A guide to extant coccolithophore taxonomy

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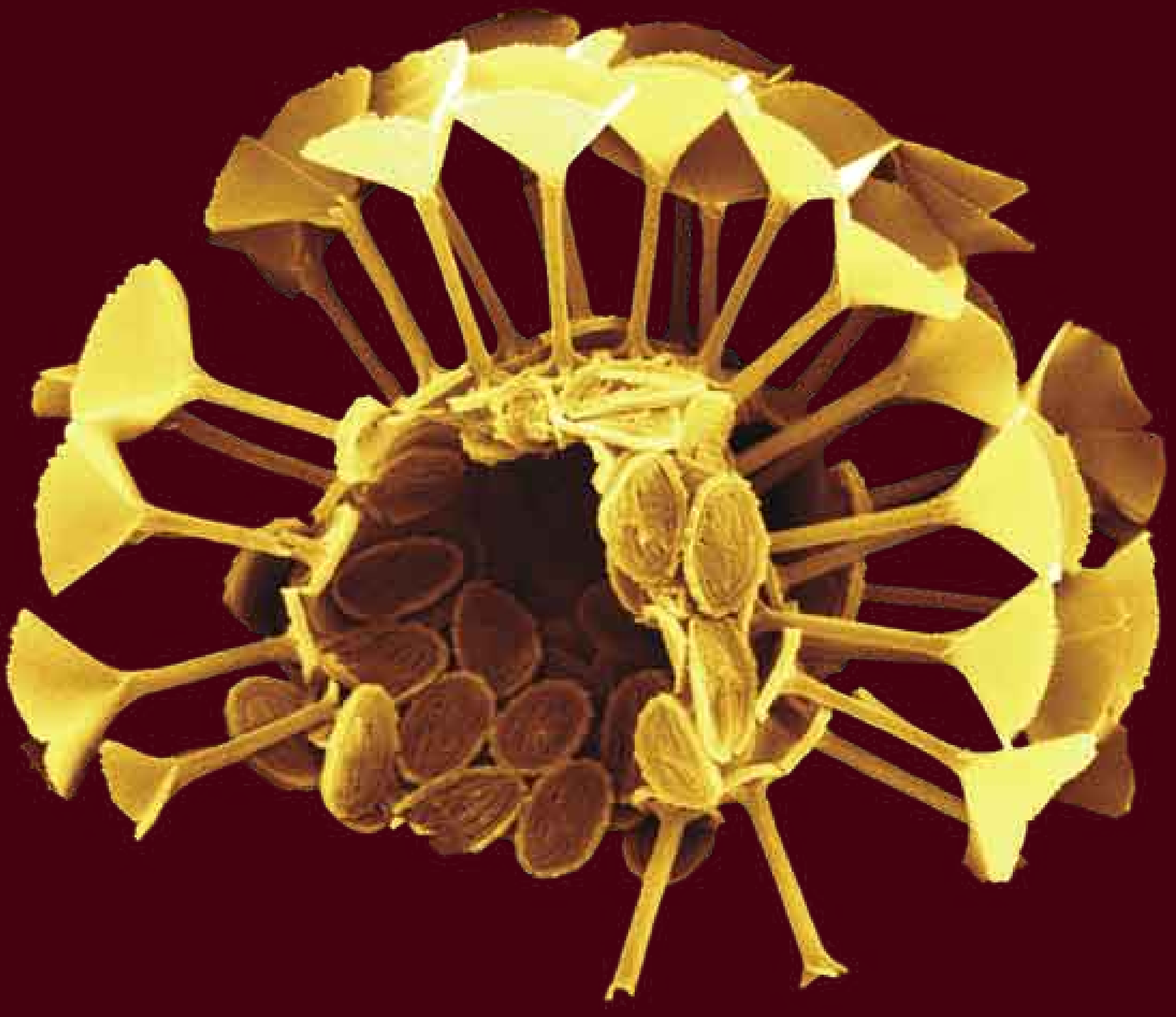

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Cover illustration: False coloured image of a *Pappomonas* sp. from the Alboran Sea, western Mediterranean. Back cover: False coloured image of *Coronosphaera mediterranea* from the S. Atlantic, off Namibia.

