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Papposphaera heldalii sp. nov. (Haptophyta, Papposphaeraceae) from Svalbard

Helge Abildhauge THOMSEN[1], Jorun Karin EGGE[2]

[1]National Institute of Aquatic Resources (DTU Aqua), Technical University of Denmark, Charlottenlund, Denmark; [2]Department of Biology, University of Bergen, Bergen, Norway

Abstract. In an attempt to establish a taxonomy for the polar contingent of lightly calcified coccolithophores, we are currently dealing with species of *Papposphaera*. Here we describe a new species, *Papposphaera heldalii* sp. nov., based on material from Svalbard. The species is unique in terms of calyx design, which is an elegant modification of the standard *P. sagittifera* theme, and also in terms of the absence of central area calcification in body coccoliths. The species thus occupies a further step in a sequence of five Arctic forms ranging from *P. sagittifera* via *P. sarion*, *P. arctica* and *P. iugifera* to *P. heldalii* showing a gradual reduction of central area calcification in body coccoliths. *P. heldalii* is unique also in the sense that the species has not been found during any of the major Arctic TEM nanoplankton surveys conducted during the last decades.

Key words: *Papposphaera*, *P. heldalii* sp. nov., Papposphaeraceae, Svalbard, scanning electron microscopy.

Abbreviations: SEM – scanning electron microscope; TEM – transmission electron microscope.

INTRODUCTION

In an ongoing effort to provide an updated survey of lightly calcified polar coccolithophores, we are in the process of dealing with species of *Papposphaera* primarily from the Arctic. The genus *Papposphaera* at present comprises nine species. The generic type, *P. lepida* Throndsen 1972, was described from Nordåsvatnet, Western Norway, and the species has since then been reported from many different sites consolidating its current status as a genuine cosmopolitan species. Two additional species have been described from low latitude sites, viz. *P. thomsenii* Norris 1983, from the Indian Ocean and *P. bourrellii* Thomsen and Buck 1998, from San Juan Islands, Washington, USA. The latter species is additionally found in samples from offshore California and from Mexico (Gulf of California) (Thomsen and Buck 1998). The remaining species all share a restricted occurrence pattern being confined to the polar regions. Arctic species comprise *P. sagittifera* Manton, Sutherland and McCully 1976, *P. sarion* Thomsen 1981, *P. arctica* (Manton, Sutherland and Oates 1976) Thomsen, Østergaard and Hansen 1991,

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Address for correspondence: Helge Thomsen, National Institute of Aquatic Resources (DTU Aqua), Technical University of Denmark, Jægersborg allé 1, DK 2920 Charlottenlund, Denmark; E-mail: hat@aqua.dtu.dk

and *P. iugifera* Thomsen and Østergaard 2016. *Papposphaera simplicissima* Thomsen in Thomsen *et al.* 1988 and *P. obpyramidalis* Thomsen in Thomsen *et al.* 1988 are so far confined to circum-Antarctic waters.

The new Svalbard species described here is morphologically at the extreme end of a variability matrix comprising all five Arctic taxa. The main theme seen across these taxa is a progressive decrease in the central area calcification and a gradual transition from forms with varimorphic coccoliths to forms with dimorphic coccoliths, i.e. having two discrete types of coccoliths building up the coccosphere.

The species is named in honour of our colleague Mikal Heldal, University of Bergen. Mikal has been instrumental in providing over the last years unique high resolution SEM images of a large number of lightly calcified polar coccolithophores. These images have proved incredibly valuable to the current process of updating our knowledge on the entire polar community of lightly calcified coccolithophores. The established recent routine has been to combine classical TEM images with selected recent SEM micrographs (see e.g. Thomsen *et al.* 2016a, b). Ironically enough we will have to abandon this routine here in as much as *P. heldalii* sp. nov. represents a taxon that has not been found during any of the extensive TEM surveys of Arctic nanoflagellates conducted during the past decades.

