ACTA
PROTOZOOLOGICA

Acta Protozool. (2015) 54: 155–169
www.ejournals.eu/Acta-Protozoologica
doi:10.4467/16890027AP.15.013.3210

# Coccolithophorids in Polar Waters: *Mercedesia* gen. nov., *Ericiolus*, *Quaternariella* and *Porsildia* gen. nov.

**Helge A. THOMSEN**[1], **Jette B. ØSTERGAARD**[2]

**[1] National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund, Denmark; [2] Nørrebrogade 52a 5th, 2200 Copenhagen N, Denmark**

**Abstract.** Coccolithophorid samples from arctic and antartic regions have been examined for an update on species morphology, life history aspects and biogeography for the coccolithophorid genera *Ericiolus* and *Quaternariella* and two other genera here described as new. *Mercedesia* gen. nov. comprises three new species, *M. aspiphora* sp. nov. from both polar regions, the arctic *M. multistellata* sp. nov. and the Antarctic *M. pusilla* sp. nov. The genus is characterized by its monomorphic nannoliths that are shaped like three-armed stars. The new arctic monospecific genus *Porsildia* gen. nov. is established for the heterococcolith-bearing species *P. acerviphora* sp. nov. Combination cells, from the arctic region, bearing holococcoliths of *Quaternariella obscura* and previously undescribed heterococcoliths, with a Papposphaeracean affinity, are described here for the first time.

**Key words:** coccolithophorid, *Mercedesia*, *Ericiolus*, *Quaternariella*, *Porsildia*, Polar Regions, electron microscopy.

**Abbreviations:** TEM – transmission electron microscope; SEM – scanning electron microscope; LM – light microscope; AMERIEZ, EPOS, ANT X/3 – acronyms for Antarctic cruises (see Materials and Methods); NEW, NOW – acronyms for Arctic cruises (see Materials and Methods); AS – Arctic Station

## INTRODUCTION

A range of 3–5 µm sized, weakly calcified and non-photosynthetic coccolithophorids (Haptophyta) are found to be persistently present at high latitude sampling sites during investigations using transmission electron microscopical techniques (Manton and Oates 1975, Manton and Sutherland 1975, Manton *et al.* 1976a, b, 1977, Thomsen 1980a, b, c, d, 1981, Thomsen *et al.* 1988, 1991, 1995).

We are currently in the process of preparing a series of papers that in turn updates our understanding of aspects of biodiversity, biogeography, life history events etc. with reference to each of the polar coccolithophorid genera and species (Thomsen *et al.* 2013, Thomsen and Østergaard 2014a, b, 2015). Since the first descriptions of these taxa, that date back three decades or more, little additional information has been published with respect to the occurrence of these forms in polar seas. Due to their small size and slight calcification these organisms

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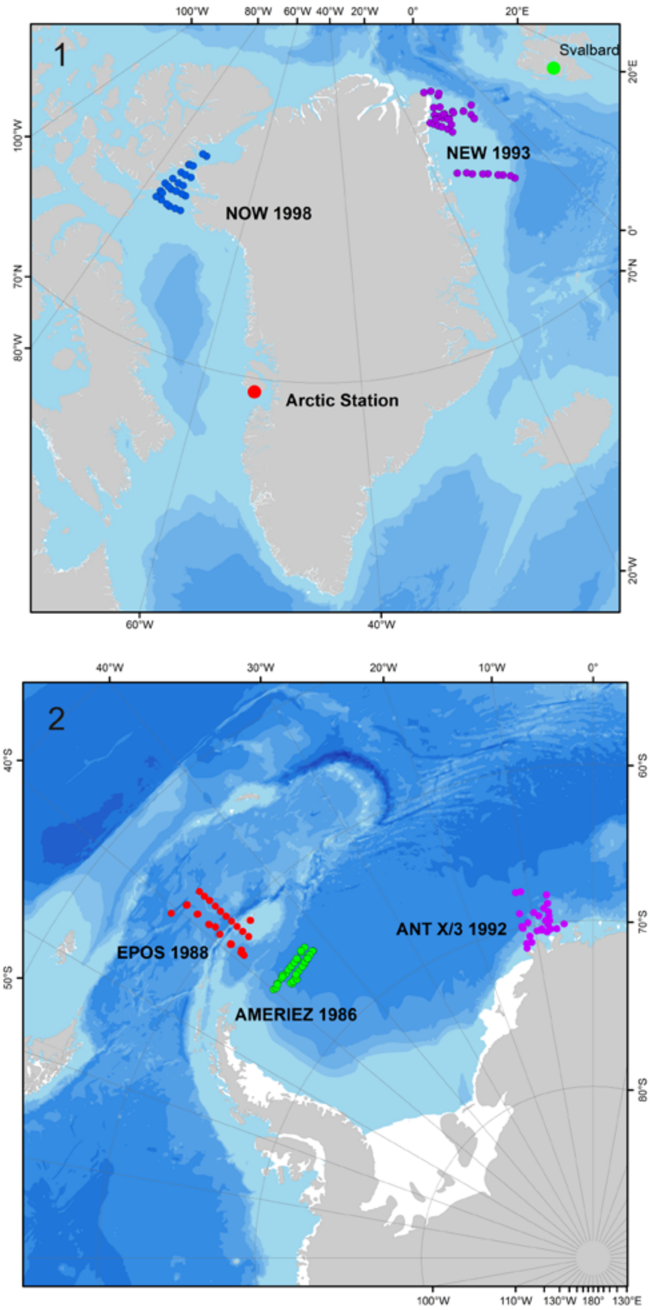
Address for correspondence: Helge A. Thomsen, DTU Aqua, Jægersborg Allé 1, 2920 Charlottenlund, Denmark. E-mail: hat@aqua.dtu.dk. Fax: +45 3588 3333

are most easily documented from TEM work, which, however, is considerably more time consuming than the routine examination of coccolithophorids on filters prepared for scanning electron microscopy (SEM). We are fortunate enough to have access to fairly vast sources of TEM material that has been collected mainly during the nineties, as well as from recent and still on-going SEM sampling programs conducted in e.g. the fiord systems of the high arctic Svalbard.

In this paper we discuss the morphology and distribution of species of the genera *Ericiolus* Thomsen in Thomsen *et al.* 1995*,* and *Quaternariella* Thomsen 1980d. A new genus, *Mercedesia* gen. nov., is described to accommodate three new species. Two of these have been previously referred to as 'Coccolithophorid sp. 1' by Thomsen *et al.* (1988; loc. cit. Figs 46 and 47 respectively). The heterococcolithophorid genus, *Porsildia* gen. nov., is described to accommodate a new species from arctic waters. *Porsildia acerviphora* sp. nov. is characterized by its dimorphic coccosphere and has its affinity to *Papposphaera* as well as to the heterococcolithophorid counterpart of *Quaternariella*. While *Quaternariella* clearly is a holococcolithophorid taxa, both *Ericiolus* and *Mercedesia* can only be referred to as nannolith-bearing genera incertae sedis (Jordan *et al.* 2004; Young *et al.* 2003).



**Figs 1–2.** Collection sites. **1** – map of the Arctic (Greenland) indicating sampling sites; **2** – map of the Antarctic (Weddell Sea) showing the location of sampling sites.

## MATERIALS AND METHODS

In this paper we compare material from the Southern Ocean, from south of the Antarctic Convergence, with samples from the Northern Hemisphere, from the Arctic Ocean and its surrounding ice-covered seas.

The Arctic material originates from the R/V 'Polarstern' ARK IX/3 North-East Water Polynya (NEW) cruise June–July 1993 and the R/V 'Pierre Radisson' North Water Polynya cruise (NOW) April–May 1998 (Fig. 1). Additional northern hemisphere sampling of relevance to this paper took place at the University of Copenhagen Arctic Station (Disko Bay, West Greenland) during the summers of 1988, 1990 and 1994, and from the Adventsfjord and Isfjord, Svalbard, during June 2012 and August 2013 respectively (Fig. 1).

