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Coccolithophorids in Polar Waters: *Pappomonas* spp. Revisited

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Abstract. A contingent of weakly calcified coccolithophorid genera and species were described from polar regions almost 40 years ago. In the interim period a few additional findings have been reported enlarging the realm of some of the species. The genus *Pappomonas* is revisited here with the purpose of providing, based on additional sampling from both polar regions, an update on species morphology, life history aspects and biogeography that can serve as a reference for the future. The examination of a substantial number of cells unequivocally supports the elevation to species level of *P. borealis* stat. nov. (previously referred to as *P. flabellifera* var. *borealis*) as a separate taxon which is different from *P. flabellifera* in a number of critical morphological features. Additional evidence in favour of linking *P. virgulosa* and *Balaniger balticus* in a shared life history in combination with significant differences in coccolith morphology between the *Pappomonas* type species (*P. flabellifera*) and *P. virgulosa* has prompted us to synonymise *Balaniger balticus* with *Pappomonas virgulosa*, while informally keeping the names of the phases as *Balaniger virgulosa* HET (= *Pappomonas virgulosa* phase) and *Balaniger virgulosa* HOL (= *Balaniger balticus* phase). A new species, *Pappomonas garrisonii* sp. nov. is described to accommodate Antarctic material from the Weddell Sea. While fitting into the *Pappomonas* generic concept, the species adds new dimensions to the overall appearance of the coccolith armour of the cell and emphasizes the close relationship between species of *Pappomonas* and *Papposphaera*.

Key words: coccolithophorid, *Pappomonas*, *Balaniger*, *P. garrisonii* sp. nov., 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).

INTRODUCTION

Lightly calcified coccolithophorids are persistently present in high latitude marine habitats. It has furthermore been evident since the early qualitative description of these taxa (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, 1991), that a majority of these are biogeographically confined to polar waters.

Using a quantitative and qualitative approach and multivariate statistics Charalampopoulou *et al*. (2011) has verified the existence of such a high latitude community of lightly calcified coccolithophorids (comprising species of *Wigwamma*, *Pappomonas*, and

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Papposphaera) that is highly distinct from all other assemblages studied along a transect from the southern part of the North Sea to the marginal ice edge north of Svalbard. Shared features among the contingent of polar coccolithophorids are modest cell dimensions (< 5 µm), lightly calcified coccoliths, elevated tolerance against low temperatures and high pH levels (Charalampopoulou *et al.* 2011), and lack of chloroplasts as an ultimate adaptation to life in a low light regime (Marchant and Thomsen 1994). The aplastidic condition indicates that these organisms are dependent for survival on scavenging bacteria and other small sized particles.

We are currently preparing a series of papers (Thomsen *et al.* 2013, Thomsen and Østergaard 2014) that will in turn and based on extensive additional sampling from both polar regions provide an update with regard to species diversity, life history events etc. with reference to each weakly calcified polar coccolithophorid genera. The current paper provides an overview of the genus *Pappomonas* Manton and Oates 1975, including the description of *P. garrisonii* sp. nov. from the Weddell Sea, Antarctica, and the transfer of *P. virgulosa* Manton and Sutherland 1975 to *Balaniger* Thomsen and Oates 1978. Circumstantial evidence exists in favour of linking species of *Pappomonas* with species of *Trigonaspis* Thomsen 1980a in a shared life cycle (Thomsen *et al.* 1991). The current status with regard to species diversity within *Trigonaspis* will be covered in a subsequent paper.

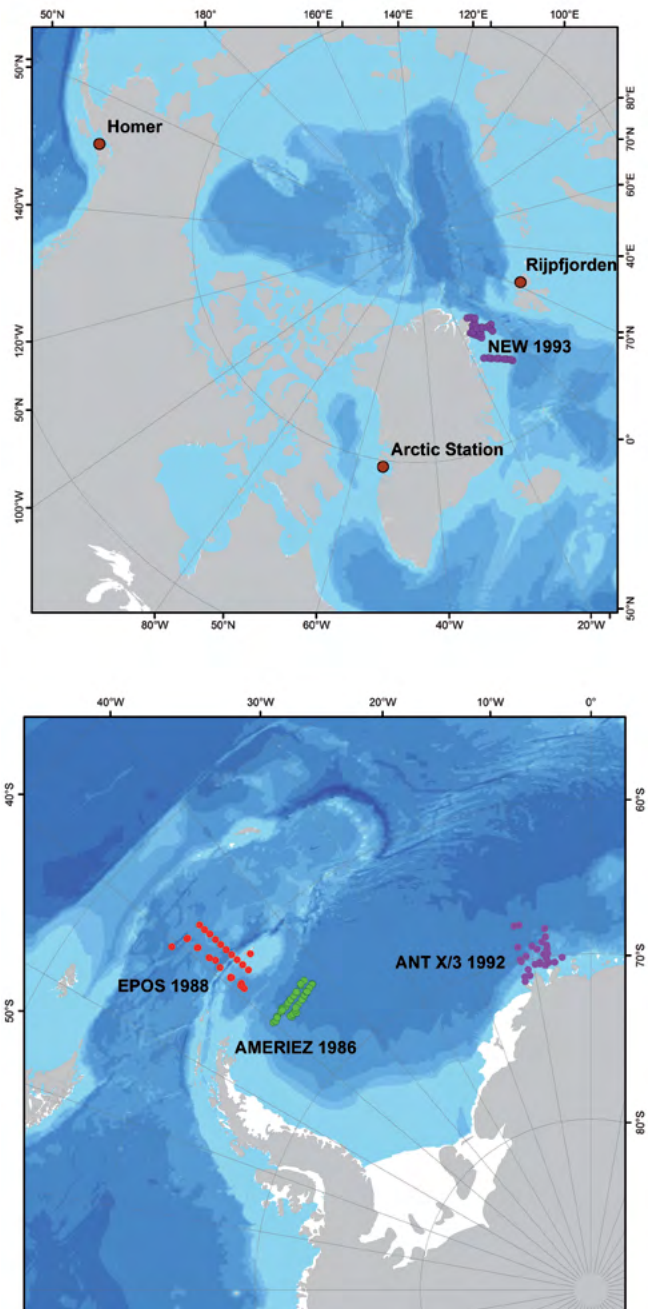
MATERIALS AND METHODS

For the purpose of this paper we have with regard to the Southern Ocean considered material sampled from south of the Antarctic Convergence, and in 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 here took place at the University of Copenhagen Arctic Station (Disko Bay, West Greenland) during the summers of 1988, 1990 and 1994 (Fig. 1) and from the Rijpfjorden, Svalbard (Fig. 1), during 2012.

The Antarctic material originates from 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 both cruises occupying stations in the Weddell Sea region (Fig. 2).

Material from California (Monterey Bay) and Mexico (Sea of Cortez), collected 1989–1990, has been included to address morphological variability within the *P. flabellifera* complex.



Figs 1–2. Collection sites. **1** – map of the Arctic showing the location of *Pappomonas* spp. sampling sites; **2** – map of the Weddell Sea, Antarctica, indicating *Pappomonas* sampling sites during three cruises.

The protocol for processing water samples for both the TEM and the LM were 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 20 µm) water sample or centrifugation of pre-

filtered material resuspended from an initial filtration of cells on top of e.g. a 1 µm Nuclepore filter. Small droplets of cells from the resuspended final pellet of material were – irrespective of the initial concentration procedure – placed on either carbon coated grids for the TEM or rinsed coverslips for the LM. Cells were subsequently fixed for ca. 30 seconds in the vapour from a 1–2% solution of OsO_4. After drying both grids and coverslips 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. Coverslips intended for the LM were air mounted upside down in order to render possible the use of a × 100 objective. Material for the SEM 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.

RESULTS AND INTERPRETATION

Pappomonas Manton and Oates 1975

Manton and Oates (1975) established the genus *Pappomonas* in a publication where they additionally analysed specimens of the closely related genus *Papposphaera* Tangen 1972. The *Pappomonas flabellifera* type material originated from Cape Town, S. Africa, while additional material from West Greenland served to substantiate features of the new taxon and provide from the outset an indication of intraspecific morphological variability. A transcription of the generic description is included below:

> *Biflagellate coccolithophorids with a short haptonema, the flagellar pole surrounded by a projecting tuft of calcified appendages each composed of a central unbranched shaft, a distal extremity of different shape and a proximal attachment to a subcircular base plate. Elsewhere the cell covered by oval calcified plates with shallow rims, the elements in the plates mainly in the form of approximately rectangular bars arranged roughly parallel to the long axis of the plate.*
>
> *Type species: Pappomonas flabellifera*

The genus *Pappomonas* additionally comprises *P. virgulosa* Manton and Sutherland 1975 (type locality: West Greenland), *P. flabellifera* var. *borealis* Manton *et al.* 1976a (type locality: Homer, Alaska), and *P. weddellensis* Thomsen in Thomsen *et al.* 1988 (type locality: Weddell Sea, Antarctica). Based on a substantial collection of new material from a wide range of geographical sites (see Figs 1, 2) each taxon, including also *P. garrisonii* sp. nov., will in turn be thoroughly described and illustrated below to provide a reference document for future investigations. Biogeographical details of all taxa are accounted for under a separate heading.