MATERIALS AND METHODS

Samples yielding *P. heldalii* originate from the project MicroPolar [µP]. MicroPolar focuses on the processes and players in Arctic marine pelagic food webs. The aim of the µP cruises, located west and north of Svalbard was to characterize microbial abundance, biomass, biodiversity and activity, and biogeochemical parameters and processes in Polar and Atlantic Water masses during an annual cycle.

Material for scanning electron microscopical analyses was collected during µP cruises on board RV 'Helmer Hanssen' or RV 'Lance', in January, March, May, August and November 2014 north and west of Svalbard. Samples were collected from several depths, from the surface, and if possible, down to 1000 m. The master plan for all cruises was to mainly sample north of Svalbard, but due to ice formations this area was only reached in January and March (Fig. 1). Specific samples yielding *P. heldalii* are listed in Table 1.

Material for the SEM was prepared by gentle filtration of a water sample (500–1500 ml) onto a 25 mm polycarbonate filter (Poretics, OSMONICS Inc.) with a pore size of 1 µm. 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 stored individually in a 15 ml Falcon tube. Filters were sputter coated (Polaron SC502 Sputter Coater) with gold or gold/palladium and examined in a Zeiss Supra 55VP scanning electron microscope at the Bergen University Laboratory for Electron Microscopy.

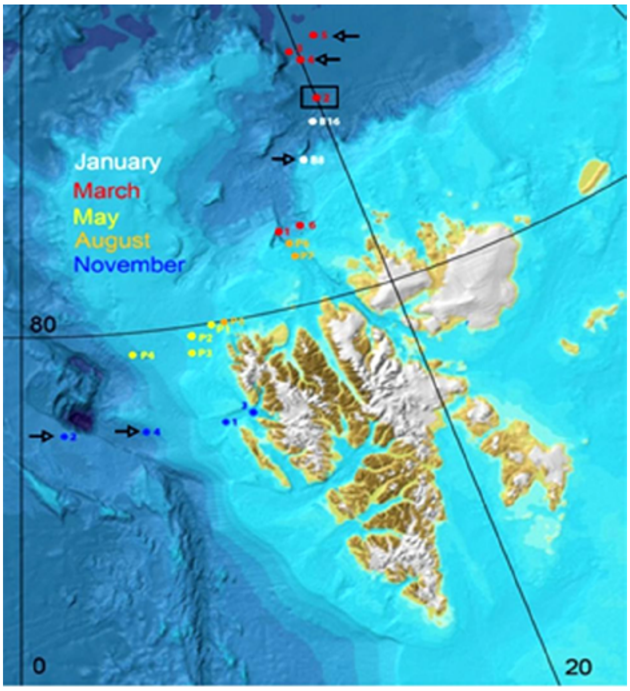


Fig. 1. Svalbard sampling sites during MicroPolar cruises. The type locality of *P. heldalii* is marked by a square, and arrows point to additional sampling sites yielding *P. heldalii* material.

Table 1. MicroPolar [µP] samples yielding *P. heldalii* sp. nov.

2014	Station #	Latitude N	Longitude E	Depth (m)
January	B8	81°25.52	17°49.60	1
March	B2	81°59.45	20°00.67	320
	B4	82°22.56	19°52.21	0
	B5	82°33.10	21°01.59	120
May	*P. heldalii* not recorded			
August	*P. heldalii* not recorded			
November	D2	78°59.34	02°03.22	500
	D4	79°01.46	06°02.98	5/50/500

The terminology follows wherever possible Young *et al.* (1997, 2003). The calyx takes in *P. sagittifera* and related species (including *P. heldalii*) a distinct shape which justifies the use of a special term for this. In order to simplify future descriptions of these structures we recommend that the *P. sagittifera* type of calyx is referred to as a four-winged rosette, and further that each element is referred to as a wing.

RESULTS AND INTERPRETATION

Papposphaera heldalii sp. nov.

