Baltic Sea coccolithophores – an overview of insights into their taxonomy and ecology from the last 40 years

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Abstract It is an established fact that coccolithophores are of little importance with respect to biomass and diversity in the Baltic proper. The likely biogeochemical and environmental reasons for this have recently been critically analyzed and reviewed. The main conclusion is that the calcium carbonate saturation of the Baltic Sea is the main controlling feature, and that in particular an undersaturation during wintertime remains the critical bottleneck for coccolithophores to prevail in the Baltic proper. While there is no reason to question these observations, it is still relevant to put on record the actual findings of coccolithophores from the Baltic proper. Examinations of Baltic Sea material from the Bothnian Sea, the Bothnian Bay and the Gulf of Finland prepared for transmission electron microscopy has thus revealed a consistent presence of a low diversity community of lightly calcified coccolithophores (i.e. *Balaniger virgulosa* HOL and HET, *Papposphaera arctica* HOL cfr. and *Papposphaera iugifera*). When including here also material examined from the Danish transitional waters connecting the North Sea and the Baltic proper, it is possible to generally support the presence in the western Baltic, the Sounds and the Kattegat of a contingent of coccolithophores that appear to be either persistently present within the area or episodically occurring as determined by larger scale hydrographical events within the North Sea/Baltic Sea confluence area.

Keywords coccolithophores (coccolithophorids), Baltic Sea, Kattegat

1. Introduction

It is a well-established fact the coccolithophore diversity is very much reduced when moving from the full saline North Sea-Skagerrak area towards the innermost brackish parts of the Baltic Sea (Pankow, 1990; Hällfors, 2004). Tyrell *et al.* (2008) have critically examined the possible explanations behind this scenario (including salinity and silicate concentrations) but concluded that a winter time $CaCO_3$ undersaturation was the most likely explanation. The Baltic Sea winter time surface waters are, according to their findings, distinctly undersaturated with respect to aragonite and borderline undersaturated with respect to calcite. This leads to a situation where coccolithophores will be unable to prevent the dissolution of their coccoliths, which in turn, in all likelihood, impacts the ecological competitiveness of these organisms.

Meier *et al.* (2014) provided an overview of the calcareous nannoplankton from the Kieler Förde and prepared a table that summarized the findings of coccolithophores from the entire Baltic Sea. The current paper summarizes observations from the last four decades of coccolithophore research from the Baltic Sea entrance area (i.e. the Kattegat, the Sounds and the western Baltic), as well as from the innermost and low saline parts of the Baltic Sea, with salinities ranging from 2–8. The observations presented here are for the purpose of future studies within the region thoroughly illustrated. The description of each taxon observed is kept as short as possible and primarily highlights new observations that add to previous descriptions. An updated version of the table compiled by Meier *et al.* (2014) is a key element of this publication.

2. Material and Methods

Material from Danish waters (Figure 1A) comes from a variety of individual projects carried out during the last four decades and will be summarized below in chronological order. All salinities are reported according to the practical salinity scale 1978 (Unesco, 1981).

The 'Belt Project' (1975–76) had an extensive sampling grid throughout the inner shallow Danish waters (Figure 1A). The platform used was the RV 'Martin Knudsen', and the actual sampling was based on water bottles mounted in sequence on the wire on top of a CTD. Material for TEM (Transmission Electron Microscope) examination was prepared at selected stations on four occasions (October 1975; January, March and June 1976). The station coverage on each of these cruises (with the exception of the January 1976 cruise) is indicated in Figure 1A using color-coded squares. Whereas the October and March cruises had fairly complete station coverage, the June cruise did not cover the Kattegat area because of a severe storm event. Also, the January 1976 sampling was impacted by a severe storm which resulted in a very much reduced sampling programme limited to a few stations in the Sound (not indicated in Figure 1A). The vast majority of the samples processed for TEM are from surface waters (Figure 1B; salinities 8–25 and 0–15°C). Non-surface samples stand out clearly in Figure 1B with salinities above 25.
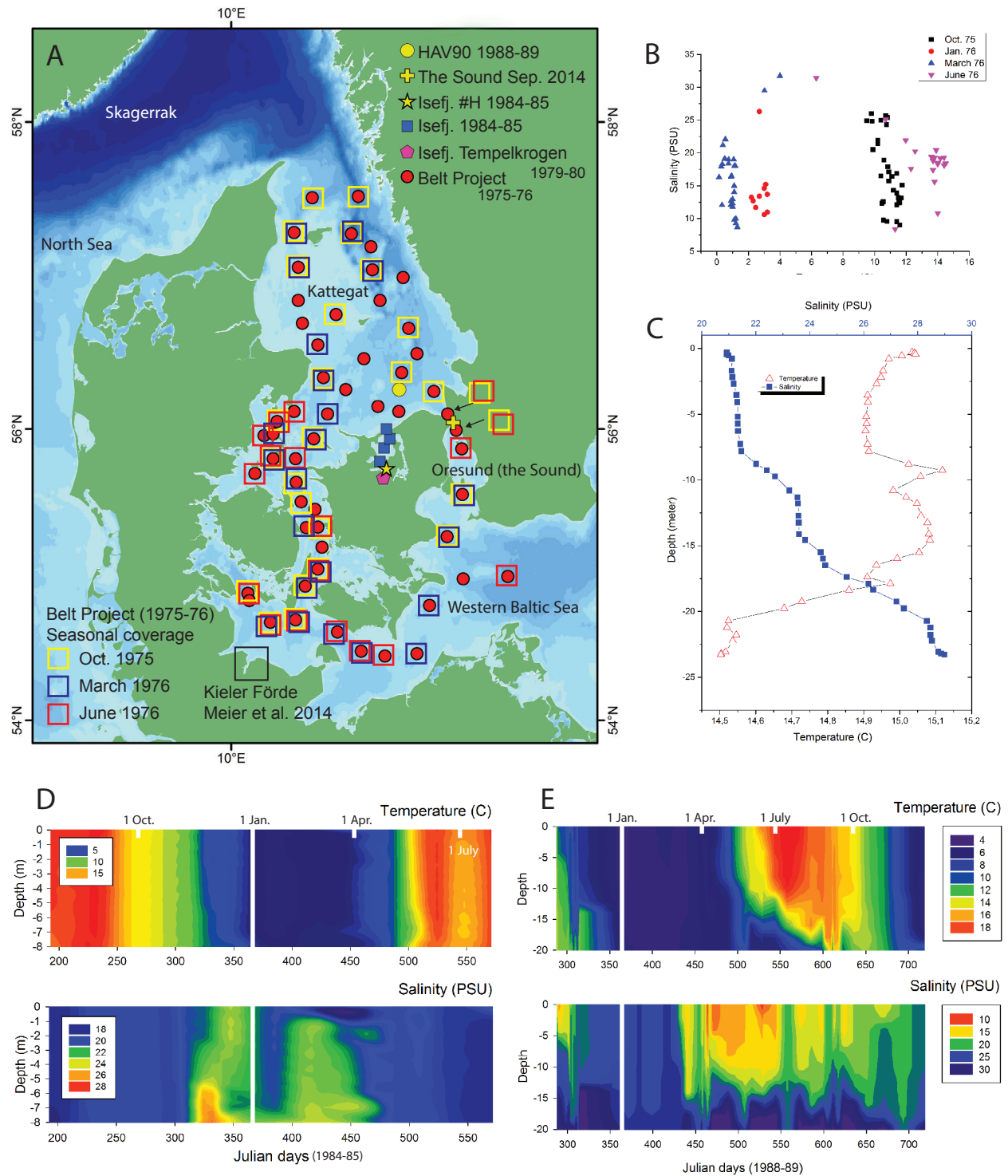
Figure 1: Danish sampling and basic environmental variability. (**A**) Map of the transition area (the Kattegat, the Belt Sea, and the western Baltic) between the Baltic Sea proper and the North Sea. The main geographic sources of material used for this survey are identified (viz. legend in the upper right corner). The colored squares (viz. legend in the lower left corner) show the extent of sampling during three Belt Project cruises. Also indicated (square box) is the Kieler Förde area examined by Meier *et al.* (2014). (**B**) Temperature-salinity plots of samples examined from four Belt Project cruises as an indication of the overall annual variability in basic environmental parameters. (**C**) Depth profiles of temperature and salinity at a station in the Sound sampled 25 September 2014. (**D**) Contour graphs (temperature and salinity) showing the annual parameter variability in the Isefjord inner broad. (**E**) Contour graphs (temperature and salinity) showing the annual parameter variability at the HAV90 permanent station in the southern Kattegat region

Sampling from the Isefjord has been a recurrent event over the last four decades. The main sources of material utilized here originate from annual sampling campaigns conducted in the innermost broad of the fjord system (Tempelkrogen/1979–80) as well as from #H (Vellerup Vig) and selected stations in the Isefjord outer broad sampled during 1984–85. Sampling was either from the shore (Tempelkrogen) or utilizing small boats, i.e. a University of Copenhagen dinghy at #H or a torpedo recovery vessel from the Kongsøre Naval Facility in the Isefjord outer broad. The Isefjord system maintains a fairly high salinity (>18) due to a frequent exchange of water through the entrance to the Kattegat and also because of a rather limited drainage area. The temperature varies annually between 0 and 20°C. The Isefjord system is very shallow and characterized by a water column that rarely becomes stratified (Figure 1D).

A large scale and multifaceted research programme ('HAV 90') was conducted using the University of Copenhagen RV 'Ophelia' at a station in the southern Kattegat (Figure 1A) during 1988–89. The water depth exceeds 20m and the water column is distinctly temperature and salinity stratified during the summer months (Figure 1E). Samples intended for TEM analysis originate from surface waters and from the fluorescence maximum depth, which is typically coincident with the halocline.

Material collected on an ad hoc basis from various sites within the western Baltic/Kattegat region has also been considered with reference to this paper. Details on a specific sample will be added where relevant. More recently, single event sampling has been conducted in, e.g. the Sound (Figure 1A/Sep. 2014). Sampling was carried out from the University of Copenhagen RV 'Ophelia'. The samples analyzed originate from the brackish surface layer (5m) and from the full saline deeper waters (20m). Vertical temperature and salinity profiles are shown in Figure 1C.

Sampling from the innermost parts of the Baltic Sea took place on several occasions (Figure 2A). The Tvärminne Zoological Station was thus visited twice (1974, 1978) and extensively sampled using boats and sampling equipment from the station at sites covering the open sea, the archipelago and the near costal fjord systems (see e.g. Thomsen, 1979). A large scale coverage of the innermost parts of the Baltic Sea was made possible during cruises on the old RV 'Aranda' during July–August 1979 (Figure 2A) and on the new RV 'Aranda' during March 1994 (Figure 2A) as part of the OSIC 1994 winter expedition (see e.g. Ikävalko & Thomsen, 1997). Temperature and salinity profiles (July–August 1979) from the Gulf of Finland transect, as well as a station sequence covering the Northern Baltic, Bothnian Sea and Bothnian Bay stations, are shown in Figure 2F, G. Surface salinity is around 6 in the Gulf of Finland and decreasing towards 3 at the northernmost Bothnian Bay station. Most of the samples processed for TEM during the 1979 cruise are from the uppermost 5m of the water column. Deeper water samples (25 and 50m) were processed only at selected stations. The sampling effort during the OSIC 1994 expedition focused on the ice biota and included only a few water column samples.

The protocol for processing water samples for the TEM was similar on all sampling occasions (see Moestrup & Thomsen, 1980). The nannoplankton community was concentrated for further processing by means of either centrifugation of a prefiltered (usually 20μm) water sample (0.5–1.0l) or centrifugation of prefiltered material resuspended from an initial filtration of cells on top of, e.g. a 1μm Nuclepore filter. Small droplets of cells from the resuspended final pellet of material were placed on carbon coated grids for the TEM. Cells were subsequently fixed for c. 30 seconds in the vapor from a 1–2% solution of OsO_4. After drying the grids 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 University of Copenhagen (JEM-T8, JEOL 100SX).

Material for the SEM (Scanning Electron Microscope) was in some instances (e.g. Pl. 2, fig. 2) standard Au-coated TEM grids prepared according to the technique outlined above and examined in a JEOL 100CX fitted with a high resolution scanning device (joint property of the Botanical and Genetics Inst, Univ. Copenhagen). Images of cells from the Sound (Pl. 1, figs 1, 7, 11; Pl. 2, fig. 7) originate from Au-coated coverslip preparations that were prepared in accordance with the TEM grid routine and examined in a FEI Quanta 200 ESEM FEG (property of DTU Cen). The Bergen SEM material (Pl. 6, fig. 3) was prepared by gentle filtration of a water sample on top of a 1.0μm Nuclepore filter. The formation of salt crystals that might obstruct the visibility of cells was minimized by allowing the pumping system to almost completely dry out the filter. Filters were sputter coated with gold and examined on a Zeiss Supra 55VP scanning electron microscope at the Bergen University Laboratory for Electron Microscopy.

The taxonomic-morphological terminology used here largely follows Young *et al.* (1997, 2003 and references therein). There is no exact quantitative data available to support the qualitative information assembled here. When an organism is described as frequent or abundant, it is merely a subjective statement based on the number of cells encountered when examining the non-quantitative TEM preparations.

