. sarion*. In a companion publication (Thomsen et al. 2016) we document that *T. arctica* sensu Manton et al. (1976b) forms combination coccospheres with an as yet undescribed Arctic species of *Papposphaera*.

In this paper we will reexamine *P. sarion* (HET, HOL and combination coccospheres) and provide an emended description of the species based on extensive material from West Greenland, NE Greenland, and Svalbard.

MATERIAL AND METHODS

The Arctic material that comprised *P. sarion* HET and HOL specimens originates from the R/V 'Polarstern' ARK IX/3 North-East Water Polynya (NEW) cruise June-July 1993, and from the University of Copenhagen Arctic Station (Disko Bay, West Greenland) where sampling was conducted during the summers of 1988, 1990 and 1994. An ongoing sampling programme yielding material for a scanning electron micro-



TEXT-FIGURE 1
Map of Arctic sampling sites. All NEW sampling sites are indicated. Stations on the southern transect leading into the polynya had by far the highest abundances of *P. sarion* (HET, HOL and combination coccospheres; 0-50 m depth).

scope (SEM) analysis has been conducted in the fiord systems of Svalbard since 2012. All sampling sites are shown in text-figure 1.

The protocol for processing water samples for the transmission electron microscope (TEM) was similar on all sampling occasions (see Moestrup and Thomsen 1980). The nanoplankton community was concentrated for further processing by means of either centrifugation of a prefiltered (usually 20µm) water sample (0.5-1 litre) or centrifugation of prefiltered material resuspended from an initial concentration of cells on top of e.g. a 1µm Nuclepore filter. Small droplets of cells from the resuspended final pellet of material were - irrespective of the initial concentration procedure - placed on carbon coated grids. Cells were subsequently fixed for ca. 30 seconds in the vapour from a 1-2% solution of OsO₄. After drying the grids were carefully rinsed in distilled water in order to remove salt crystals. Grids were shadow cast with either Au/Pd or Cr prior to the examination in JEOL electron microscopes property of the Botanical Institute at the Univ. of Copenhagen. Material for the SEM was prepared by gentle filtration of a water sample on top of a 1.0µm Nuclepore filter. The formation of salt crystals that might obstruct the visibility of cells was minimized by allowing the pumping system to almost completely dry out the filter. Filters were sputter coated with gold and examined on a Zeiss Supra 55VP scanning electron microscope at the Bergen University Laboratory for Electron Microscopy.

The terminology follows wherever possible Young et al. (1997, 2003).

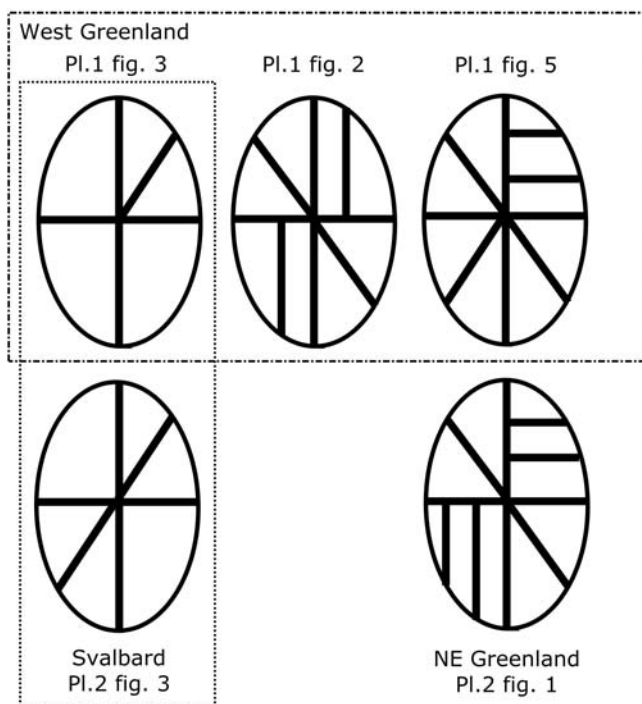
OBSERVATIONS

Papposphaera sarion HET Plates 1-2

The cell is spherical to ellipsoidal and measures ca. 6 x 5µm. It carries two flagella and a haptonema (Pl. 1 fig. 1) which is the typical hallmark of a prymnesiophycean flagellate.