Description of the heterococcolithophore phase: Coccosphere outer diameter ca. 10 µm; inner diameter 4–5 µm (Figs 3–5). Dimorphic coccoliths. Body coccoliths are narrowly elliptical and typically measure 0.9–1.0 × 0.5–0.6 µm. The coccolith rim (Fig. 2) is formed by two cycles of elements. A proximal cycle of rod-shaped elements (0.1–0.2 × 0.04 µm) and a distal cycle of pentagonal elements that give the rim a regular serrated appearance. Elements from the distal cycle are regularly shifted half the length of a rod-shaped element from the proximal cycle and an extension from the pentagonal elements separates the rod-like elements (Figs 2, 7; arrows). The coccolith rim flares slightly relative to the subtending organic base plate, and is variable in height (0.2–0.3 µm). There is no central area calcification. Clusters of coccoliths with calicate central spines occur at the apical and antapical poles of the cell (Figs 3–5). These coccoliths are narrowly elliptical and measure 1.0–1.2 × 0.8 µm. The coccolith rim (Fig. 7) is similar to that described above for the body coccoliths. Central area calcification is in the shape of an axial cross (Figs 3, 5–6) that leads into a central shaft (2.1–3.6 µm) which in turn carries a calyx 0.9–1.2 µm in height. The calyx (Fig. 2) is formed by four triangular wings arranged in a cross-shaped perpendicular pattern. Each wing is distally and laterally terminated by a prominent tooth and overlaps proximally for a short distance with the central stem.

Holotype: Figs 3, 6 (same cell).

Type locality: Collected March 2014 from St. B2 (Fig. 1) at 320 m depth (cold Atlantic water / < 2°C / > 34.92 PSU).

Type depository: The filter and the stub examined are maintained in the archives of the Bergen University Laboratory for Electron Microscopy which is affiliated with the Faculty of Mathematics and Natural Sciences.

Etymology: The species epithet '*heldalii*' honours the contribution of Mikal Heldal, Univ. Bergen, to the recent exploration of lightly calcified coccolithophores from high Arctic sites.

There is little additional information required in support of the details embedded in the formal species diagnosis. We have not observed flagella and haptonema in association with any of the complete coccospheres examined. However, the occurrence of coccoliths with calicate spines in distinct clusters and with a noticeable difference in length of the central structure when comparing clusters within the same cell (see e.g. Fig. 4) clearly indicates that these cells have distinct polarity which is commonly linked to the presence in the living cell of flagella and haptonema. Since all other species of *Papposphaera* are flagellated there is every reason to believe that these cells are too.

Table 2. Size variability (µm) among body coccoliths.

Body coccoliths	Source	Mean	SD	Min	Max	n
Fig. 3	Lenght	1.05	0.114	0.84	1.27	12
	Width	0.56	0.097	0.44	0.74	13
Fig. 4	Lenght	0.95	0.144	0.51	1.20	23
	Width	0.61	0.102	0.37	0.77	21
Fig. 5	Lenght	0.92	0.137	0.54	1.20	33
	Width	0.60	0.092	0.37	0.73	32

