

Papposphaera obpyramidalis (Haptophyta, Papposphaeraceae): New findings from both Polar Regions

Thomsen, Helge Abildhauge; Egge, Jorun Karin; Heldal, Mikal

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1	Papposphaera obpyramidalis (Haptophyta, Papposphaeraceae): New findings from both Polar
2	Regions
3	
4	Papposphaera obpyramidalis (Haptophyta, Papposphaeraceae): Nouvelles découvertes provenant
5	des deux régions polaires.
6	
7	Helge Abildhauge Thomsen ^a , Jorun Karin Egge ^b , Mikal Heldal ^b
8	^a National Institute of Aquatic Resources (DTU Aqua), Technical University of Denmark,
9	Charlottenlund, Denmark;
10	^b Department of Biology, University of Bergen, Thormøhlensgate 53, 5020 Bergen, Norway
11	
12	* Corresponding author
13	E-mail address: <u>hat@aqua.dtu.dk</u> (H. Thomsen)
14	

16 Abstract

17	Papposphaera obpyramidalis is reinvestigated based on additional high latitude sampling from
18	the southern hemisphere. The material used here comprises better preserved TEM material
19	including several cells with complete flagellation, as well as LM of living material. The re-
20	examination basically confirms the findings that were part of the species description but also adds
21	details on e.g. nutritional mode and the presence of an underlayer of unmineralized scales.
22	Papposphaera obpyramidalis has hitherto been considered confined to Antarctic waters. However,
23	here we present also findings of the species from Arctic realms based on recent SEM surveys from
24	the Svalbard region, indicating a bipolar distribution.
25	
26	Keywords: Coccolithophore, coccolithophorid, Papposphaera, P. obpyramidalis, polar regions, electron microscopy
27	Résumé
28	Papposphaera obpyramidalis est de nouveau étudiée à partir des échantillons provenant des
29	hautes latitudes de l'hémisphère Sud. Le matériel utilisé ici comprend du materiel
30	MET mieux préservé avec notamment plusieurs cellules à flagellations complètes, ainsi que du LM
31	de matériaux vivants. Le réexamen confirme les résultats qui faisaient déjà partie de la description
32	de l'espèce, mais apporte aussi des détails, comme par exemple sur le mode nutritionnel et la
33	présence d'une sous-couche d'écailles non minéralisées. Papposphaera obpyramidalis était jusqu'à
34	présent considérée restreinte aux eaux de l'océan Austral. Cependant, nous présentons également ici
35	des résultats de l'espèce provenant des eaux arctiques, basé sur des observations récentes au MEB
36	de matériel provenant de Svalbard, indiquant ainsi une distribution bipolaire de l'espèce.
27	

Mots clés: Coccolithophore, coccolithophoridés, *Papposphaera*, *P. obpyramidalis*, régions polaires, microscopie
 39 électronique

- 40 **Abbreviations:** TEM transmission electron microscope; SEM scanning electron microscope;
- 41 LM light microscope; AMERIEZ, EPOS, ANT X/3 acronyms for Antarctic cruises (see
- 42 Materials and Methods)

43 **1. Introduction**

Papposphaera obpyramidalis Thomsen in Thomsen et. al. 1988 was described based on the 44 45 finding of four coccospheres among the Weddell Sea AMERIEZ material. The main feature of this species, i.e. the large calvees each formed by four triangular plates, renders this taxon easily 46 recognizable and it has accordingly been observed in a number of subsequent TEM and SEM based 47 surveys of coccolithophores along transects and station grids leading into the Antarctic region. 48 Papposphaera obpyramidalis is thus established as an iconographic representative of the Antarctic 49 50 community of lightly calcified coccolithophores. We present here further details, e.g. the collapsed nature of the pyramids and the presence of underlayer scales, on *P. obpyramidalis* based on light 51 microscopy and transmission electron microscopy of material collected during the EPOS and ANT 52 53 X/3 Antarctic cruises.

We have until recently considered *P. obpyramidalis* as being confined to the southern hemisphere. The reasoning behind this is that whilst there are frequent recordings from Antarctic waters, the taxon is absent from species lists from the large scale Arctic TEM nannoflagellate surveys conducted over the last decades. However, bipolarity within *P. obpyramidalis* has now become an issue in as much as this organism has been found on some occasions during recent SEM surveys of material mostly from the Svalbard region. We will below illustrate these findings and make some initial comparisons of the two subsets of material.