The coccosphere consists of monomorphic to varimorphic muroliths. All coccoliths appear to be basically identical, however, with a certain variability in size of the central spine dependent on the position within the coccosphere. The individual coccolith is normally elliptical (Pl. 1, figs. 2, 5; Pl. 2, fig. 3) and measures 1.0-1.4 x 1.5-2.0µm. Due to the limited calcification of the wide central area the organic base plate is often visible (Pl. 1, figs. 2, 5). When viewed from the distal side the radiating ridges are prominent (Pl. 1, fig. 2), whereas when viewed from the proximal side the radiating ridges are seen to be overlaid by concentric ridges (Pl. 1, fig. 5). The rim calcification comprises the two cycles of elements that are typical for a Papposphaeracean murolith. The proximal cycle is thus formed by linearly organized rod-shaped elements (0.20-0.24µm long and ca. 0.06µm wide) that occur interspaced between the elements of the wall proper (Pl. 1, figs. 2-4; Pl. 2 fig. 1). The second cycle of large pentagonal elements (0.2-0.6µm high and quite variable within the same coccolith) form a dense and slightly flaring wall that arises from the coccolith periphery at an angle of approx. 100 degrees (Pl. 2, fig. 3).

Examination of a large number of cells from a wide geographical range clearly highlights that central area calcification in *P. sarion* is subject to considerable variability. The original description of *P. sarion* (Thomsen 1981) was based on the examination of only 5 cells supported by the fortunate finding of a few detached coccoliths such as the one reproduced here as Plate 1 figure 3. In this coccolith the central area calcification consists of a cross-bar arranged roughly along the main axes of the coccolith (axial cross). A single radial arm (Pl. 1, fig. 3, arrow) is seen in the upper quadrant of the coccolith almost concealed by the central spine. In retrospect and when taking into account the entire material now available to us it appears that the single enlarged rectangular tile present within the central area (Pl. 1, fig. 3, arrowhead) is likely an artefact within this particular coccolith. The central area configuration comprising an axial cross and a single additional radial arm is exactly mirrored in some *P. sarion* coccoliths from Svalbard (Pl. 2, fig. 3, arrows), although in most of the Svalbard coccoliths there are two radial arms in opposite quadrants. In the *P. sarion* material from the West Greenland type locality the majority of the cells examined had additional elements present as part of the central area calcification (Pl. 1, figs. 2, 5). The axial cross is still evident, however, there are typically radial arms traversing more than one quadrant and some of the arms of the central cross (typically one or two) support additional calcified bars attached at right angles to the arm of the central cross. Material from NE Greenland (Pl. 2, fig. 1) shares with the West Greenland material the presence of both radial arms in between the arms of the central cross and additional elements (bars) organized at right angles to the individual arm of the central cross. Schematic drawings are provided in text-figure 2 indicating the variability observed. The exact coccoliths that serve as background for the schematic drawings are pointed out in Plate 1, figures 2, 5 and Plate 2, figure 1. It is obvious when examining the coccoliths displayed in e.g. Plate 1, figure 5 and Plate 2, figure 1, that the central area



TEXT-FIGURE 2
Schematic drawings of central area calcification (distal surface view). The origin and exact source of each drawing is indicated.

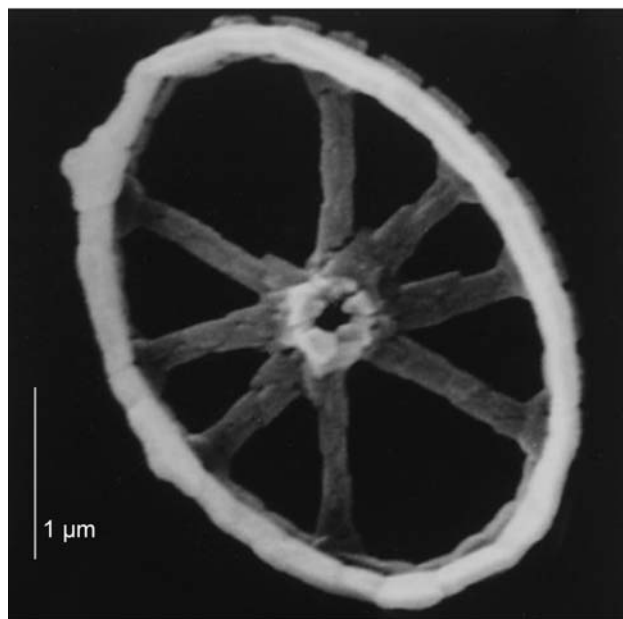
calcification easily becomes dis-arranged rendering an exact reconstruction of the original layout difficult. It appears rational, at least for the time being and without access to molecular data on *P. sarion* strains from different sites, that a certain plasticity with respect to central area calcification should be accepted within *P. sarion*. The allocation of the material examined here (West Greenland, NE Greenland and Svalbard) to *P. sarion* is additionally based on a marked similarity with respect to rim calcification and in particular the elaboration of the central spine. The fact that the documented variability with respect to central area calcification (text-fig. 2) represents a progression of overlapping complexity (with the NEW material representing the most extreme case) also adds to the necessity of dealing with this variability within the context of a single species.