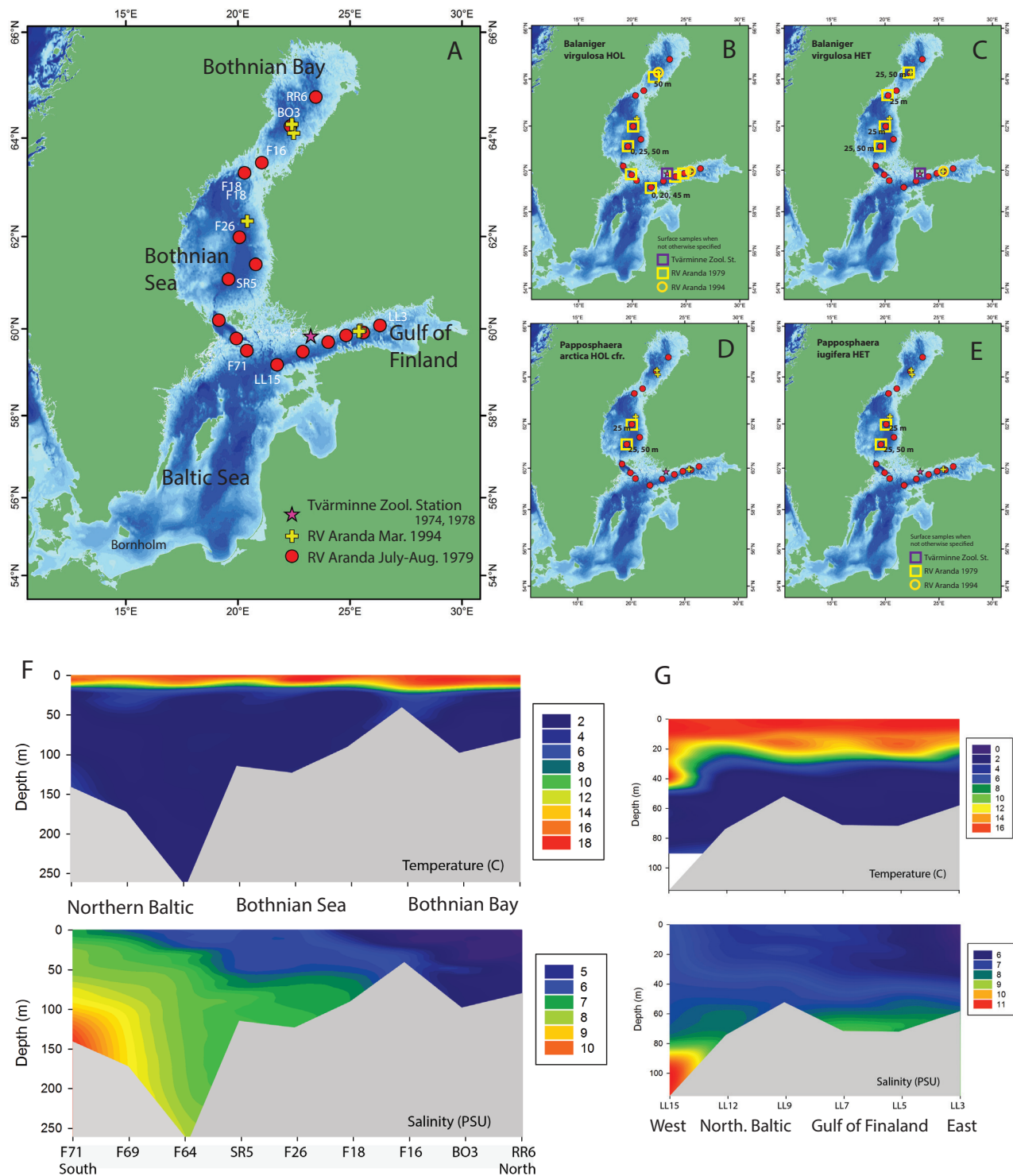The exact origin of material selected for illustration appears in Table 1.

Figure 2: Sampling from the Gulf of Finland, Bothnian Sea and Bothnian Bay, occurrence patterns of selected species, and basic environmental variability. **(A)** Map of sampling sites distributed among two RV 'Aranda' cruises and multiple visits to the Tvärminne Zoological Station and its immediate surroundings. **(B)** *Balaniger virgulosa* HOL. **(C)** *Balaniger virgulosa* HET. **(D)** *Papposphaera arctica* HOL cfr. **(E)** *Papposphaera iugifera* HET. **(F)** Contour graphs (temperature and salinity) showing the variability along a south to north transect in the Bothnian Sea and the Bothnian Bay. **(G)** Contour graphs (temperature and salinity) along a west to east transect in the Gulf of Finland

Plate	Taxon	Illustration	Origin	Date	Misc.
1	*Syracosphaera nodosa*	Fig. 1	Denmark, the Sound	Sept. 2014	20m depth
	Calciopappus caudatus	Figs 2–4	Denmark, Helgenæs, Kattegat	June 1976	15m depth
	Ceratolithus cristatus	Figs 5–6	Denmark, Hals, N. Kattegat	Oct. 1975	Surface sample
	Algirosphaera robusta	Fig. 7	Denmark, the Sound	Sept. 2014	20m depth
	Syracosphaera corolla	Fig. 8	Denmark, Tempelkrogen, the Isefjord	Feb. 2015	Surface sample
	Braarudosphaera bigelowii	Figs 9–10	Denmark, Tempelkrogen, the Isefjord	Sept. 1980	Surface sample
	Emiliania huxleyi	Fig. 11	Denmark, the Sound	Sept. 2014	20m depth
	Pleurochrysis roscoffensis cfr.	Figs 12–13	Finland, Ajax, Tvärminne Zool. Station	Aug. 1978	Surface sample
2	*Acanthoica quattrospina* HOL	Figs 1–6	Denmark, the Isefjord outer broad	Aug. 1984	Surface sample
	Acanthoica quattrospina HET	Fig. 7	Denmark, the Sound	Sept. 2014	20m depth
		Fig. 8	Denmark, the Isefjord outer broad	Aug. 1984	Surface sample
3	*Syracosphaera borealis*	Figs 1–4	Denmark, the Isefjord outer broad	Aug. 1984	Surface sample
	Corisphaera strigilis cfr.	Fig. 5	Denmark, HAV90 station, S. Kattegat	Sept. 1989	Surface sample
4	*Corisphaera strigilis* cfr.	Figs 1–5	Denmark, the Isefjord outer broad	Aug. 1984	Surface sample
5	*Balaniger virgulosa* HOL	Fig. 1	Denmark, Køge Bight, W. Baltic	Oct. 1977	Surface sample
		Fig. 2	Denmark, the Isefjord outer broad	Aug. 1984	Surface sample
		Figs 3–5	Denmark, Tempelkrogen, the Isefjord	Sept. 1980	Surface sample
6	*Balaniger virgulosa* HET and HOL	Figs 1–2	Finland, Bothnian Sea, #SR5	Aug. 1979	25m depth
	Balaniger virgulosa HET	Fig. 3	Norway, Bergen area		
		Fig. 4	Denmark, coastal North Sea	July 1975	Surface sample
		Fig. 5	Denmark, N. Kattegat	March 1976	15m depth
7	*Balaniger virgulosa* HET	Fig. 1	Finland, Bothnian Sea, #SR5	Aug. 1979	25m depth
		Fig. 2	Finland, Bothnian Sea, #SR5	Aug. 1979	50m depth
		Fig. 3	Finland, Bothnian Sea, #SR5	Aug. 1979	25m depth
		Fig. 4	Finland, Bothnian Bay, #BO3	Aug. 1979	50m depth
		Fig. 5	Finland, Bothnian Sea, #SR5	Aug. 1979	50m depth
		Fig. 6	Finland, Bothnian Sea, #F16	Aug. 1979	25m depth
8	*Trigonaspis minutissima*	Fig. 1	Denmark, Læsø Ø, N. Kattegat	Mar. 1976	15m depth
		Fig. 2	Denmark, Als, W. Baltic	June 1976	Surface sample
		Fig. 3	Denmark, Læsø Ø, N. Kattegat	Mar. 1976	15m depth
		Fig. 4	Denmark, Kolby Kås, S. Kattegat	June 1976	10m depth
	Pappomonas borealis HOL	Figs 5–6	Denmark, Læsø Ø, N. Kattegat	Mar. 1976	15m depth
		Fig. 7	Denmark, Endelave, S. Kattegat	June 1976	Surface sample
	Pappomonas borealis HET	Fig. 8	Denmark, Als, W. Baltic	Oct. 1975	Surface sample
		Fig. 9	Denmark, Als, W. Baltic	June 1976	Surface sample
		Fig. 10	Denmark, HAV90 station, S. Kattegat	April 1989	Surface sample
9	*Papposphaera arctica* HOL	Fig. 1	Denmark, Knudshoved, the Great Belt	Mar. 1976	Surface sample
		Figs 2–3	Denmark, Drogden, the Sound	Mar. 1976	Surface sample
		Figs 4–5	Denmark, Stevns, W. Baltic	Jan. 1976	Surface sample
	Papposphaera arctica HOL cfr.	Figs 6, 8	Finland, Bothnian Sea, #SR5	Aug. 1979	25m depth
		Fig. 7	Finland, Bothnian Sea, #F71	Aug. 1979	45m depth
10	*Papposphaera lepida*	Figs 1–2	Denmark, the Sound	Jan. 1976	10m depth
	Pseudowigwamma scenozonion	Figs 3–4	Denmark, Læsø Rende, N. Kattegat	Mar. 1976	10m depth
	Wigwamma arctica	Fig. 5	Denmark, Læsø E, N. Kattegat	Mar. 1976	15m depth

Table 1: Overview of the origin of material selected for illustration (Plate 1–10)

3. Results and discussion
3.1 Isochrysidales
3.1.1 Noelaerhabdaceae

Emiliania huxleyi (Lohmann, 1902) Hay & Mohler *in* Hay *et al*., 1967
Pl. 1, fig. 11

The only variety observed in inner Danish waters is *E. huxleyi* type A. This taxon occurs year round in inner Danish waters (Figure 3A) and sometimes forms dense blooms in the northern Kattegat region (Andersson & Eilola, 2006). The recorded temperature and salinity intervals are 0.3–14.5°C and 8.4–31.7, respectively. *Emiliania huxleyi* has been observed as far east as Bornholm (May 1975/see Figure 2A).

3.1.2 Pleurochrysidaceae

Pleurochrysis roscoffensis (Dangeard, 1934) Fresnel & Billard, 1991 cfr.
Pl. 1, figs 12–13

Observed twice in near-coastal samples from sites nearby the Tvärminne Zoological Station. It appears from Pl. 1, fig. 13 that this species has nodes on both the distal shield and the tube inner wall which are characteristics of *P. roscoffensis*.

3.2 Syracosphaerales
3.2.1 Rhabdosphaeraceae

Acanthoica quattrospina Lohmann, 1903/*Sphaerocalyptra* sp.
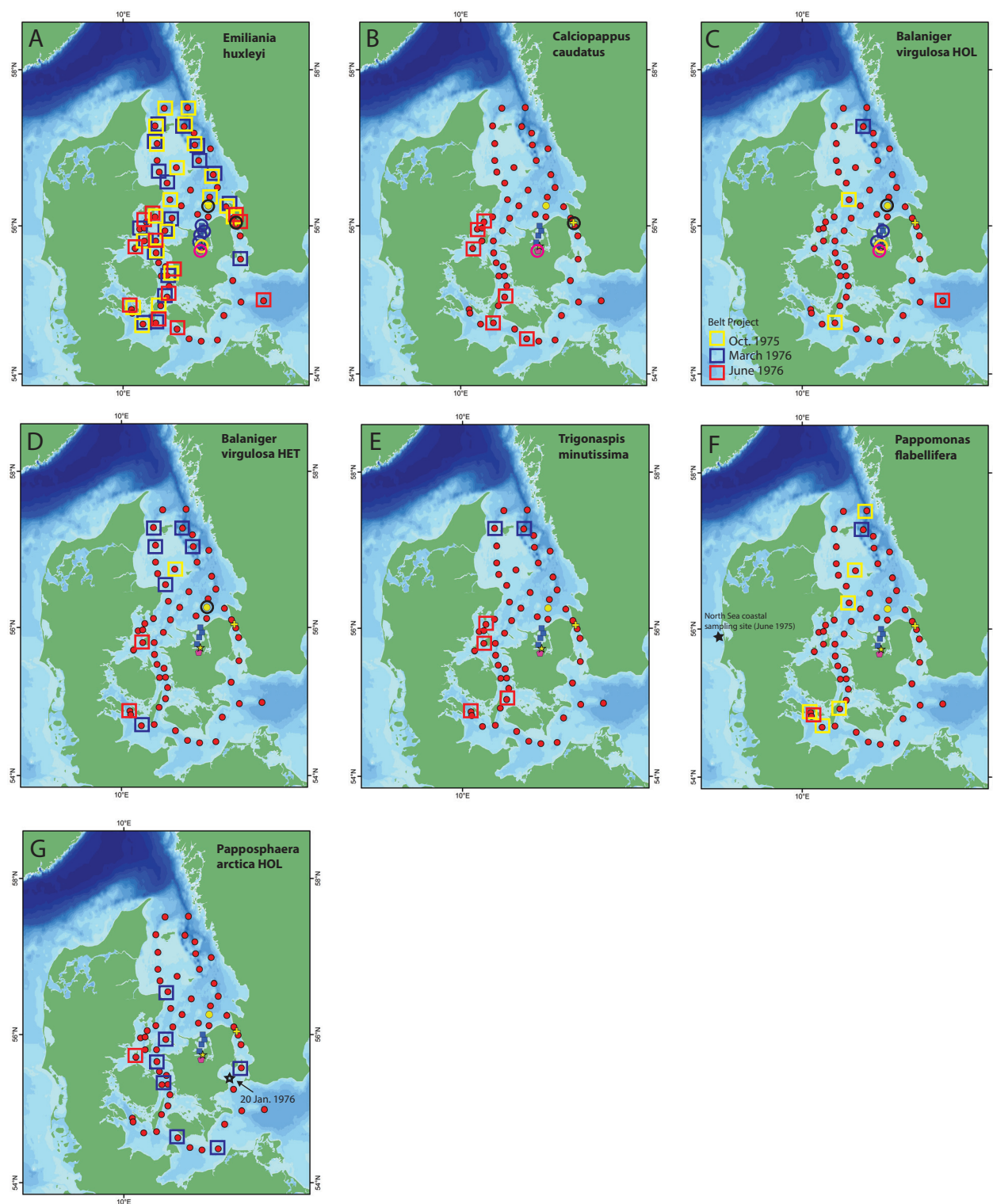Pl. 2, figs 1–8

Figure 3: Findings of selected coccolithophores from inner Danish waters. **(A)** *Emiliania huxleyi*; **(B)** *Calciopappus caudatus*; **(C)** *Balaniger virgulosa* HOL; **(D)** *Balaniger virgulosa* HET; **(E)** *Trigonaspis minutissima*; **(F)** *Pappomonas flabellifera* HET; **(G)** *Papposphaera arctica* HOL

A life cycle involving *Acanthoica quattrospina* (Pl. 2, figs 7–8) and a previously undescribed holococcolithophore with affinity to *Sphaerocalyptra* sp. has been suggested on multiple occasions (e.g. Cros *et al.*, 2000; Cros & Fortuño, 2002; Meier *et al.*, 2014; Šupraha *et al.*, 2014). Combination coccospheres are missing in our material. However, the two stages co-occurred and were abundantly present in samples from the Isefjord Outer Broad during August 1985.