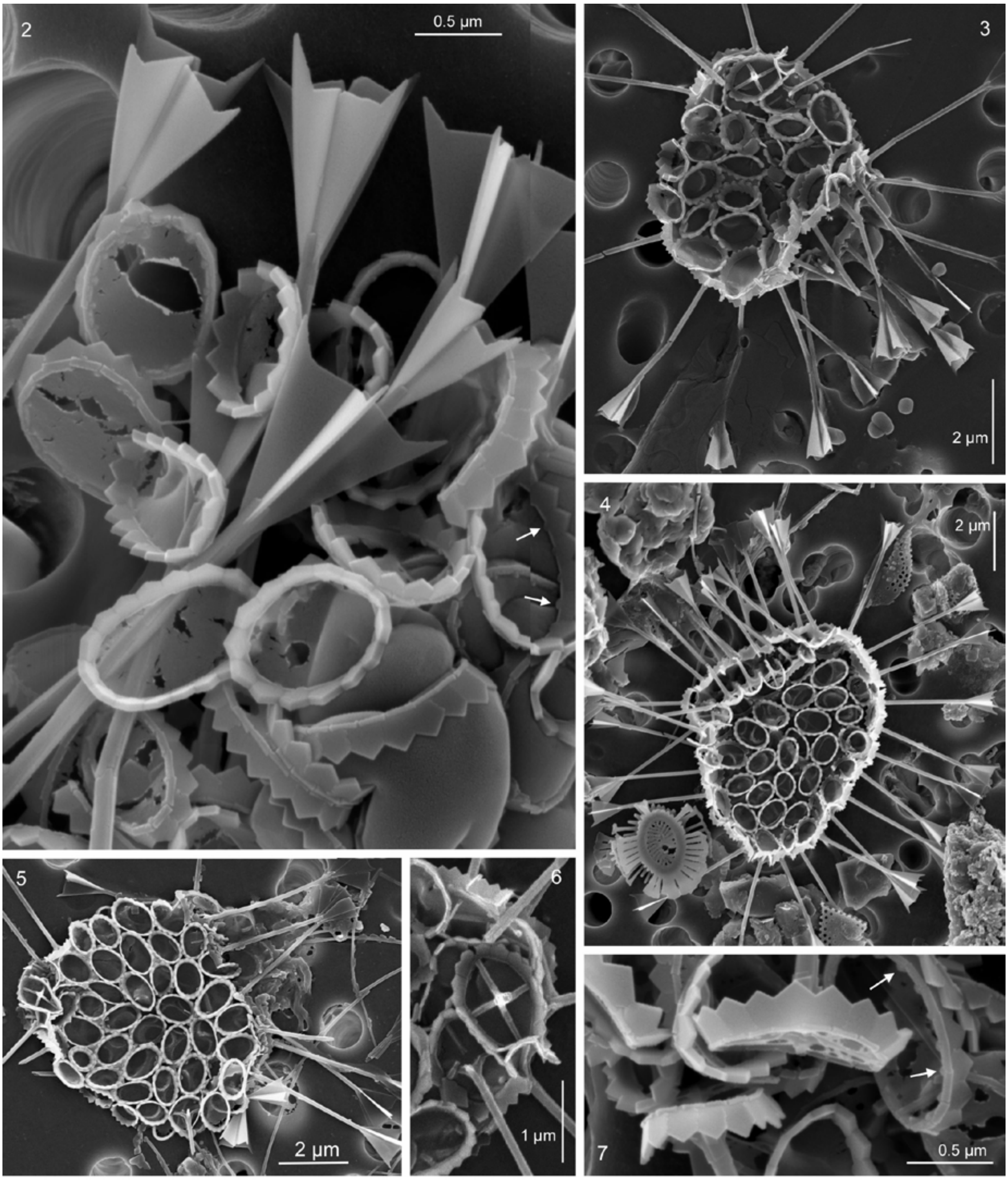
In *P. heldalii* there is a large variability in size (Figs 3–5) among body coccoliths within the same coccosphere exceeding what is typically observed within species of *Papposphaera*. Table 2 summarizes the variability encountered, with the cell in Fig. 5 representing the most extreme case with mean values of 0.9 ± 0.14 × 0.6 ± 0.09 and overall size ranges between 0.5–1.2 and 0.4–0.7 µm respectively.

There is no evidence of unmineralized underlayer scales nor can we at this stage provide information with reference to a possible life history counterpart of *P. heldalii*.