The central calicate spine (2.3-2.5µm) appears more or less identical across the geographic realms and time ranges sampled. The stem (ca. 1.1µm) is a continuation of the arms of the axial cross (Pl. 2, fig. 3) and thus comprises four rods with a square cross-section and a central cavity. It appears that each rod can be irregularly divided into shorter elements (see e.g. Pl. 1, fig. 3). The calyx is formed by four closely appressed and differently sized elongate elements (Pl. 1, figs 2, 3).

***P. sarion* combination coccospheres**

Plate 3

Thomsen et al. (1991; loc cit. figs. 5-7) provided evidence for the existence of *P. sarion* combination coccospheres in West Greenland waters involving *Turrisphaera* sp. as a life-cycle counterpart. Here we add additional examples of combination coccospheres (*P. sarion* / *Turrisphaera* sp.) from NE Greenland (Pl. 3, figs. 1-4). A single enlarged heterococcolith (Pl. 3, fig.



TEXT-FIGURE 3
SEM image of *Stradnerlithus fragilis*. Reproduced with permission from Bown and Cooper (1998).

4) from the cell illustrated in Plate 3, figure 3 corroborates the identification of these cells as *P. sarion*. All three specimens are characterized by extended and contiguous areas of each type of coccolith. Although SEM images are preferable with respect to illustrating the authenticity of a combination coccosphere, there is no doubt that the images shown here do not display a chance stacking of autonomous coccolithophores. The cells illustrated here measure ca. 7 x 6 µm. The calicate spines from combination coccospheres tend to be longer (2.7-3.7 µm) than those described above for *P. sarion* HET.

The *Turrisphaera* sp. holococcoliths are exactly similar to those previously encountered in the West Greenland combination coccospheres (Thomsen et al. 1991) and will be further described below.

The *P. sarion* counterpart was erroneously identified by Thomsen et al. (1991) as *Turrisphaera arctica* Manton, Sutherland and Oates 1976 (type locality: Resolute Bay, Cornwallis Island, Canada). Our current access to a vastly increased number of combination coccospheres from in particular the high-arctic region clearly establishes the fact that *Turrisphaera arctica* has a shared life-cycle with an as yet undescribed species of *Papposphaera* (Thomsen et al. 2016). The distinguishing feature of *T. arctica* is a pronounced asymmetry of the distal part of the individual coccolith (Manton et al. 1976b; loc. cit. figs 25-29) where one side of the tube halfway up the coccolith is unidirectionally pulled out and tilted with reference to the main axis of the coccolith. This is particularly evident in coccoliths at either end of the cell, whereas coccoliths from the middle part of the cell tend to be generally shorter and fairly symmetrical in overall appearance. This reinterpretation of *T. arctica* puts the species somewhere in the middle of a variability matrix that encompasses on the one hand the highly symmetrical *T. borealis* Manton, Sutherland and Oates 1976 (= *Papposphaera*

sagittifera Manton, Sutherland and McCully 1976 HOL) and on the other hand the highly assymetrical *T. polybotrys* Thomsen 1980. Manton et al. (1976b) in the original description of *T. arctica* mentioned occasional assymetry and coiling at the distal end of individual *T. arctica* coccoliths. However, they were primarily focused on distinguishing *T. arctica* from *T. borealis*, to the extent that the very explicit assymetry of the *T. arctica* coccolith receives in the original publication too little attention as a keystone taxonomic feature. They even write that ‘...at some future time our second species, now designated *T. arctica* sp.nov., may have to be relegated to the status of a variety or a collection of local or teratological growth-forms modified environmentally from our first species *T. borealis* sp. nov.’ All currently available evidence supports the circumscription of *T. arctica* as a valid taxon.

***P. sarion* HOL**
Plate 4

The NE Greenland material provided a rich suite of complete specimens of *P. sarion* HOL. The cell is circular to ovoid (5-8 x 8µm), with two flagella and a haptonema (Pl. 4, figs. 1, 2).

The coccosphere comprises monomorphic to varimorphic tubular coccoliths. There is in almost all cells examined a variability in size among coccoliths (Pl. 4, fig. 2: 2.2 – 3.3µm). The largest coccoliths cluster around the flagellar pole, shorter ones are positioned at the posterior cell end, while coccoliths within a median band around the cell are smaller than the others. The individual tubular coccolith is symmetrical along the longitudinal axis and widened at both ends. The distal end is sometimes clearly funnel-shaped (Pl. 4, fig. 3) but in most cases it appears occluded because of what we interpret as a likely collapse of the tube opening caused by the handling and drying of the material. A monolayer of hexagonal crystallite plates cover the coccolith surface in what appears to be a helical coiling pattern. The crystallite plates have a mean distance between opposite and

parallel sides of $0.134 \pm 0.011 \mu\text{m}$ (n=50) and an overall size range between 0.104-0.164µm. There is no evidence of a central pore in the individual hexagonal plate. Manton et al. (1976b) reported such central perforations in both *T. borealis* and *T. arctica*. No unmineralized under layer scales have been observed so far.