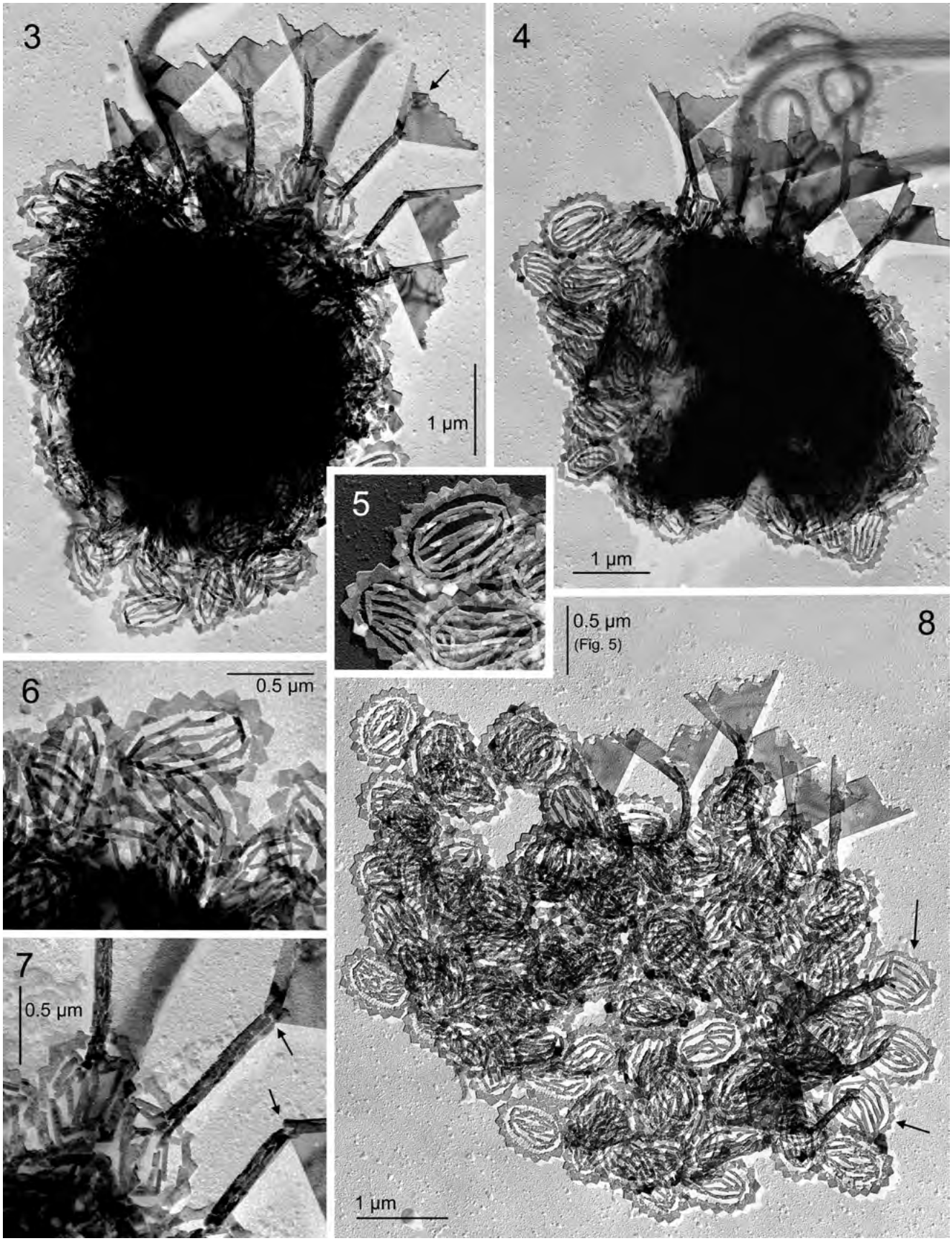
Pappomonas flabellifera Manton and Oates 1975

When first described (Manton and Oates 1975) the material examined comprised as also acknowledged by the authors three morphotypes that were basically distinguished by differences in the appearance of the blades that terminate the circumflagellar coccoliths. While the West Greenland morphotype (loc.cit. Figs 9–12, 14, 20, 21) was later singled out as the variety '*borealis*' (Manton *et al.* 1976a), the two remaining morphotypes both of S. African origin were maintained within *P. flabellifera* var. *flabellifera*. The S. African type material (Manton and Oates 1975; loc.cit. Figs 5, 6) which is further substantiated by additional micrographs (loc.cit. Figs 7, 8, 16, 17) represents a morphotype of *P. flabellifera* that is rarely encountered and to the best of our knowledge not illustrated in any subsequent publication. The feature that most clearly identifies the type material is the V-shaped circumflagellar coccolith appendage. The second S. African morphotype (loc.cit. Figs 13, 15, 18, 19) has, however, become the de facto *P. flabellifera* var. *flabellifera* which has later been found and reported from a range of geographic sites. The inclusion of no less than three morphotypes in the original description of *P. flabellifera* has created confusion in as much as the diagnosis as it stands (and despite the precise identification of a type specimen) does in fact include morphological features and dimensions sampled across the whole range of morphotypes encountered.

The below reexamination of a substantially larger material of *Pappomonas flabellifera* var. *flabellifera* and *P. flabellifera* var. *borealis* (under the heading *P. borealis* stat. nov.) provides in our opinion the insight needed to set up a more robust future taxonomic framework.

The vast majority of the *P. flabellifera* cells examined in preparation for the current paper and also those illustrated in Figs 3–12 come from the North East Water Polynya (NEW / Figs 3–8) and Svalbard (Figs 9–12).

The *P. flabellifera* body coccolith is oval and displays a fairly narrow variability in length and width in the material examined here (see Fig. 18 and Table 1). The rim is more or less perpendicular to the base plate scale (Fig. 10) and comprises a distal cycle of 15–20 quasi-pentagonal and closely abutted elements (Fig. 6) and interspersed between these a proximal/inner cycle


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

of short rod-like elements (see Fig. 58A). The central area calcification comprises rod-shaped elements joined end to end. In larger coccoliths (Fig. 5) there is typically a ring of elements running roughly in parallel with the rim and with a number of more or less parallel lines of elements (3–4) occupying the interior and spanning the entire length of this oval. In smaller coccoliths the central area calcification is limited to 3–4 lines of elements arranged along the longitudinal axis of the coccolith (Fig. 10). In most cases these patterns can be interpreted as a ring of elements arranged more or less parallel to the scale rim and with a single line of rods arranged along the longitudinal axis of the scale. Elements from the peripheral ring frequently come into contact with the rim calcification at either end of the coccolith.

The circumflagellar coccoliths, typically 10–15, are organized as a fairly compact ring at the anterior cell end (Figs 3, 9, 11). The hollow process (0.8–10 µm) which is formed by a dense layer of minute rods (Fig. 7) is proximally attached to an oval base plate scale (Figs 7 and 8) that does not deviate markedly from an ordinary body coccolith in size, shape or central area calcification. However, the central process is supported also by lines of elements that run more or less perpendicular to the longitudinal axis of the coccolith forming a transverse bar. It is also apparent from Figs 7 and 8 that the rim in circumflagellar pole coccoliths is less elaborate in comparison with body coccoliths. The pentagonal elements are less abundant and more widely spaced. The central process distally carries a triangular structure formed in most cases by two slightly overlapping, asymmetrically sized and obtusely angled blades (Figs 3 and 4) that are terminated distally by a jagged and irregular rim of crystalline facets, and often terminated on either side by a prominent tooth-like projection. The lateral edges of the triangle measure in our material 0.8–1.0 µm and the upper edge from tip to tip 1.0–1.2 µm. The overlap between the central shaft and the two terminal blades is fairly short (Figs 7, 12). The angle formed by the two blades is at this point approximately 85 degrees.

Table 1. Dimensions of body coccoliths in *P. flabellifera* and *P. borealis.*

Species		Length	Width
Pappomonas flabellifera	Mean value	0.75	0.46
	Stand. dev.	0.07	0.05
	n	51	51
Pappomonas borealis	Mean value	1.34	0.81
	Stand. dev.	0.15	0.11
	n	55	55

It is obvious that Manton and Oates (1975) were very cautious when circumscribing *P. flabellifera* realizing that it summarizes features sampled across three acknowledged morphotypes. However, it will be evident when dealing with *P. borealis* below that substantial evidence exists in favour of treating *P. borealis* as a separate species and not merely as a variety of *P. flabellifera.* This obviously impacts on the formal circumscription of *P. flabellifera* and calls for an emended description of this taxon. The diagnosis is filtered for *P. borealis* effects in terms of size ranges provided and a lack of informative morphological details caused by the amalgamation of taxonomic units that were in fact too different to be handled at the subspecific level. The emended diagnosis below is building directly upon the original species diagnosis and only revised in places where additional precision is called for.

Pappomonas flabellifera **Manton and Oates 1975 emend. Thomsen and Østergaard**

Protoplast ca. 6 × 4 µm, with flagella up to 20 µm and a haptonema up to 8 µm long. The cell surface covered with oval calcified plates, 0.75 ± 0.07 × 0.46 ± 0.05 µm; the rims composed of 15–20 spade-shaped segments bluntly pointed distally and

◀◀

Figs 3–8. *Pappomonas flabellifera* TEM whole mounts from the Arctic (NEW). **3** – whole cell with details accounted for in Figs 6–7; the arrow points to the demarcation line between the significantly different sized half blades of the triangle; **4** – whole cell with flagella and a curled up haptonema; **5** – detail from Fig. 4 showing body coccoliths with a fairly extensive central area calcification; reversed printing; **6** – body coccoliths (detail from Fig. 3) showing rim and central area calcification; **7** – oval flagellar pole coccolith with extensive central area calcification; notice the minute elements making up the stalk and the short overlap between stalk and triangle (arrows); **8** – detached armour of coccoliths; circumflagellar coccoliths (arrows) are oval, nearly of the same size as body coccoliths and with fairly extensive calcification.

Table 2. Biogeography of *Pappomonas* spp. and *Balaniger virgulosa*. Type localities are indicated by using bold face.

Hemisphere	Northern hemisphere									Southern hemisphere				
Region	Arctic				Non-Arctic						Antarctica			
Locality	W. Greenland (Disko)	North East Water Polynya (NEW)	Svalbard	Homer, S. Alaska	Norway	Denmark	Finland	California, Monteray Bay	Mexico, Sea of Cortez	Cape Town, S. Africa	Weddell Sea (Ameriez)	Weddell Sea (EPOS)	Weddell Sea (ANT X73)	Australian sector / Southern Ocean
Pappomonas														
P. flabellifera (S.Afr. type mat.)								16		**1**				
P. flabellifera (main morphotype)	6,9,12,13	18	18		8	7			16	1				
P. borealis	1,3,6,9,12,13	18	18	**3**		7								
P. weddellensis											**10**	18	18	17
P. garrisonii													**18**	
Balaniger														
B. virgulosa HET	2,6,9,12,13	18		3	8	7	5,14,19							
B. virgulosa HOL	6	19				4,19	5,11,14,15,19							

1) Manton and Oates 1975
2) Manton and Sutherland 1975
3) Manton *et al*. 1976a
4) Thomsen and Oates 1978
5) Thomsen 1979
6) Thomsen 1981
7) Christensen *et al*. 1985
8) Espeland and Throndsen 1986
9) Hansen *et al*. 1988
10) Thomsen *et al*. 1988
11) Vørs 1992
12) Østergaard 1993
13) Clausen *et al*. 1994
14) Ikävalko and Thomsen 1997
15) Ikävalko 1998
16) Thomsen and Buck 1998
17) Findlay and Giraudeau 2000
18) This publication
19) Thomsen unpublished

ca. 0.1 µm high, separated at the base by narrow rod-shaped to triangular spacers; the plate surface a mosaic of elongated elements, with their long dimension parallel to the long sides of the oval except at the ends where the outermost bars continue to follow the line of the plate edge. The number of lines of elements that can be counted along the short axis of a body coccolith is dependent on the overall size of the coccolith and varies from 3–6 with 3 being the most commonly observed number. At the flagellar pole of the cell, up to 15 conspicuous calcified appendages crowded together, each composed of a straight shaft ca. 1.0 µm long attached proximally to the surface of an oval base plate, marginally smaller than the ordinary oval plates but structurally similar, albeit with a less compact rim. Each appendage ends distally in an almost completely flattened fan-like blade ca. 1 µm long and up to 1.5 µm wide, in outline approximating to an inverted triangle with a point of 90° or less attached to the top of the shaft; the blade typically consists of two asymmetrically sized elements; the overlap between the shaft and the blade is short; the contour of the distal edge of the triangle variable but a central cleft always present; a few similar but smaller appendages, sometimes almost sessile on their base plates, scattered elsewhere on the cell.