The redescription and overall update on current knowledge with reference to *P. obpyramidalis* is part of an ongoing effort to establish a coherent overview of the community of lightly calcified coccolithophores from Polar Regions. The first paper in this series targeted the genus *Wigwamma* Manton, Sutherland and Oates 1977 (Thomsen et. al., 2013), and we are currently in turn dealing with species of *Papposphaera* (Thomsen and Egge, 2016; Thomsen and Østergaard, 2016;

66 Thomsen et. al., 2015a,b; Thomsen et al., 2016).

69

68 **2. Materials and methods**

'Melville' AMERIEZ cruise (March 1986), the R/V 'Polarstern' ANT VII/3 'EPOS II' cruise (Nov. 70 1988 – Jan. 1989) and the R/V 'Polarstern' ANT X/3 'Herbst im Eis' cruise (April-May 1992), with 71 72 all cruises occupying stations in the Weddell Sea region (Fig. 1A). The Arctic material derives from an ongoing sampling programme collecting material for scanning electron microscopical analysis 73 74 that has been conducted since 2012 in the fjord systems of Svalbard and also at other Arctic sites. 75 The sampling site yielding P. obpyramidalis (#D2 at 78.59.3°N, 3.03.2°E; 15 Nov. 2014; 2 and 20 meter depth) is shown in Fig. 1B. 76 77 The light microscopy (Fig. 2 E-J) was carried out during the ANT X/3 cruise. The microscope, a Dialux 20 fitted with a x100 Nomarski objective, was placed on a vibration damped 78 79 table in a cold container thus being operated at ambient sea temperatures. A Wild MPS-55 photographic unit and a flash system were used to optimize photography and to further reduce any 80 vibrations generated by the ship. 81 82 Table 1 summarizes collection specific data for the material actually used here for illustration purposes. 83 The protocol for processing water samples for transmission electron microscopy (TEM) was 84 85 similar on all sampling occasions (see Moestrup and Thomsen, 1980). The nannoplankton community was concentrated for further processing by means of either centrifugation of a 86 prefiltered (usually 20 µm) water sample or centrifugation of prefiltered material resuspended from 87 88 an initial concentration of cells on top of e.g. a 1 µm Nuclepore filter. Small droplets of cells from the resuspended final pellet of material were placed on carbon coated grids for the TEM. Cells 89 were subsequently fixed for ca. 30 seconds in the vapour from a 1-2% solution of OsO₄. After 90

The Antarctic material for transmission electron microscopy originates from the R/V

drying the grids were carefully rinsed in distilled water in order to remove salt crystals. Grids were 91 shadow cast with either Au/Pd or Cr prior to the examination in JEOL electron microscopes 92 93 property of the Botanical Institute at the Univ. of Copenhagen. Material for the SEM was prepared by gentle filtration of a water sample on top of a 1.0 µm 94 Nuclepore filter. The formation of salt crystals that might obstruct the visibility of cells was 95 minimized by allowing the pumping system to almost completely dry out the filter. Filters were 96 sputter coated with gold and examined on a Zeiss Supra 55VP scanning electron microscope at the 97 Bergen University Laboratory for Electron Microscopy. 98 The terminology follows wherever possible Young et. al. (1997, 2003). 99

100

102 **3. Observations**

103 **3.1** Antarctic material / light microscopy (Fig. 2E-J)

104 P. obpyramidalis was abundantly present in ANT X/3 samples to the extent that it was repeatedly observed live in the light microscope. Fig. 2E-J represent images of one particular cell. 105 When focusing through the cell different features become visible. The cell is flagellated and the 106 107 haptonema is visible curled up at the front end of the cell (Fig. 2E, I, arrows). The coccoliths with their oversized calvces are clearly visible in Fig. 2G-H, J. These LM images also clearly show the 108 109 size differences within the individual coccosphere with the largest and tallest coccoliths clustering around the flagellar pole. The outline of coccolith bases can be seen in Fig. 2E, I (arrows). Figure 110 2F focuses on the outer edge of the coccosphere and displays the most distal edges of the individual 111 112 coccoliths. The short and sharp lines, that are more or less perpendicular to the longitudinal axis of the cell, are definitive proof of the fact that the calvx in this species is flattened and 2-dimensional. 113 The species epithet was chosen based on the erroneous assumption that the four triangular blades in 114 an undisturbed cell would form an inverted pyramidal structure. 115