The Antarctic material originates from the R/V 'Melville' AMERIEZ cruise (March 1986), the R/V 'Polarstern' ANT VII/3 'EPOS II' cruise (Nov. 1988 – Jan. 1989) and the R/V 'Polarstern' ANT X/3 'Herbst im Eis' cruise (April–May 1992), with all cruises occupying stations in the Weddell Sea region (Fig. 2). The protocol for processing water samples for the TEM were similar on all sampling occasions (see Thomsen *et al.* 2013 for further details). Material for the SEM (Svalbard / Figs 40–41) was prepared by gentle filtration of a water sample on top of a 1.0 µm 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 used in the taxonomic descriptions largely follows Young *et al.* 1997.

## RESULTS

### *Mercedesia* gen. nov.

Diagnosis: Small biflagellate coccolithophorids with a short haptonema. Nannoliths monomorphic and star-shaped (triradiate). A lamina sometimes fills the spaces between the three rays of the stellate nannolith. Small organic underlayer scales not observed.

Type species: *Mercedesia aspiphora* sp. nov.

Etymology: '*Mercedesia*' is used here because of the reminiscence to the three-pointed star in the centre piece of the Mercedes-Benz logo.

*Mercedesia* is a highly distinct genus that cannot be confused with any extant coccolithophorid taxon. Triradiate stellate nannoliths are known from the geological record, e.g. *Discoaster triradiatus* Tan (Young 1998) and *Marthasterites tribrachiatus* (Bramlette & Riedel) Deflandre (Black 1968). Apart from the morphological differences there is also a profound tenfold size difference between these nannofossils and the nannoliths of the type species *M. aspiphora* and the other species, rendering a direct relationship very unlikely. The calcified nature of the *Mercedesia* coccosphere has been verified by an X-ray elemental analysis of the periplast (Thomsen *et al.* 1988).

### *M. aspiphora* sp. nov. (Figs 3–8)

Syn.: 'Coccolithophorid sp. 1' in Thomsen *et al.* 1988 (loc. cit. Fig. 47).

Diagnosis: Cell quasispherical (diam. 3–5 μm) with two flagella (ca. 20 and ca. 25 μm long) and a somewhat shorter haptonema (10–15 μm). The coccosphere (Fig. 5) consists of a dense layer of monomorphic triangular, slightly convex nannoliths. The nannoliths have three slightly concave sides (ca. 0.5 μm long) and a central three-armed rib pattern on the distal side (Figs 3, 4, 7). Most cells have nannoliths with a small central nodule on the distal side (Figs 3, 7).

Holotype: Figs 3, 6 (same cell) from the Weddell Sea, Antarctica (EPOS st. #161 at 57°30.3 S / 47°00.6 W) occurring in a mixed sample from 10 and 20 meters depth and processed on 13 December 1988.

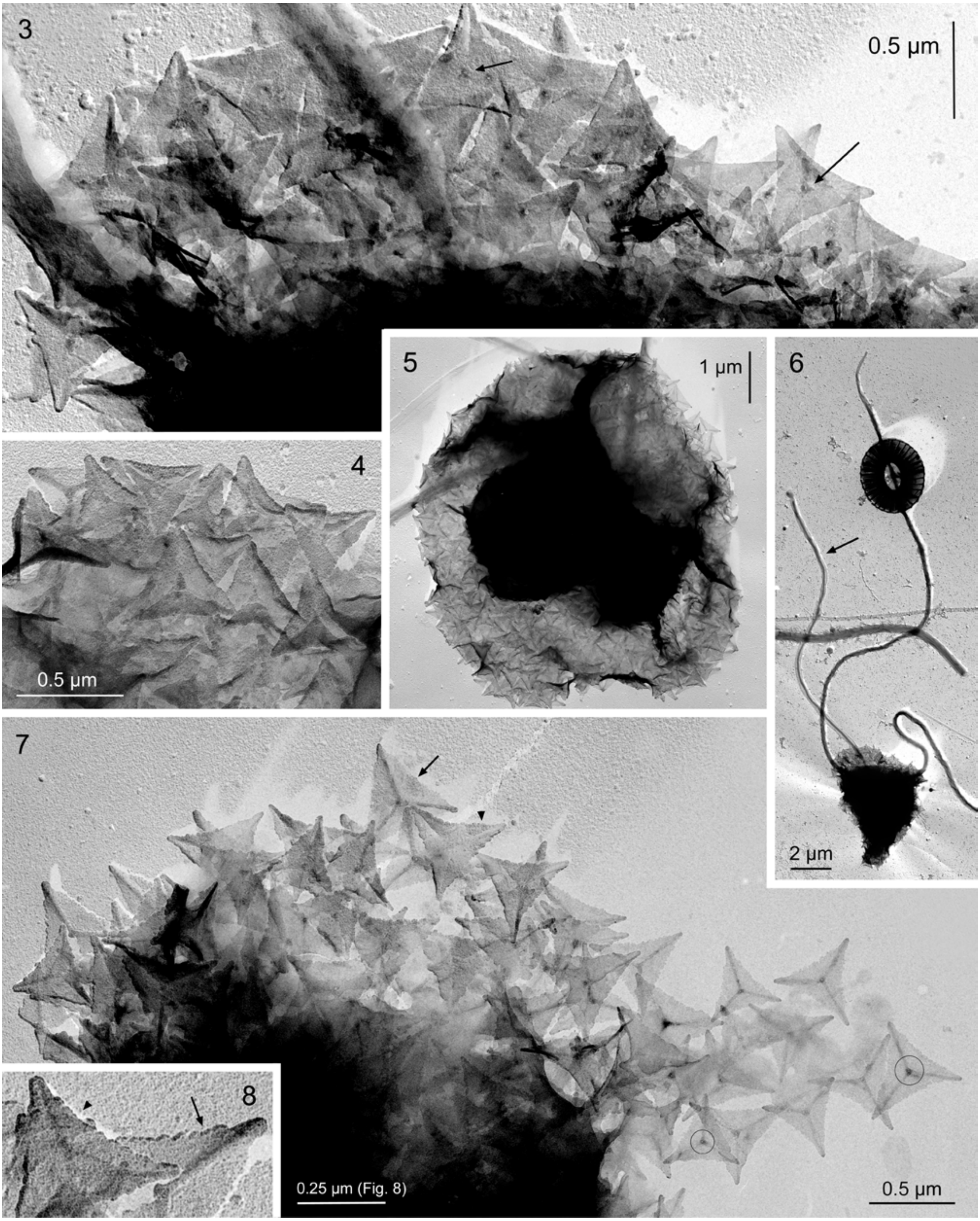
Etymology: 'aspis' (Gr.) shield and 'phora' (Gr.) carrying.

Numerical details of *M. aspiphora* have been accounted for in Table 1. The interpretation above of nannolith shape and form, in particular with respect to the distal convexity of the liths, remains questionable and can most likely only be fully ascertained from sectioned material studied in the TEM. The critical question is whether the nannoliths are in fact triangular and convex with the 3 ribs on top or if they are rather concave with 3 radial depressions. We have here assumed for geometrical reasons that the concave face of the triangular nannolith is most likely representing the proximal side. Figs 7–8 show both sides of the nannoliths. The arctic coccospheres originating from NEW deviates slightly from the antarctic EPOS material in having minutely serrate edges on the triangular nannoliths (Figs 7–8). However, this could very well be an artefact caused by partly decalcification of the nannolith rims. There is no indication for presence of organic underlayer scales in this taxon, nor have we observed combination cells involving *M. aspiphora.*

*Mercedesia aspiphora* was abundant (> 25 specimens) in samples from Antarctica (AMERIEZ, EPOS) and rare (< 5 specimens) in samples from the Arctic (NEW, NOW).