Additional material of *P. flabellifera* from non-polar regions has been included here to help elucidate global morphological variability and the possible existence of morphological clusters that correlate with geographic realms. It is thus evident that cells collected off California (Figs 15–17) are much similar to the South African type material when comparing e.g. details of the circumflagellar coccoliths (triangles with a simple median cleft separating two blades with a fairly simple geometry), whereas cells from Mexico (Figs 13–14) are almost mirror images of other South African cells (Manton and Oates 1975, loc.cit. Fig. 13) characterized by carrying – with reference to cell dimensions at large – exceptionally prominent circumflagellar coccoliths with very pronounced lateral extensions on each blade. The Californian and Mexican cells are additionally characterized by encompassing body coccoliths carrying a simplified and almost sessile central process. These coccoliths tend to be most abundantly present in particular towards the antapical end of the cell. This feature was also recognized in material from South Africa and it is obvious that the morphology of the reduced appendages is indeed very similar. While realizing the scarcity of material available there is at least an indication of a possible minor morphological separation between a 'warm' water contingent of *P. flabellifera* (S. Africa, California, Mexico) and a 'cold' water Northern Hemisphere contingent.

Thomsen *et al.* (1991) provided evidence for a shared life history among species of *Pappomonas* and species of *Trigonaspis* Thomsen 1980a. The combination cell illustrated (loc.cit. Fig. 17) involved *P. borealis* and *T. diskoensis* Thomsen 1980a and further examples of this specific partnership are added here (see below). It is worth emphasizing that a combination cell involving *P. flabellifera* has not yet been found. However, the likely candidate based on biogeographical evidence, is *T. minutissima* Thomsen 1980a.

The currently known biogeographical range of *P. flabellifera* is summarized in Table 2.

***Pappomonas borealis* (Manton, Sutherland and McCully 1976a) Thomsen and Østergaard stat. nov.**

Basionym: *Pappomonas flabellifera* var. *borealis* Manton, Sutherland and McCully 1976a

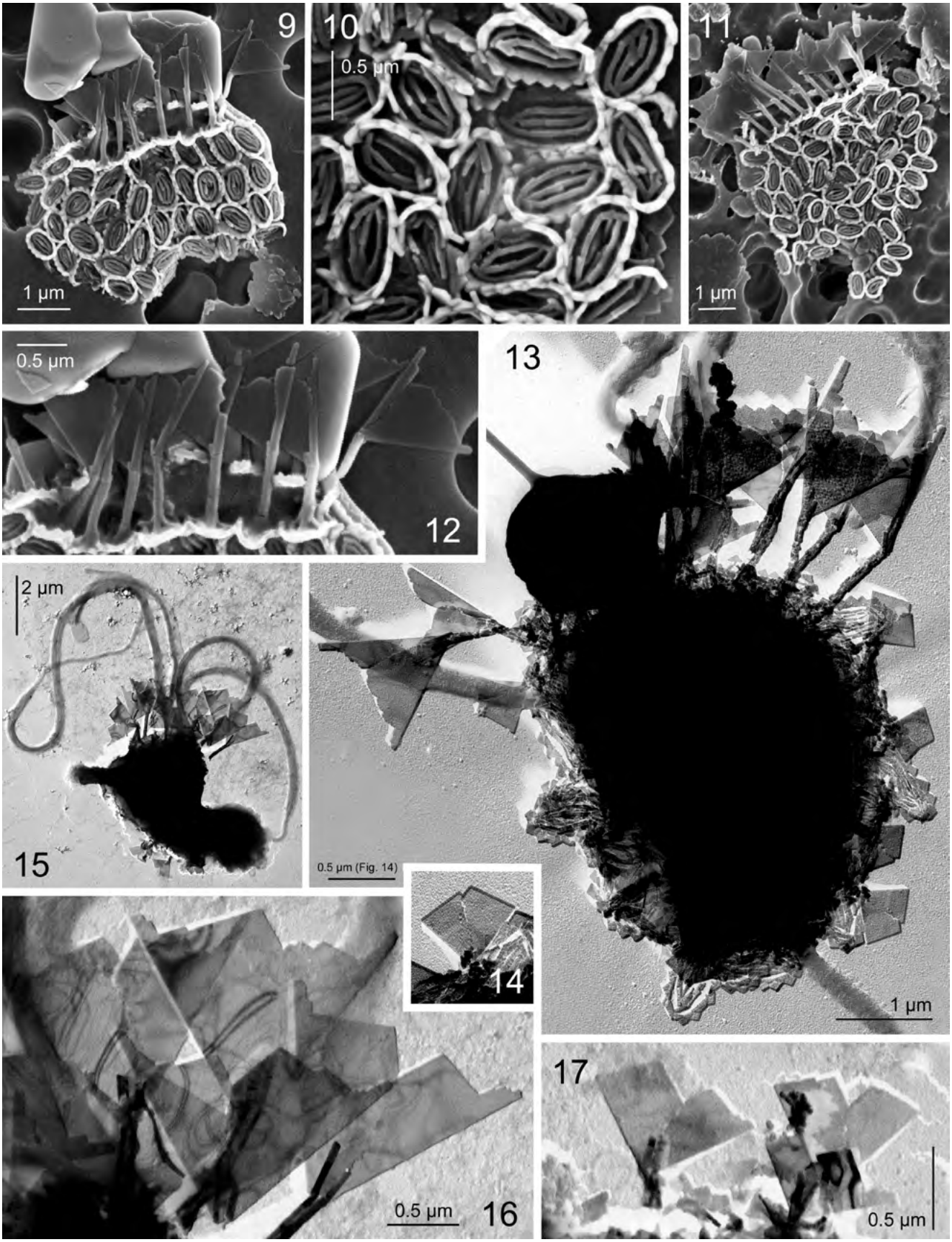
The emended diagnosis below is building directly upon the original diagnosis of the former variety and only revised in places where additional precision is called for:

Differing from the type of the genus (P. flabellifera) by more nearly triangular blades to the flabelliform appendages, the distal edge dentate or fimbriate, the central cleft more distinct with the adjacent sides of the two half-blades not overlapping, the angle between outside edges of the blade as a whole approximately 90°, each half-blade attached laterally to the end of the columnar stalk for a longer distance (about half the blade length), than in the type. The base plate of a flagellar pole coccolith is almost circular, ca. 0.7 µm in diam. and with a cross-shaped calcification where elements merge into the central shaft. Mineralized plates without appendages somewhat wider relative to their length, commonly 0.9 × 1.4 µm excluding the rim. The number of rows of elements on the plate is typically within the range 5–9.

Type material: Homer, Alaska (Manton et al. 1976a, loc.cit. Figs 12–14)

The body coccoliths of *P. borealis* are much reminiscent of those of *P. flabellifera*, however, clearly distinguishable based on size (Table 1; Fig. 18) and in derived size-related features such as the number of rim elements and the complexity of the central area calcification. The height of a single pentagonal element from the rim is up to 0.3 µm. In large coccoliths (Figs 19, 25, 27) there are usually two complete rings of elements and three to four rows of elements inside the inner oval that are arranged more or less in parallel with the longitudinal axis of the coccolith. The central area calcification in smaller coccoliths is much similar to that described for *P. flabellifera*.

Circumflagellar coccoliths (Figs 24, 25) differ from those of *P. flabellifera* both with respect to shape (almost circular; ca. 0.7 µm in diam.) and calcification


9
1 µm
10
0.5 µm
11
1 µm
0.5 µm
12
13
2 µm
15
0.5 µm (Fig. 14)
14
1 µm
0.5 µm
16
17
0.5 µm

(cross shaped arrangement of elements that merge into the shaft of the central process), and with reference to the elaboration of the triangular structure that terminates the circumflagellar coccolith (Figs 24–27). The triangle consists of two almost identical half blades in which the distal edge and the upper part of the ventral flanges are finely serrulate. The lateral edge of a triangle (straight line) measures in our material 1.25–1.5 µm while the upper edge from tip to tip measures 1.5–2 µm. The two half blades appear to be perfectly aligned forming a two-dimensional structure. The lower lateral edges are straight and adjoin at an angle that typically exceeds 90°. The central shaft (1.4–1.6 µm) is connected to the triangle for at least half the distance between the base of the triangle and the upper rim.

Deviant cells of *P. borealis* in which rim elements (1–2 on each coccolith) are hypertrophied have been observed in samples from both W. Greenland (Fig. 28) and NEW (Fig. 29). The aberrant element takes the shape of an oblique pointed triangle.

A combination cell with coccoliths belonging to *P. borealis* (HET) and *Trigonaspis diskoensis* (HOL) was discussed by Thomsen *et al*. (1991; loc.cit. Fig. 17). We are fortunate enough here to be able to present further cells (Figs 30–32) that substantiate the life history relationship between these two taxa.

The currently known biogeographical range of *P. borealis* is summarized in Table 2.