Complete cells of *A. quattrospina* HOL are shown in Pl. 2, figs 1–3. The coccosphere has a triangular outline

(width × length c. 4 × 5μm) and carries two flagella (c. 14μm) and a markedly shorter haptonema (c. 7μm). Little information can be obtained from Pl. 2, fig. 1 on features of the individual holococcoliths due to the inability of the electrons to pass through the coccosphere. However, it is at least apparent that there is a marked difference between circumflagellar and body coccoliths in terms of the degree to which the central part of the coccolith protrudes above the base plate. It also appears that the most completely developed calyptroliths have a proximal part with parallel sides from where the cone eventually arises. Also, the cell shown in Pl. 2, fig. 3 has a haptonema. This is curled up and appears to be somewhat longer than the one shown in Pl. 2, fig. 1. The TEM examination of *A. quattrospina* HOL (=*Sphaerocalyptra* sp.) provides new information on, in particular, the unmineralized parts of the *Sphaerocalyptra* periplast. Below the large (1.6 × 1.25μm), oval organic scales that support the calyptroliths (Pl. 2, fig. 3) there are two additional layers of organic scales, i.e. medium-sized oval plates (1.0 × 0.8μm) and small scales (0.25 × 0.2μm) that tend to occur attached to the periphery of the latter (Pl. 2, figs 4, 6). The medium-sized scales in particular clearly show the characteristic radiating surface patterning typical of a haptophyte scale. In some instances, the surface of these is covered by organic material in the shape of 'columnar' structures (Pl. 2, fig. 5). Similar material has previously been observed in, e.g. *Chrysochromulina herdlensis* (Leadbeater, 1972; Manton & Leadbeater, 1974).

Algirosphaera robusta (Lohmann, 1902) Norris, 1984
Pl. 1, fig. 7
This species was fairly frequent in the September 14 sample from the Sound (20m; see Figure 1C). Meier *et al.* (2014) first reported this species from the Baltic Sea (Kieler Förde) and concluded that it was not likely a native species but rather a temporary intruder from the North Sea where it is a well-established taxon (Charalampopoulou *et al.*, 2011). Its co-occurrence in the 20m sample from the Sound, together with, e.g. a group of non-native loricate choanoflagellates (Thomsen, unpublished observations), points to that its occurrence in inner Danish waters and the western part of the Baltic Sea is indeed linked to special hydrographical events within the area. *Algirosphaera robusta* has been reported to form combination coccospheres with *Sphaerocalyptra quadridentata* (Schiller, 1913) Deflandre, 1952 (see e.g. Triantaphyllou & Dimiza, 2003). This life-phase has not so far been reported from the Baltic Sea.

3.2.2 Syracosphaeraceae
Calciopappus caudatus Gaarder & Ramsfjell, 1954
Pl. 1, figs 2–4
Commonly observed June 1975 and also found in September 2014 (Figure 3B). Flagellated cells with a haptonema (Pl. 1, fig. 3) and small under layer scales (Pl. 1, fig. 4) are sometimes observed.

Syracosphaera borealis Okada & McIntyre, 1977
Pl. 3, figs 1–4
Syracosphaera borealis was also observed by Meier *et al.* (2014) from the Kieler Förde. The axial structure, which is typically developed as a prominent irregular ridge formed by upgrowth from laths, is little pronounced in the Isefjord material (Pl. 3, figs 1–3). However, when examining the Kieler Förde material presented by Meier *et al.* (2014; their Pl. 3, figs 1–5) it is evident that this feature is highly variable across coccoliths from the very same coccosphere (i.e. from absent to pronounced), so there is every evidence to believe – considering also the proximity of the geographic sites - that the Isefjord 1975 material is also correctly identified as *S. borealis*. The coccoliths illustrated in Pl. 3, fig. 4 are furnished with irregular and isolated nodes which is a feature assigned to *S. borealis* type 2 by Kleijne (1993).

Syracosphaera corolla Lecal, 1966
Pl. 1, fig. 8
A single *S. corolla* exothecal coccolith (Pl. 1, fig. 8) was observed recently (February 2015) from the Isefjord area. Considering that *S. corolla* is ubiquitously present in North Sea waters (e.g. Charalampopoulou *et al.*, 2011) it is likely that this taxon will occasionally manifest itself also inside the North Sea-Baltic Sea boundary.

Syracosphaera nodosa Kamptner, 1941 cfr.
Pl. 1, fig. 1
Commonly observed in the September 2014 sample from the Sound (20m depth). Not previously recorded from the Baltic Sea. *Syracosphaera nodosa* is reported to form combination coccospheres with *Helladosphaera cornifera* (Schiller, 1913) Kamptner, 1937, a life-phase which has not so far been observed in the Baltic Sea.

3.3 Holococcolithophores
Corisphaera strigilis Gaarder, 1962 cfr.
Pl. 3, fig. 5; Pl. 4, figs 1–5
Frequently observed during the August 1985 coccolithophore 'bloom' in the Isefjord (Pl. 4, figs 1–5). Also observed in a single sample from the HAV90 southern Kattegat station (Pl. 3, fig. 5).

The conical cell measures c. 5μm and carries two flagella and a somewhat shorter haptonema (Pl. 4, figs 1, 4). The periplast comprises two layers of organic scales of which the largest and outermost scales (1–1.3 × 0.7–0.9μm) are mineralized. There is an underlayer of small scales (0.4–0.45 × 0.3–0.35μm) that are likely in the undisturbed periplast located along the periphery of the larger mineralized scales. The scatter of scales (Pl. 3, fig. 5) seems to indicate that there is also a medium sized, non-mineralized scale type (left side of the image, arrows). However, it appears more likely, considering the obvious calcification gradient across the image, that these are probably completely decalcified 'coccoliths'. The *C. strigilis* body coccoliths are formed by

angular crystallites arranged in regular patterns. From the micrographs available it appears that the coccoliths have no peripheral tube (as in, e.g. the closely related *C. gracilis* Kamptner, 1937). The calcification is rather limited to a peripheral band (c. 3 crystallite lines wide) which is spanned by a bridge (Pl. 4, fig. 5; single coccoliths from Pl. 3, fig. 5 and Pl. 4, fig. 4). Coccoliths in *C. strigilis* are dimorphic with flagellar pole coccoliths carrying a bridge that is extended into a leaf-like lamina. This is not evident in our material but at least hinted at in Pl. 4, fig. 4 where some anterior end coccoliths have arched median structures.

The facts that *C. strigilis* has been found (Šupraha *et al.*, 2015) to share a combination coccosphere with *Syracosphaera hirsuta* Kleijne & Cros, 2009 (formerly *S. borealis* type 2), and also that a very distinct co-occurrence of *S. borealis* and *C. strigilis* is reported from the Southern Ocean (Malinverno, pers. com.), adds further evidence to the identification of the material described here as representing form complexes of *C. strigilis* and *S. borealis*, respectively.

3.4 Coccolith families *incertae sedis*
3.4.1 Papposphaeraceae
Balaniger virgulosa (Thomsen & Oates, 1978) Thomsen & Østergaard, 2014

The established terminology used to distinguish life cycle phases (HET and HOL) is used also in the context of *B. virgulosa* although in this species the haploid phase produces calcite elements (nannoliths) which are morphologically significantly different from holococcolith crystallites in the strict sense. An update of terminology will likely be needed at some stage to address this issue.

Balaniger virgulosa HOL
Pl. 5, figs 1–5; Pl. 6, figs 1–2
Syn.: *Balaniger balticus* Thomsen & Oates, 1978
Balaniger virgulosa HOL is, despite its small overall dimensions (L = 3–5µm; W = 4–6µm), easily recognized even at the light microscope level due to its distinct heart-shaped cell contours, the two flagella and a haptonema, and the apoplastidic nature of the cell. When examined in the TEM the species is unequivocally identified from the presence of minute hollow pyramids (Pl. 5, figs 1–3) that constitute the coccosphere in this species. The presence of calcium in the periplast was verified when the species was first described (Thomsen & Oates, 1978). Decalcification experiments showed (Thomsen & Oates, 1978) that the pyramid is formed of organic material that does not change in overall appearance following acid treatment. The angular appearance of some pyramid distal tips (e.g. Pl. 5, fig. 1, arrows) points to that this is where a crystallite might be located. Groups of pyramids (or 'hats' as they are also often referred to) are attached to organic plates that cover the entire surface of the cell (Pl. 8, figs 4–5). Thomsen & Østergaard (2014) documented that *B. balticus* shares a life cycle with *Pappomonas virgulosa*, hence the recent

name change. Material of *B. virgulosa* HOL from the innermost parts of the Baltic Sea is included here as Pl. 6, figs 1–2. The shape of the individual 'hat' in material from the Baltic Sea proper is mostly of the sharp-pointed type (Pl. 6, fig. 2) that has also infrequently been observed in material from inner Danish waters (Thomsen & Oates, 1978/l.c. Pl. 3 B, C). It is tempting to hypothesize that the difference in 'hat' design is perhaps due to a complete lack of calcification in the genuine Baltic Sea material of this taxon.

The type locality of *B. virgulosa* HOL (i.e. *B. balticus*) is Tempelkrogen, the innermost part of the Isefjord system. Since its first description this coccolithophore species has been repeatedly observed in the Isefjord throughout the years and seasons sampled. Findings outside the fjord system are, however, rather sparse and scattered (Figure 3C). *Balaniger virgulosa* HOL is distributed throughout the entire Baltic Sea. It has been observed repeatedly in samples collected in the vicinity of the Tvärminne Zoological Station (Thomsen, 1979; Vørs, 1992) and was also found at several stations occupied by RV 'Aranda' cruises in 1979 and 1994 (Figure 2B). *Balaniger virgulosa* HOL is both eurythermal and euryhaline.

Balaniger virgulosa HET
Pl. 6, figs 1–5; Pl.7, figs 1–6
Bas.: *Pappomonas virgulosa* Manton & Sutherland, 1975
Recently Thomsen & Østergaard (2014) reexamined *Balaniger virgulosa* HET based on material from the Arctic. The typical Atlantic Ocean appearance of this life history phase (Pl. 6, fig. 5) is here further documented from a SEM image (Pl. 6, fig. 3; courtesy of M. Heldal, Univ. of Bergen) of material from the Bergen area, Norway. *Balaniger virgulosa* HET carries oval body coccoliths and circumflagellar coccoliths that terminate in a tuft of elongated elements (Pl. 6, fig. 3). The rim and central area calcification comprises linearly arranged sequences of erect, elongated elements separated by small adnate, rod-shaped elements (Pl. 6, fig. 4). Coccoliths at the antapical pole consistently carry reduced central appendages (shaft reduced or sometimes even missing). It appears from Pl. 6, fig. 3 that ordinary body coccoliths may also occasionally be furnished with such reduced appendages.

The Danish material (viz. Pl. 6, figs 4–5) matches the appearance of this taxon from high latitude sites fairly well (Manton & Sutherland, 1975; Thomsen & Østergaard, 2014). When examining material from the innermost parts of the Baltic Sea (Pl. 7) it becomes evident that there are two morphotypes of this species present within the area. The cell illustrated in Pl. 7, figs 4, 6 is characterized by a very clear distinction between flagellar pole coccoliths with central appendages and body coccoliths that are completely devoid of these. Coccoliths from the antapical pole (Pl. 7, fig. 4, arrow) carry reduced central appendages where the shaft is missing. However, in the majority of the cells examined from the Baltic Sea proper (e.g. Pl. 7, figs 1, 5) all coccoliths carry central appendages, yet with a marked distinction in size from the apical towards the antapical pole. In this respect, these cells

are thus reminiscent of the Bergen material (Pl. 6, fig. 3). While the cells illustrated in Pl. 7 are selected to represent the extreme ends of the observed variability, it should be emphasized that intermediate forms do also occur. It appears acceptable, based on the patterns of variability observed across the entire geographic range of *B. virgulosa,* and without access to information beyond what can be retrieved from chance observations of natural samples*,* to argue that this variability is likely reflecting environmental impact and must, therefore, be accounted for within the concept of a single species. Teratological modifications of the *B. virgulosa* calyx (solid, flattened V-like structures) sometimes occur in material from the Baltic Sea proper (Pl. 7, figs 2–3).

The findings of *B. virgulosa* HET from inner Danish waters as well as the innermost parts of the Baltic Sea are shown in Figure 3D and Figure 2C. It is evident that this species is both eurythermal and euryhaline with a potential to occur throughout the entire Baltic Sea at any specific time of the year. It deserves to be mentioned that whereas *B. virgulosa* HOL is frequently recorded from the Isefjord area we have never succeeded in finding *B. virgulosa* HET inside the fjord, despite the fact that this life history stage has been frequently recorded from the nearby 'HAV90' southern Kattegat permanent station.

Trigonaspis minutissima Thomsen, 1980
Pl. 8, figs 1–4

Trigonaspis minutissima is a diminutive coccolithophore species, 2.4–3μm in diameter, with the usual two flagella (14–21μm) and a somewhat shorter haptonema (8–12μm). The cell carries a tuft of narrow, tower-shaped flagellar pole coccoliths (Pl. 8, fig. 1). Calcification is in the form of triangular groups of crystallites. For further details see Thomsen & Østergaard (2015). There is no evidence so far of a life cycle counterpart to the holococcolithophore *T. minutissima*. However, indirect evidence (e.g. co-occurrence) supports the idea that *Pappomonas flabellifera* might be a strong candidate.

Findings of *T. minutissima* are summarized in Figure 3E. The overall temperature and salinity ranges are 3–12.3°C and 17.6–31.7, respectively.

Pappomonas borealis (Manton, Sutherland & McCully, 1976) Thomsen & Østergaard, 2014

The shared life cycle between *P. borealis* and *T. diskoensis* was first documented by Thomsen *et al.* (1991) and has later been confirmed by the finding of additional combination coccospheres in West Greenland waters (Thomsen and Østergaard, 2014).

Pappomonas borealis HOL
Pl. 8, figs 5–7
Syn. *Trigonaspis diskoensis* Thomsen, 1980

Pappomonas borealis HOL is primarily characterized by a tuft of rather prominent, tower-shaped flagellar pole coccoliths (Pl. 8, figs 5, 7) formed by an organic matrix that supports numerous triangular groups of crystallites (Pl. 8, fig. 6) organized in helical paths along the surface of a 'tower' (see also Thomsen and Østergaard, 2015).