**Table 1.** Cell and nannolith dimensions (μm) of *Mercedesia aspiphora*. Notice that none of the measurements, e.g. cell diameter, have been corrected for the transformation from a 3D to a 2D object that occurs to a variable degree during cell drying.

| Flagella | Haptonema | Cell diam. | Nannolith dimensions (edge) | | | | Source of material (microgr. #) |
|---|---|---|---|---|---|---|---|
| | | | Mean | SD | min/max | n | |
| 21/25 | 11.8 | 3.3 × 4.9 | | | | | EPOS 10007 (Fig. 6) |
| | | | 0.671 | 0.078 | 0.607–0.847 | 10 | EPOS 10006 (Fig. 3) |
| 20.4/21.7 | 10.6 | 4 × 5 | 0.486 | 0.034 | 0.398–0.520 | 18 | EPOS 11296 + 11297 |
| 19.6/24.7 | 14.6 | 4.2 × 4.8 | 0.483 | 0.073 | 0.4–0.6 | 6 | EPOS 4912 |
| | | c. 5 | 0.433 | 0.029 | 0.395–0.487 | 9 | NEW 24936 (Figs 4, 5) |
| | | | 0.549 | 0.055 | 0.432–0.638 | 18 | NEW 24896 (Fig. 7) |
| | | | 0.461 | 0.061 | 0.366–0.569 | 9 | NOW 39922 |


3
0.5 µm
4
0.5 µm
5
1 µm
6
2 µm
7
8
0.25 µm (Fig. 8)
0.5 µm

***Mercedesia multistellata*** **sp. nov. (Figs 9, 10, 14, 15)**

Diagnosis: Cell elongate (c. 4 × 5 µm) with two flagella (12.5/9.5 µm) and a shorter haptonema (ca. 7 µm) (Fig. 10). Nannoliths are monomorphic three-pointed stars (Figs 9, 14, 15), with arms slightly bent in proximal direction. The individual arms gradually taper towards the tip. The mean value 'tip-to-tip' distance is 0.46 µm.

Holotype: Figs 9, 10, 14, 15 (same cell) from the Kane Basin, NW Greenland (NOW st. #B7 at 79°00.096 N / 73°19.964 W) occurring in a sample from 40 meters depth and processed on 12 May 1998.

Etymology: from 'multi' (L) meaning many and 'stella' (L) meaning star.

Numerical details of *M. multistellata* have been accounted for in Table 2. The tip-to-tip distance between neighbouring arms is 0.46 µm (mean value) which is basically identical to the edge length in *M. aspiphora* coccoliths from the same geographical area (Table 1).

The star-shaped nannoliths somewhat resemble the central three-armed rib-pattern on the nannoliths of *M. aspiphora* but without the membranous material between the arms of the ribs. However, we don't think that *M. multistellata* nannoliths represent an extreme variation of the *M. aspiphora* morphological theme, because of the robust appearance of the stars in *M. multistellata* and the absence of intermediate forms in our material.

In nannoliths resting on all three arms these appear to be equally long (Figs 9, 14, 15). A tilted position of nannoliths often causes these to display two complete arms and a 'short' arm (Figs 9, 15 arrows), with the short arm appearing much darker in the micrograph as a microscopy artefact. Organic under layer scales have not been observed and there is no indication of life cycles involving *M. multistellata*.

The nature of the small spherical structures that appear among the nannoliths (Figs 9, 10) is unknown to us.

*Mercedesia multistellata* was found in three different samples from NW Greenland (NOW) and has also been observed in a single sample from NE Greenland (NEW) (Gammelgaard, personal communication). A cluster of nannoliths reminiscent of *M. multistellata* have been observed by Østergaard (unpublished results) from tropical waters (Phuket, Thailand).

***Mercedesia pusilla*** **Thomsen & Østergaard (Figs 11–13)**

Syn.: 'Coccolithophorid sp. 1' in Thomsen *et al.* 1988 (loc. cit. Fig. 46).

Diagnosis: Cell elongate (c. 2.5 × 4 µm) with two flagella (19.5/22 µm) and a shorter haptonema (ca. 13 µm). Nannoliths are monomorphic, shaped like three-pointed stars with arms slightly bent in proximal direction. The central part, the base of the arms is fairly broad. The nannolith centre is characterized by a central pore. The mean value 'tip-to-tip' distance is 0.28 µm.

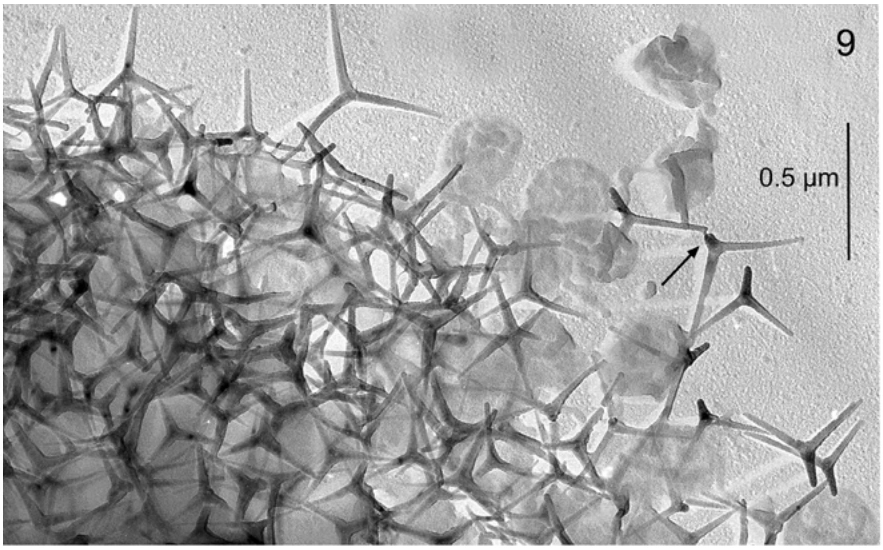
Holotype: Figs 11, 13 (same cell) from the Weddell Sea, Antarctica (EPOS st. #186 at 57°57 S /49°00 W) occurring in a mixed sample from 10 and 20 meters depth and processed on 28 December 1998.

Etymology: 'pusillus' (L) meaning very small.

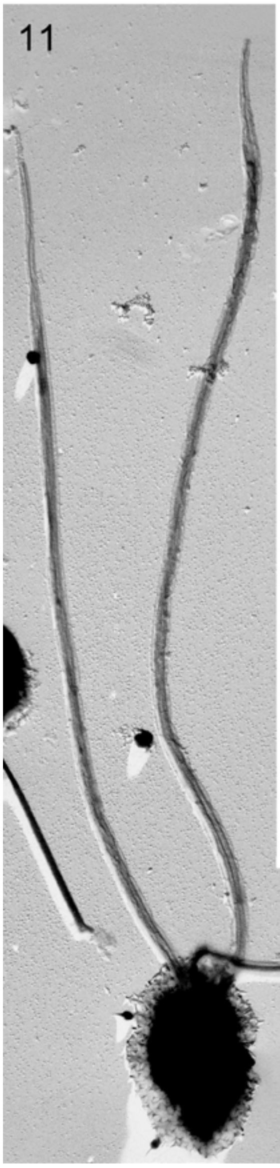
The Antarctic EPOS material comprised a few cells (Figs 11–13) closely reminiscent of *M. multistellata* in many aspects except for the dimensions and the shape of the central part of the three-armed, star-shaped nannoliths (Figs 12, 13). Numerical details have been accounted for in Table 2. It appears that *M. pusilla* is on the average half the size of *M. multistellata* when comparing dimensions of the individual nannolith. The central nannolith pore, which is very conspicuous in the material examined here (Figs 12–13), was also evident in the AMERIEZ cell previously illustrated by Thomsen *et al.* (1988; loc. cit. Fig. 46). This structural element thus appears to constitute a fairly prominent diagnostic feature of this new taxon.