A GUIDE TO EXTANT COCCOLITHOPHORE TAXONOMY

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Dedication

To Peter Westbroek and Jan van Hinte, for inspiring coccolithophorid research,
and enriching our lives

Journal of Nannoplankton Research Special Issue 1

Foreword

Coccolithophores are beautiful organisms and also important ones. They are one of the main groups of marine phytoplankton playing key roles in the marine ecosystem as primary producers and in marine biogeochemistry as producers of organic carbon, carbonate and dimethyl sulphide. In addition they are major sediment formers, key biostratigraphic marker fossils and valuable indicators of palaeoceanographic change. These diverse interests have lead to intensive research on extant coccolithophores over the past decade. Interdisciplinary research has been promoted through the European projects EHUX (Coccolithophorid Dynamics: The European *Emiliania huxleyi* Programme) and CODENET (Coccolithophorid Evolutionary Biodiversity and Ecology Network) projects. In addition there has been extensive work, especially in Europe and Japan, on coccolithophore communities in the plankton and on fluxes of coccoliths in sediment traps.

As a result of this recent research the taxonomy of coccolithophores has advanced significantly over the past decade, i.e. since the seminal syntheses of Jordan & Kleijne (1994) and Jordan et al. (1994). So there is a need for a new synthesis, and especially for an identification guide. There is still work to be done, especially formal description of many now well-established informally described species, but coccolithophores are now one of the most comprehensively described, and most reliably identifiable groups of oceanic microplankton. In consequence they are an ideal group for developing study of the pattern and role of biodiversity in plankton ecology. We hope this identification guide will facilitate such studies, as well as informing palaeontologists studying fossil coccoliths of the nature of the modern biota.

Acknowledgements

This work is a synthesis of many years work and the authors have been assisted by many colleagues. This has included extended discussion of taxonomy and exchange of samples with other nannoplankton taxonomy enthusiasts, especially Mara Cortes, Doan Nhu Hai, Ric Jordan, Vita Pariente, Christian Samtleben and Alexandra Zeltner. Other colleagues have encouraged the work, assisted with sampling and provided invaluable assistance with electron microscopy, the following list may seem improbably long but all these colleagues have made real contributions for which we are indebted: Laura Arin, Alex Ball, Karl-Heinz Baumann, Chantal Billard, Babette Boeckel, Jörg Bollmann, Paul Bown, Sandra Broerse, Mario Cachão, Daniella Crudeli, Marta Estrada, Claire Findlay, Jacqueline Fresnel, José-Manuel Fortuño, Jan van Hinte, Marc Hockfield, Aude Houdan, Andy Howard, Chris Jones, Michael Knappertsbusch, Ramon Margalef, Linda Medlin, Marie-Helene Noel, Hisatake Okada, Richard Pearce, Patrick Quinn, Alberto Sáez, Blair Steel, Hans Thierstein, Maria Triantaphyllou, Peter Westbroek, Emma Williamson, Patrizia Ziveri.
Financial and logistic support has been provided by all of our institutions, recognising the fundamental importance of taxonomy in underpinning all biological research. More specifically the EU TMR CODENET project (Coccolithophorid Evolutionary Biodiversity and Ecology Network) directly funded our collaboration and this volume is a contribution of the project.

Image credits
The illustrations are primarily the authors but we are very grateful to the following for providing images; Babette Boeckel (Plates 1/6; 6/8, 12; 16/4; 23/3; 25/15; 31/6, 9; 39/10); Marie-Helene Noel (Plate 32/1-3), Vita Pariente (Plates 21/1-3; 23/7, 9, 10, 13; 27/1, 6, 9; 50/1), Tien-Nan Yang (plate36/5-6); Jacqueline Fresnel (Plates 5/10, 9/3-6).