Pappomonas weddellensis Thomsen in Thomsen *et al.* 1988

The original description of this taxon was based on only two specimens (Thomsen *et al.* 1988). Additional sampling from the Weddell Sea, in particular during the ANT X/3 cruise, has provided a multitude of cells that renders possible a reexamination of the validity of morphological details emphasized in the original description. There is complete agreement between the original description and subsequent findings in almost all features; e.g. with regard to: 1) the central process of circumflagellar coccoliths which is terminated by two markedly differently sized half blades (Fig. 34, arrows) one of which is drawn out into a pointed triangular blade, 2) the quasicircular base of a circumflagellar coccolith, and 3) the presence of reduced and non-stalked central processes on coccoliths at the antapical cell end. Whereas most of the body coccoliths observed display a cruciform central area calcification (Fig. 37) in agreement with that of the type material, other cells (Fig. 36) have a more elaborate central area calcification where each quadrant of the base plate scale has an additional line of rectangular elements organized along the long axis of the coccolith (Fig. 35). However, it is worth emphasizing that the cell shown in Fig. 36 in addition to this deviant type of body coccolith also encompasses body coccoliths with the more typical arrangement of elements in a simple cross (Fig. 36, arrow) plus the occasional irregularly positioned single element. The iso-

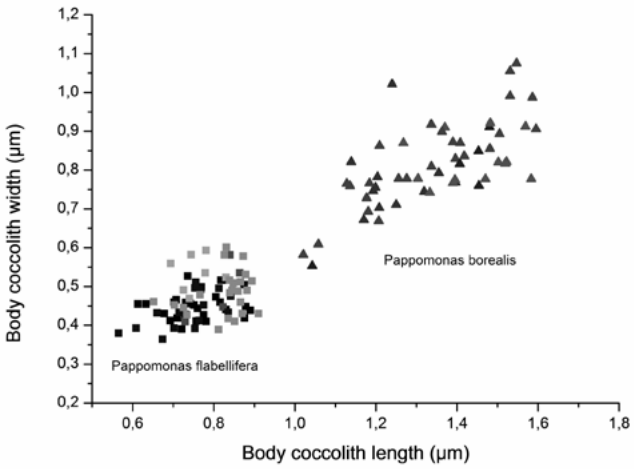
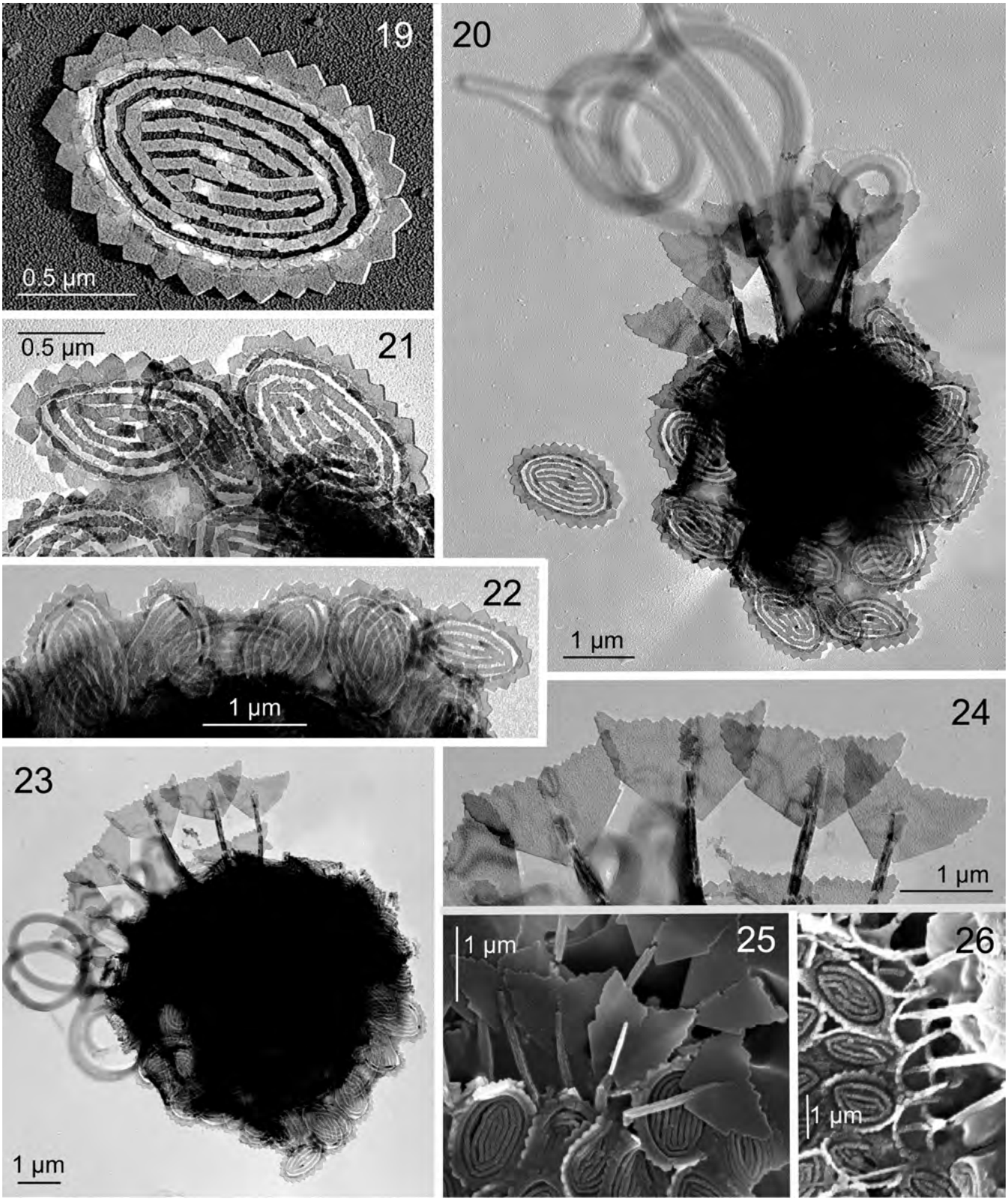


Fig. 18. *Pappomonas flabellifera* (squares) and *P. borealis* (triangles) body scale dimensions.

Figs 9–17. *Pappomonas flabellifera* from Svalbard (9–12), Mexico (13–14) and California (15–17). SEM (9–12) and TEM (13–17) whole mounts. **9** – complete cell showing closely packed body coccoliths and a very well defined ring of circumflagellar coccoliths (ca. 15); **10** – detail of body coccoliths showing the upright position of rim elements; **11** – complete cell; **12** – detail of circumflagellar coccoliths (from Fig. 9) indicating that neighbouring 'half blades' of a triangle are joined at a blunt angle; **13** – whole cell very reminiscent of material previously published from S. Africa; see text for further details; **14** – detail of a reduced central appendage formed by two equally sized half blades; **15** – whole cell with flagella and haptonema; **16** – detail from Fig. 15 showing triangles that are reminiscent of those of the S. African type cell; see text for further details; **17** – detail from Fig. 15 of reduced, yet stalked central appendages.


19
0.5 µm
20
1 µm
21
0.5 µm
22
1 µm
23
1 µm
24
1 µm
25
1 µm
26
1 µm

lated body coccolith (Fig. 35 from the cell shown in Fig. 36) shows a typical *Pappomonas* configuration of the rim with ca. 20 upright polygonal elements interspersed at the base by a sequence of rod-shaped elements (Fig. 58C).

Pappomonas weddellensis is similar to both the type species *P. flabellifera* and *P. borealis* in so many crucial morphological aspects that a shared generic affiliation still appears justified. Combination cells involving *P. weddellensis* and *Trigonaspis* sp. have not yet been encountered. *Trigonaspis melvillea* Thomsen 1988 is abundant in Antarctic waters and might thus be a possible candidate.

The currently known biogeographical range of *P. weddellensis* is summarized in Table 2.

***Pappomonas garrisonii* Thomsen and Østergaard sp. nov.**

Diagnosis: Cell spherical, ca. 5 µm in diameter with two flagella and a somewhat shorter haptonema. Coccoliths of two types. Body coccoliths (Fig. 39) are oval, 1.0 ± 0.095 × 0.65 ± 0.09 µm. The rim consists of large pentagonal elements (0.2–0.25 µm in height) forming a densely aggregated and upright ring. Adnate and rod-shaped elements occur interdispersed at the base of the pentagonal elements (Fig. 58D). The central area is supporting ca. 5 lines of rod-shaped elements arranged in parallel with the longitudinal axis of the coccolith and crossed in the middle by a single line of elements arranged along the shortest axis of the coccolith. Radial elements from the base plate scale upper surface ornamentation are visible in between elements. Other coccoliths carry central processes that are diagnostic for the species. These coccoliths are best developed at the flagellar pole but occur scattered all over the cell surface (Fig. 41). The quasi-circular coccolith (diam. 0.7–0.8 µm) has a rim that is basically similar to that of the

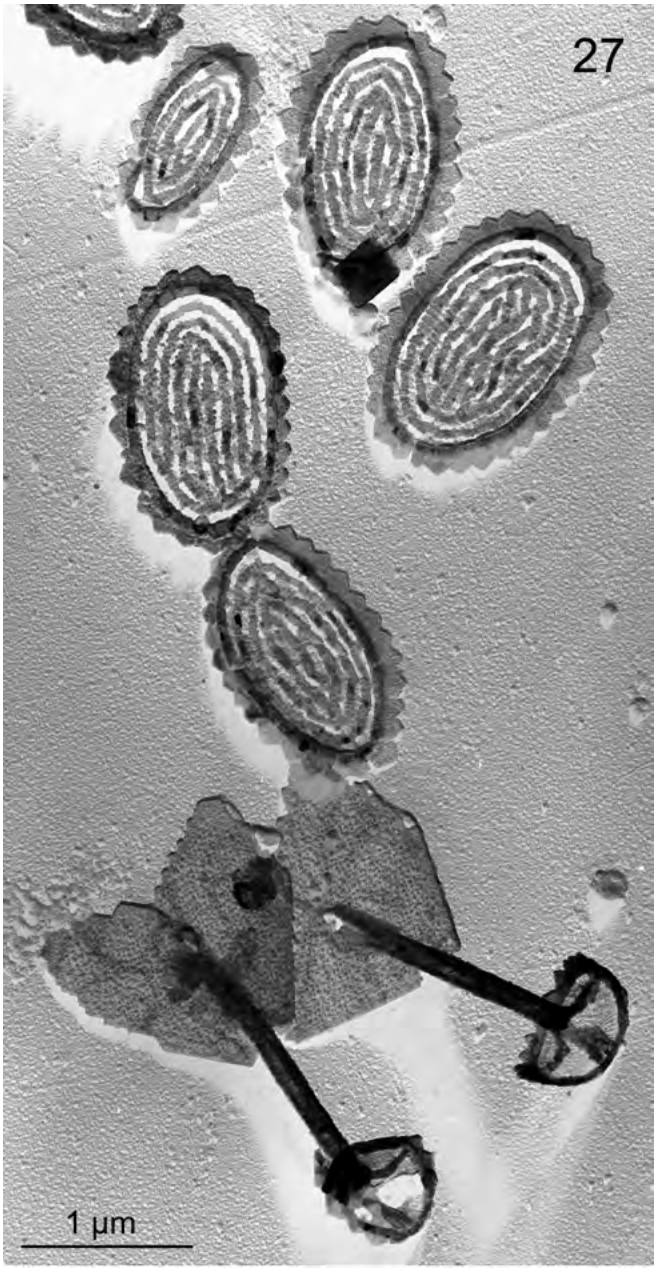


Fig. 27. *Pappomonas borealis* (TEM whole mount) from the Arctic (West Greenland). Scatter of body and circumflagellar coccoliths illustrating differences in size and ornamentation among body coccoliths and the highly dissimilar base of the circumflagellar coccoliths.