The final feature to comment on here is the appearance of the cytoplasm. Most controversial is the fact that this cell is devoid of a chloroplast. We have observed many live cells none of which had any trace of a chloroplast, and the absence of a chloroplast has also been verified based on fluorescence microscopy. The generally accepted paradigm within coccolithophores at large is that they are photosynthetic with the occasional possibility of supplementing the carbon sequestering by mixotrophy. Polar coccolithophores, and in particular members of the Papposphaeraceae, are unique in relying exclusively on heterotrophy for their survival.

123

124 3.2 Antarctic material / transmission electron microscopy (Fig. 2A-D, K; Fig. 3A-B)

125 The examination of a large amount of material of P. obpyramidalis from the EPOS and ANT X/3 cruises basically confirms the observations that were part of the first AMERIEZ based 126 127 description of the species (Thomsen et. al., 1988). We have added images showing cells with complete flagellation and haptonema (Fig. 2A, D; Fig. 3A-B) which represents the normal 128 appearance of *P. obpyramidalis*. The coccosphere typically measures 8-10 µm in external diameter 129 and 4- 5 μ m in interior diameter. It is obvious from the complete cells shown in Fig. 1A, D that 130 there is a pronounced difference in the size of coccoliths from one end of the cell to the other, i.e. 131 132 the coccoliths are varimorphic. The proximal part of a coccolith is narrowly elliptical and measures 1.1-1.3 x 0.6-0.9 µm. The coccolith rim is standard for a papposphaeracean murolith and the height 133 varies from 0.25-0.30 µm. It comprises two cycles of overlapping and interlocking elements (Fig. 134 135 2K). The central area calcification is an axial cross (Fig. 2B-C, K) that leads into a central calicate spine where the stem varies in size $(0.5-1.6 \,\mu\text{m})$ with the most long-stemmed coccoliths encircling 136 the flagella. When measuring the size of the terminal 'pyramid' between its lateral extremes the 137 mean value is 2.1±0.42 µm (Fig. 2A) and 2.1±0.25 µm (Fig. 2D) with absolute ranges from 1.7-2.6 138 µm (Fig. 2A) and 1.4-2.8 µm (Fig. 2D). 139

A high magnification of coccoliths (Fig. 2K) documents the presence in this species of organic underlayer scales each with a fine pattern of radiating and concentric threads. The dimensions of these are $0.25-0.3 \times 0.3-0.4 \mu m$. It is important to mention that the presence of organic underlayer scales of this morphology is confirmed also from other micrographs, to rule out the possibility that the linkage between coccoliths and organic scales illustrated here is just fortuitous.

146

147 3.3 Arctic material / scanning electron microscopy (Fig. 3C-D)

148 The Arctic material includes coccospheres (Fig. 3C) and scatters of coccoliths (Fig. 3D) that comprise individual coccoliths which are dimensionally and morphologically very similar to those 149 150 from Antarctica. The coccolith thus measures 1.26±0.13 x 0.80±0.08 µm with an overall size range of 1.1-1.5 x 0.65-0.95 µm, while the maximum size span of the calyx ranges from 1.6 to 2.0 µm. 151 The stem of the central process is similarly short as previously seen in Antarctic specimens. It is 152 obvious from Fig. 3C-D that the calyx is also here a flattened 'pyramid' although damage to some 153 of the coccoliths as part of the preparational procedure has caused some of the calyces to bend and 154 155 the flattened pyramid to 'open up'.