The geographical distribution of *P. heldalii* is currently almost exclusively limited to the Svalbard region (Fig. 1). However, the species has also been found in 'MicroPolar' samples from Young Sound (East Greenland / approx. 74°15N and 20°10W) (Heldal, Egge, Larsen and Paulsen, unpublished observations), and it is likely to have a panarctic distribution similar to what appears to be the case for many other lightly calcified coccolithophores from northern hemisphere high latitudes.

DISCUSSION

While *P. heldalii* on the one hand has very unique species characteristics, i.e. no central area calcification in body coccoliths, and a design of the calyx that is not previously observed among any species of *Pap-*



Figs 2–7. *Papposphaera heldalii* SEM images of cells from the Svalbard region collected during Jan. 2014 (Figs 4–5) and March 2014 (Figs 2–3, 6–7). **2** – cluster of coccoliths shown at high magnification. Notice in particular details of the calyx and coccolith rim calcification. The arrows point to extensions from the pentagonal elements separating the rod-like elements. See also ruptures in the organic base plates of body coccoliths; **3** – whole cell (type specimen) showing the general disposition of types of coccoliths within the coccosphere. A single coccolith (enlarged in Fig. 6) shows the central area calcification of a calicate coccolith; **4** – whole cell. Notice the difference in length of the central process among the two clusters of coccoliths carrying these. See also the conspicuous size differences between neighboring body coccoliths; **5** – body coccoliths showing large individual size differences; **6** – detail of central area calcification in a coccolith that carries a central process (broken away here); 7 – detail of coccolith rim from coccoliths that carry a central process. The arrows point to extensions from the pentagonal elements separating the rod-like elements.

posphaera, it is similarly evident that this species can also be defined as an end or starting point in a developmental sequence of five closely related Arctic species of *Papposphaera* (Fig. 8). In three of these, viz. *P. sagittifera* (Fig. 8A), *P. arctica* (Fig. 8C) and *P. iugifera* (Fig. 8D) the structure of the calyx – a four-winged rosette – appears to be exactly the same. Each wing has parallel edges. The exterior edge is straight, whereas the interior edge is stepwise reduced in width towards the distal end. The degree to which the individual wing diverges from the stem is dependent on the angle between the exterior edge of the wing and the line connecting this to the interior edge. Any variability in calyx design or dimensions can in our experience be found both between these three species and within the same species. *P. heldalii* (Fig. 8E) obviously represents a particularly elegant variation over the calyx motif shared by the other three species, whereas *P. sarion* (Fig. 8B) at first sight appears to deviate substantially from the rest. However, as hypothesized by Thomsen and Østergaard (2016) the *P. sarion* calyx can in fact be interpreted as e.g. a *P. sagittifera* calyx in which the only remaining parts of the four wings that form the calyx are the outermost longest 'steps' in each of these. In all five species the central area calcification in coccoliths carrying central processes is an axial cross (Fig. 8), yet in *P. sagittifera* supplemented also by some longitudinal bars and in *P. sarion* by bars that can be radial and/or perpendicular to the arms of the axial cross.

When examining the body coccolith central area calcification across these five taxa, it is evident that a sorting is possible from a heavily calcified case in *P. sagittifera* (Fig. 8A) where the axial cross is supplemented by 5–7 longitudinal bars, to *P. heldalii* that is characterized by having no central area calcification at all (Fig. 8E). Stages in between these extremes are occupied by: (1) *P. sarion* which has, in addition to the axial cross, radial arm(s) often supplemented by longitudinal or transverse bars that occupy one or two coccolith quadrants (Fig. 8B), (2) *P. arctica* with just a plain axial cross, and (3) *P. iugifera* which typically has a complete transverse bar and remnants of a longitudinal bar. For further details see Thomsen *et al.* (2016a, b) and Thomsen and Østergaard (2016).

Apart from documenting similarities and dissimilarities among the five Arctic species and arguing for sequential development in morphological features, the more profound difference from top to bottom (Fig. 8A–E) is in fact a shift from varimorphic coccoliths in *P. sagittifera* to genuine dimorphic coccoliths in *P. heldalii*.