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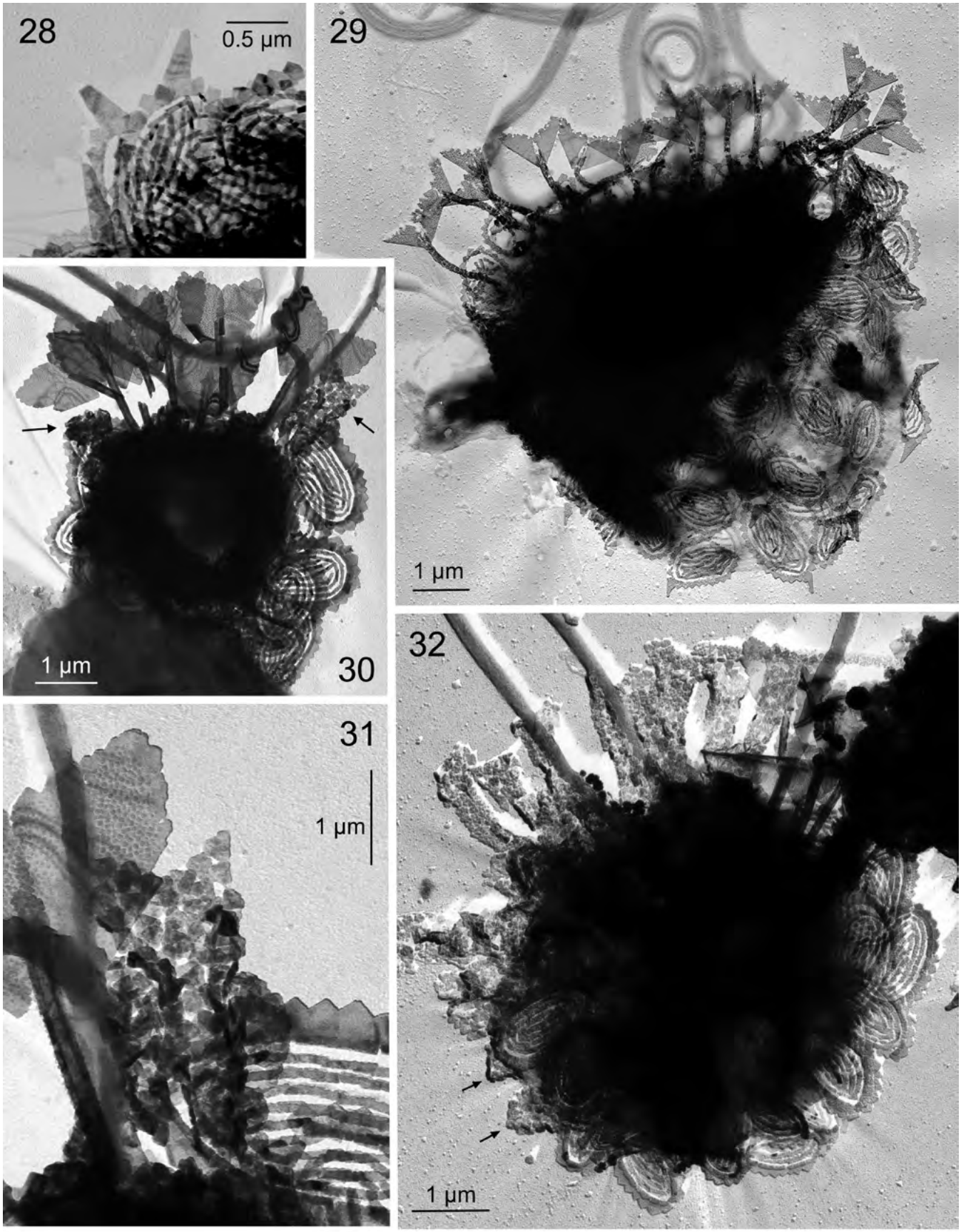
Figs 19–26. *Pappomonas borealis* from the Arctic (NEW / Figs 19–24; Svalbard / Figs 25–26); TEM (Figs 19–24) and SEM whole mounts (Figs 25–26). **19** – single body coccolith (reversed printing / detail from Fig. 20) showing rim (pentagonals and rods) as well as central area calcification consisting of two ovals and four embedded lines of rod-shaped elements in the middle; notice that the radiating fibrils on the upper surface of the base plate scale are visible in between elements of the central area calcification; **20** – whole cell with flagella and a curled up haptonema; **21** – detail of posterior cell end body coccoliths from the cell shown in Fig. 20; **22** – detail of body coccoliths from the cell shown in Fig. 23; **23** – whole cell; **24** – detail of circumflagellar coccoliths; notice the extended overlap between shaft and triangular blade; **25** – detail of anterior cell end to show the flattened triangular blade and the upright rim on body coccoliths; **26** – a sequence of circumflagellar coccoliths showing the upright rim and the cruciform central area calcification.


28
0.5 µm
29
1 µm
30
1 µm
31
1 µm
32
1 µm

body coccoliths, whereas the central area calcification is reduced to a cross-like structure where the arms coalesce at the centre to support the central shaft (Figs 38, 42). The central shaft is up to 1.5 µm long and formed by densely aggregated elements (Fig. 39). Two elongated elements (1.2–1.3 µm in circumflagellar coccoliths and 0.8–0.9 µm in coccoliths at the posterior cell end) diverge from the tip of the central shaft. They are each furnished with two triangular and wing-like blades. The smaller blades from each pair are placed centrally. The cleft between these is terminated above the tip of the central shaft through the insertion of a rhomboid element (Fig. 39). The width of the terminal structure varies from 1–2 µm. Small unmineralized under layer scales (ca. 0.35 × 0.5 µm) can be observed scattered among the coccoliths (Figs 39, 40). These scales display radiating ridges and loose concentric fibrils.

Combination cells with *Trigonaspis* sp. have been observed (Figs 43–45).

Type specimen: Fig. 41 (TEM micrograph 20454).

Type locality: Weddell Sea (7°19.3 W, 68°14 S), Antarctica; collected on 13 April 1992 at 10 m depth.

Etymology: The species is named in honour of Dr. David L. Garrison who has contributed significantly to our understanding of pelagic polar ecology and who was also instrumental in providing the possibility of participating in the ANT X/3 cruise.

Pappomonas garrisonii shares with other species of *Pappomonas*: 1) an armour of dimorphic coccoliths which with reference to patterns of calcification and elaboration of the central process on 'flagellar pole' coccoliths have diagnostic features in common, and 2) a life history that implements species from the holococcolithophorid genus *Trigonaspis* (Thomsen 1980a). However, *P. garrisonii* also deviates from the mainstream *Pappomonas* concept as defined by *P. flabellifera*, *P. borealis* and *P. weddellensis*, by having: 1) coccoliths with central processes evenly distributed over the entire cell surface (albeit with the largest ones encircling the flagellar pole), 2) a central process termination that is not a simple modification of the 'triangle' theme, 3) a rim calcification on body coccoliths which in size and overall morphology is much reminiscent of that observed in species of *Papposphaera*, e.g. *P. sagittifera* (Fig. 58D, E), and 4) a layer of organic underlayer scales.

Despite the fairly long list of features that distinguishes *P. garrisonii* form the core species of *Pappomonas* we prefer for the time being to ascribe the new taxon to *Pappomonas*. The life history relationship with *Trigonaspis* sp. is a strong supporting argument behind this decision. Unpublished findings indicate that species which are at present allocated to *Papposphaera*, e.g. *P. sagittifera* Manton, Sutherland and McCully 1976a, are in fact often found with dimorphic coccoliths (Thomsen, Østergaard and Heldal, unpublished findings) thus in this aspect critically blurring the distinction between *Pappomonas* and *Papposphaera*. It can be anticipated that any strategy with regard to a possible redefinition of the genera *Pappomonas* and *Papposphaera* will need to be assisted by gene sequencing techniques and preferably also TEM thin sectioning.

The currently known biogeographical range of *P. garrisonii* is summarized in Table 2.

Balaniger virgulosa (Thomsen and Oates 1978) Thomsen and Østergaard comb. nov.

Syn. *Pappomonas virgulosa* Manton and Sutherland 1975

Balaniger balticus Thomsen and Oates 1978

Balaniger virgulosa HET (Figs 46, 50) carries oval body coccoliths and circumflagellar coccoliths that terminate in a tuft of elongated elements. Body coccoliths measure 0.8 ± 0.10 × 0.5 ± 0.04 µm. The rim consists of erect and slightly tilted rectangular elements (0.1 µm) that are distinctly separated by small rod-shaped elements arranged along the base plate scale surface (Figs 49, 58F). The central area calcification typically comprises a single oval ring arranged in parallel to the rim and a line of elements inside the oval. The calcification is formed by a sequence of upright larger elements distinctly separated by small adnate rod-shaped elements.