156 **4. Discussion**

While the starting point here is evidence for an aplastidic condition in *P. obpyramidalis* it is 157 158 important to emphasize that this appears to be in fact a general characteristic of the entire community of polar lightly calcified coccolithophores. We have over the last decades examined 159 hundreds of dried cells of lightly calcified polar coccolithophores (across all genera and species) at 160 high magnification in freshly prepared material and searched for a chloroplast using primarily 161 epifluorescence techniques. Whereas nearby control cells, e.g. small diatom cells, always fluoresced 162 163 distinctly red when excited, this was never the case for any of the lightly calcified coccolithophores. 164 The first member of the lightly calcified coccolithophore community that was found to be non-photosynthetic was in fact Balaniger virgulosa HOL (Thomsen and Oates 1978) Thomsen and 165 166 Østergaard 2014 (= Balaniger balticus Thomsen and Oates 1978). Although this was not specifically mentioned in the TEM description of this species (Thomsen and Oates, 1978), it has 167 due to the frequent occurrence of this form in Danish coastal waters, become a regularly confirmed 168 169 fact since then. The B. virgulosa signature when observed live is unmistakable, i.e. a heart-shaped greyish-whitish cell body with two long flagella and a somewhat shorter haptonema. While few of 170 the lightly calcified coccolithophores can be convincingly identified in the light microscope – with 171

P. obpyramidalis being one of the rare exceptions –the group as such has a very distinct appearance
due to the unique combination of the colourless cell interior, the typical haptophyte appendages
(flagella and haptonema) and a scaly periplast.

While it is evident to us that the polar lightly calcified coccolithophore communities are genuinely non-photosynthetic across the entire range of genera and species, it remains to be verified whether their relatives from tropical waters share their heterotrophic life mode. Is the lack of chloroplasts in polar forms a primary feature or is it a secondary derived feature selected for due to environmental stress, e.g. prolonged periods of darkness? In order to properly address this issue cultures of one or more of these enigmatic organisms will be needed.

It is a well-established fact that species of *Papposphaera* and species of *Turrisphaera* form 181 182 part of the same life cycles even though it has so far only been documented in a few cases (P. sagittifera/T. borealis; P. sp. nov./Turrisphaera arctica; P. sarion/Turrisphaera sp. nov.; see 183 Thomsen et. al., 1991, 2016a,b). It should be emphasized that also the generic type, P. lepida 184 Tangen 1972, appears in combination cells with a species of *Turrisphaera* (Young et al., 2015). It is 185 thus to be expected, based on e.g. the convincing similarity between the generic type and P. 186 187 obpyramidales that a partnership with a species of Turrisphaera will eventually be documented for *P. obpyramidalis*. The species diversity within *Turrisphaera* seems to be falling short in 188 comparison with the diversity observed in Papposphaera. This applies to the Polar Regions and 189 190 interestingly enough also to warm water habitats that have recently been found to accommodate many species of Papposphaera, but, very few species of Turrisphaera. The features available in 191 Turrisphaera for rapid species identification are limited which could indicate that a cryptic species 192 193 concept is perhaps in operation here. This is an issue that needs to be pursued using DNA sequencing which is the proper tool for detecting and differentiating morphologically similar 194 species. 195

196 When browsing through the literature on lightly calcified polar coccolithophores the question 197 arises whether minute unmineralized underlayer scales are to be found across the genus and species 198 matrix according to some kind of masterplan. So far we have seen these scales in all five species of Wigwamma (i.e. W. arctica, W. annulifera, W. antarctica, W. triradiata, and W. armatura / see 199 Thomsen et. al., 2013) and also within Calciarcus (see Thomsen and Østergaard, 2014a) which is 200 201 strongly expected to share a life history with species of *Wigwamma*. Unmineralized underlayer scales are also a shared feature among species of Turrisphaera (i.e. T. borealis, T. polybotrys / see 202 203 Manton et. al., 1976 and Thomsen, 1980a), Trigonaspis (i.e. T. diskoensis, T. minutissima, and T. 204 melvillea / see Thomsen, 1980b and Thomsen and Østergaard, 2015), and Quaternariella (i.e. Q. 205 obscura / see Thomsen, 1980c). It thus appears safe to conclude (based on the multiple occurrences 206 within a number of genera) that the presence of unmineralized underlayer scales is a basic feature of 207 at least the genera Wigwamma, Turrisphaera and Trigonaspis. The only formally described species from this cluster of genera which is not so far associated with unmineralized scales is Turrisphaera 208 arctica, and the reason behind this is most likely a lack of adequate material to document their 209 presence. The presence of small unmineralized underlayer scales in P. obpyramidalis (Fig. 2K) is 210 211 somewhat unexpected, because this is in fact the first species of *Papposphaera* in which these have 212 been found. However, it should be mentioned that such scales have also been found in a single 213 species of Pappomonas, i.e. P. garissonii Thomsen and Østergaard 2014 (see Thomsen and 214 Østergaard, 2014b). It is premature to conclude anything about the possible consequences of these findings. Is the presence or absence of these scales critical at the level of the circumscription of 215 genera? – or is it merely a species characteristic? In many cases negative evidence with respect to 216 217 the occurrence of these scales is not very helpful, because the species in question may be either seriously under sampled or the material available not of a quality that allows for the recognition of 218 these scales even when using a TEM. However, when it comes to the genera Papposphaera and 219