Findings of *P. borealis* HOL are restricted to the northernmost Kattegat area and only during wintertime and in subsurface samples (17 March 1976, 3–4°C, salinity range 29.5–31.7).

Pappomonas borealis HET
Pl. 8, fig. 10

Pappomonas borealis HET has recently (Thomsen & Østergaard, 2014) been redefined as a separate taxon (formerly referred to as *P. flabellifera* var. *borealis*) based on differences in the design of the flagellar pole coccoliths, and also size and central area calcification of the body coccoliths.

Pappomonas borealis HET has so far only been found twice in Danish waters (western Baltic [Als], June 1976, 12.3°C, salinity 17.6; southern Kattegat [HAV90], April 1989, 7°C, salinity 14).

Pappomonas flabellifera Manton & Oates, 1975 emend. Thomsen & Østergaard, 2014
Pl. 8, figs 8–9

The Danish material of *P. flabellifera* (Pl. 8, figs 8–9) mirrors exactly the Arctic material of this taxon as illustrated by, e.g. Thomsen & Østergaard (2014; l.c. Fig. 3) with reference to morphological details as well as dimensions.

Pappomonas flabellifera has been found on several occasions (Figure 3F) within a temperature range of 4–12°C and at salinities ranging from roughly 12–32. The species is additionally known from the coastal North Sea (Figure 3F) in samples dating back to June 1975 (15°C, salinity 32).

Papposphaera arctica (Manton, Sutherland & Oates, 1976) Thomsen, Østergaard & Hansen, 1991 HOL
Pl. 9, figs 1–5
Bas. *Turrisphaera arctica* Manton, Sutherland & Oates, 1976

Based on the finding of combination coccospheres, Thomsen *et al.* (1991) demonstrated that species of *Papposphaera* share a life history with species of *Turrisphaera*. This has since been further substantiated in, e.g. a series of publications on species of *Papposphaera* (Thomsen *et al.*, 2015a, b; 2016). *Turrisphaera* spp. are characterized by a coccosphere that comprises tower-shaped coccoliths where an organic matrix supports a surface monolayer of hexagonal groups of crystallites. The three species described so far under the genus name *Turrisphaera* (*borealis*, *arctica*, *polybotrys*) are distinguished primarily on the basis of morphological features with reference to the distal part of the flagellar pole coccoliths (Manton *et al.*, 1976; Thomsen, 1980). In *T. arctica* the flagellar pole coccoliths are thus unilaterally hypertrophied towards the distal end. This particular feature is also evident in images of *Turrisphaera* sp. from inner Danish waters (Pl. 9,

figs 1–3). It has recently been shown (Thomsen *et al.,* 2015a) that *T. arctica* shares a life history with a *Papposphaera* sp. that differed from previously described species of *Papposphaera*. In this species the coccolith central area calcification is in the shape of a simple axial cross and the calicate spines are of the *P. sagittifera* type (see e.g. Thomsen, 1981). In accordance with these recent observations the material examined here is, therefore, formally referred to as *P. arctica* HOL. A single combination coccosphere was found from inner Danish waters (Pl. 9, figs 4–5). While it is obviously *T. arctica* based on the asymmetrical flagellar pole coccoliths (Pl. 9, fig. 4, arrow), it is unfortunately not possible to fully account for the identity of the *Papposphaera* sp. (Pl. 9, fig. 5). While the rim calcification is clearly of the *Papposphaera* type, it is not possible to analyze the pattern of central area calcification which is critical in this context.

Papposphaera arctica HOL is fairly frequently observed in inner Danish waters (Figure 3G) at temperatures and salinities ranging from 1.6–3.6°C and 9.3–19.2, respectively. The finding of *P. arctica* in a June sample (14.2°C) somehow 'spoils' the picture of a stenothermal and euryhaline occurrence pattern.

Papposphaera arctica (Manton, Sutherland & Oates, 1976) Thomsen, Østergaard & Hansen, 1991 HOL cfr.
Pl. 9, figs 6–8

Whereas there is no doubt about the generic affiliation of this material (*Turrisphaera*) based on the presence of hexagonal groups of crystallites (Pl. 9, fig. 8), the Bothnian Sea material of *P. arctica* HOL cfr. (Pl. 9, figs 6–7) unfortunately provides little information with respect to the design of the flagellar pole coccolith, which is the key to species identification. The material is here tentatively referred to as *P. arctica* HOL cfr. despite the fact that it is not possible to convincingly demonstrate the presence of the asymmetrical circumflagellar coccoliths that is the key figure of this taxon in this material (see e.g. Pl. 9, fig. 2). The logic behind illustrating the material under this heading is the fact that this species tends to be the most frequently observed form of *Turrisphaera* in the confluence area between the Baltic Sea and the North Sea. It is tempting to hypothesize, considering that *Papposphaera iugifera* (Thomsen & Østergaard, 2016) is observed from the very same Bothnian Sea stations (Figure 2E), that the specimens illustrated here could rather be the thus far unknown life history counterpart of this newly described species of *Papposphaera*.

The occurrence of *P. arctica* HOL cfr. (Figure 2D) is limited to only two stations (SR5, 25m, 2 August 1979; F71, 25 and 50m, 1 August 1979).

Papposphaera lepida Tangen, 1972
Pl. 10, figs 1–2

Papposphaera lepida is an easily recognizable species that was originally described from the Bergen area (western Norway) and since then observed worldwide (Tangen, 1972). The coccosphere comprises monomorphic coccoliths furnished with a highly conspicuous calicate spine. The calyx is a flattened, circular structure formed from four separate elements and placed perpendicular to the stem (Pl. 10, fig. 1). There is a certain size variability among the individual calyces depending on their position within the coccosphere – with the largest ones clustering around the apical pole. A wristlet supports the transition from stem to calyx (Pl. 10, fig. 2).

Papposphaera lepida has only been observed twice from the entire Baltic Sea region: south-western Kattegat area (16 June 1976, 15m, 6.3°C, salinity 31.4), northernmost entrance to the Sound (19 January 1976, 2.7°C, salinity 26.3). Tangen (1972) summarized that *P. lepida* occurred within a wide range of both temperatures (6.5–20.5°C) and salinities (10.3–30.3). Considering that the findings reported here extend the lower temperature limit a few degrees and that the species is also known from, e.g. Thailand coastal waters (Thomsen, unpublished), it is obvious that this is a truly eurythermic species. At the same time there is an indication that brackish water (<10; e.g. the Baltic Sea east of Bornholm) is likely to present a barrier towards the distribution of this species.

Pseudowigwamma scenozonion (Thomsen, 1980) Thomsen *in* Thomsen, Østergaard & Heldal, 2013
Pl. 10, figs 3–4
Bas.: *Wigwamma scenozonion* Thomsen, 1980

The coccolith calcification in this tiny (4–6μm) species is limited to the rim of an otherwise uncalcified plate (Pl. 10, fig. 3). A characteristic feature of the species is the occurrence of a single, enlarged and almost quadratic element (Pl. 10, fig. 4) among the normal rod-shaped elements forming the peripheral rim. The transfer of this species to a monotypic genus (Thomsen *et al.*, 2013) was argued by significant differences in rim architecture when comparing this species to *Wigwamma* spp., and the lack of a coccolith superstructure. Finally, there is also circumstantial evidence (Thomsen *et al.*, 2013) indicating that *P. scenozonion* has a life cycle counterpart that deviates markedly from that of *Wigwamma* spp.

Pseudowigwamma scenozonion occurred only once in samples from the Baltic Sea at large, i.e. at a station in the northernmost part of the Kattegat (Læsø west, 17 March 1976, 10m, 3.0°C, salinity 29.5).

Wigwamma arctica Manton, Sutherland & Oates, 1977
Pl. 10, fig. 5

Thomsen *et al.* (2013) recently reexamined the genus *Wigwamma* and all described species. While doing so they were looking for consistent patterns in the morphological variability of, e.g. *W. arctica*. Features such as how the arms of the pyramidal coccolith superstructure meet (single point versus one rod protruding distally above the others), and also details in the assembly of coccolith rim and superstructure (enlargement versus no enlargement of the rim elements that 'carry' the superstructure), were used in an effort to search for obvious morphological patterns reflecting large scale regions of occurrence. The approach

taken was not adequate even in terms of distinguishing between Arctic and Antarctic populations of *W. arctica*. It was therefore concluded that the variability observed had to be dealt with within the context of a single species. The Danish specimen illustrated here (Pl. 10, fig. 5; one spine protruding and rim crystallite enlargement) clusters with Antarctic material rather than material from either the West Greenland type locality or NE Greenland (NEW polynya).

Wigwamma arctica occurred only twice in samples from the Baltic Sea at large, i.e. at a station in the northernmost part of the Kattegat (Læsø east, 17 March 1976, surface: 0.5°C, salinity19.1, and at 15m depth: 4.0°C, salinity 31.7).

3.5 Nannolith families *incertae sedis*
3.5.1 Braarudosphaeraceae
Braarudosphaera bigelowii (Gran & Braarud, 1935)
Deflandre, 1947
Pl. 1, figs 9–10

The *B. bigelowii* coccosphere is a regular, pentagonal dodecahedron (Pl. 1, fig. 9). The individual liths are pentagonal (Pl. 1, fig. 10) and with a side length of c. 5μm.

Observed a few times in samples from the Isefjord inner broad. Hagino *et al.* (2013) showed that in the 18S rDNA tree of the Prymnesiophyceae, *Chrysochromulina parkeae* Green & Leadbeater, 1972 fell within the *B. bigelowii* clade, and it was hypothesized that *C. parkeae* could be the alternate life cycle stage of *B. bigelowii* sensu stricto. It is mentioned here because *C. parkeae* is frequently observed in samples from, e.g. the Isefjord inner broad.

3.5.2 Ceratolithaceae
Ceratolithus cristatus HET *coccolithomorpha* type
(Lecal-Schlauder, 1950) Young *et al.*, 2003
Pl. 1 Figs 5–6

Only observed once in samples from inner Danish waters (Hals, N. Kattegat, 22 October 1975, surface: 10.4°C, salinity 25.0). The planoliths (Pl. 1, figs 5–6) are morphologically similar to material illustrated in, e.g. Young *et al.* (2003), however, markedly smaller in cross section (1.3–1.4μm).

Concluding remarks
The current status with respect to the overall occurrence of coccolithophore species in the Baltic Sea is summarized in Table 2. This is basically an update of an earlier table provided by Meier *et al.* (2014). The total number of forms recorded is in excess of 30. The vast majority of these are known only from the western Baltic and Kattegat area, and only a few of these (e.g. *Emiliania huxleyi*) are of any importance in terms of algal biomass and productivity within the area. The number of species repeatedly recorded from the innermost parts of the Baltic Sea (the Gulf of Finland, the Bothnian Sea and the Bothnian Bay) is limited to c. 5 taxa. In the context of the winter time CaCO$_3$ undersaturation scenario outlined by Tyrell *et al.* (2008), it is interesting to speculate about why the only coccolithophore species that are persistently present in the most brackish, open water parts of

the Baltic Sea are lightly calcified genera and, e.g. represent species that are otherwise typically associated with polar waters. Is calcification less critical in these apoplastidic forms, or do they possess, e.g. high amounts of organics (polysaccharides) to protect their coccoliths from dissolution? It is obvious that further studies, including attempts to culture these organisms and also an application of a range of cell biological and molecular tools, will be needed to address these issues beyond mere speculation.

The material examined, in preparation for this compilation of findings of coccolithophore species from the Baltic Sea, encompasses two unique sampling events that deserve further comments. The 'coccolithophore bloom' encountered in August 1985 when sampling the Isefjord outer broad remains unique in terms of diversity and abundance of cells. The community comprised *Acanthoica quattrospina* HET and HOL, *Balaniger virgulosa* HOL, *Corisphaera strigilis*, *Emiliania huxleyi*, *Ericiolus spiculiger*, and *Syracosphaera borealis*. Is the presence of a similar assemblage of coccolithophore species a recurrent phenomenon in the southern Kattegat and its associated fjords and belts? - or was the August 1985 scenario genuinely unique? There is unfortunately not material available to answer this question. In as much as the standard Danish monitoring of phytoplankton relies on samples fixed in standard acid Lugol's iodine, the possible presence of a coccolithophore community has never been an issue. It is unfortunately also a fact that the number of samples available for a TEM/SEM community analysis of phytoplankton from this area is by far too fragmented to substantially contribute to an overall picture of coccolithophore occurrence patterns over a time span of decades.

The deep water Øresund sample from September 2014 was unique both in terms of species diversity and abundance of coccolithophores (*Acanthoica quattrospina* HET, *Algirosphaera robusta*, *Emiliania huxleyi*, *Syracosphaera nodosa*), but also in terms of their co-occurrence with a number of loricate choanoflagellate species that had not hitherto been observed in Danish waters (Thomsen, unpublished results). Some of these were known only from faraway places such as the Indian Ocean and thus represent a genuine warm water microbial community. It appears most likely that the September 2014 community represents a recent major inflow of Atlantic waters into the Kattegat area. In as much as the reference for the occurrence pattern of loricate choanoflagellates in inner Danish waters also dates back a couple of decades (Thomsen, unpublished results), it is important to emphasize that what appears (Sep. 2014) to be a completely new community of microorganisms in a Kattegat/Belt Sea context might also, in fact, represent a new 'normal'. It is a possibility that climate change, which impacts, e.g. sea water temperatures and hydrographical flows, may be a decisive factor in shaping microbial communities in local waters that may already now appear much different from the old 'normal'.