A GUIDE TO EXTANT COCCOLITHOPHORE TAXONOMY

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Introduction

This is an annotated species-level overview and classification of living coccolithophores. It is primarily intended to act as an *aide memoire* to coccolithophorid taxonomy, with brief notes serving as a reminder to the distinguishing features of taxa, extended descriptions can be found in the primary literature. The biology of coccolithophores is well summarised in the review volumes of Winter & Siesser (1994), Green & Leadbeater (1994) and Thierstein & Young (in press), so notes are only needed here on a few topics directly related to taxonomy and identification.

Terminology

The terminology used here essentially follows the Guidelines for Coccolith and Calcareous Nannofossil Terminology of Young et al. (1997), key aspects are summarised in figure 1, and the full guide is available online, via the INA website. An additional glossary of terms for haptophytes is provided by Jordan et al. (1995). The following aspects are worth noting.

1. Coccolithophores produce two very different types of coccoliths: (a) *heterococcoliths*, which are formed of a radial array of complex crystal-units. (b) *holococcoliths,* which are formed of numerous minute (ca. 0.1 μm) euhedral crystallites. We now know that holococcoliths and heterococcoliths are products of respectively haploid and diploid life-cycle phases and form via very different biomineralisation processes (see e.g. Young et al. 1999). A few structures do not conform to either pattern and so have been termed *nannoliths*, following palaeontological usage. Nannoliths are probably formed by different biomineralisation processes, and in some cases possibly not by coccolithophores.

2. We use the terms *placolith*, *murolith* and *planolith* as descriptors of heterococcolith shape, independent of structure.

3. Each of the heterococcolith types can conveniently be subdivided into a *rim* and *central area*.

4. The terms segment, crystal-unit and element form a hierarchy of structural components: *Elements* are the superficially discrete units observed on the surface of a coccolith. *Crystal-units* are single crystals and typically are composed of several interconnected but superficially discrete elements. A *segment* consists of the different crystal-units that constitute one radially repeated portion of a heterococcolith rim.

5. A basic characteristic of coccoliths is that their morphology and structure is highly variable, with the result that homology is limited. Elaborate specialist terminology would therefore be counter-productive, instead we have tried as far as possible to avoid obscure terms. In particular, following Young et al. (1997), we have avoided the more obscure terms coined for coccoliths of particular taxa (e.g. cricolith, cyrtolith, fragariolith).

Coccolith crystallography and growth

Kamptner (1954), Prins (1969) and Romein (1979) showed that crystallographic orientation was an invaluable key to understanding coccolith ultrastructure and phylogenetic relationships. Young et al. (1992, 1999) showed further that the typical heterococcolith rim structure was composed of two interlocking crystal-units with respectively sub-vertical (V-units) and sub-radial (R-units) c-axes. These two crystal-unit types originate from a proto-coccolith ring of alternating V-unit and R-unit nuclei. This proto-coccolith ring is formed within the cell, on an organic baseplate scale, as the first phase of coccolith growth. This basic structure provides a key to interpreting cross-polarised light images and to elucidating relationships, so the structure of coccoliths in these terms is discussed in the family and order descriptions. Within family groups the coccolith structure and crystallography is usually constant, so for species-level identification, especially in SEM, it is a feature that can be ignored. However, it should be noted that this crystallographic aspect of the classification means that it is based on variation in rather stable biomineralisation processes and so is much more robust than might appear superficially. An important development of the V/R model is recognition that the radial laths in the Syracosphaeraceae represent a third crystal-unit type with tangential c-axis orientations (Young et al. subm.). This provides the basis for grouping of the Syracosphaeraceae, Rhabdosphaeraceae, and Calciosoleniaceae into the order Syracosphaerales.