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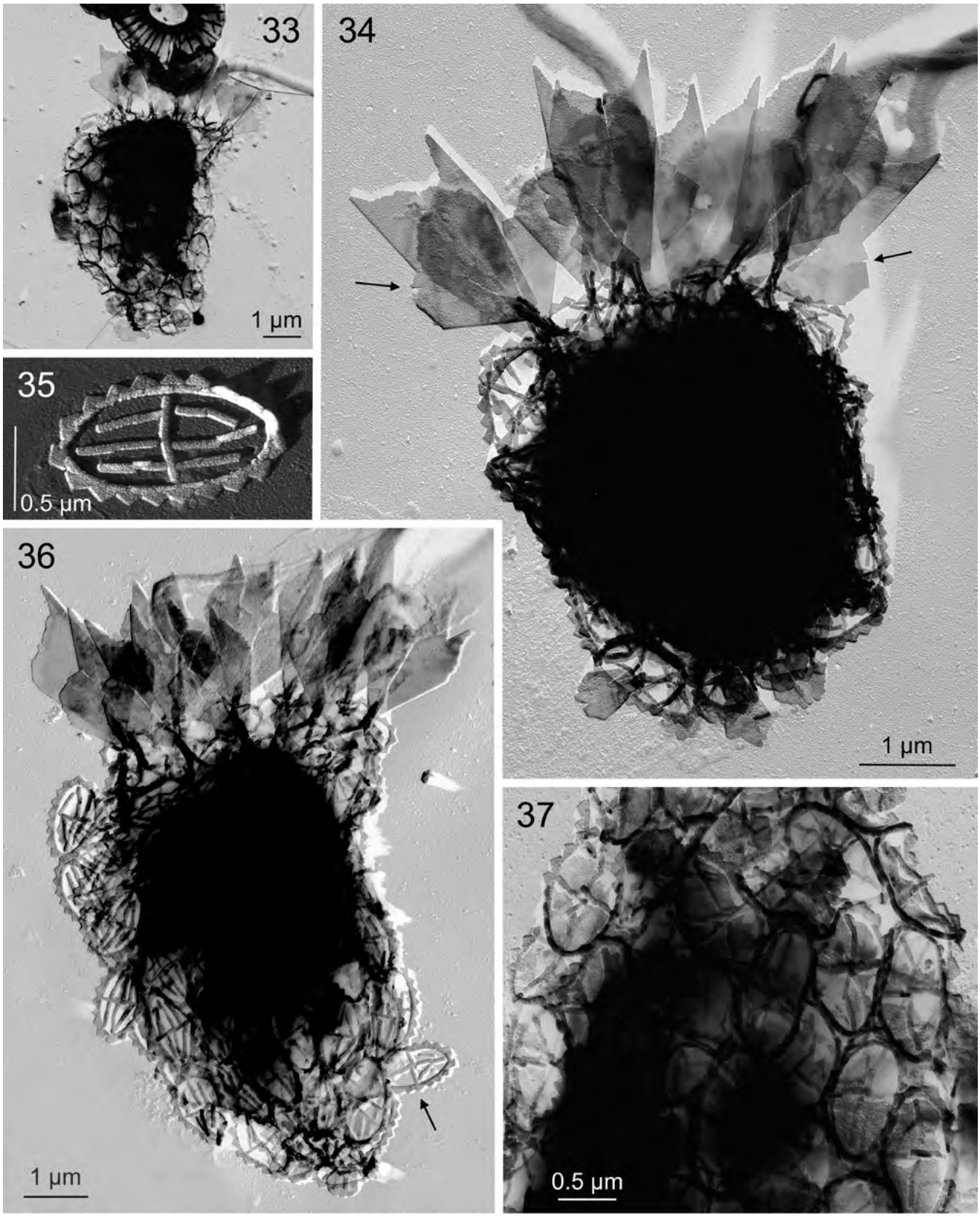
Figs 28–32. *Pappomonas borealis* (TEM whole mounts) from the Arctic (West Greenland / Figs 28, 30–32; NEW / Fig. 29). **28** – detail of body coccoliths with triangular hypertrophied elements within the rim; **29** – whole cell with rim hypertrophy on body coccoliths at the cell rear end; **30** – combination cell; '*Trigonaspis diskoensis*' elements are pointed out; **31** – detail from Fig. 30 clearly displaying the '*Trigonaspis*' triangles composed of three individual calcite crystals; **32** – a second combination cell with a well-developed *T. diskoensis* half-cell with a corona of circumflagellar coccoliths and body coccoliths (arrows); the '*borealis*' part of the cell is recognized based on the central area morphology.


33
1 µm
34
1 µm
35
0.5 µm
36
1 µm
37
0.5 µm

This arrangement thus basically mirrors that of the coccolith rim with the exception that the upright elements are not inclined but appear to be positioned at right angles to the base plate scale (Figs 49, 58G).

The circumflagellar coccolith is oval (Fig. 48; material from Bergen, Norway). The rim and central area calcification mirrors that of the body coccoliths while also integrating a cruciform arrangement of elements that lead into the central shaft. The central shaft (ca. 1 µm) is terminated (Fig. 47) by a characteristic tuft of four elongated elements (0.6–0.9 µm). Coccoliths with a reduced central appendage (shaft missing) are frequently observed at the posterior cell end (Fig. 46).

We are here providing evidence (Figs 52–57) that *Pappomonas virgulosa* and *Balaniger balticus* are part of the very same life history. The combination cells shown in Figs 54 and 57 thus comprise periplast areas where the characteristic pyramid-like structures of *B. balticus* occur mixed in between *P. virgulosa* coccoliths. The two morphotypes of *B. balticus* pyramids (Figs 55–56) were introduced already when the species was originally described (Thomsen and Oates 1978). In a single specimen from Svalbard (Fig. 52) it is apparent that the body coccoliths are widely separated. When scrutinizing the area between the coccoliths (Fig. 53) it was revealed that these areas comprised clusters of *B. balticus* pyramids. The Svalbard cell illustrated in Fig. 52 is thus yet another combination cell further strengthening the *P. virgulosa* and *B. balticus* life history case.

The finding of combination cells that link *P. virgulosa* to *B. balticus* in combination with: 1) an aberrant organization of rim and central area calcification in comparison with the generic type species *P. flabellifera*, and 2) a markedly different concept with regard to the termination of circumflagellar coccolith processes, renders impossible the continued inclusion of *P. virgulosa* within *Pappomonas*. The straightforward solution is to synonymise *P. virgulosa* with *B. balticus* (as *B. virgulosa* because '*virgulosa*' takes precedence over '*balticus*') and to refer in the future to the specific stages using the informal keyword HET for the heterococcolithophorid stage *Pappomonas virgulosa* and HOL for the holococcolithophorid stage *Balaniger balticus*.

The original diagnosis (Manton and Sutherland 1975) is detailed enough to unequivocally circumscribe the heterococcolithophorid stage. The observations provided here basically corroborates the information in Manton and Sutherland 1975, however also adds information previously lacking with regard to the exact configuration of the circumflagellar coccolith and new knowledge with regard to life history stages of this taxon. As none of these features are crucial to species identification it is not considered relevant to emend the original description.

The currently known biogeographical range of *B. virgulosa* HET and HOL is summarized in Table 2.

BIOGEOGRAPHY

Three patterns emerge from the biogeographical survey presented in Table 2. First of all it appears, when examining the cold water environments sampled, that *Pappomonas* albeit being bipolar in distribution when considering the genus as such, is represented at each pole by different sets of species, i.e. *P. weddellensis* and *P. garrisonii* in Antarctica and in the Arctic *P. flabellifera* and *P. borealis*. Secondly it is interesting to note the persistent occurrence of *B. virgulosa* HET in West Greenland, at North Atlantic lower latitudes, and in the inner parts of the Baltic Sea. Whereas the holococcolithophorid phase of *B. virgulosa* is less frequently observed at high latitudes it is frequently reported from Danish coastal waters (Thomsen, unpublished results) and from the Baltic Sea at large. It is furthermore interesting to note that while the *B. virgulosa* HOL stage is almost always present in water samples from a Danish