SYSTEMATIC DESCRIPTION

An emended description of *P. sarion* is called for considering the above documented variability in central area calcification of *P. sarion* HET, and the fact that *P. sarion* HOL represents a species of ‘*Turrisphaera*’ that has not been previously described.

Division HAPTOPHYTA Hibberd 1972
Class PRYMNESIOPHYCEAE Hibberd 1976
Order COCCOLITHALES Schwarz 1932
Family PAPPOSPHAERACEAE Jordan and Young 1990 emend
Andruleit and Young 2010

***Papposphaera sarion* (Thomsen 1981) Thomsen, Heldal and Østergaard emend.**

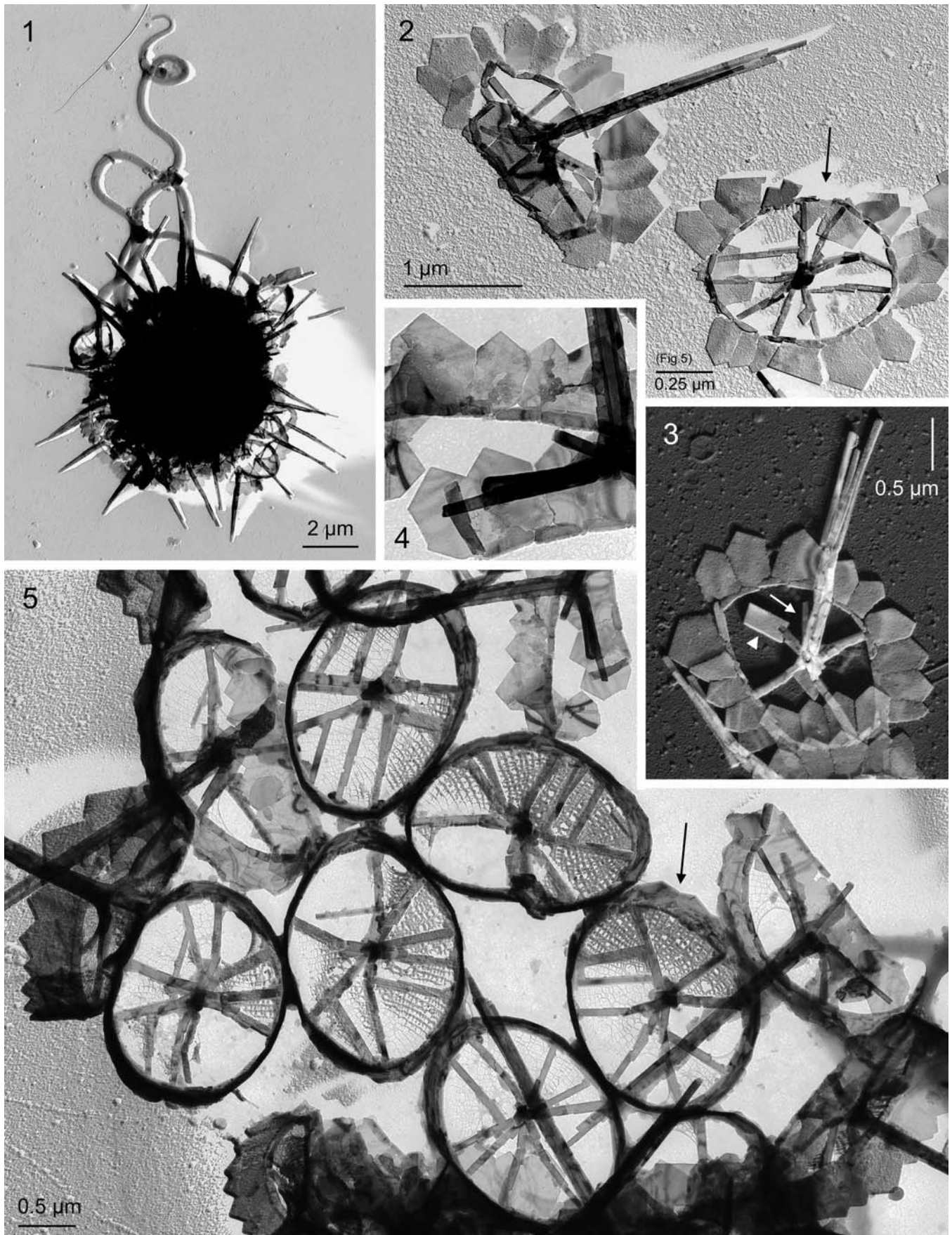
Emended diagnosis: The species exists in two distinct life cycle forms (HET, HOL). Combination coccospheres are found within the biogeographical realms of the species (the Arctic seas).

