



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

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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

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14

15

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 matériel
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.

37

38 **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**

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

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

61 The redescription and overall update on current knowledge with reference to *P. obpyramidalis*
62 is part of an ongoing effort to establish a coherent overview of the community of lightly calcified
63 coccolithophores from Polar Regions. The first paper in this series targeted the genus *Wigwamma*
64 Manton, Sutherland and Oates 1977 (Thomsen et. al., 2013), and we are currently in turn dealing
65 with species of *Papposphaera* (Thomsen and Egge, 2016; Thomsen and Østergaard, 2016;
66 Thomsen et. al., 2015a,b; Thomsen et al., 2016).

67

68 **2. Materials and methods**

69 The Antarctic material for transmission electron microscopy originates from the R/V
70 'Melville' AMERIEZ cruise (March 1986), the R/V 'Polarstern' ANT VII/3 'EPOS II' cruise (Nov.
71 1988 – Jan. 1989) and the R/V 'Polarstern' ANT X/3 'Herbst im Eis' cruise (April-May 1992), with
72 all cruises occupying stations in the Weddell Sea region (Fig. 1A). The Arctic material derives from
73 an ongoing sampling programme collecting material for scanning electron microscopical analysis
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
76 meter depth) is shown in Fig. 1B.

77 The light microscopy (Fig. 2 E-J) was carried out during the ANT X/3 cruise. The
78 microscope, a Dialux 20 fitted with a x100 Nomarski objective, was placed on a vibration damped
79 table in a cold container thus being operated at ambient sea temperatures. A Wild MPS-55
80 photographic unit and a flash system were used to optimize photography and to further reduce any
81 vibrations generated by the ship.

82 Table 1 summarizes collection specific data for the material actually used here for illustration
83 purposes.

84 The protocol for processing water samples for transmission electron microscopy (TEM) was
85 similar on all sampling occasions (see Moestrup and Thomsen, 1980). The nanoplankton
86 community was concentrated for further processing by means of either centrifugation of a
87 prefiltered (usually 20 µm) water sample or centrifugation of prefiltered material resuspended from
88 an initial concentration of cells on top of e.g. a 1 µm Nuclepore filter. Small droplets of cells from
89 the resuspended final pellet of material were placed on carbon coated grids for the TEM. Cells
90 were subsequently fixed for ca. 30 seconds in the vapour from a 1-2% solution of OsO₄. After

91 drying the grids were carefully rinsed in distilled water in order to remove salt crystals. Grids were
92 shadow cast with either Au/Pd or Cr prior to the examination in JEOL electron microscopes
93 property of the Botanical Institute at the Univ. of Copenhagen.

94 Material for the SEM was prepared by gentle filtration of a water sample on top of a 1.0 μm
95 Nuclepore filter. The formation of salt crystals that might obstruct the visibility of cells was
96 minimized by allowing the pumping system to almost completely dry out the filter. Filters were
97 sputter coated with gold and examined on a Zeiss Supra 55VP scanning electron microscope at the
98 Bergen University Laboratory for Electron Microscopy.

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

100

101

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

116 The final feature to comment on here is the appearance of the cytoplasm. Most controversial
117 is the fact that this cell is devoid of a chloroplast. We have observed many live cells none of which
118 had any trace of a chloroplast, and the absence of a chloroplast has also been verified based on
119 fluorescence microscopy. The generally accepted paradigm within coccolithophores at large is that
120 they are photosynthetic with the occasional possibility of supplementing the carbon sequestering by
121 mixotrophy. Polar coccolithophores, and in particular members of the Papposphaeraceae, are unique
122 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
126 X/3 cruises basically confirms the observations that were part of the first AMERIEZ based
127 description of the species (Thomsen et. al., 1988). We have added images showing cells with
128 complete flagellation and haptonema (Fig. 2A, D; Fig. 3A-B) which represents the normal
129 appearance of *P. obpyramidalis*. The coccosphere typically measures 8-10 μm in external diameter
130 and 4- 5 μm in interior diameter. It is obvious from the complete cells shown in Fig. 1A, D that
131 there is a pronounced difference in the size of coccoliths from one end of the cell to the other, i.e.
132 the coccoliths are varimorphic. The proximal part of a coccolith is narrowly elliptical and measures
133 1.1-1.3 x 0.6-0.9 μm . The coccolith rim is standard for a papposphaeracean muralith and the height
134 varies from 0.25-0.30 μm . It comprises two cycles of overlapping and interlocking elements (Fig.
135 2K). The central area calcification is an axial cross (Fig. 2B-C, K) that leads into a central calicate
136 spine where the stem varies in size (0.5-1.6 μm) with the most long-stemmed coccoliths encircling
137 the flagella. When measuring the size of the terminal ‘pyramid’ between its lateral extremes the
138 mean value is $2.1\pm 0.42 \mu\text{m}$ (Fig. 2A) and $2.1\pm 0.25 \mu\text{m}$ (Fig. 2D) with absolute ranges from 1.7-2.6
139 μm (Fig. 2A) and 1.4-2.8 μm (Fig. 2D).