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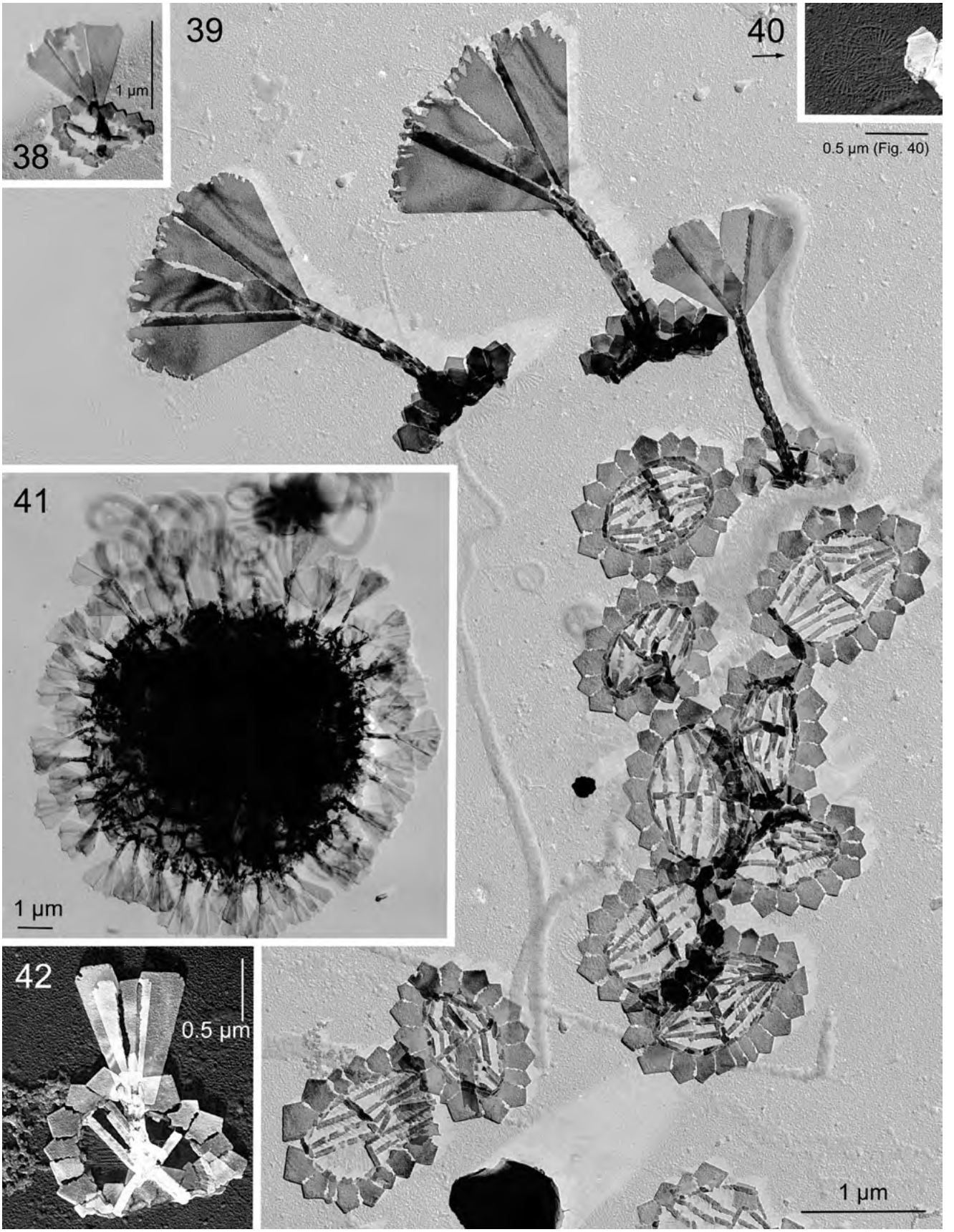
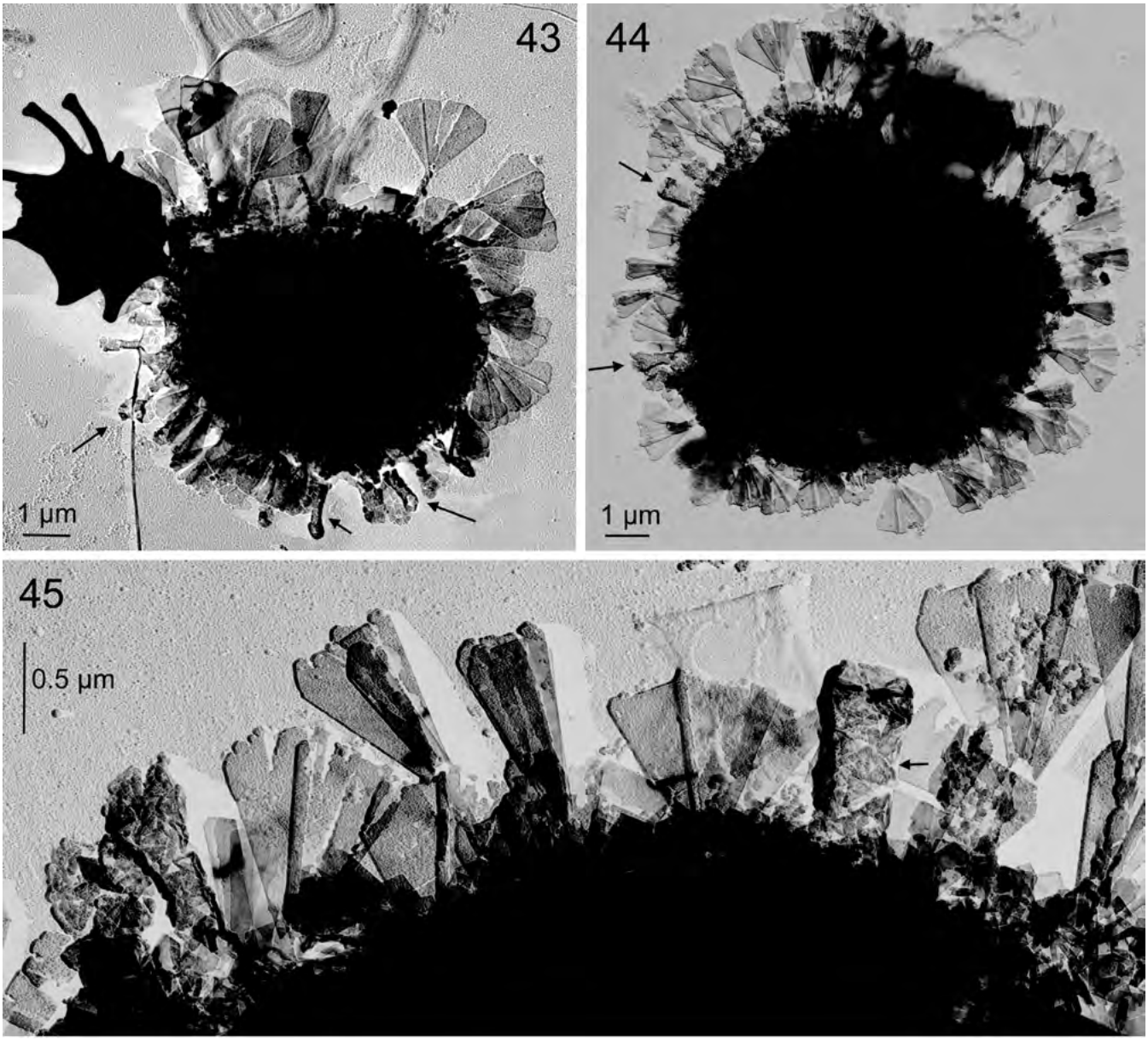
Figs 33–37. *Pappomonas weddellensis* (TEM whole mounts) from the Weddell Sea, Antarctica (EPOS / Figs 33, 37; ANT X/3 / Figs 34–36). **33** – whole cell, notice the size of the cell in comparison with the *Emiliania huxleyi* single coccolith above the cell; **34** – whole cell with a corona of elaborate circumflagellar coccoliths and coccoliths with reduced central appendages at the posterior cell end. Arrows indicate the demarcation line between the half blades of the central process termination; **35** – single body coccolith (reversed printing) showing details of calcification; **36** – whole cell where most body coccoliths are similar to that shown in Fig. 35, however also comprising body coccoliths where the central area calcification is almost limited to a cross-like structure (arrow); **37** – detail of the posterior cell end of the organism shown in Fig. 33; body coccoliths display a cross-like calcification of the central area.


38
1 µm
39
40
0.5 µm (Fig. 40)
41
1 µm
42
0.5 µm
1 µm



Figs 43–45. *Pappomonas garrisonii* sp. nov. combination cells with *Trigonaspis* sp. TEM whole mounts from the Weddell Sea, Antarctica (ANT X/3). **43** – whole cell with *Trigonaspis* parts pointed out; **44** – a second combination cell with *Trigonaspis* parts pointed out; **45** – detail of the periplast from Fig. 44 showing the *Trigonaspis* tower-like coccoliths and their triangular substructure (arrow).

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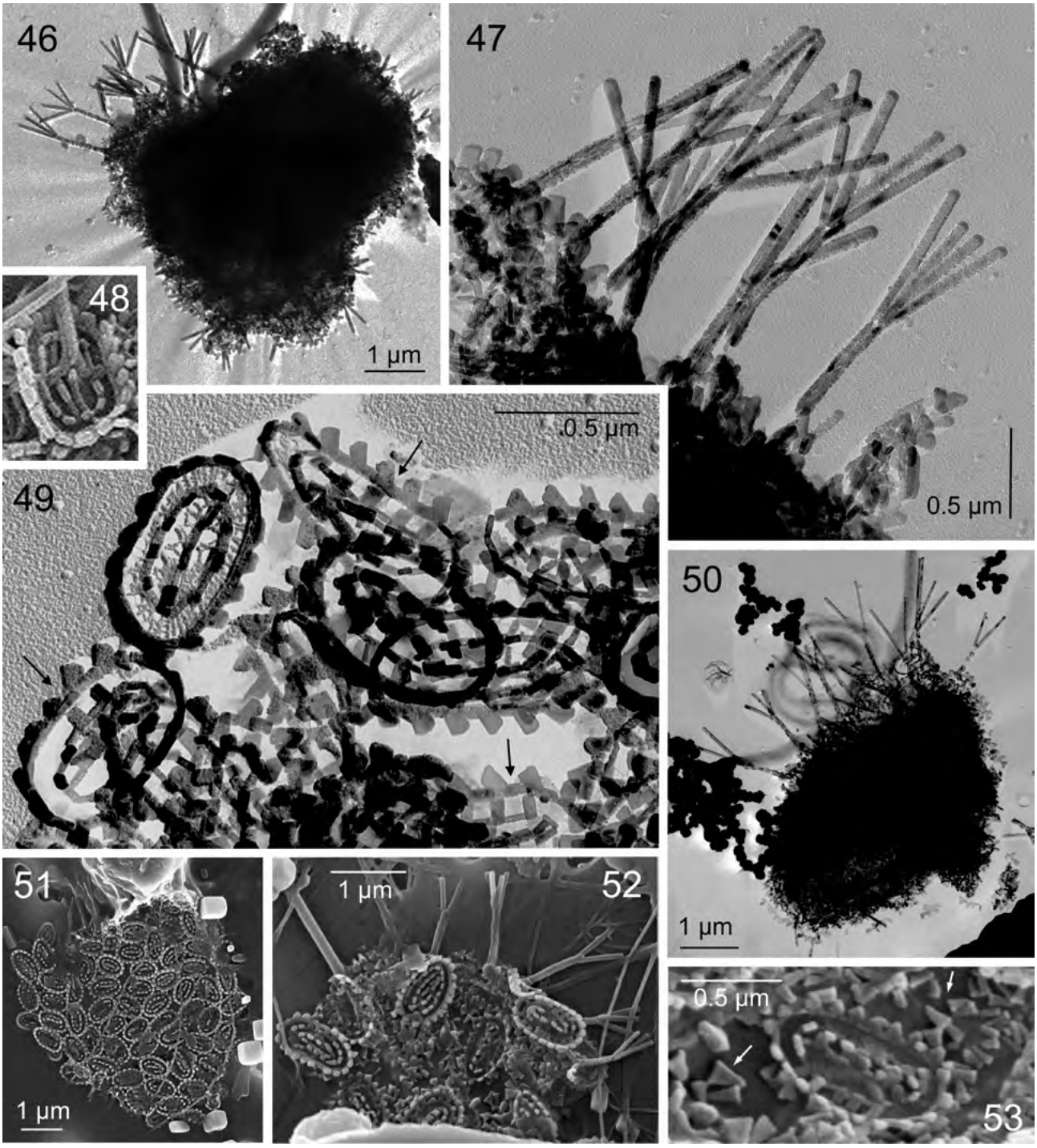
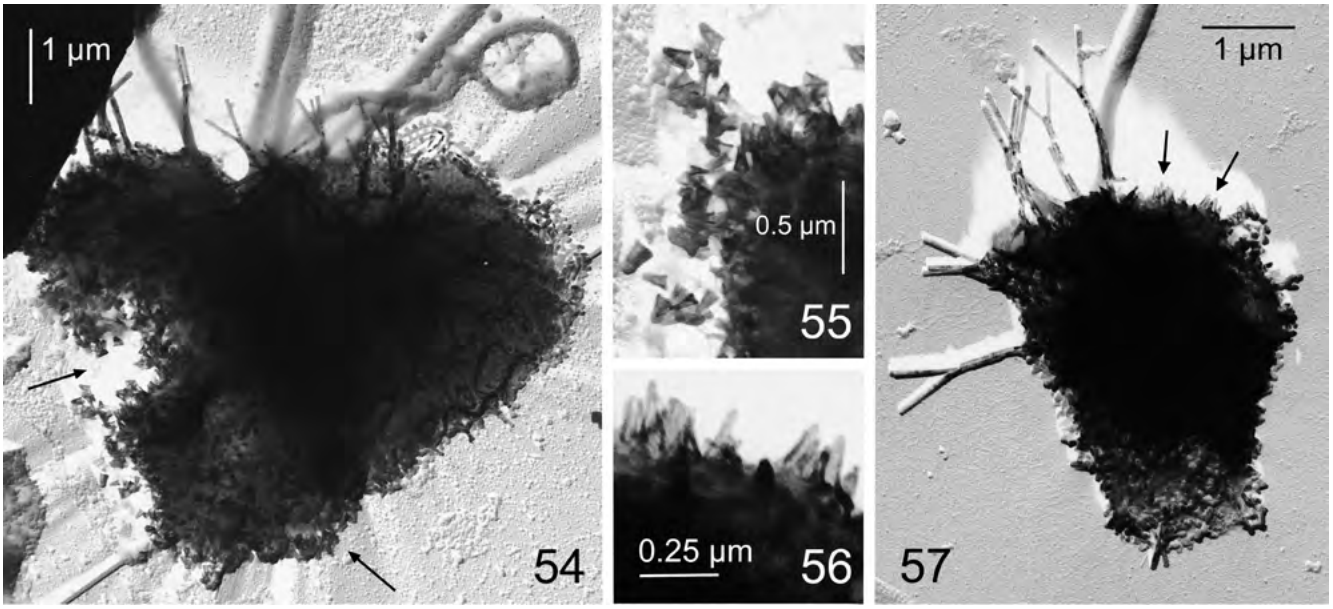
Figs 38–42. *Pappomonas garrisonii* sp. nov. (TEM whole mounts) from the Weddell Sea, Antarctica (ANT X/3). **38** – coccolith with reduced central appendage; notice the cruciform central area calcification; **39** – scatter of body and circumflagellar coccoliths; **40** – unmineralized under layer scales (reversed printing); **41** – complete cell (holotype) with flagella and haptonema; coccoliths with central appendages occur over the entire cell; the largest of these are grouped at the anterior cell end; **42** – coccolith with small central appendage and cruciform central area calcification (reversed printing).