Heterococcolithophore phase: Cell spherical to ovoid (ca. 5 x 7µm) with two flagella and a haptonema. Coccolith (murolith) monomorphic to varimorphic (size variability of spine), elliptical in outline and ca. 1.2 x 1.8µm. The rim comprises two cycles, i.e. a proximal cycle of rod shaped elements and a distal palisade of pentagonal elements giving the rim a toothed upper margin. Central area calcification is sparse and variable. An axial cross is always present and supplemented by (1) 1-3 radial

PLATE 1

Transmission electron microscope images of material from Arctic Station, West Greenland (1977: fig. 3; 1988: fig. 2; 1990: figs 1, 4, 5)

- 1 Complete specimen with curled up flagella and haptonema.
- 2 Isolated coccoliths showing details of rim and central area calcification. The arrow points to the coccolith that has been used for the schematic reconstruction in text-fig. 2.
- 3 Isolated coccolith in reverse printing. The arrow points to a calcified arm traversing one of the quadrants. A hypertrophied rod element from the central cross is marked by an arrowhead. Details of the stem and the calyx stand out clearly.
- 4 Detail of rim calcification (from fig. 5).
- 5 Scatter of coccoliths. The organic base plate pattern is evident and the visibility of concentric fibres in combination with the general appearance of the rim indicate that this cluster of coccoliths expose the proximal face. The arrow points to the coccolith that has been used for the schematic reconstruction in text-fig. 2. Notice that the image in text-fig. 2 is a mirror image because these are drawn to show the distal face.



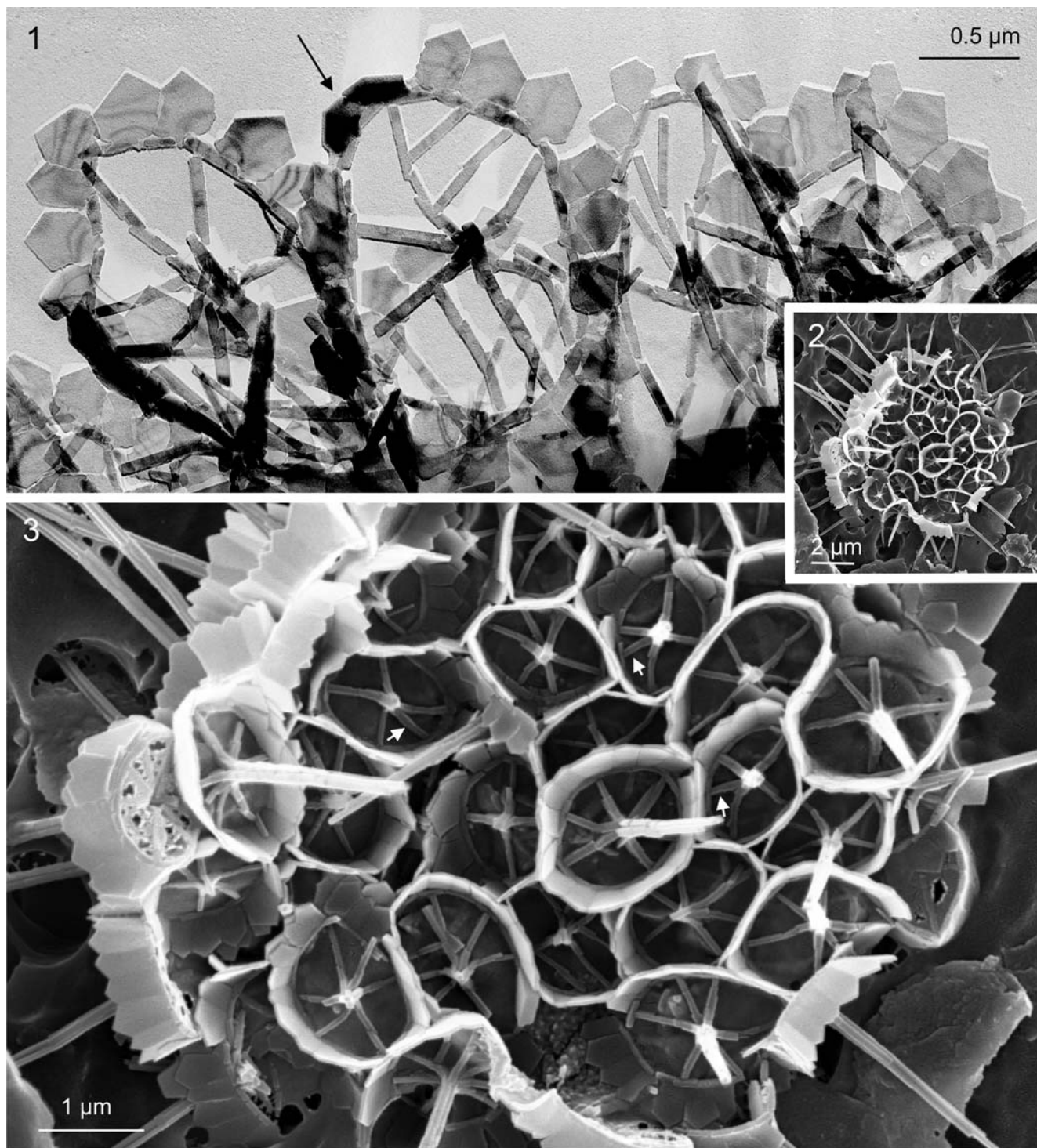


PLATE 2

Transmission electron image of material from NE Greenland (fig. 1) and scanning electron images (figs 2, 3) of material from Svalbard.