140 A high magnification of coccoliths (Fig. 2K) documents the presence in this species of
141 organic underlayer scales each with a fine pattern of radiating and concentric threads. The
142 dimensions of these are 0.25-0.3 x 0.3-0.4 μm . It is important to mention that the presence of
143 organic underlayer scales of this morphology is confirmed also from other micrographs, to rule out
144 the possibility that the linkage between coccoliths and organic scales illustrated here is just
145 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
149 comprise individual coccoliths which are dimensionally and morphologically very similar to those
150 from Antarctica. The coccolith thus measures $1.26\pm 0.13 \times 0.80\pm 0.08 \mu\text{m}$ with an overall size range
151 of $1.1\text{-}1.5 \times 0.65\text{-}0.95 \mu\text{m}$, while the maximum size span of the calyx ranges from 1.6 to 2.0 μm .
152 The stem of the central process is similarly short as previously seen in Antarctic specimens. It is
153 obvious from Fig. 3C-D that the calyx is also here a flattened ‘pyramid’ although damage to some
154 of the coccoliths as part of the preparational procedure has caused some of the calyces to bend and
155 the flattened pyramid to ‘open up’.

156 **4. Discussion**

157 While the starting point here is evidence for an aplastidic condition in *P. obpyramidalis* it is
158 important to emphasize that this appears to be in fact a general characteristic of the entire
159 community of polar lightly calcified coccolithophores. We have over the last decades examined
160 hundreds of dried cells of lightly calcified polar coccolithophores (across all genera and species) at
161 high magnification in freshly prepared material and searched for a chloroplast using primarily
162 epifluorescence techniques. Whereas nearby control cells, e.g. small diatom cells, always fluoresced
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
165 non-photosynthetic was in fact *Balaniger virgulosa* HOL (Thomsen and Oates 1978)Thomsen and
166 Østergaard 2014 (= *Balaniger balticus* Thomsen and Oates 1978). Although this was not
167 specifically mentioned in the TEM description of this species (Thomsen and Oates, 1978), it has
168 due to the frequent occurrence of this form in Danish coastal waters, become a regularly confirmed
169 fact since then. The *B. virgulosa* signature when observed live is unmistakable, i.e. a heart-shaped
170 greyish-whitish cell body with two long flagella and a somewhat shorter haptonema. While few of
171 the lightly calcified coccolithophores can be convincingly identified in the light microscope – with

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

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

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

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
199 *Wigwamma* (i.e. *W. arctica*, *W. annulifera*, *W. antarctica*, *W. triradiata*, and *W. armatura* / see
200 Thomsen et. al., 2013) and also within *Calciarcus* (see Thomsen and Østergaard, 2014a) which is
201 strongly expected to share a life history with species of *Wigwamma*. Unmineralized underlayer
202 scales are also a shared feature among species of *Turrisphaera* (i.e. *T. borealis*, *T. polybotrys* / see
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
208 from this cluster of genera which is not so far associated with unmineralized scales is *Turrisphaera*
209 *arctica*, and the reason behind this is most likely a lack of adequate material to document their
210 presence. The presence of small unmineralized underlayer scales in *P. obpyramidalis* (Fig. 2K) is
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
215 findings. Is the presence or absence of these scales critical at the level of the circumscription of
216 genera? – or is it merely a species characteristic? In many cases negative evidence with respect to
217 the occurrence of these scales is not very helpful, because the species in question may be either
218 seriously under sampled or the material available not of a quality that allows for the recognition of
219 these scales even when using a TEM. However, when it comes to the genera *Papposphaera* and

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

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

232

233 **Disclosure of interest**

234 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 *P. obpyramidalis* 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*.

319

| Cruise | Station | Date | Position | | 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

Fig. 2B

Fig. 2C

Fig. 2D, 2K

Fig. 2E-J

Fig. 3A-B

Fig. 3C-D

∶ *P. obpyramidalis* .