Pappomonas under sampling is generally not an issue, nor is the overall quality of the material a
problem, so in these particular cases negative evidence will most likely have to be accepted as valid
evidence. As indicated above we will for the time being have to leave this case open and basically
proceed whenever possible to simply accumulate additional evidence on the presence or absence of
these structures.

The final issue to be briefly introduced here is that of bipolarity. The general picture is here that the two poles share genera while species tend to be found in only one or the other polar region. The apparent exceptions from this general rule of thumb are *Wigwamma arctica*, *W. annulifera*, *Calciarcus alaskensis* 'morphotype 3', *Papposphaera sagittifera* (Antarctic material yet referred to as *P. sagittifera* cfr.) and finally *P. obpyramidalis* as reported here. Without access to molecular data to provide the final proof of bipolarity, there is not much that can be done at this moment apart from continue to keep track on forms that potentially have a bipolar distribution.

232

233 Disclosure of interest

The authors declare that they have no competing interest.

235

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- 246

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295	
296	
297	Legends
298	Fig 1. Collection sites. A. Map of the Weddell Sea, Antarctica, showing stations sampled during
299	three cruises. Papposphaera obpyramidalis occurred at all three sites. B. Map of the Arctic
300	Svalbard area showing the location of the single sampling site from where <i>P. obpyramidalis</i> has
301	been observed.
302	
303	Fig. 2. Papposphaera obpyramidalis TEM (Figs A-D, K) and LM (Figs E-J) / Antarctic material
304	from the ANT X/3 cruise. A. Complete cell with curled up flagella and haptonema. B. Detail of
305	proximal part of coccolith showing rim structure and central area calcification. C. High
306	magnification of three differently sized coccoliths. D. Complete cell with curled up flagella and
307	haptonema. E-J. Light micrographs showing different focal levels of the same cell; the haptonema
308	and coccolith base outlines (arrows) are visible in Figs E, I. The scale bar (Fig. 2F) applies to all
309	light micrographs. K. Reversed print of coccoliths showing unmineralized scales from the
310	underlayer (arrows).
311	

312	Fig. 3. Papposphaera obpyramidalis TEM (Figs A-B / Antarctic material from the Ant X/3 cruise)
313	and SEM (Figs C-D / Arctic material from #D2). A. Detail from Fig. B showing the haptonema. B.
314	Complete cell with partly extended flagella and haptonema. C. Complete coccosphere. D. High
315	magnification of coccoliths.
316	
317	
318	Table 1: Collection specific details pertinent to material selected here to illustrate P. obpyramidalis.

Cruise	Station	Date	Posi	tion	Depth (m)
ANT X/3	#21/355	12-apr-92	70°22.06 S	7°19.95 W	2
ANT X/3	#21/426	20-apr-92	70°21.64 S	9°44.6 W	2+10
ANT X/3	#21/391	16-apr-92	70°21.64 S	8°54.84 W	15
ANT X/3	100	09-apr-92	70°30.5 S	8°01.5 W	10
ANT X/3	#21/431	21-apr-92	70°59.3 S	11°00.1 W	2+10
ANT X/3	#21/458	28-apr-92	69°06.6 S	12°03.6 W	100
μPolar	#D2	15-nov-14	78°59.3 N	3°03.2 E	2 and 20

Table 1: Collection specific details pertinent to material selected here to illustrate

Illustration	
Fig. 2A	ļ.
Fig. 2B	
Fig. 2C	
Fig. 2D, 2K	
Fig. 2E-J	
Fig. 3A-B	-
Fig. 3C-D	

P. obpyramidalis .



100°W 110°W 130°W 180° 130°E