- 1 Detail of coccoliths showing rim and central area calcification. The arrow points to the coccolith that has been used for the schematic reconstruction in text-fig. 2.
- 2 Low magnification of a cell to show the size variability among the central spines.
- 3 High magnification detail of the cell shown in fig. 2. Notice the robust appearance of the rim and the central area calcification. Arrows point to coccoliths in which there is only a single arm traversing one of the quadrants. In all remaining coccoliths there are consistently two oppositely located arms (see also text-fig. 2).

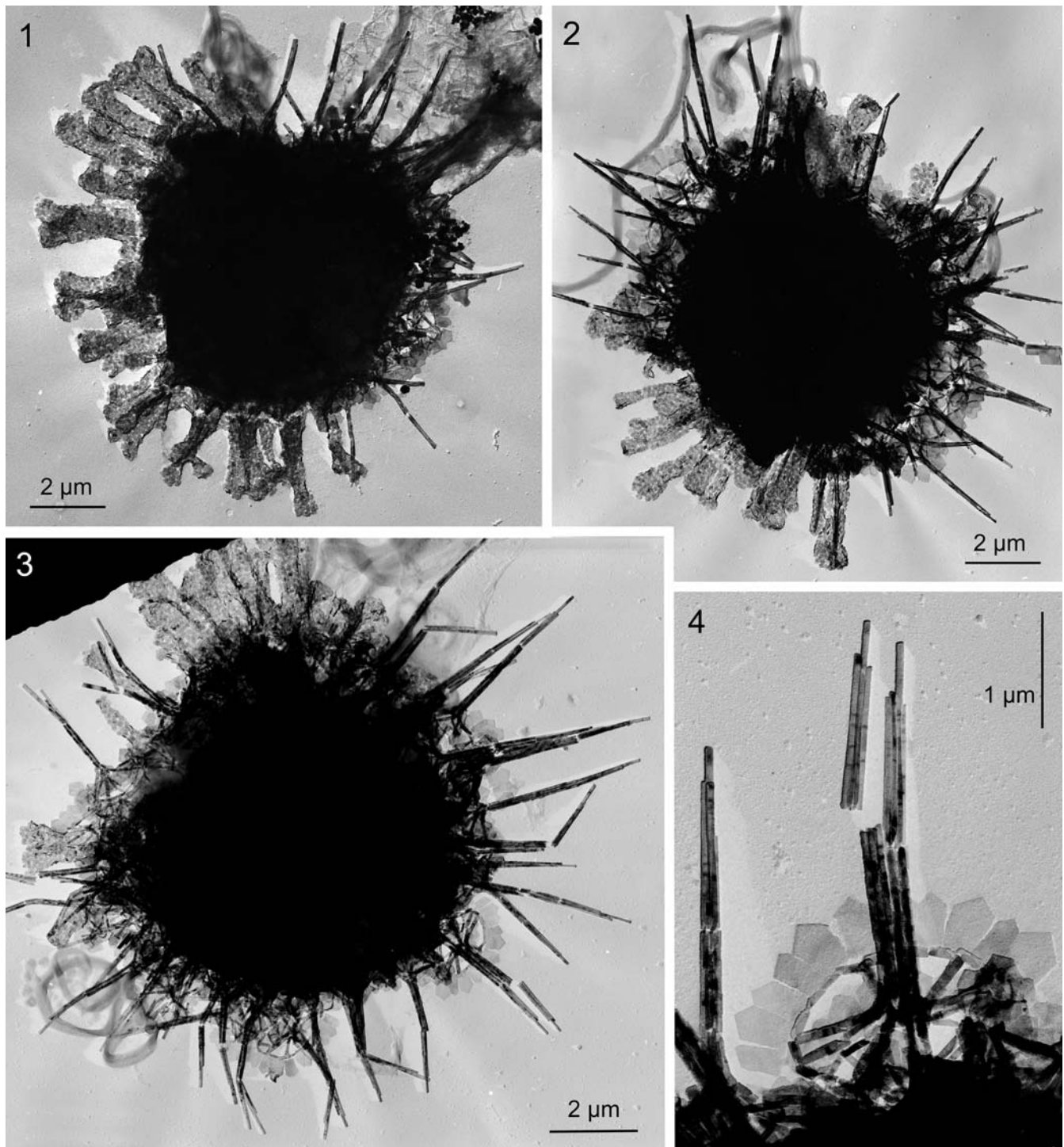


PLATE 3

Transmission electron micrographs of combination coccospheres from NE Greenland.