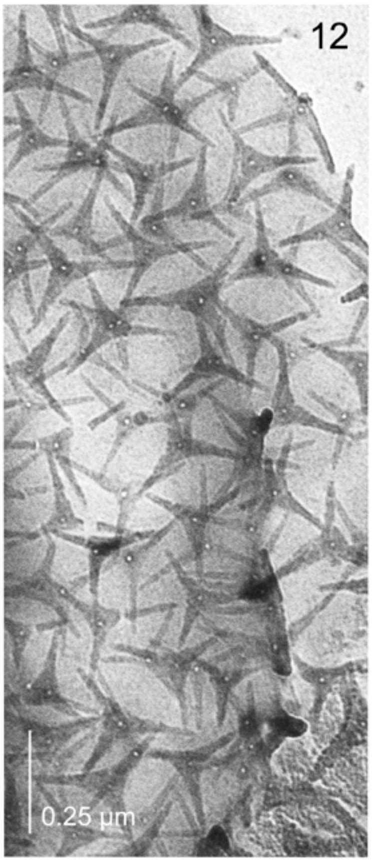
◂◂

**Figs 3–8.** *Mercedesia aspiphora*. TEM whole mounts (Figs 3, 6) from Antarctica (EPOS) and (Figs 4, 5, 7, 8) from the Arctic (NEW). **3** – high magnification of triangular nannoliths from the cell shown in Fig. 6; arrows point to distinct central knobs; **4** – high magnification of nannoliths from Fig. 5; **5** – complete cell with armour of triangular nannoliths; **6** – complete cell (type material) with appendages; the haptonema (arrow) is both shorter and thinner than the flagella; a single coccolith (*Emiliania huxleyi*) almost the size of the entire *M. aspiphora* cell obscures part of the flagellum; **7** – high magnification of nannoliths; the arrow points to a nannolith with the distal face upwards, whereas an arrowhead points to a nannolith with the proximal face exposed; circles indicate distinct central knobs; **8** – detail from Fig. 7 showing the finely serrate margin of the nannoliths in distal (arrow) and proximal (arrowhead) views.

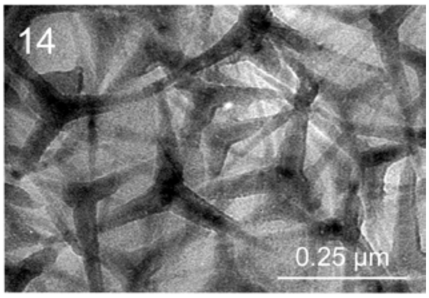

9
0.5 µm


10
1 µm


11
2 µm


12
0.25 µm


13
0.25 µm


14
0.25 µm

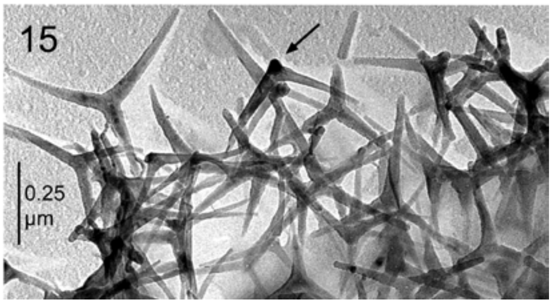

15
0.25 µm

**Table 2.** Nannolith dimensions (µm) of *Mercedesia multistellata* and *M. pusilla*.

| Nannolith dimensions (µm) | Spine length | | | | "Tip-to-tip" distance | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Range | n | Mean | SD | Range | n |
| ***Mercedesia multistellata*** | | | | | | | | |
| NOW (Figs 9, 15) | 0.292 | 0.032 | 0.244–0.369 | 20 | 0.459 | 0.057 | 0.369–0.599 | 20 |
| ***Mercedesia pusilla*** | | | | | | | | |
| EPOS (Fig. 13) | 0.133 | 0.012 | 0.110–0.158 | 25 | 0.22 | 0.025 | 0.173–0.279 | 25 |
| EPOS (Fig. 12) | 0.17 | 0.014 | 0.144–0.198 | 20 | 0.284 | 0.022 | 0.238–0.327 | 20 |
| AMERIEZ (Thomsen *et al.* 1988, loc. cit. Fig. 46) | 0.117 | 0.013 | 0.094–0.144 | 20 | 0.204 | 0.021 | 0.167–0.248 | 11 |

### *Ericiolus frigidus* Thomsen in Thomsen *et al.* 1995 (Figs 16–20)

Syn.: 'Coccolithophorid sp. 2' in Thomsen et al. 1988 (loc. cit. Figs 48–49).

The morphological interpretation of the calcified tetrads of spines ('caltrops') encasing the cell (Fig. 16) is somewhat hampered due to the fact that the coccosphere rarely breaks apart and almost no individual nannoliths are exposed. Tetrads of spines shown in Figs 17–18 represent the rare exceptions. A re-examination of material from Antarctica (EPOS) does not add substantial new information to the original description (Thomsen *et al.* 1995). The individual lith is four-armed (Figs 17–18) with one outwardly pointing spine commonly more robustly developed, slightly longer (0.264 ± 0.021 µm / n = 14) and wider (0.052 ± 0.01 µm / n = 20) than the other three arms (0.24 ± 0.039 µm / n = 6). The re-examination of *E. frigidus* has not revealed organic under layer scales, nor have we observed combination cells involving *E. frigidus*. Two complete cells of *E. frigidus* are shown in Figs 19–20. The cell body is very characteristically heart shaped with dimensions ranging between 3.6 and 4.4 µm. The flagella are of slightly dissimilar length (Fig. 19: 20.8/22.9 µm and Fig. 20: 18.4/21 µm). The haptonema is much shorter (Fig. 19: 12.4 µm).

*Ericiolus frigidus* is regularly occurring in samples from Antarctica (AMERIEZ, EPOS, ANT X/3) but has not so far been observed in samples from the Arctic. The *Ericiolus* type species, *E. spiculiger* Thomsen in Thomsen *et al.* 1995, was described from Danish coastal waters, and has not so far been observed outside this area.

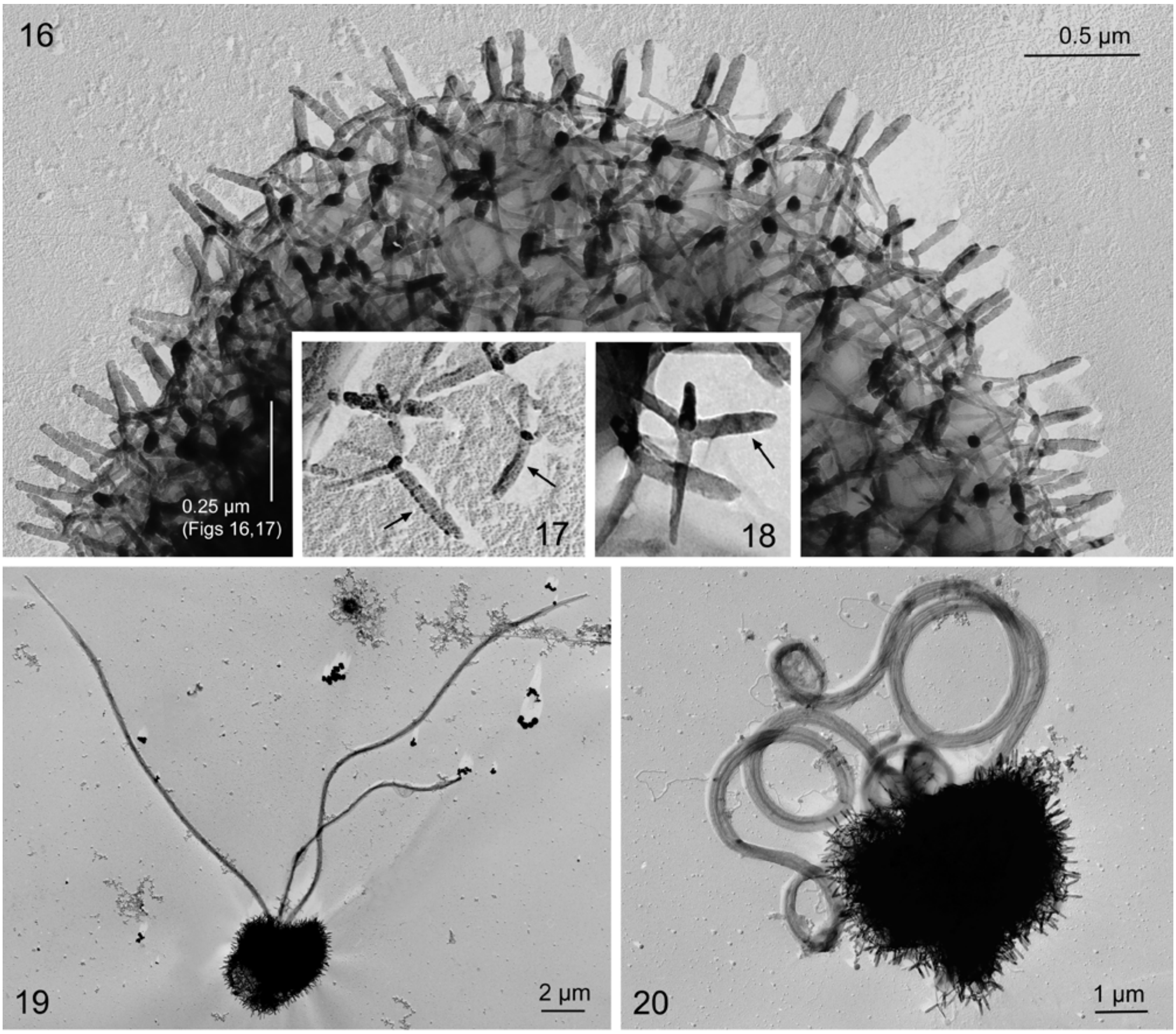
*Ericiolus frigidus* bears a slight resemblance to *Polycrater* sp. in Cros & Furtoño (2002; loc. cit. Figs 82C, D). However, the additional proximal part of the coccoliths of that taxon, with its four-sided symmetry is very different.