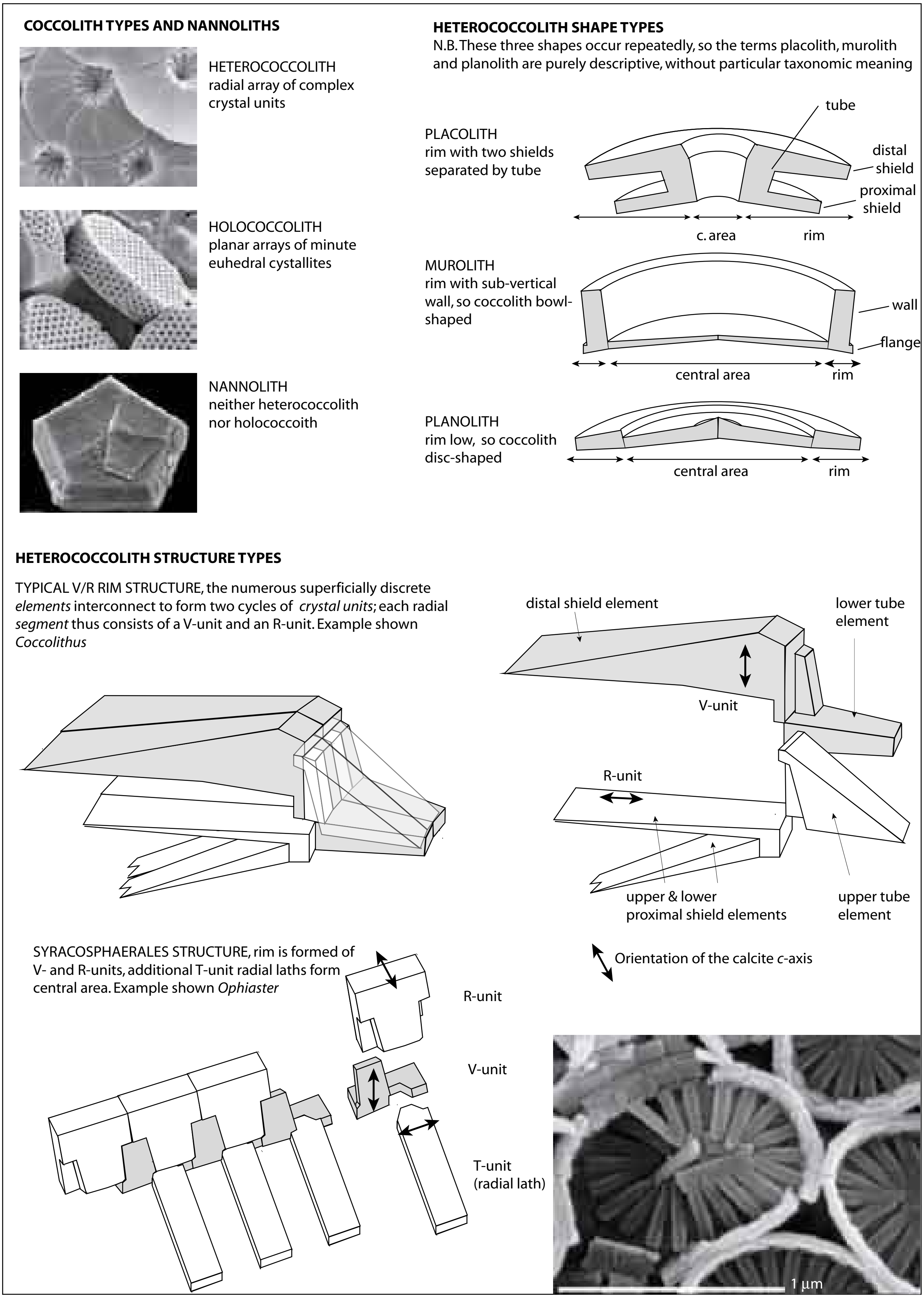


Figure 1 - Key terms related to coccolith morphology and structure

Species list

The species list used here was based initially on that of Jordan & Kleijne (1994), and Jordan & Green (1994). However, this has been significantly revised in the light of subsequent research. All species described in the last few years are included. In addition, we have included numerous species and morphotypes for which formal descriptions are in preparation, including most of those described in Cros & Fortuño 2002. (NB Cros & Fortuño 2002 is a published atlas based on the PhD Thesis of Cros 2001, only the former publication is cited). It is perhaps unfortunate that so many taxa have been introduced informally, however, since in almost all cases full formal descriptions are in preparation it was not appropriate here to introduce Linnean names. To maintain stability of nomenclature the original authors' terms are used (e.g. *Syracosphaera* sp. type D of Kleijne 1991). One new genus and species is introduced, *Placorhombus ziveriae,* and two new families, the Alisphaeraceae and Umbellosphaeraceae. The following new combinations are introduced here, *Algirosphaera cucullata, Reticulofenestra maceria, Umbilicosphaera anulus*, *Calciosolenia brasiliensis*, *Helladosphaera vavilovii*. In addition, as a result of recognition of life-cycle associations numerous holococcolithophores are now considered to be alternate phases of heterococcolithophores rather than discrete species, as discussed below.

Life-cycles

It has long been suspected that haplo-diplontic life-cycles are widespread in haptophytes and that the different phases bear different coccoliths and/or organic scales (Billard 1994). For coccolithophores, only limited data is available from culture studies (e.g. Parke & Adams 1960, Gayral & Fresnel 1983, Medlin et al. 1996, Geisen et al. 2002, Houdan et al. subm., Noel et al. subm.). However, supplementary data is available from combination coccospheres recording the transition between life-cycle stages and bearing coccoliths characteristic of both stages (e.g. Thomsen et al. 1991, Kleijne 1991, Alcober & Jordan 1997, Cros et al. 2000, Cros & Fortuño 2002, Geisen et al. 2002). From this work, it appears that three life-cycle types are common in coccolithophores.