1-3 Complete cells with flagella and haptonema and a coccosphere mixture of hetero- and holococcoliths. 4.

Detail from fig. 3 to corroborate the diagnostic features of *P. sarion*.

arms that traverse the quadrants, and (2) also the occasional calcified bars (1-4) that are arranged perpendicular to the arms of the central cross. The stem of the calicate spine is formed by a continuation of the arms of the central cross. The calyx consists of a dense cluster of 4 differently sized narrow elements. The length of the central spine typically varies between 2.3 – 2.5 µm.

Holococcolithophore phase: Cell spherical to ovoid (ca. 5-8 x 8 µm) with two flagella and a haptonema. Coccolith monomorphic to varimorphic (variability primarily in length), each a slender and symmetrical tube (2.2 – 3.3 µm) that is widened at both ends. Minute hexagonal plates (ca. 0.13 µm) organized in a helical pattern cover the entire surface of the coccolith.

DISCUSSION

One of the important lessons learnt from revisiting *P. sarion* HET is the amount of variability that can be seen in central area calcification of the species when examining specimens that cover a large timespan and geographical area. The validity of dealing with this variability within a single species can of course be questioned and needs ultimately to be verified by means of molecular tools once the techniques to deal with single cell sequencing of organisms that are too small to be recognizable in the LM have been fine tuned.

Due to the overall minuteness and weak calcification of the polar coccolithophorid genera and species (to which *P. sarion* belongs) it has generally not been considered possible to even tentatively link these extant forms with items from the fossil records. However, it has been pointed out to us recently that there is a striking similarity between the *P. sarion* HET coccolith and coccoliths from the genus *Stradnerlithus* Black 1971. Among the species of *Stradnerlithus* it appears relevant to point in particular towards *S. fragilis* (Rood and Barnard 1972) Perch-Nielsen 1984, which is characterised by a simple rim structure and a central area calcification that comprises 8 radial bars which can (in alignment with the description of the *P. sarion* central area calcification above) be interpreted as an axial cross and four additional radial arms that traverse each of the four quadrants. A central spine is also a characteristic feature of the coccolith which measures 3-3.5 x 2.2-2.5 µm. The *S. fragilis* coccoliths are thus distinctly bigger than those of *P. sarion* but still within at least a neighbouring size range. There is a striking overall similarity when comparing an image of *S. fragilis* (e.g. Bown and Cooper 1998; loc. cit. fig. 4 reproduced here as text-fig. 3) with in particular the SEM image of *P. sarion* (Pl. 2, fig. 3). The geological range of *S. fragilis* is the late Jurassic epoch with first occurrence at the start of the Oxfordian stage (ca. 165 Ma). The *stradnerlithids* have a very patchy fossil record. They are usually completely absent but also occasionally present in high abundances and diversities typically in laminated marl facies where there has been no bioturbation (e.g. Goy 1981). A study of sediments with this sort of exceptional preservation has also led to the description of *Pocillithus spinulifer* Dunkley Jones, Bown and Pearson, 2009 from the Pande Clays in Tanzania, a species that may be related to extant narrow-rimmed muroliths, i.e. the Papposphaeraceae (Dunkley Jones et al. 2009).

The reported stratigraphic ranges of *Stradnerlithus* spp., *Pocillithus* sp. and other fossil forms with a possible papposphaeracean affinity will remain discontinuous due to the preservation demands. Yet it is promising that tentative evidence exist that potentially roots the papposphaeraceans way back in the earliest part of the coccolithophore evolutionary history.

An additional core finding is that the holococcolithophorid life-cycle counterpart of *P. sarion* is not as previously alleged *T. arctica* but rather an undescribed form of *Turrisphaera*. It was postulated at an early stage (Thomsen et al. 1991) that for organisms that cannot easily be cultured nor sequenced, the finding of combination coccospheres in samples processed directly from the sea was likely to become an important tool with reference to circumscribing troublesome taxa. Historically it has been very difficult to separate species of in particular *Turrisphaera*. There are at present three species described (*T. borealis*, *T. arctica*, *T. polybotrys*) and a range of undescribed forms. We are fortunate enough to have access to combination coccospheres of several *Papposphaera* species. This will allow us during the process of dealing with the species of *Papposphaera* one by one to gradually improve our possibilities to also identify species of *Papposphaera* HOL (= *Turrisphaera*) when they are encountered in the holococcolithophore phase.