### *Quaternariella obscura* Thomsen 1980d (Figs 21–33)

This taxon was described based on material from West Greenland (Arctic Station). The main diagnostic feature is packages of rhombohedral crystallites (typically in groups of four) evenly distributed over the entire cell surface. The coccolith base plate scale is circular and rimmed and has a diameter of approx. 0.6 µm (Thomsen 1980d). Evidence is also available documenting the presence of small non mineralized under layer scales (Thomsen 1980d; loc. cit. Fig. 6).

◀◀

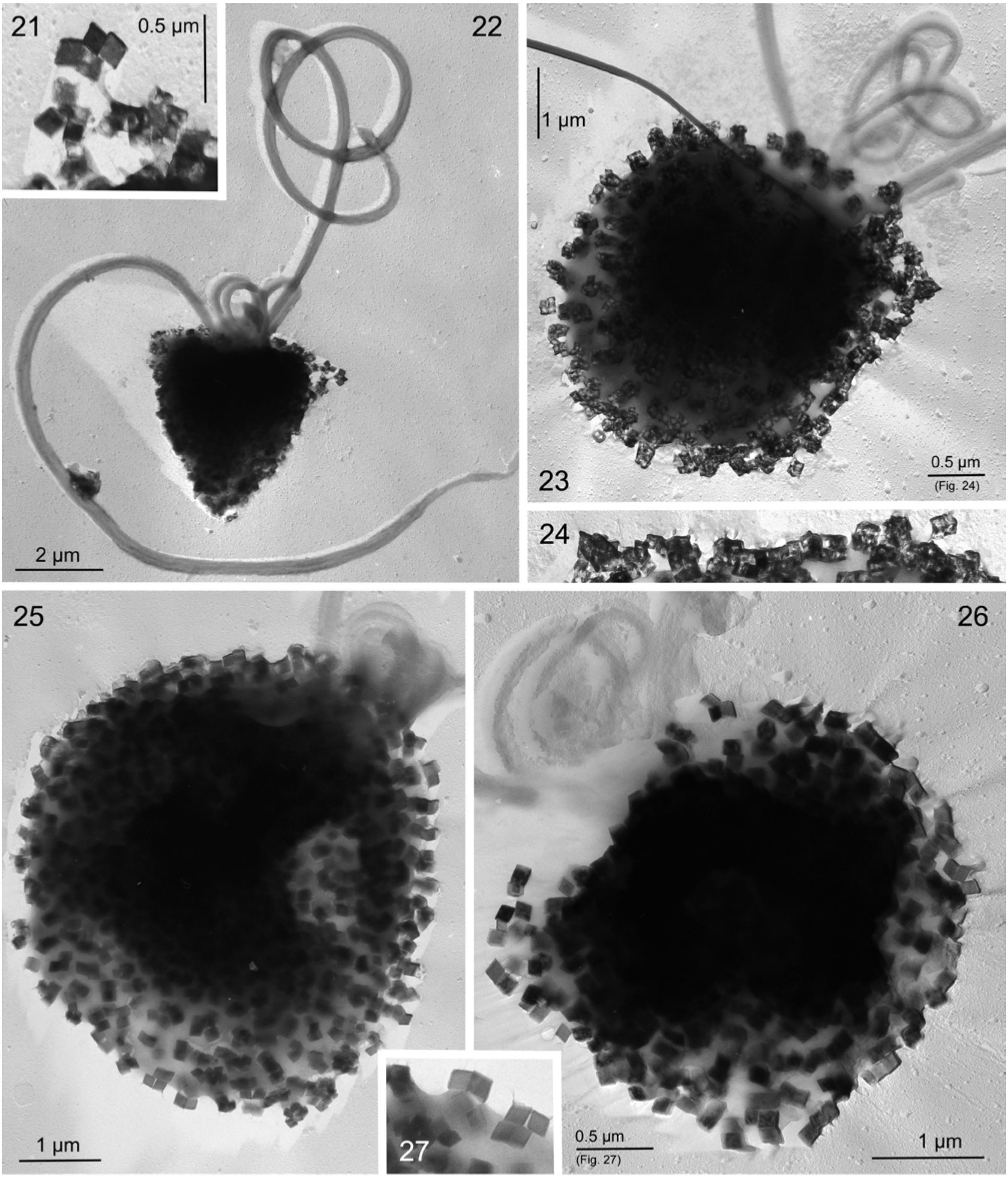
**Figs 9–15.** *Mercedesia* spp. TEM whole mounts of *M. multistellata* (Figs 9, 10, 14, 15) from the Arctic (NOW) and *M. pusilla* (Figs 11–13) from Antarctica (EPOS). **9** – scatter of nannoliths from the cell shown in Fig. 10; arrow points to an asymmetrically positioned 'two-armed' nannolith; spherical structures of unknown origin occur among the nannoliths; **10** – complete cell (*M. multistellata* type specimen) with stretched out flagella and haptonema (arrow); **11** – whole cell (*M. pusilla* type specimen) with flagella and a shorter haptonema that stretches out perpendicular to the cell (arrow); **12** – detail of nannoliths showing the central pore; **13** – high magnification of nannoliths from the cell shown in Fig. 11; **14** – detail of nannoliths (from Fig. 10) showing the rather robust appearance of some nannoliths; **15** – detail of nannoliths (from Fig. 10) showing a perfectly aligned nannolith and others that are tilted to the extent that one arm is 'reduced' to a dark spot (arrow).



**Figs 16–20.** *Ericiolus frigidus*. TEM whole mounts from Antarctica (EPOS). **16** – detail of anterior cell end showing the entangled armor of nannoliths with the most solid spine pointing outwards; **17** – detail of single nannoliths showing the tetrads of spines; the outwardly projecting spine (arrows) is more robust than the other three spines; **18** – more robust single nannolith; the arrow points to the outwardly directed spine; **19** – whole cell with extended flagella and a somewhat shorter haptonema; notice the highly characteristic heart-shaped cell body; **20** – a second example of a heart-shaped coccopshere with appendages.

Most probably there is a cluster of four crystallites in the centre of each scale. Here we illustrate additional material from the type locality (Figs 21–22) and also document the occurrence of this taxon in NE Greenland (NEW / Figs 23–27) as well as from Antarctica (EPOS / Figs 28–29). Irrespective of the origin of the material the general appearance is very similar. Numerical details have been accounted for in Table 3.

We provide here for the first time evidence for the existence of different life cycle phases in *Q. obscura* (Figs 30–33). We found three combination cells in the Arctic that display typical *Q. obscura* holococcoliths in one half of the cell whereas the other half carries heterococcoliths that bear resemblance to e.g. *Papposphaera* spp. (Figs 30, 32). The contours of the individual heterococcolith can be traced and we can additionally



**Figs 21–27.** *Quaternarielle obscura*. TEM whole mounts from the Arctic, viz. West Greenland/Arctic Station (Figs 21, 22) and NEW (Figs 23–27). **21** – groups of crystallites; **22** – complete cell with appendages; **23** – complete cell with curled up haptonema and nicely organized packages of crystallites; **24** – detail from Fig. 23 showing the boxed organization of crystallites; dissolution phenomena are obvious; **25, 26** – complete cells showing an even spread of crystallite packages; **27** – high magnification of single rhombohedral crystallites.