1. Diploid phase heterococcolith-bearing, haploid phase non-calcifying - Noelaerhabdaceae, Hymenomonadaceae and Pleurochrysidaceae.

2. Diploid phase heterococcolith-bearing, haploid phase holococcolith-bearing - Calcidiscaceae, Coccolithaceae, Helicosphaeraceae, Syracosphaeraceae, Rhabdosphaeraceae and Papposphaeraceae (figure 2).

3. Diploid? phase heterococcolith-bearing, haploid? phase nannolith-bearing - Ceratolithaceae, and Alisphaeraceae.

Since holococcolith and heterococcolith phases have traditionally been described as separate species, the recognition of life-cycle combinations is leading to widespread revision of nomenclatural taxonomy. We agree with Thomsen et al. (1991) and Cros et al. (2000) that a single formal name should be applied to both phases of a life-cycle. Whenever needed, an informal indication of whether the heterococcolith phase or holococcolith phase has been observed can be added to the species name - e.g. *Syracosphaera anthos* HET, *Syracosphaera anthos* HOL. The appropriate name should be based on normal taxonomic rules of priority. This system is followed here, but since this is an identification guide holococcoliths and heterococcoliths are considered separately. To allow comparison with the literature the traditional names are also given, in curly brackets, e.g. {*Crystallolithus hyalinus*}.

Additional complexity occurs in several **c**ases where two or more traditional holococcolith species are associated with a single traditional heterococcolith species (Geisen et al. 2002). In some of these cases, there is parallel variation in the holococcoliths and heterococcoliths (e.g. *Coccolithus pelagicus* and *Calcidiscus leptoporus*), in these cases separate species or sub-species can be defined. In other cases the holococcolith variation is not paralleled by any obvious variation in heterococcolith morphology (e.g. *Syracosphaera pulchra, Coronosphaera mediterranea*), in these cases a more informal notation is used e.g. *S. pulchra* HOL *oblonga* type.