Figs 46–53. *Balaniger virgulosa* HET from the Arctic (West Greenland / Figs 46–47, 49; NEW / Fig. 50; Spitsbergen / Figs 51–53; Bergen, Norway / Fig. 48); TEM (Figs 46–47, 49–50) and SEM (Figs 48, 51–53) whole mounts. **46** – complete cell with reduced central appendages on some coccoliths at the posterior cell end; **47** – detail of cirtcumflagellar coccolith central processes showing the shaft and the tuft of four elongate elements that terminate the structure; **48** – detail of specimen from western Norway showing central area features of a circumflagellar coccolith; **49** – detail of body coccoliths showing the rim and central area calcification; the arrows point to areas where the calcification is particularly evident; **50** – complete cell with flagella and a curled up haptonema; **51** – whole cell which shows the irregular arrangement of densely packed body coccoliths; **52** – combination cell comprising *Pappomonas virgulosa* and *Balaniger balticus*; interspersed between the widely separated body coccoliths is a layer of pyramidal appendages known from *B. balticus*; **53** – detail from Fig. 52 showing (arrows) the *B. balticus* pyramids.



Figs 54–57. *Balaniger balticus* / *Pappomonas virgulosa* combination cells. TEM whole mounts from West Greenland. **54** – complete cell with flagella and a single haptonema; arrows point to areas of the periplast where *B. balticus* HOL elements occur; **55** – detail from Fig. 54 showing *B. balticus* HOL pyramids; **56** – detail from Fig. 57 showing a pointed variant of the *B. balticus* HOL pyramids; **57** – complete cell with the *B. balticus* HOL periplast elements pointed out.

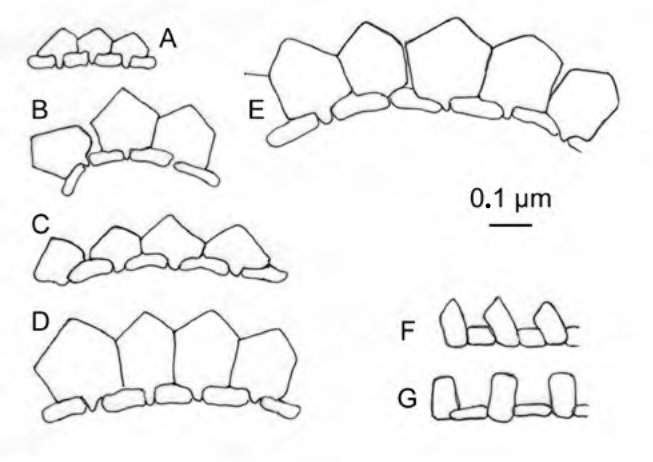


Fig. 58. Interpretation of rim calcification (body coccoliths) in species of *Pappomonas* and *Papposphaera*. **A** – *Pappomonas flabellifera* (NEW / micrograph 25036); **B** – *Pappomonas borealis* (NEW / micrograph 24879); **C** – *Pappomonas weddellensis* (ANT X/3 / micrograph 20549); **D** – *Pappomonas garrisonii* sp.nov. (ANT X/3 / micrograph 21149); **E** – *Papposphaera sagittifera* (NEW / micrograph 24930); **F–G** – *Balaniger virgulosa* HET scale rim (F) and base plate calcification (G) (West Greenland / micrograph 10322).

fiord, Isefjorden, that has been sampled annually on more occasions (Thomsen, unpublished) the *B. virgulosa* HET stage has never been found from this particular habitat. Although based on limited material it appears safe to conclude that it is a characteristic feature of *B. virgulosa* that its occurrence at a specific site appears to be dominated by one phase (HET in West Greenland and HOL in the Isefjord) and that so far only the Baltic proper appears to present a physical environment to *B. virgulosa* that favours both phases. Finally, *P. flabellifera* appears to have the largest biogeographical range of all species examined.

DISCUSSION

The genus *Pappomonas* as currently circumscribed encompasses four species (viz., *flabellifera*, *borealis*, *weddellensis* and *garrisonii*) while a former species (*virgulosa*) has been transferred to *Balaniger*. It is important to emphasize that this will represent only an interim status for the genus, in as much as there is a wealth of mostly low-latitude undescribed species (see e.g. Cros

and Fortuño 2002; *Pappomonas* sp. types 1–5) that share critical morphological features with *Pappomonas*. Prior to formally describing any of these forms it will, however, be relevant to also critically reexamine all taxa that have so far been allocated to the genus *Papposphaera* Tangen 1972. The main distinguishing feature between *Papposphaera* and *Pappomonas* is a monomorphic or varimorphic heterococcosphere in *Papposphaera* while *Pappomonas* is characterized by a polymorphic heterococcosphere. However, both *P. garrisonii* sp. nov. as well as some of the known undescribed forms of *Pappomonas,* seem to challenge this straightforward and simple distinction between the two genera. Also when examining new material of species of *Papposphaera* (Thomsen, Østergaard and Heldal, unpublished results) it becomes increasingly difficult to advocate that the *Papposphaera* heterococcosphere is monomorphic-varimorphic rather than straightforward dimorphic. Combination cells indicate that the holococcolithophorid genera *Trigonaspis* and *Turrisphaera* are alternate life-cycle phases of *Pappomonas* and *Papposphaera* respectively. The main distinguishing features are hexagonal (*Turrisphaera* spp.) versus triangular (*Trigonaspis* spp.) crystallite groups and a monomorphic or varimorphic holococcosphere (*Turrisphaera*) versus dimorphic holococcosphere (*Trigonaspis*). In subsequent papers we will in turn reexamine polar species of *Trigonaspis*, *Papposphaera* and *Turrisphara* to provide the best possible platform based on morphological evidence to subsequently deal with the wealth of undescribed forms (*Pappomonas* spp. and *Papposphaera* spp.) mostly from low-latitude sites. However, there is no doubt that molecular evidence will be needed to substantiate any circumscription of taxa based on morphological evidence exclusively. The establishment of cultures of a selection of these lightly calcified polar coccolithophorids will obviously represent a major step forward in our understanding of these organisms. However, a more realistic approach, realizing the difficulties involved in establishing and maintaining cultures of coccolithophorids at large, is perhaps to rely on sequence data that stem from single cell analysis. Attempts were recently made (Lundholm and Thomsen, unpublished results) at the Arctic Station (W. Greenland, June 2013) to isolate single cells using a traditional pipetting technique. The challenge encountered when picking out a single cell from a mixed community under direct visual LM control, is the lack of resolution which in most cases renders impossible a proper (and crucial) species identification of these modestly sized target cells (< 5 µm). Whereas it is fairly straightforward to recognize as such a lightly calcified coccolithophorid cell based on cell appendages (flagella and haptonema), the occurrence of calcified structures encasing the cell and the aplastidic condition of the cell, we also had to conclude that *Turrisphaera borealis* (Manton *et al.* 1976b) was in fact the only taxon that could be recognized beyond doubt when examining a mixed sample in an inverted microscope at 40 × phase contrast magnification. It needs to be emphasized that even when examining live material in a standard microscope at × 100, using either phase contrast or Nomarski optics, it is rarely possible to unambiguously identify specific cells to species level. We are therefore currently looking into techniques that combine undisputed species identification (e.g. a SEM examination of uncoated material) with the availability of manipulating tools that, either inside or outside the scope, can subsequently secure the cell examined for further processing, e.g. a PCR analysis.

The aphorism 'everything is everywhere, but the environment selects' asserts that microbial taxa are found everywhere on earth that there is suitable habitat for them (Fenchel and Finlay 2004, Bass and Boenigk 2011). The genus *Pappomonas* while being recorded from both polar regions is represented in each area by different subsets of species. We should emphasize perhaps that although the morphospecies concept applied here is by nature subjective there is hardly any doubt about the validity of the four taxa currently assigned to the genus, and we also strongly believe that the sampling efforts in both polar areas are large enough to rule out undersampling as a decisive factor when analysing patterns of large scale distribution. The documented existence of persistent communities of lightly calcified coccolithophorids at both the North and South Pole can be taken as an indication of a large degree of similarity among the habitats being offered at either site. On the other hand it still remains a possibility that the fact that species are not in all cases found to be ubiquitous can be explained by minor causative differences among otherwise seemingly identical habitats. It appears valid, despite a limited sampling effort in some parts of the world's oceans, to conclude that low latitude habitats are obviously not suitable for the vast majority of the lightly calcified polar coccolithophorids. A plausible explanation for the restricted distribution of the individual species as contrasted to the bipolar occurrence of the genus itself might simply be that an exchange

of genetic material across the warm water low latitude water masses has not taken place in recent geological time. These organisms are not known to produce stable resting cysts for long range dispersal and even though they are not dependent on photosynthesis a pole to pole transport via e.g. cold deep water currents would be very challenging.

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