**Table 3.** Coccolith dimensions (µm) of *Quaternariella obscura*. Notice that none of the measurements, e.g. cell diameter, have been corrected for the transformation from a 3D to a 2D object that occurs to a variable degree during cell drying.

| Flagella | Haptonema | Cell diam. | Crystallite (edge) | | | | Source of material |
|---|---|---|---|---|---|---|---|
| | | | Mean | SD | min/max | n | |
| 20.8/25.4 | | 3.8 | 0.119 | 0.011 | 0.099/0.132 | 8 | Arctic Station, W. Greenland (Figs 21,22) |
| | | 4.3 × 5.3 | 0.097 | 0.013 | 0.078/0.122 | 18 | Arctic Station, W. Greenland (Fig. 30) |
| | 13.2 | 4.3 × 4.8 | | | | | NEW (Figs 23,24) |
| | | | 0.127 | 0.014 | 0.110/0.152 | 14 | NEW (Figs 25, 27) |
| | | 3.1 × 3.5 | 0.129 | 0.016 | 0.09/0.16 | 18 | NEW (Fig. 26) |
| | | 2.5 × 3.8 | 0.115 | 0.013 | 0.087/0.139 | 21 | EPOS (Figs 28–29) |

account for at least some details of the rim calcification. In the combination cells (Figs 30, 32) the heterococcolith rims have fallen apart into the individual elements. This probably is due to the very delicate structure of the rim. The heterococcolith central area is oval and measures 0.47–0.61 × 0.82–0.96 µm which is within the size range typical for species of *Papposphaera*. Unfortunately we were not able to resolve the exact structure of the central area calcification, although Fig. 33 shows that it seems to consist of a heap of irregularly placed elements. The rim consists of a proximal/inner cycle of rod shaped elements aligned end-to-end (Figs 30, 32–33). The distal/outer cycle is built of differently sized pentagonal and square elements (height: 0.27–0.38 µm). In an undisturbed coccosphere these element most likely will closely adjoin to form a somewhat widening tube encircling the central area. The overall appearance and the dimensions of the rim thus coincide with those described from species of *Papposphaera* (see e.g. Thomsen *et al.* 1981, loc. cit. Fig. 5).

The cell illustrated in Figs 34–35 is interpreted as a complete specimen of the heterococcolithophorid stage within the *Quaternariella obscura* life cycle. The absence of muroliths with a central process must be noted although more material obviously needs to be examined to verify whether this is a persistent feature of this species. An enlargement of selected coccoliths in Fig. 35 shows, in support of the morphological interpretation of the coccolith shown in Fig. 33, that the central area calcification comprises a flat layer of irregular aggregations of elements of different size and shape. It is also evident that this cell shares the irregular appearance of the outer edge of the coccolith rim with the cells illustrated in Figs 30, 32.

Although the rim of the heterococcoliths in the combination cells resembles that of *Papposphaera* coccoliths, the absence of a central process and the aberrant structure of the central area makes it is difficult to assign these heterococcoliths to *Papposphaera* or any other known heterococcolithophorid genus. However, from a taxonomic point of view it is in the future sufficient to refer to the heterococcolith phase as *Q. obscura* HET.

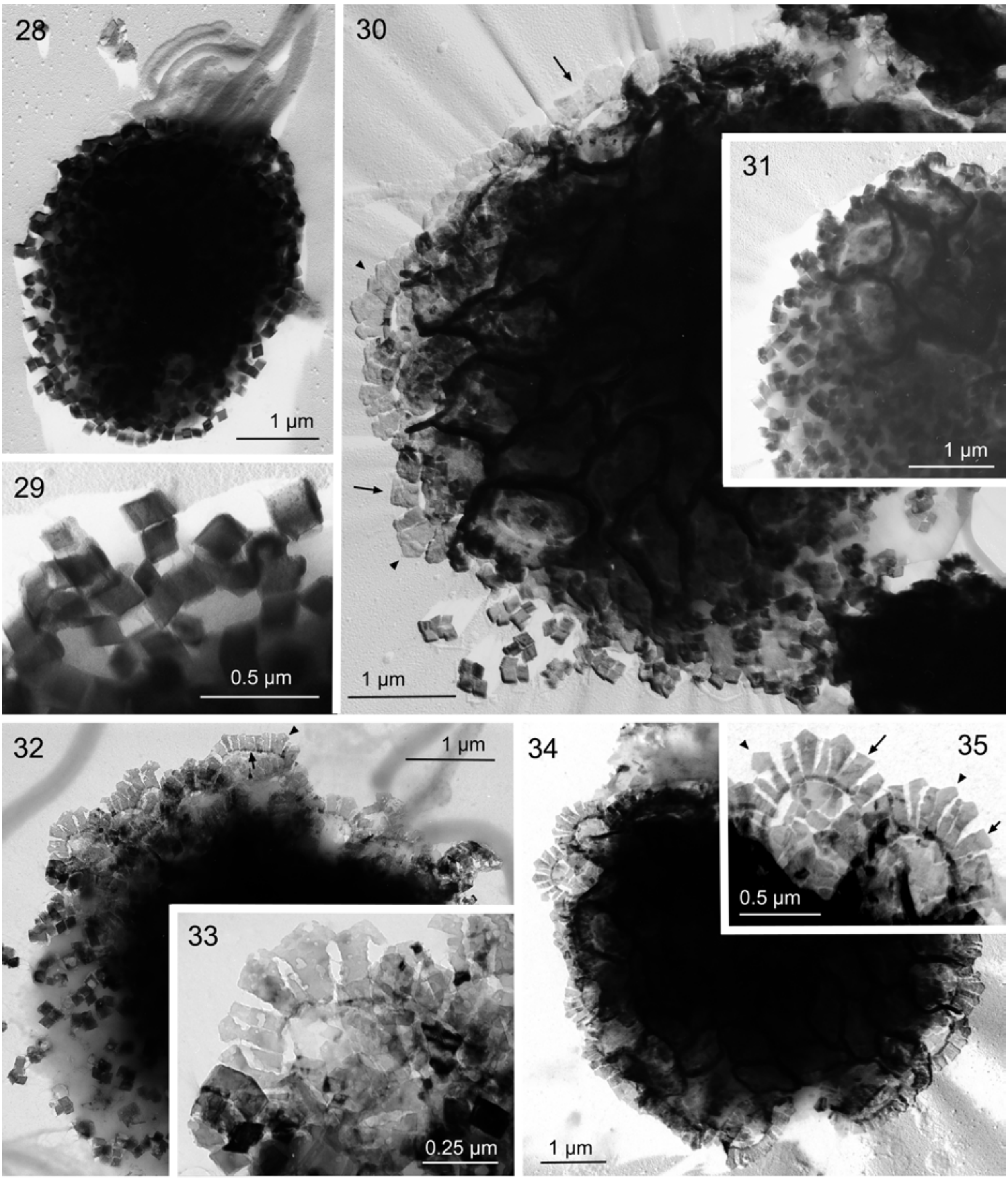
### ***Porsildia* gen. nov.**

Diagnosis: Coccosphere dimorphic. Circumflagellar coccoliths have a central process formed proximally by numerous densely aggregated elements and distally terminating in two closely aligned elongate elements. Body coccoliths oval. In both coccolith types the vertical wall consists of slightly overlapping elements that vary in size and shape. The central area of the body coccoliths has a low central structure of irregularly piled elements that vary in size and shape; this structure is not connected to the rim.

Type species: *Porsildia acerviphora* sp. nov.

Etymology: Genus named in honour of Dr. Morten Porsild – a Danish botanist – who founded the University of Copenhagen Arctic Station (Qeqertarsuaq, West Greenland) in 1906.

*Porsildia* gen. nov. bears resemblance to genera of the Papposphaeraceae Jordan and Young 1990, and in particular to *Papposphaera* Tangen 1972 and *Pappomonas* Manton and Oates 1975. Both genera have coccoliths with a characteristic murolith rim, a narrow wall, and a distally protuding structure in a wide variety of shapes on the central area. Central area and process structure are the key features with respect to species identification. The coccosphere may be monomorphic, dimorphic, varimorphic or polymorphic. *Porsildia* body coccoliths on the other hand have a unique and very different structure of the central area.