The overarching conclusion to be drawn from the observations above is that there is a critical need for new

Species	Distribution	Source
Acanthoica quattrospina HET	Kattegat and Belt Sea, Kieler Förde, Isefjord, Øresund	Pankow 1990, Hällfors 2004, Meier *et al.* 2014, this study
Acanthoica quattrospina HOL	Kieler Förde, Isefjord	Meier *et al.* 2014, this study
Algirosphaera robusta	Kieler Förde, Øresund	Meier *et al.* 2014, this study
Alisphaera extenta	Kieler Förde	Meier *et al.* 2014
Balaniger virgulosa HET	Kattegat and Belt Sea, Gulf of Finland, Bothnian Sea, Bothnian Bay	Thomsen 1979, Thomsen *et al.* 1988, Ikävalko & Thomsen 1997, this study
Balaniger virgulosa HOL	Kattegat and Belt Sea, Gulf of Finland, Bothnian Sea, Bothnian Bay	Thomsen & Oates 1978, Thomsen 1979, Thomsen *et al.* 1988, Ikävalko & Thomsen 1997, this study
Braarudosphaera bigelowii	Kattegat and Belt Sea	Hällfors 2004, this study
Calciopappus caudatus	Kattegat and Belt Sea	Pankow 1990, Hällfors 2004, this study
Calyptrosphaera sp.	Kattegat and Belt Sea	Hällfors 2004 (= Acant. quattrospina HOL?)
Ceratolithus cristatus	Kattegat	This study
Coccolithus pelagicus	Arkona Basin, S. Baltic proper, Centr. Baltic proper, N. Baltic proper, Gulf of Finland, Bothnian Sea, Bothnian Bay	Hällfors 2004
Corisphaera strigilis	Isefjord	This study
Coronosphaera mediterranea	Kattegat and Belt Sea	Hällfors 2004
Discosphaera tubifera	Gdansk Bay (once), ? S. Baltic proper	Pankow 1990, Hällfors 2004
Emiliania huxleyi	Kattegat and Belt Sea, Kiel Bight, Kieler Förde, Isefjord	Pankow 1990, Lohmann 1908, Hällfors 2004, Wasmund *et al.* 2008, Meier *et al.* 2014, this study
Ericiolus spiculiger	Isefjord	Thomsen *et al.* 1995
Hymenomonas roseola	Gulf of Finland	Pankow 1990
Hymenomonas sp.	Kieler Förde	Meier *et al*. 2014
Pappomonas borealis HET	Kattegat and Belt Sea	Thomsen *et al.* 1988
Pappomonas borealis HOL	Kattegat and Belt Sea	Thomsen *et al.* 1988
Pappomonas flabellifera HET	Kattegat and Belt Sea	Thomsen *et al.* 1988
Papposphaera lepida	Kattegat and Belt Sea	Thomsen *et al.* 1988
Papposphaera arctica HOL	Kategat and Belt Sea, N. Baltic proper	Thomsen *et al.* 1988, this study
Papposphaera arctica HOL cfr.	Bothnian Sea	This study
Papposphaera iugifera	Bothnian Sea	Thomsen & Østergaard 2016
Pleurochrysis carterae	Kattegat and Belt Sea, Arkona Basin,	Pankow 1990, Hällfors 2004
Pleurochrysis roscoffensis cfr.	Gulf of Finland	This study
Pseudowigwamma scenozonion	Kattegat and Belt Sea	Thomsen *et al.* 1988
Syracosphaera borealis	Kieler Förde, Isefjord	Meier *et al*. 2014, this study
Syracosphaera corolla	Isefjord	This study
Syracosphaera nodosa	Øresund	This study
Trigonaspis minutissima	Kattegat and Belt Sea	Thomsen *et al.* 1988
Wigwamma arctica	Kattegat and Belt Sea	Thomsen *et al.* 1988

Table 2: Summary of species recorded from the Baltic Sea (based on Meier *et al.*, 2014)

baseline studies on the marine microbial/nannoflagellate diversity from Danish waters, i.e. the confluence region between the Baltic Sea and the North Sea, as an aid in our understanding of the impacts of climate change on local ecosystems, and hence also as a general instrument to better be able to evaluate both historical and recent findings.

References
Andersson, P. & Eilola, K. 2006. Comparison of satellite images of the *Emiliania huxleyi* bloom in the Skagerrak and the Kattegat during 2004 to modeled surface currents. *Geophysical Research Abstracts*, **8**: 04360, 2006.

Charalampopoulou, A., Poulton, A.J., Tyrell, T. & Lucas, M.I. 2011. Irradiance and pH affect coccolithophore community composition on a transect between the North Sea and the Arctic Ocean. *Marine Ecology Progress Series*, **431**: 25–43.

Cros, L. & Fortuño, J. 2002. Atlas of Northwestern Mediterranean coccolithophores. *Scientia Marina*, **66**: 7–182.

Cros, L., Kleijne, A., Zeltner, A., Billard, C. & Young, J.R. 2000. New examples of holococcolith-heterococcolith combination coccospheres and their implications for coccolithophorid biology. *Marine Micropaleontology*, **39**: 1–34.

Hagino, K., Onuma, R., Kawachi, M. & Horiguchi, T. 2013. Discovery of an Endosymbiotic Nitrogen-Fixing Cyanobacterium UCYN-A in *Braarudosphaera bigelowii* (Prymnesiophyceae). *PLoS ONE*, **8**(12): e81749. doi:10.1371/journal.pone.0081749.

Hällfors, G. 2004. Checklist of Baltic Sea Phytoplankton Species (including some heterotrophic protistan groups). *Baltic Sea Environment Proceedings*, **95**: 1–208.

Ikävalko, J. & Thomsen, H.A. 1997. The Baltic sea ice biota (March 1994): A study of the protistan community. *European Journal of Protozoology,* **33**: 229–243.

Kleijne, A. 1993. *Morphology, Taxonomy and distribution of extant coccolithophorids (Calcareous nanoplankton)*. Druk-kerij FEBO B.V.: 321 pp.

Leadbeater, B.S.C. 1972. Fine structural observations in six new species of *Chrysochromulina* (Haptophyceae) from Norway with preliminary observations on scale production in *C. microcylindra* sp. nov. *Sarsia*, **49**: 65–80.

Lohmann, H. 1908. Untersuchungen zur Feststellung des vollstän-digen Gehaltes des Meeres an Plankton. *Wissenschaftliche Meeresuntersuchungen. Neue Folge, Abt. Kiel*, **10**: 130–370.

Manton, I. & Leadbeater, B.S.C. 1974. Fine-structural observa-tions on six species of *Chrysochromulina* from wild Danish marine nanoplankton, including a description of *C. cam-panulifera* sp. nov. and a preliminary summary of the nano-plankton as a whole. *Det Konglige Danske Videnskabernes Selskab, Biol. Skrifter,* **20**: 1–26.

Manton, I. & Sutherland, J. 1975. Further observations on the genus *Pappomonas* Manton et Oates with special reference to *P. virgulosa* sp. nov. from West Greenland. *British Phycologi-cal Journal*, **10**: 377–385.

Manton, I., Sutherland, J. & Oates, K. 1976. Arctic coccolitho-phorids: two species of *Turrisphaera* gen. nov. from West Greenland, Alaska and the Northwest Passage. *Proceedings Royal Society London, Ser. B. Biol. Sci.,* **194**: 179–194.

Meier, K.J.S., Kinkel, H. & Young, J. 2014. A note on calcareous nannoplankton from the Kieler Förde (Baltic Sea). *Journal of Nannoplankton Research*, **33**: 29–37.

Moestrup, Ø. & Thomsen, H.A. 1980. Preparation of shadow-cast whole mounts. *In*: E. Gantt (*Ed.*). *Handbook of Phycological methods, Vol. III.* Cambridge University Press, Cambridge: 385–390.

Pankow, H. 1990. *Ostsee-Algenflora*. Gustav Fischer Verlag, Jena: 648pp.

Šupraha, L., Ljubešić, Z., Mihanović, H. & Henderiks, J. 2014. Observations on the life cycle and ecology of *Acanthoica quattrospina* Lohmann from a Mediterranean estuary. *Jour-nal of Nannoplankton Research*, **34**: 49–56.

Šupraha, L., Ljubešić, Z. & Henderiks, J. 2015. Combination coccospheres from the eastern Adriatic coast (Mediterranean Sea). *Journal of Nannoplankton Research*, **35**: 81.

Tangen, K. 1972. *Papposphaera lepida*, gen. nov. n. sp., a new marine coccolithophorid from Norwegian coastal waters. *Norwegian Journal of Botany*, **19**: 171–178.

Thomsen, H.A. 1979. Electron microscopical observations on brackish-water nannoplankton from the Tvärminne area, SW coast of Finland. *Acta Botanica Fennica*, **110**: 11–37.

Thomsen, H.A. 1980. *Turrisphaera polybotrys* sp.nov. (Prymne-siophyceae) from West Greenland. *Journal Marine Biologi-cal Association U.K.,* **60**: 529–537.

Thomsen, H.A. 1981. Identification by electron microscopy of nanoplanktonic coccolithophorids (Prymnesiophyceae) from West Greenland, including the description of *Papposphaera sarion* sp.nov. *British Phycological Journal*, **16**: 77–94.

Thomsen, H.A. & Oates, K. 1978. *Balaniger balticus* gen. et sp.nov. (Prymnesiophyceae) from Danish coastal waters. *Journal Marine Biological Association U.K.*, **58**: 773–779.

Thomsen, H.A. & Østergaard, J.B. 2014. Coccolithophorids in polar waters: *Pappomonas* spp. revisited. *Acta Protozoolog-ica,* **53**: 233–254.

Thomsen, H.A. & Østergaard, J.B. 2015. Coccolithophorids in polar waters: *Trigonaspis* spp. revisited. *Acta Protozoolog-ica*, **54**: 85–96.

Thomsen, H.A. & Østergaard, J.B. 2016. *Papposphaera iugifera* nov. sp. from West Greenland, Svalbard, and the Baltic Sea. *Revue de Micropaléontologie*, **59**: 71–79.

Thomsen, H.A., Bjørn, P.P., Højlund, L., Olesen, J. & Pedersen, J.B. 1995. *Ericiolus* gen. nov. (Prymnesiophyceae), a new coccolithophorid genus from polar and temperate regions. *European Journal of Phycology*, **30**: 29–34.

Thomsen, H.A., Buck, K.R., Coale, S.L., Garrison, D.L. & Gowing, M.M. 1988. Nanoplanktonic coccolithophorids (Prymnesiophyceae, Haptophyceae) from the Weddell Sea, Antarctica. *Nordic Journal of Botany*, **8**: 419–436.

Thomsen, H.A., Heldal, M. & Østergaard, J.B. 2015a. Cocco-lithophores in polar waters: *Papposphaera arctica* HET and HOL revisited. *Micropaleontology*, **61**: 419–427.

Thomsen, H.A., Heldal, M. & Østergaard, J.B. 2015b. Cocco-lithophores in polar waters: *Papposphaera sarion* HET and HOL revisited. *Micropaleontology*, **61**: 429–438.

Thomsen, H.A., Østergaard, J.B. & Hansen, L.E. 1991. Hetero-morphic life histories in arctic coccolithophorids (Prymnesio-phyceae). *Journal of Phycology*, **27**: 634–642.

Thomsen, H.A., Østergaard, J.B. & Heldal, M. 2013. Coccolitho-phorids in polar waters: *Wigwamma* spp. revisited. *Acta Pro-tozoologica*, **52**: 237–256.

Thomsen, H.A., Østergaard, J.B. & Heldal, M. 2016. Coccolitho-phores in Polar Waters: *Papposphaera sagittifera* HET and HOL Revisited. *Acta Protozoologica*, **55**: 33–50.

Triantaphyllou, M. & Dimiza, M. D. 2003. Verification of the *Algirosphaera robusta - Sphaerocalyptra quadriden-tata* (coccolithophores) life-cycle association. *Journal of Micropalaeontology*, **22**: 107–111.

Tyrell, T., Schneider, B., Charalampopoulou, A. & Riebesell, U. 2008. Coccolithophores and calcite saturation in the Baltic and Black Seas. *Biogeosciences*, **5**: 485–494.

Unesco 1981. The Practical Salinity Scale 1978 and the Interna-tional Equation of State of Seawater 1980. *Technical Papers Marine in Science*, **36**.

Wasmund, N., Göbel, J. & Bodungen, B. 2008. 100-years changes in the phytoplankton community of Kiel Bight (Baltic Sea). *Journal of Marine Systems*, **73**: 300–322.

Young, J.R., Bergen, J.A., Bown, P.R., Burnett, J.A., Fiorentino, A., Jordan, R.W., Kleijne, A., van Niel, B.E., Romein, A.J.T. & von Salis, K. 1997. Guidelines for coccolith and calcareous nannofossil terminology. *Palaeontology*, **40**: 875–912.

Young, J., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I., & Østergaard, J. 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannopankton Research, Special Issue*, **1**: 1–132.

Vørs, N. 1992. Heterotrophic amoebae, flagellates and heliozoa from the Tvärminne area, Gulf of Finland in 1988–1990. *Ophelia*, **36**: 1–109.

Plate 1
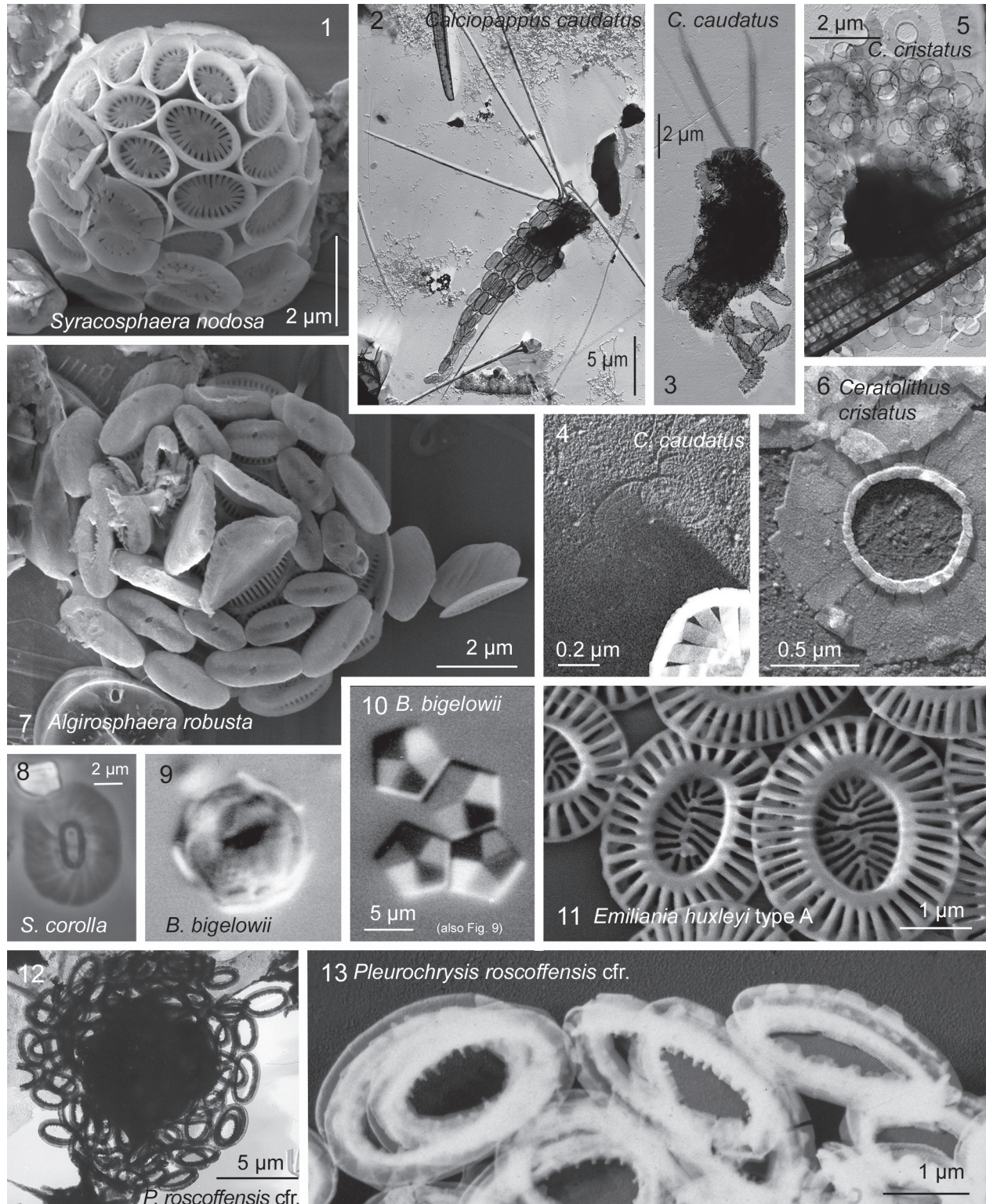
Coccolithophores from inner Danish waters (Figs 1–11) and Finland (Figs 12–13). SEM: Figs 1, 7, 11; TEM: Figs 2–6, 12–13; LM (Light Microscope): Figs 8–10 (phase contrast and nomarski interference contrast); reverse printing: Figs 4, 6, 13.