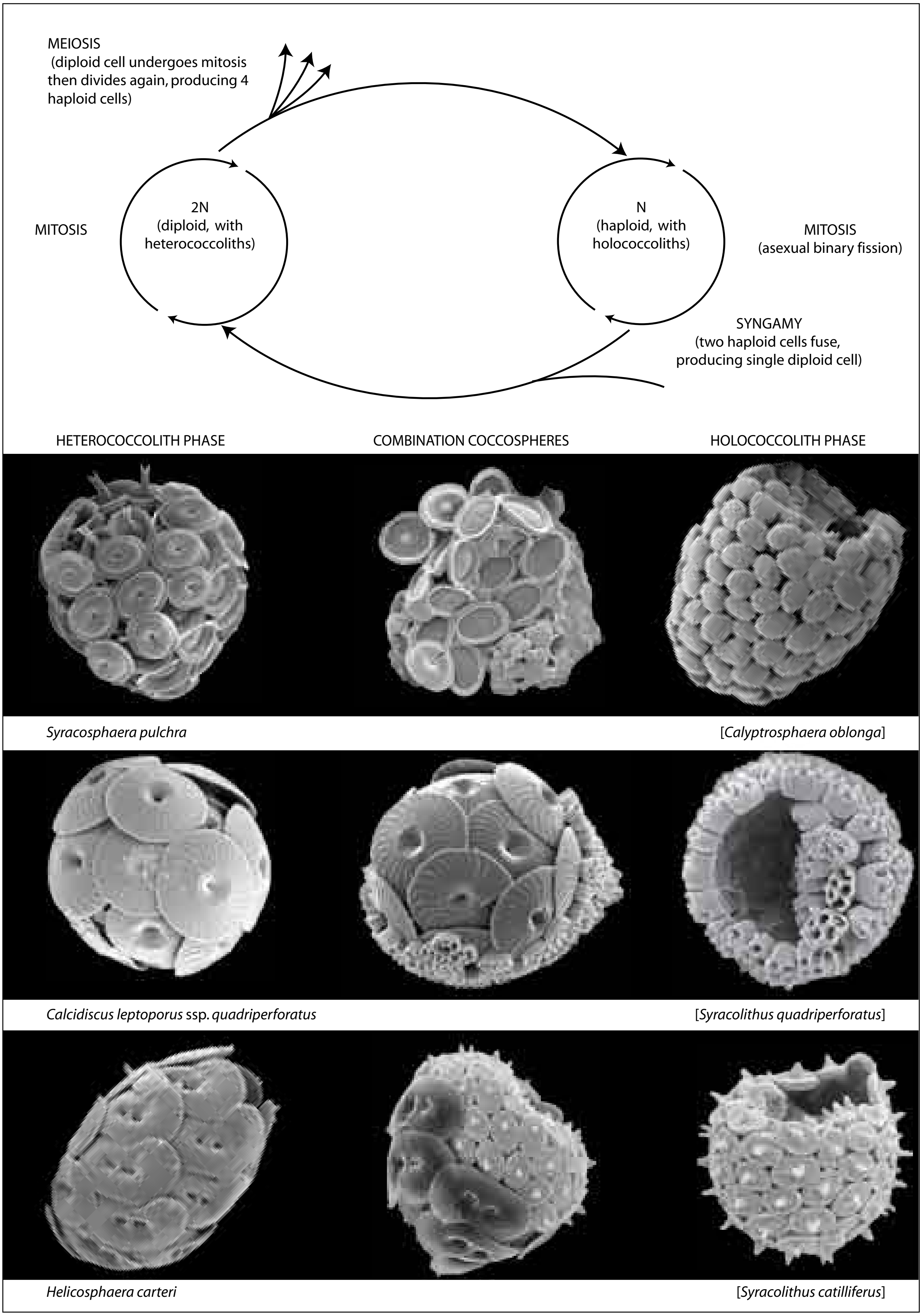


Figure 2 - Typical coccolithophore life-cycle, and three examples

Higher classification

The higher classification is based on that of Young & Bown (1997a), including use of a three-level, order-family-genus, classification. This is based primarily on coccolith structure and crystallography but also on other data as available, from both biological and palaeontological research. Changes have been made in light of new knowledge as follows (see also figure 3 and see main text for longer explanations):

(1) The order Isochrysidales Pascher 1910 is used instead of Prinsiales Young & Bown 1997, since it has priority and since results from molecular genetic and biochemical studies have supported the grouping of *Isochrysis* and various other non-calcifying genera into the family Isochrysidaceae as a sister taxon to the Noelaerhabdaceae (Edvardsen et al. 2000).