**Figs 28–35.** *Quaternariella obscura*. TEM whole mounts from Antarctica (EPOS) (Figs 28–29) and (Figs 30–35) West Greenland (Arctic Station). **28** – complete cell from the southern hemisphere; **29** – detail of the periplast from Fig. 28; **30** – *Q. obscura* combination cell (Arctic Station 1990) showing *Papposphaera*-like coccoliths along one side of the cell; arrows point to square rim elements and arrowheads to pentagonal elements; **31**– a second combination cell (Arctic Station 1990) where heterococcoliths are visible as dark, oval structures; **32** – combination cell collected near Arctic Station during 1988; arrow points to square rim elements and arrowhead to pentagonal elements; **33** – Detail from Fig. 32; **34** – complete coccosphere with heterococcoliths that are similar to those shown in Figs 30, 32; **35** – detail from Fig. 34. Arrows point to square rim elements and arrowheads to pentagonal elements; notice also the irregular elements in the central area of the coccolith.

***P. acerviphora*** **sp. nov. (Figs 36–41)**

Diagnosis: With all characteristics of the genus. Up to 10 circumflagellar pole coccoliths. The central process measures 1.7–1.9 µm in length and 0.2–0.3 µm in width. The length of the distal twin pair of elongate elements is 0.5–0.7 µm. Body coccoliths oval (1.0–1.2 × 0.6–0.7 µm) with an irregular outline and a central heap of calcified elements. The rim has an irregular upper margin and it is asymmetrical; one end bears a distinctly larger, widening and pointed, element of variable shape. The height of the rim is variable within the range 0.2–0.4 µm.

Holotype: Figs 37, 39 (same cell) from Arctic Station, Disko Bay, West Greenland, occurring in a sample from 50 metres depth (34 PSU, 2°C) processed 1 Sep. 1990.

Etymology: from 'acervus' (L) pile and 'phora' (Gr.) carrying.

The material from West Greenland, comprising only two specimens, is supplemented with material from Svalbard (courtesy of M. Heldal, Univ. of Bergen) collected from the Adventsfjord (June 2012) and the Isfjord (Aug. 2013). The SEM images (Figs 40–41) document the general appearance of the robust central process. The solid and somewhat irregular rim is also evident from both micrographs, as is also the pile of rectangular elements found in the central area of a body coccolith. Numerical data comparing material from West Greenland and Svalbard is provided in Table 4. It is evident that the cells examined, irrespective of geographical origin or times of collection, are basically identical. It is evident from Fig. 41 that the central area heap of calcified elements in body coccoliths shows much diversity with regard to shape and dimensions of the individual elements. Some are square while others are rectangular. Typical dimensions are within the range 0.12–0.23 µm and the thickness of a plate ca. 0.05 µm. The material examined so far does not allow for conclusions with regard to the structure of the central area in the circumflagellar coccoliths.

*Porsildia acerviphora* is included in this paper because of its Arctic origin and also because its body coccoliths have a structure similar to those found on the heterococcolithophorid species that forms part of the *Quaternariella obscura* life cycle (Figs 30–35). Shared characteristics are 1) the coccolith wall formed by an irregular mix of square (Figs 30, 32, 35, 39; arrows), rectangular and pentagonal (Figs 30, 32, 35, 39; arrowheads) elements, and 2) the occurrence of a central structure of differently sized and shaped elements in the central area of the body coccoliths (Figs 33, 35, 39, 41).

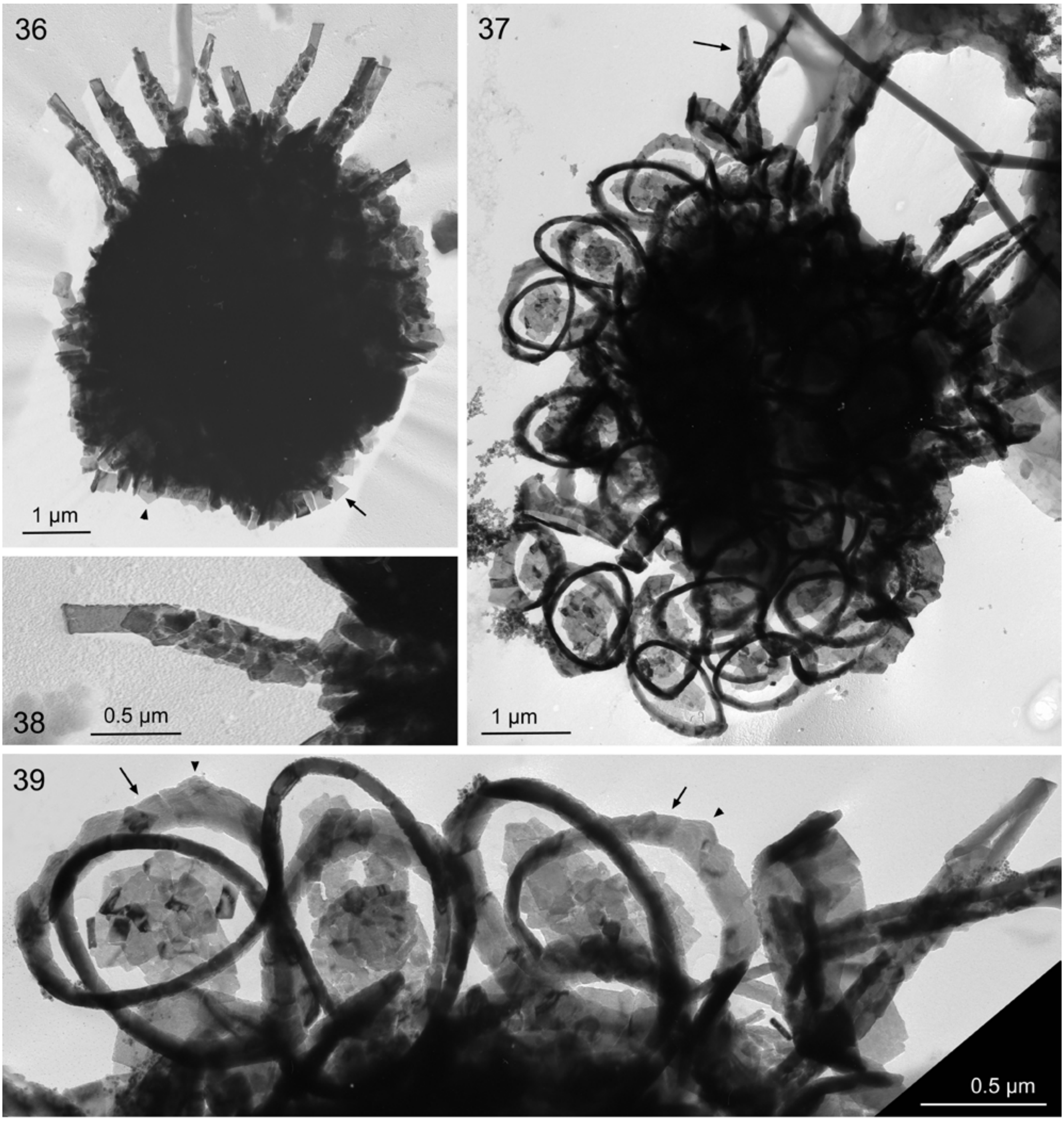
## DISCUSSION

Due to their small size and rare occurrence these forms will be found only coincidentally. Modest cell dimensions and the lack of conspicuous external features makes identification of these forms almost impossible unless examined as whole mounts in the TEM. The current biogeographical pattern as given in Table 5, therefore will only represent a small fraction of the true distributional range of these enigmatic taxa.