Fig. 2. Complete coccosphere. **Fig. 3.** Cell with flagella and haptonema. **Fig. 4.** Uncalcified under layer scales. **Fig. 8.** Phase contrast. **Fig 9.** Live cell. **Fig. 10.** Detached liths (Nomarski interference contrast).

Plate 2 – *Acanthoica quattrospina*
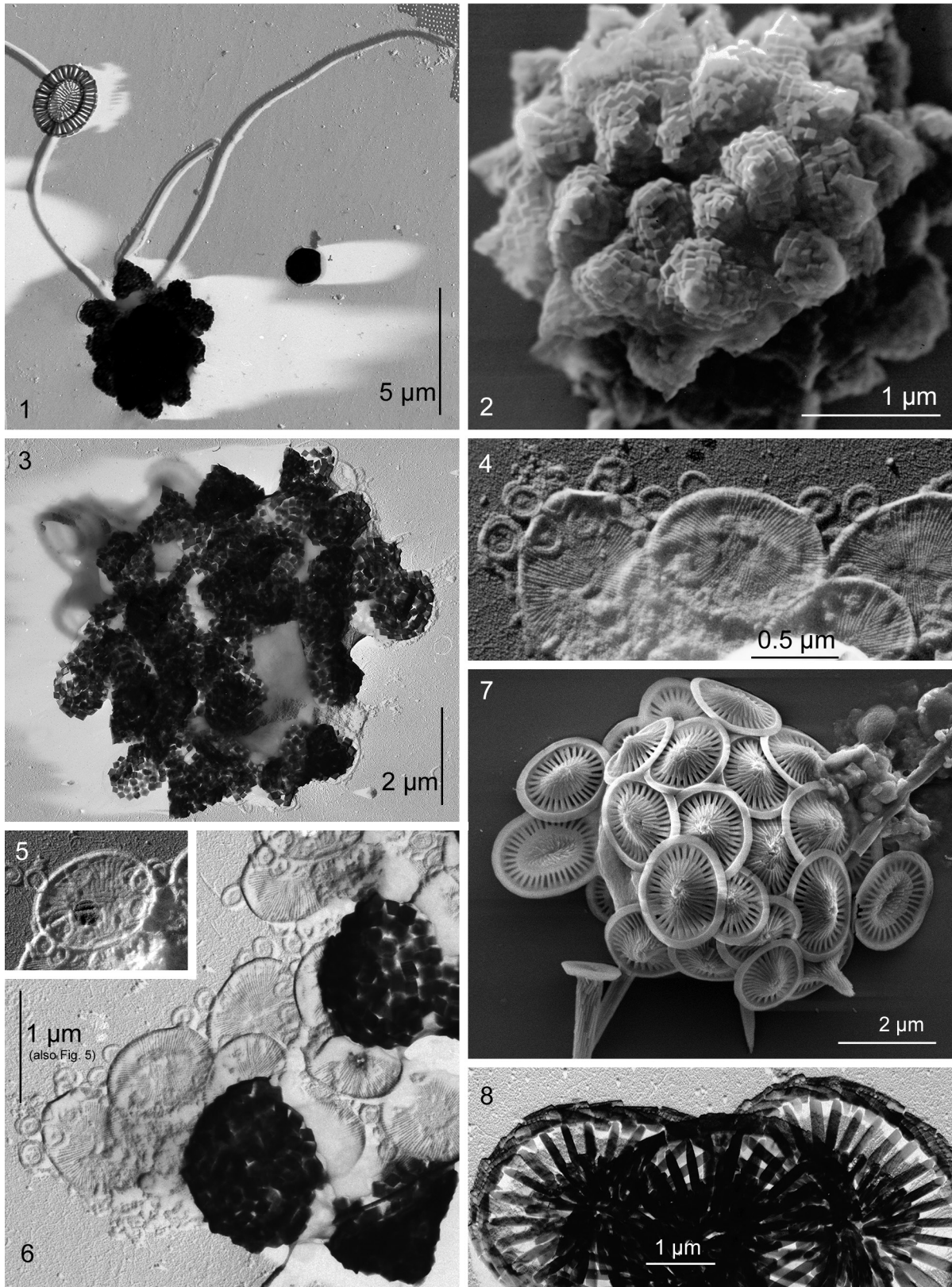
HOL (Figs 1–6) and HET (Figs 7–8) from Danish waters; TEM: Figs 1, 3–6, 8; SEM: Figs 2, 7; reverse printing: Figs 4–5.
**Fig. 1.** Complete cell. **Fig. 2.** Calyptroliths. **Fig. 3.** Calyptroliths in TEM. Notice the curled up haptonema. **Fig. 4.** Unmineralized large and small under layer scales. **Fig. 5.** Unmineralized scale carrying columnar or 'worm-like' material. **Fig. 6.** Scatter of calyptroliths and under layer scales. The small scales tend to occur along the periphery of the larger unmineralized scales. **Fig. 7.** Complete coccosphere. **Fig. 8.** Detail of body coccoliths.

Plate 3
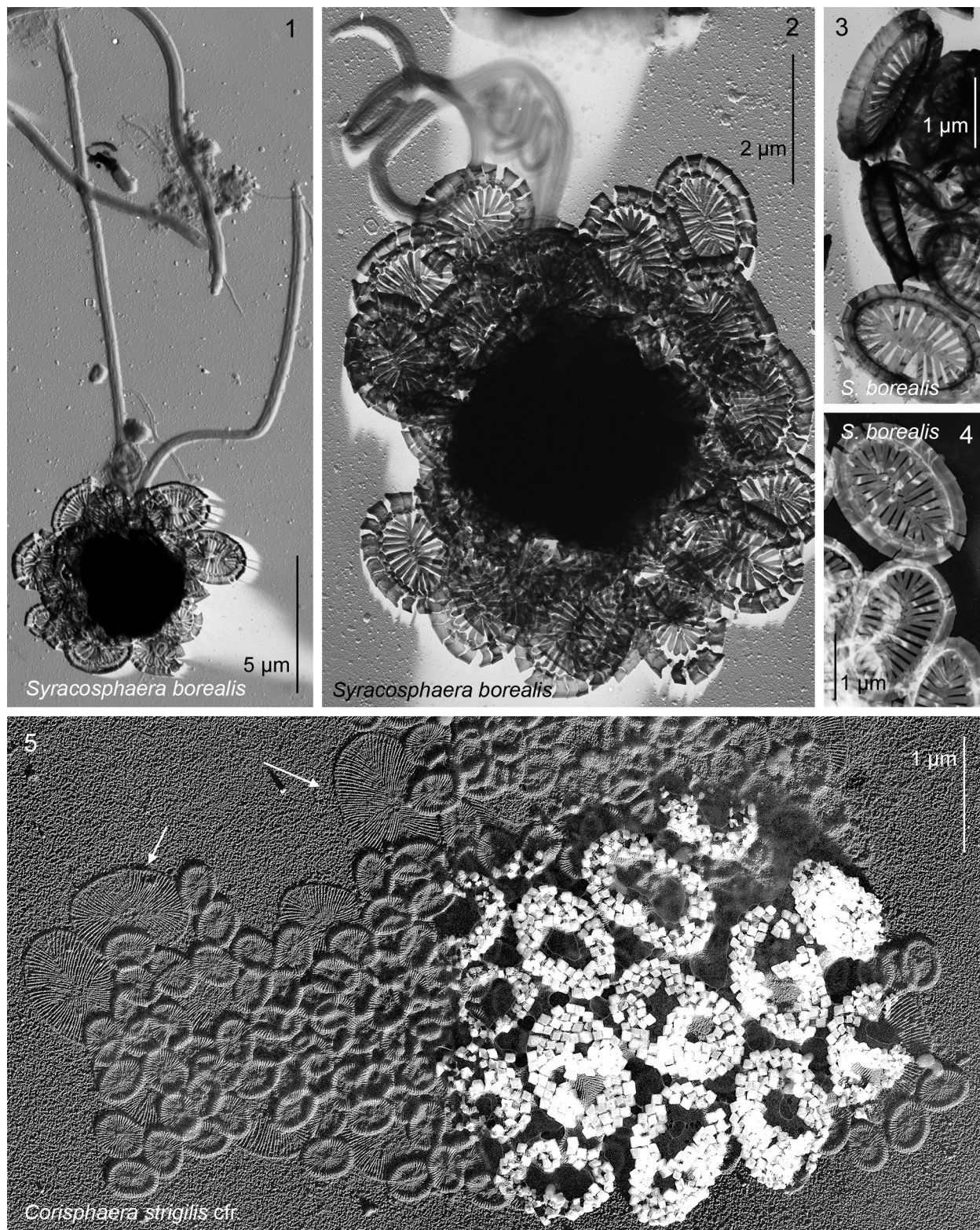


TEM: Figs 1–5; reverse printing: Figs 4–6.
Fig. 1. Complete cell. **Fig. 2.** Coccosphere; notice the curled up haptonema next to a single flagellum. **Figs 3–4.** Coccoliths. **Fig. 5.** Scatter of zygoliths and unmineralized scales. There is a gradual decalcification from right to left which makes it probable that the large unmineralized scales (arrows) are in fact the organic scale supporting the zygoliths. These are in turn 'encircled' by numerous and small unmineralized scales.

Plate 4 – *Corisphaera strigilis* cfr.
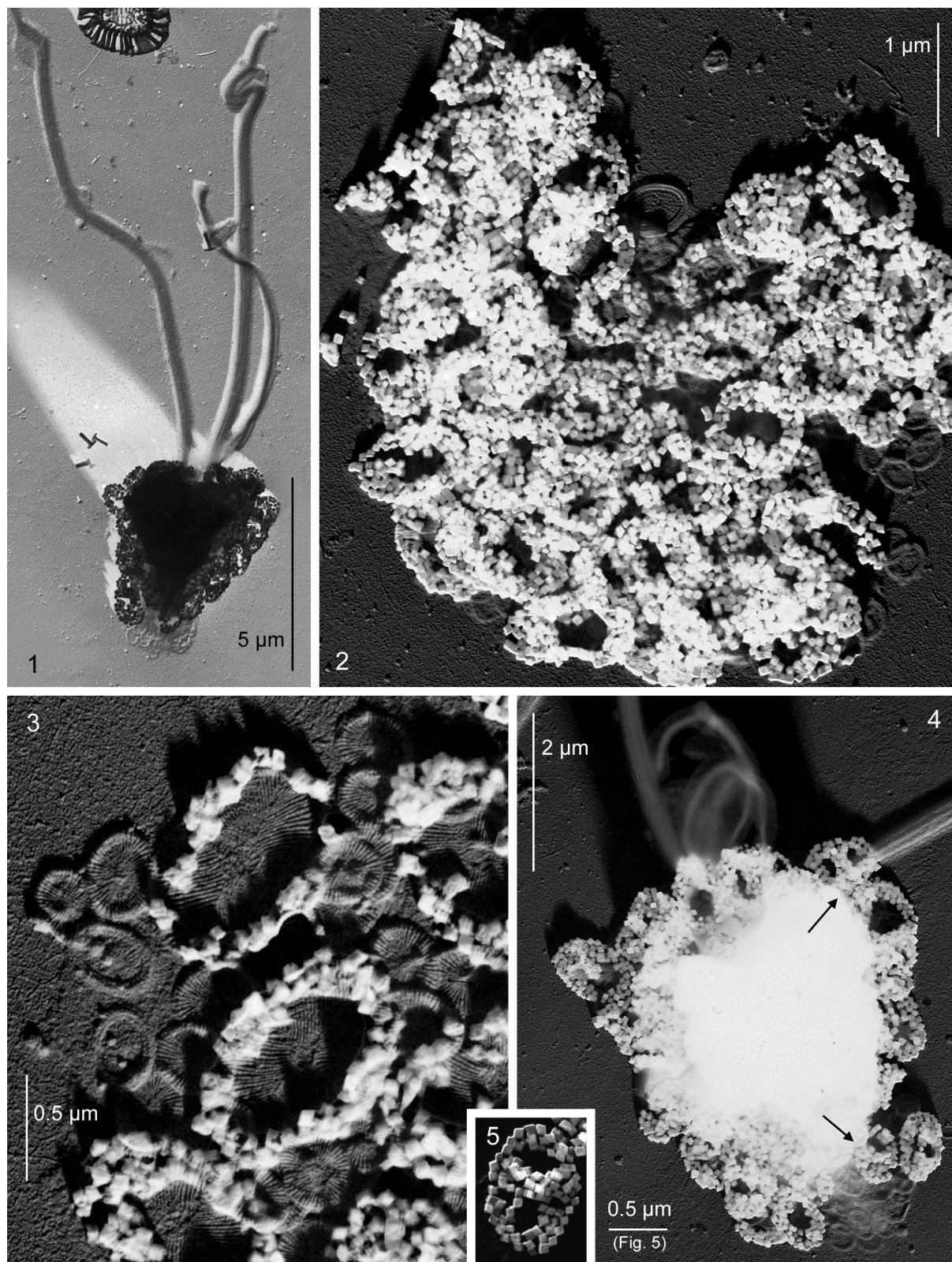
TEM images from the Isefjord; reverse printing: Figs 2–5.