The known geographical range of *P. sarion* HET and HOL is at present the Arctic (Svalbard, NE Greenland) and the sub-arctic (Disko Bay, West Greenland). Combination coccospheres are known from NE Greenland and West Greenland. It is thus likely that *P. sarion* is ubiquitously present in the arctic and sub-arctic realms and that the lack of extensive recordings of the species should only be attributed to undersampling and the specific preparational and microscopical demands for proper identification.

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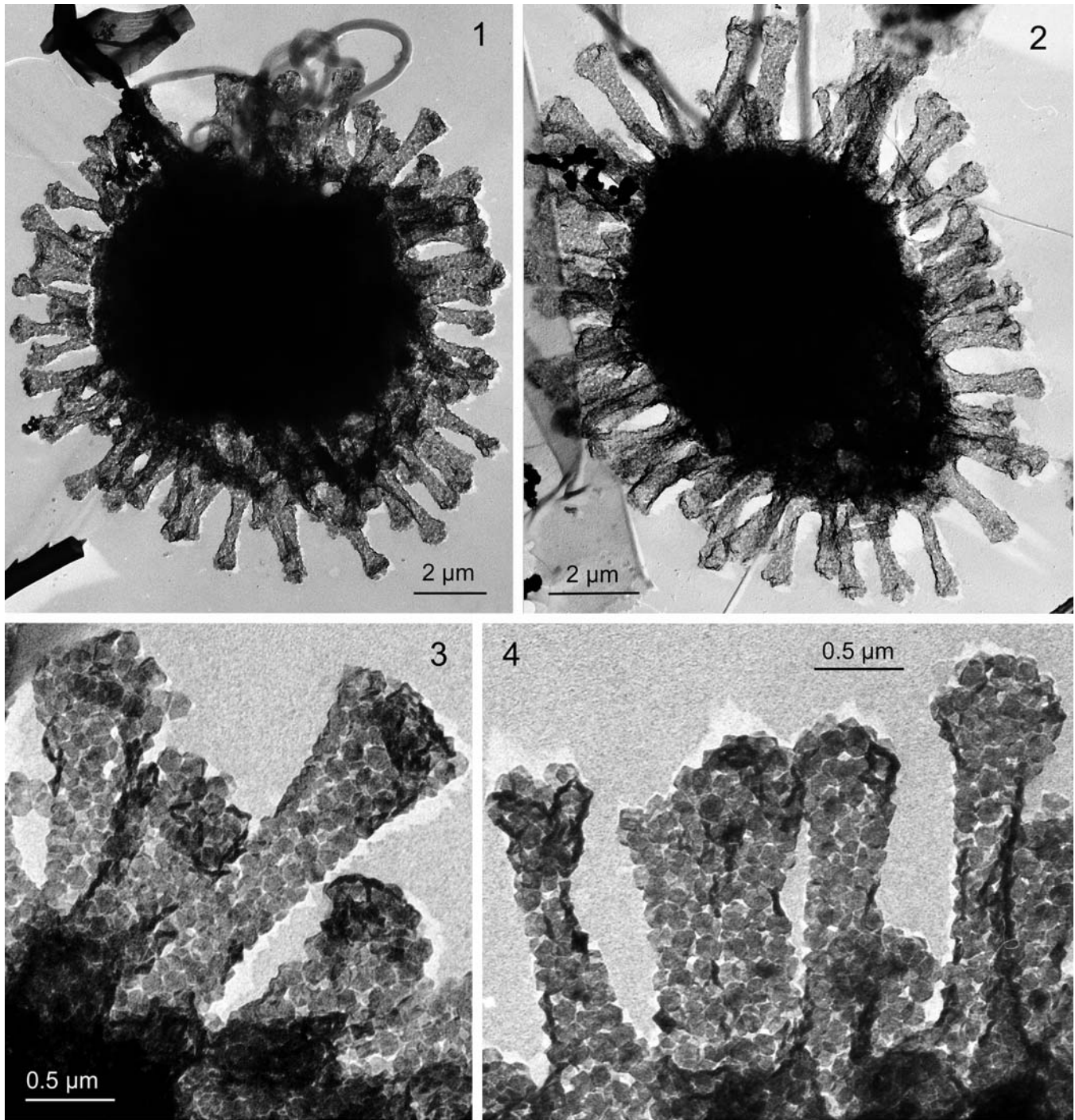


PLATE 4

Transmission electron micrographs of *P. sarion* HOL from NE Greenland.

- 1-2 Two complete specimens with flagella and haptonema. Notice the size difference (particularly evident in fig. 2) between individual coccoliths in different positions within the coccosphere.
- 3 Detail from fig. 1 to show the surface layer of hexagonal plates and a single coccolith with a funnel-shaped distal opening.
- 4 Detail of coccosphere (from fig. 1) to show the typical occluded appearance of the coccolith distal end.

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