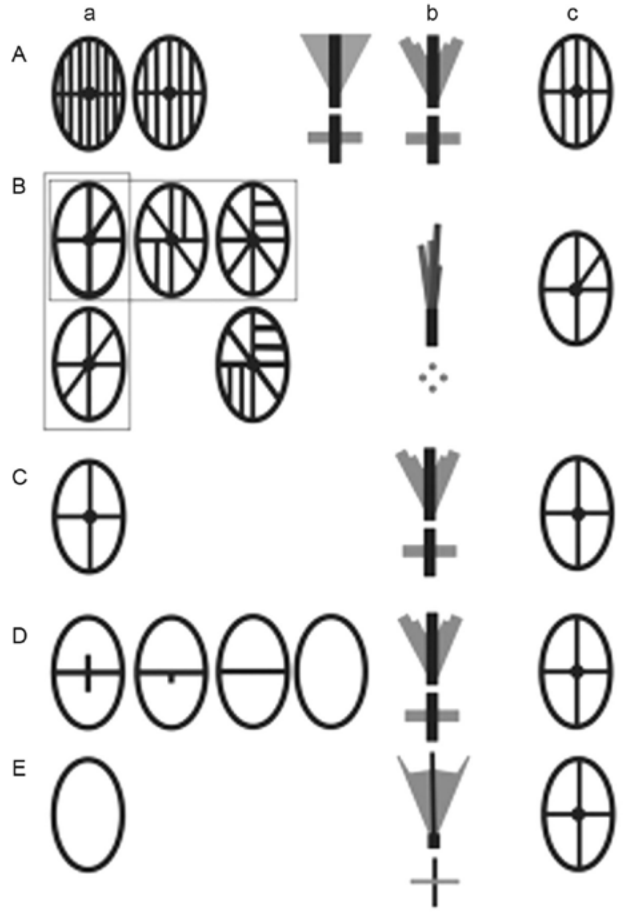


Fig. 8. Schematic drawings of coccolith structures in species of *Papposphaera* (not drawn to scale). **a** – body coccoliths; **b** – calyx design; **c** – coccoliths with central processes; **A** – *P. sagittifera*; **B** – *P. sarion*; **C** – *P. arctica*; **D** – *P. iugifera*; **E** – *P. heldalii*. Notice that alternative shapes are included for some species (A/a, B/a, D/a) and that the *P. sarion* design for a coccolith with a central process (B/c) is potentially as variable as B/a.

In our opinion the five species discussed here form a natural grouping that by all probability will remain accommodated in a single genus. Whether this cluster of species will ultimately be maintained within the genus *Papposphaera* is a relevant question with no obvious immediate answer. Decisions here must await a thorough reanalysis of the type species *P. lepida* and preferably also molecular evidence. However, it deserves to be mentioned that the life history counterpart of *P. sagittifera*, *P. sarion* and *P. arctica* is a species of *Turrisphaera* which is also the case for *P. lepida* (Young *et al.* 2015). A holococcolithophore life history counterpart has not so far been associated with *P. iugifera* or *P. heldalii*.

It finally also appears to be a unifying characteristic for species of *Papposphaera* that they have a calyx design that is based on a four-fold symmetry. This is in contrast to the current situation within *Pappomonas* Manton and Oates 1975 (Thomsen and Østergaard 2014a) which as presently circumscribed comprises species with a two-fold symmetry pattern in calyx design.

In summary it thus appears that *Papposphaera* is characterized by e.g. possessing varimorphic or dimorphic coccoliths (muroliths), a calyx with a four-fold symmetry, and a life history counterpart to be found among species of *Turrisphaera*. *Pappomonas* on the other hand has dimorphic coccoliths, a calyx with a two-fold symmetry, and a life history counterpart to be found among species of *Trigonaspis* Thomsen 1980 (see Thomsen and Østergaard 2014b).

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