Fig. 1. Complete cell. **Fig. 2.** Detail of coccoliths from a vacated coccosphere. Most coccoliths appear somewhat disturbed. The most prominent unifying feature is a peripheral band of densely packed crystallites. Unmineralized under layer scales are present (lower right). **Fig. 3.** Weakly calcified coccoliths overlaying small unmineralized scales. **Fig. 4.** Complete cell. Notice the cluster of unmineralized scales that are visible at the antapical pole. A couple of fairly well defined zygoliths are pointed out. **Fig. 5.** Well-developed zygolith.

Plate 5 – *Balaniger virgulosa* HOL
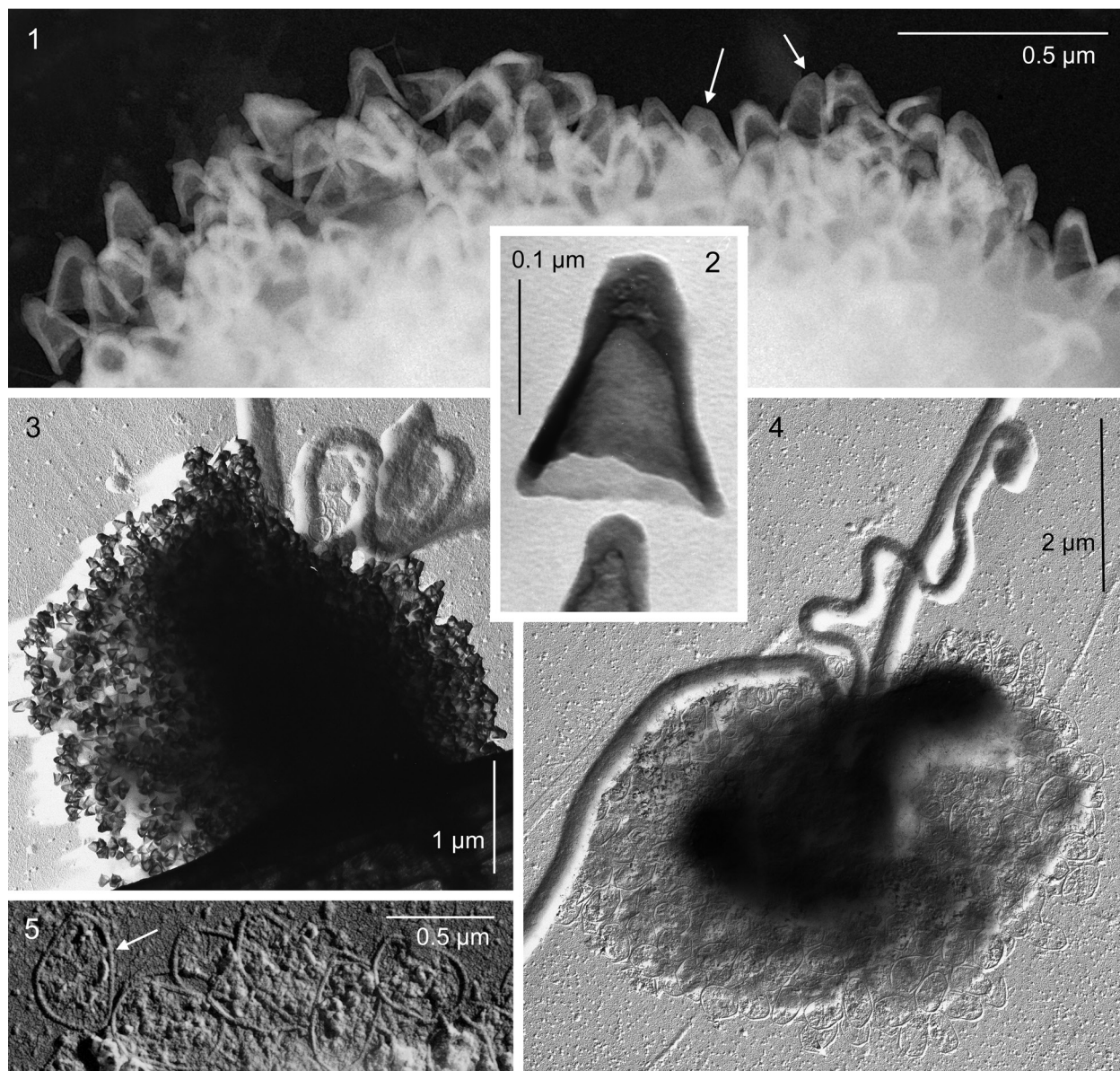
TEM images from Danish inner waters.
Fig. 1. Reversed print showing the typical appearance of the *B. virgulosa* pyramids. Some pyramids (arrows) have a distinct angular distal end which indicates that a minute crystallite might be positioned here. **Fig. 2.** High magnification of a single pyramid. **Fig. 3.** Detail of complete cell with flagella and haptonema showing the characteristic grouping of pyramids in clusters that match individual supporting organic scales. **Fig. 4.** Weakly mineralized specimen with flagella and haptonema. **Fig. 5.** Detail (from Fig. 4) of organic scales with traces of pyramids (arrow).

Plate 6 – *Balaniger virgulosa* HET and HOL
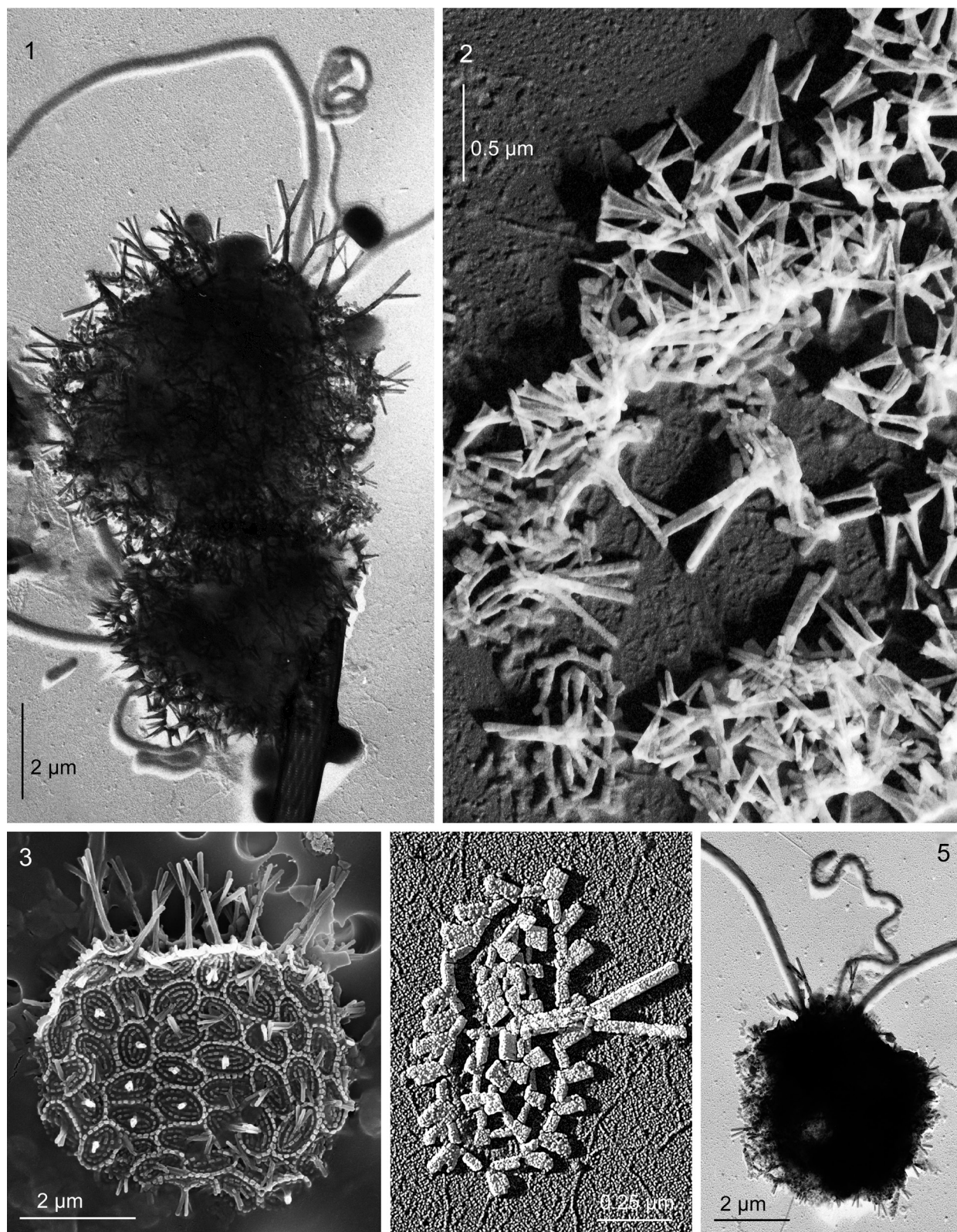
From the Baltic proper (Figs 1–2), Norway (Fig. 3) and Denmark (Figs 4–5). TEM: Figs 1–2, 4–5; SEM: Fig. 3; reverse printing: Figs 2, 4.
Figs 1–2. From the Baltic proper; **Fig. 3.** Norway; **Figs 4–5.** Denmark. Image type: TEM - Figs 1–2, 4–5; SEM - Fig. 3; Reversed printing - Figs 2, 4.
Fig. 1. Complete cells of *P. virgulosa* HET (top) and *P. virgulosa* HOL (bottom). **Fig. 2.** Scatter of heterococcoliths and holococcoliths (pyramids) indicating that this might be a broken combination coccosphere. Notice that the individual pyramid is sharp pointed and fairly different from those shown in e.g. Pl. 5, fig. 1. **Fig. 3.** Complete coccosphere with a distinct cluster of calicate flagellar pole coccoliths. **Fig. 4.** Detail of body coccolith. **Fig. 5.** Complete cell.
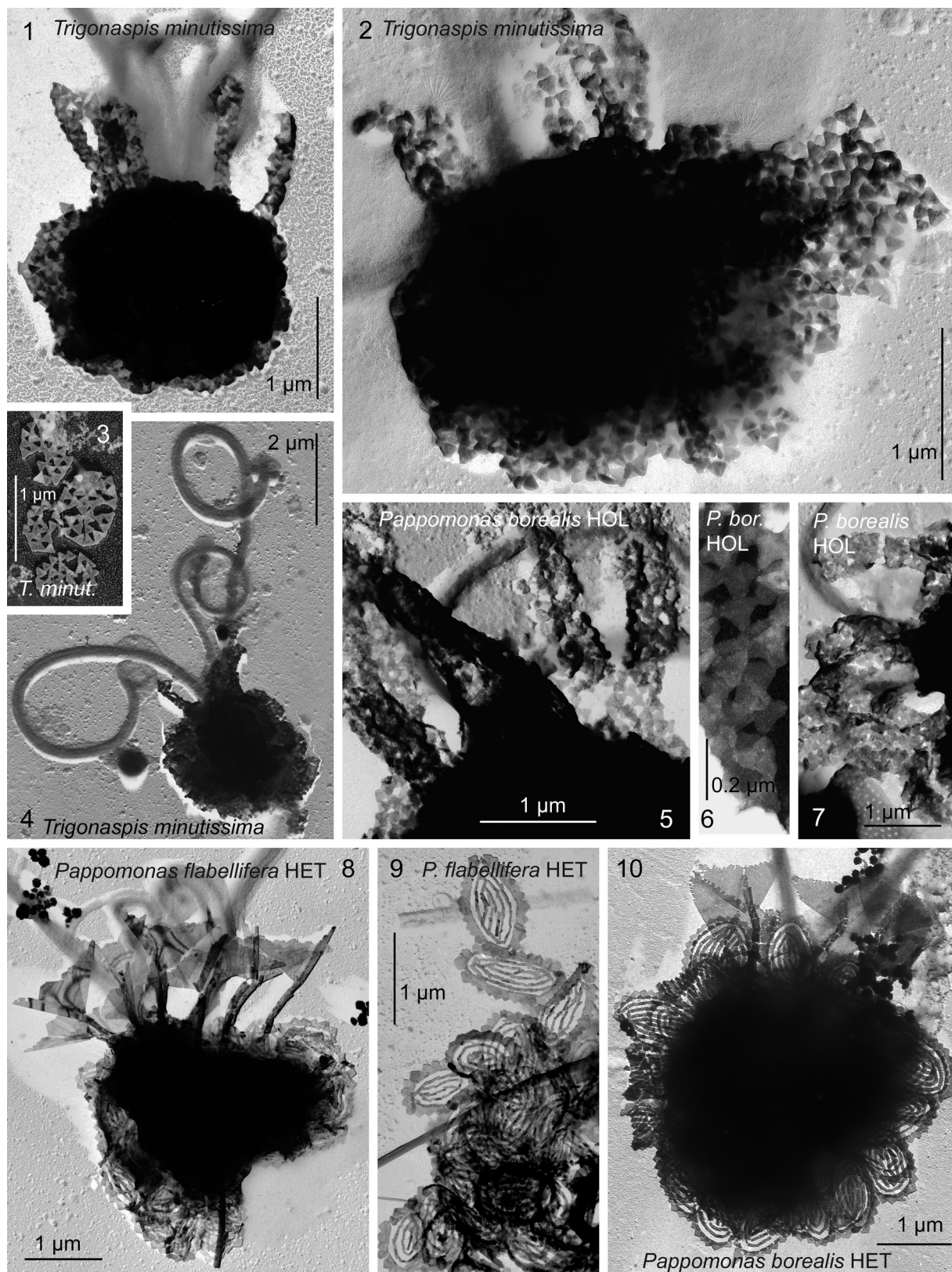
Plate 7 – *Balaniger virgulosa* HET
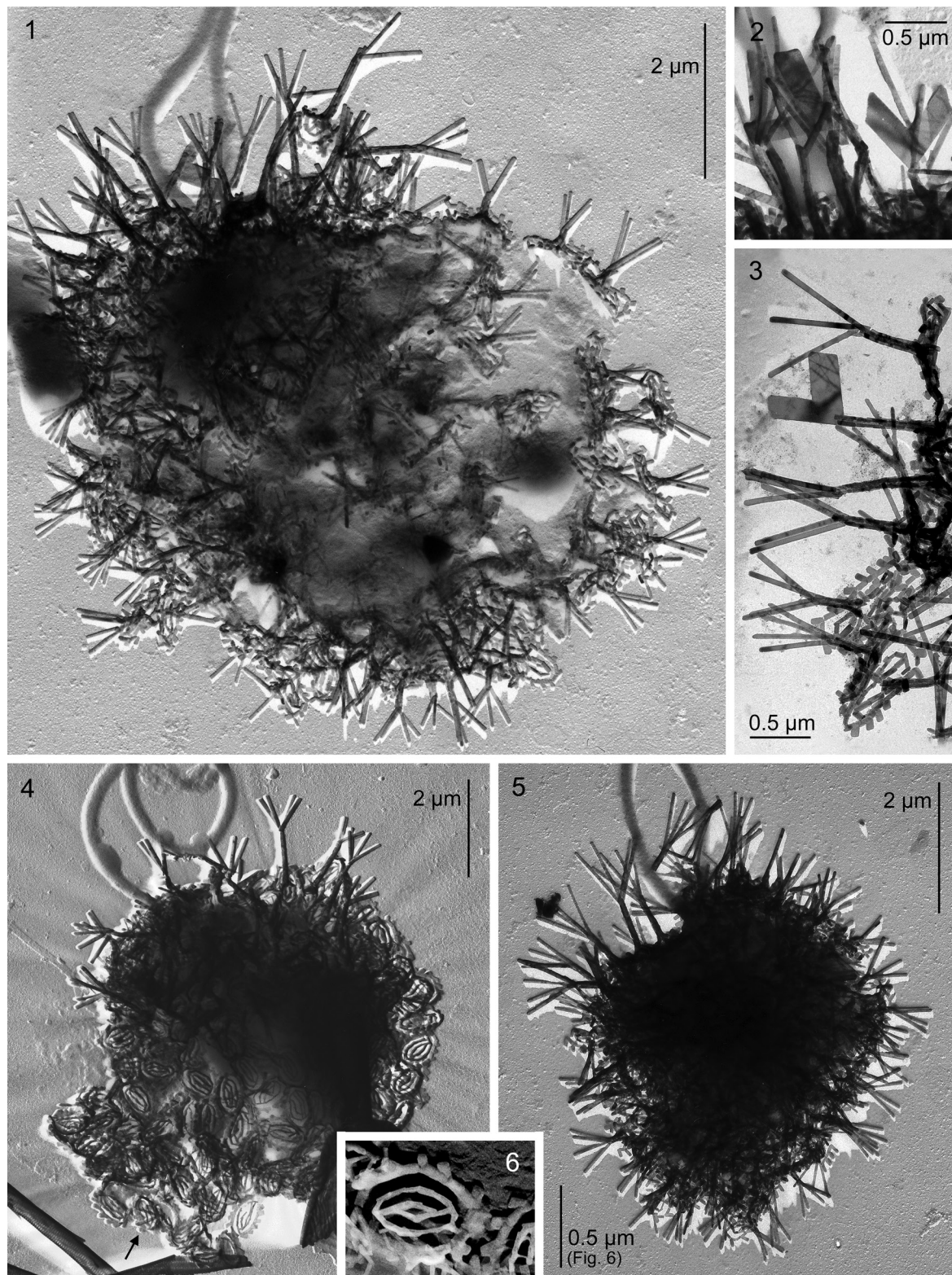
TEM images from the Baltic.