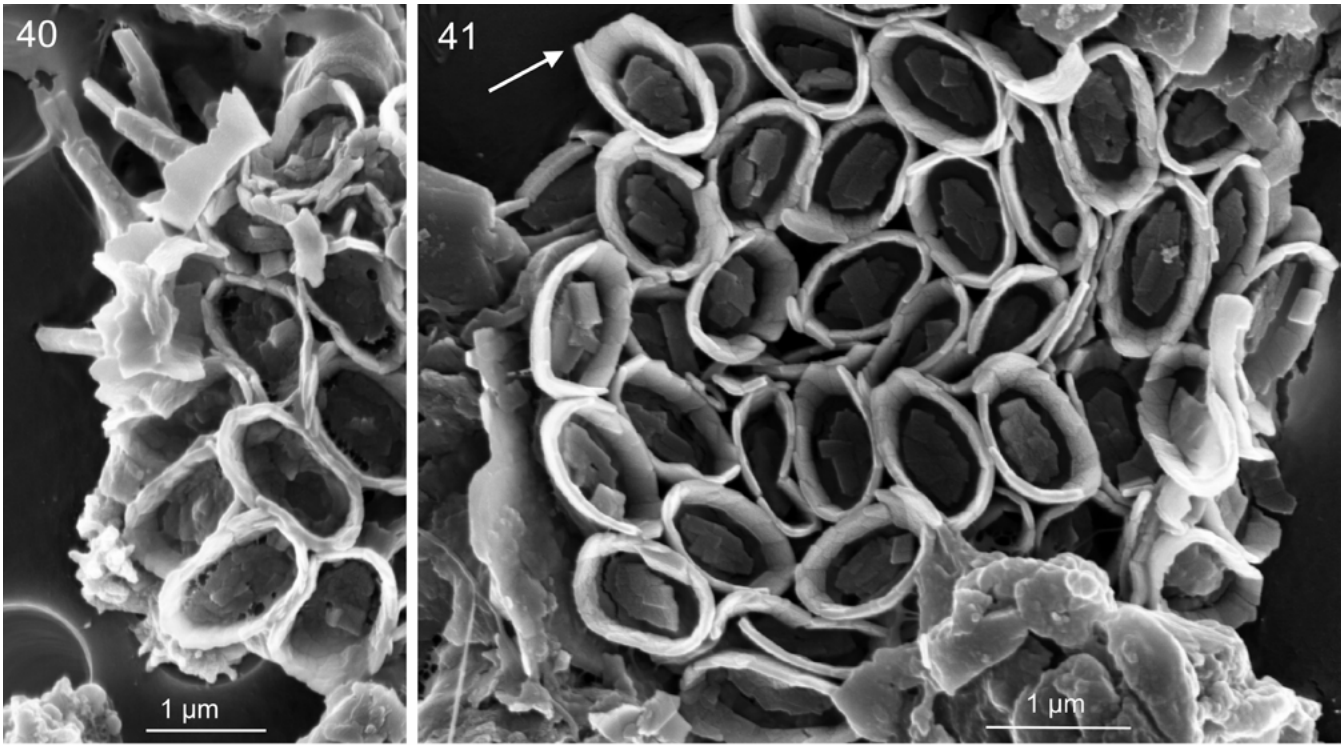
It is somewhat surprising, considering the occurrence in the NOW polynya and the multi decadal and intensive sampling effort ca. 1000 km further south, that so far *M. aspiphora* has not been recorded from Disko Bay (Arctic Station). It might be hypothesized that this species is biogeographically confined to the high Arctic while not being similarly competitive at a sub-arctic site. It is similarly worth emphasizing that neither *M. aspiphora* nor *M. pusilla* has been recorded while examining the ANT X/3 material despite the fact that the AMERIZ, EPOS and ANT X/3 material is very similar in terms of coccolithophorid diversity. The apparent bipolar distribution of *M. aspiphora* calls for verification by means of molecular tools.

**Table 4.** Coccolith dimensions (µm) of *Porsildia acerviphora*.

| Source of material | Cell diam. | Central appendage (flag. pole coccolith) | | | Body coccolith | | Rim |
|---|---|---|---|---|---|---|---|
| | | Length (total) | Length (term.) | Width | Length | Width | Height |
| Arctic Station, W. Greenland (Figs 36–39) | c. 5 | 1.6–1.9 | 0.5–0.7 | 0.2–0.3 | 1.0–1.2 | 0.6–0.7 | 0.2–0.4 |
| Svalbard, Adventsfjord | c. 5 | 1.6 | | 0.2 | 0.9–1.0 | 0.5–0.7 | 0.2–0.3 |
| Svalbard, Isfjord (Figs 40–41) | c. 5 | 1.3–1.5 | 0.40–0.45 | 0.2–0.3 | 0.7–1.0 | 0.5–0.6 | 0.2–0.3 |



**Figs 36–39.** *Porsildia acerviphora*. TEM whole mounts from Arctic Station, West Greenland, collected during 1990. **36** – cell with incomplete flagellation (only one flagellum visible); ten flagellar pole coccoliths with a central process; body coccoliths with an irregular rim formed by a mixture of differently shaped elements with squares (arrow) and pentagons (arrowhead); **37** – holotype; arrow points to a central appendage termination which is clearly divided into two elongate parallel elements; **38** – flagellar pole coccolith (detail from Fig. 36); **39** – high magnification of coccoliths (detail from Fig. 37); the central heap of elements as well as the irregular rim are evident; arrows point to square rim elements while toothed elements are denoted by arrowheads.



**Figs 40–41.** *Porsildia acerviphora*. SEM whole mounts from Isfjorden, Svalbard, collected during august 2013. **40** – detail of anterior cell end showing flagellar pole coccoliths; notice the highly irregular rim on the coccolith that is laterally profiled; **41** – body coccoliths showing solid rims as well as heaps of elements covering the central parts of the coccolith central area; an arrow points to a particularly enlarged rim element.

**Table 5.** Summary of biogeographical data for species of *Mercedesia, Ericiolus, Quaternariella* and *Porsildia.* Type localities are indicated by using bold face.

| Region | Arctic | | | | Antarctica | | |
|---|---|---|---|---|---|---|---|
| Locality | W. Greenland (Disko) | North East Water Polynya (NEW) | North Water Polynya (NOW) | Svalbard | Weddell Sea (AMERIEZ) | Weddell Sea (EPOS) | Weddell Sea (ANT X/3) |
| ***Mercedesia*** | | | | | | | |
| *M. aspiphora* | | 6 | 6 | | 3 | **6** | |
| *M. multistellata* | | 6 | **6** | | | | |
| *M. pusilla* | | | | | 3 | **6** | |
| ***Ericiolus*** | | | | | | | |
| *E. frigidus* | | | | | 3 | **6** | 6 |
| ***Quaternariella*** | | | | | | | |
| *Q. obscura* | **1**,2,4,5 | 6 | | | | 6 | |
| ***Porsildia*** | | | | | | | |
| *P. acerviphora* | **6** | | | 6 | | | |

1) Thomsen 1980d
2) Hansen *et al.* 1988
3) Thomsen *et al.* 1988
4) Østergaard (unpubl.)
5) Clausen *et al.* 1994
6) This paper

Future issues to resolve with respect to the species accounted for here will be to provide further morphological documentation of the heterococcolithophorid counterpart of *Q. obscura*, and complement our understanding of the genus *Mercedesia* by also providing evidence for its life history counterparts. The search for combination cells is most likely to be successful when based on future large scale surveys of live material processed for electron microscopy. The rationale behind this is that a two-step process of first establishing any of these forms in culture and subsequently manipulating environmental parameters to trigger a life-cycle switch is by no means a straightforward approach. Irrespective of this a critical future goal will anyway be to establish cultures or secure single cell isolates with an unequivocal species identification that can provide e.g. genetic sequence data, which will in turn help aligning the enigmatic forms studied here with other clusters of haptophytes.

**Acknowledgements.** Thanks are due to crew members and scientific personnel participating in the research cruises that supplied material for this publication. Staff at the Arctic Station, W. Greenland, are acknowledged for granting us access to the station and its facilities on many occasions. The work was supported by the ERC Advanced Grant project "MINOS" (project number 250254) and the NRC project MicroPolar (project number 225956/E10) through M. Heldal, University of Bergen. We greatly appreciate – courtesy of M. Heldal – the possibility to include SEM micrographs from various Svalbard localities. Thanks are due to an anonymous reviewer for providing multiple valuable suggestions for improving the manuscript.

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Received on 14th January, 2014; revised on 16th October, 2014; accepted on 16th October, 2014.