Fig. 1. Complete coccosphere. The circumflagellar coccoliths have long calicate spines (top left) while other coccoliths have calicate spines in which the stem is significantly shortened. **Figs 2–3.** Details of coccospheres in which aberrant types of calyces mix in between normal ones. **Fig. 4.** Specimen from the most brackish part of the Baltic Sea. Body coccoliths are without a central spine. The arrow points to an antapical pole coccolith that carries a reduced central appendage **Fig. 5.** A second coccosphere which shares with Fig. 1 the presence in all coccoliths of a central calicate spine. **Fig. 6.** Reverse printing. Detail of body coccolith calcification.

Plate 8

Figs 1–10 (TEM images).

Fig. 1. *Trigonaspis minutissima*

Fig. 2. *Trigonaspis minutissima*

Fig. 3. *T. minut.*

Fig. 4. *Trigonaspis minutissima*

Fig. 5. *Pappomonas borealis* HOL

Fig. 6. *P. bor.* HOL

Fig. 7. *P. borealis* HOL

Fig. 8. *Pappomonas flabellifera* HET

Fig. 9. *P. flabellifera* HET

Fig. 10. *Pappomonas borealis* HET

TEM images from inner Danish waters; reverse printing: Figs 3, 6.
Fig. 1. Complete cell. **Fig 2.** Complete coccosphere in which some of the body coccoliths have broken loose. **Fig. 3.** Detached body coccoliths showing the triangular crystallite groups united to form regular patterns. **Fig. 4.** Complete cell. **Fig. 5.** Detail of flagellar pole coccoliths. **Fig. 6.** Detail from Fig. 5 showing the triangular crystallite groups. **Fig. 7.** Flagellar pole coccoliths. **Fig. 8.** Complete cell. **Fig. 9.** Body coccoliths. **Fig. 10.** Complete cell.

Plate 9
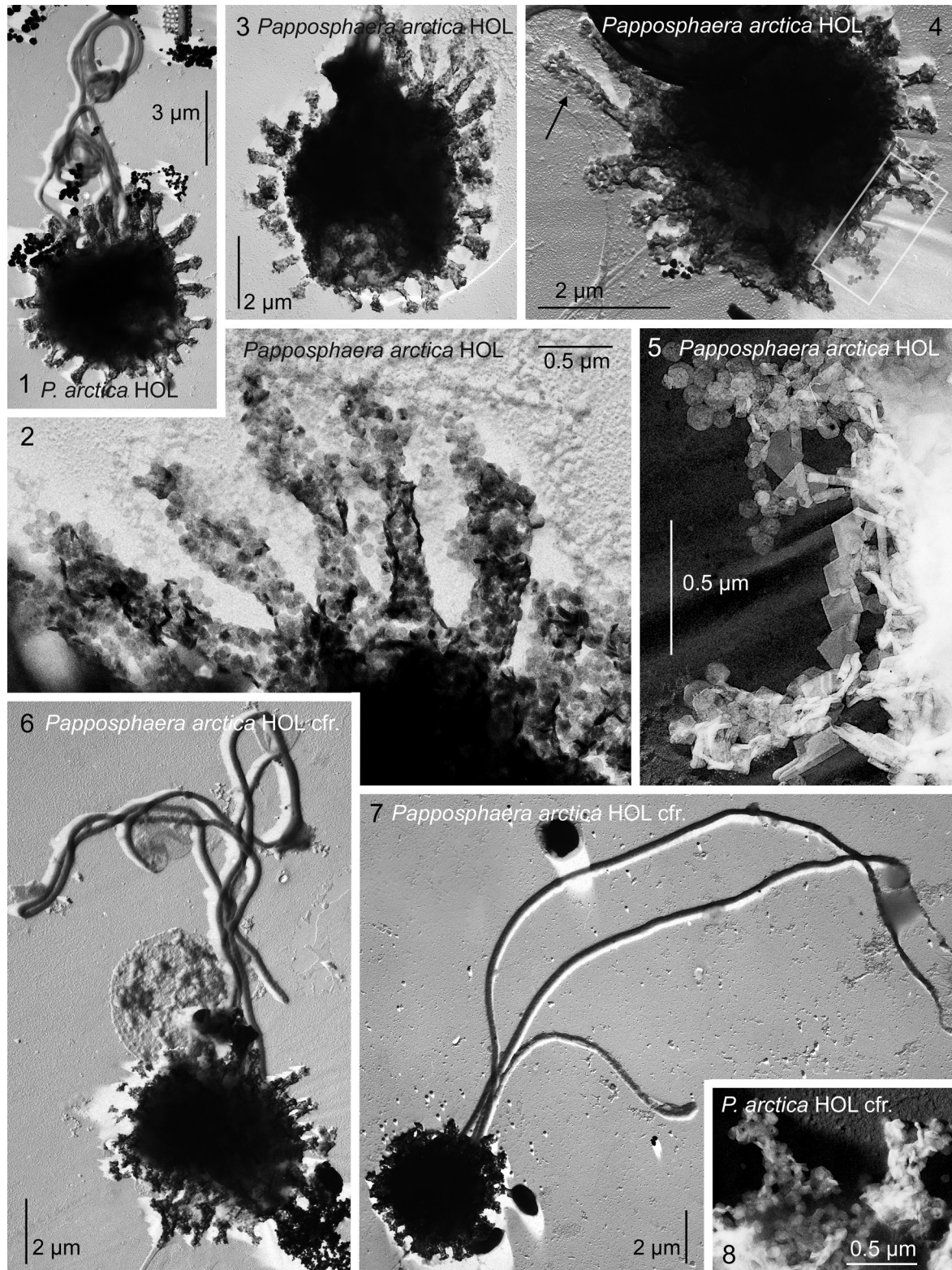
Papposphaera arctica HOL and combination coccosphere from inner Danish waters (Figs 1–5/TEM images). *Papposphaera arctica* HOL cfr. from the Bothnian Sea (Figs 6–8/TEM images); reverse printing: Figs 5, 8.

Fig. 1. Complete cell with flagella and haptonema. The unilateral distal proliferation of the flagellar pole coccoliths is only little pronounced. **Fig. 2.** Flagellar pole coccoliths (detail from Fig. 3); notice the unilateral distal hypertrophy. **Fig. 3.** Complete coccosphere. **Figs 4–5.** Combination coccosphere. The area that displays both hetero- and holococcoliths is marked in Fig. 4, and enlarged in Fig. 5. **Fig. 6–7.** Complete cells. **Fig. 8.** Detail from Fig. 6 showing a coccolith from the antapical pole. The hexagonal groups of crystallites are evident.

Plate 10
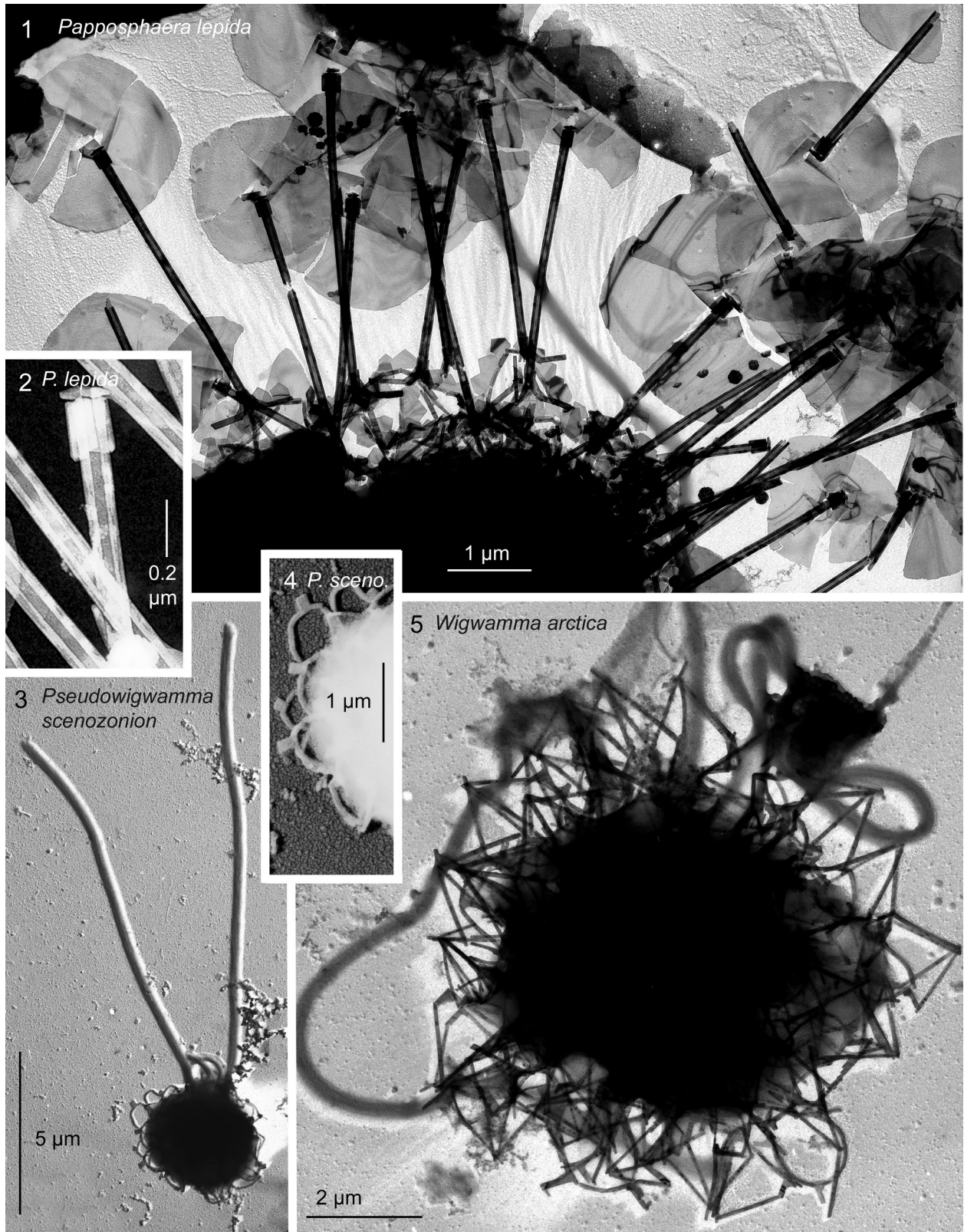
Images from inner Danish waters; reverse printing: Figs 2, 4.
Fig. 1. Pappoliths. **Fig. 2.** Detail of the collar at the distal end of the stem. **Fig. 3.** Complete cell. **Fig. 4.** Detail from Fig. 3 showing the rim calcification in the species. **Fig. 5.** Complete cell.