(2) The families Hymenomonadaceae and Pleurochrysidaceae are included in the Coccosphaerales, based on: molecular genetic data (Sáez et al. in press); new data from ultrastructure studies of *Pleurochrysis* (Marsh 1999); and cytological evidence for close affinity of the Hymenomonadaceae and Pleurochrysidaceae.

(3) The order Syracosphaerales is revised to include the Calciosoleniaceae, Syracosphaeraceae and Rhabdosphaeraceae, all of which are characterised by radial lath cycles.

(4) The genus *Alveosphaera* is included in the Calciosoleniaceae, and the genus *Anoplosolenia* is considered a synonym of *Calciosolenia*.

(5) The genera *Alisphaera* and *Canistrolithus* are removed from the Syracosphaeraceae to form a new family, the Alisphaeraceae, since they have a very different structure (Kleijne et al. 2002).

(6) The nannolith genus *Polycrater* is included in the Alisphaeraceae since it is the alternate lifecycle stage of *Alisphaera* and *Canistrolithus* (Cros & Fortuño 2002).

(7) The important genus *Umbellosphaera* is removed from genera *incertae sedis* to be placed in a new family Umbellosphaeraceae. This family is monogeneric but the morphology and structure of *Umbellosphaera* is well enough characterised for us to be confident that it does not fall into any other family.

(8) The heterococcolithophore "*Neosphaera"* has now been shown to be a life-cycle stage of *Ceratolithus* (Alcober & Jordan 1997, Sprengel & Young 2000). Therefore, the coccoliths which were previously described as species of *Neosphaera* are now included in *Ceratolithus cristatus*.

(9) The category of genera *incertae sedis* has now been subdivided: (a) As mentioned above *Neosphaera, Umbellosphaera* and *Polycrater* have been removed to respectively the Ceratolithaceae, Umbellosphaeraceae and Alisphaeraceae; (b) *Tetralithoides*, *Turrilithus*, the heterococcolith stage of "*Calyptrosphaera" sphaeroidea* and the new genus *Placorhombus* are grouped together as "narrow-rimmed placoliths"; (c) *Picarola, Vexillarius, Wigwamma* and an undescribed genus are grouped together as "narrow rimmed muroliths, with possible affinity to the Papposphaeraceae; (d) Finally, this leaves a residual group of three, probably unrelated, nannoliths *incertae sedis*, *Florisphaera, Gladiolithus* and *Ericiolus*.

Conventions used and organisation of the Guide

The taxa are primarily arranged according to Linnean classification but to make the arrangement clearer and to allow informal subdivision of taxa this is supplemented by an informal 3-level numbered heading scheme. At each level there are usually 3-5 choices per group, which we have found a convenient number for rapid comprehension of diversity; and each sub-group is as far as possible of equal size. The first two levels are given in the table of contents and summarised in an index figure at the end of the guide.

A special effort was made to illustrate almost all taxa, and to have descriptions directly opposite illustrations. Larger size versions of the images are available via the CODENET and INA web sites and this will be extended to include the text, and information on the provenance of the images. All scale bars are one micron long unless otherwise noted.

Conventions & abbreviations used:

{}	traditional name for a life-cycle phase, when it was regarded as a discrete taxon, e.g. {*Crystallolithus hyalinus*}
[]	invalid taxa and previous generic assignments, e.g. [*Crenalithus*]
HOL	holococcolithophore stage of life-cycle
HET	heterococcolithophore stage of life-cycle (NB We use HOL/HET rather than HO/HE as recommended in Cros et al. (2000b), since the former abbreviations are less cryptic, and more easily pronounceable)
BC	body coccolith
CFC	circum-flagellar coccolith
AAC	antapical coccolith
XC	exothecal coccolith (*Syracosphaera* only)
V/R-units	crystal-units with sub-vertical/sub-radial calcite c-axes (cf. Young et al. 1992)
lith	coccolith
LM	light microscopy
SEM	scanning electron microscopy

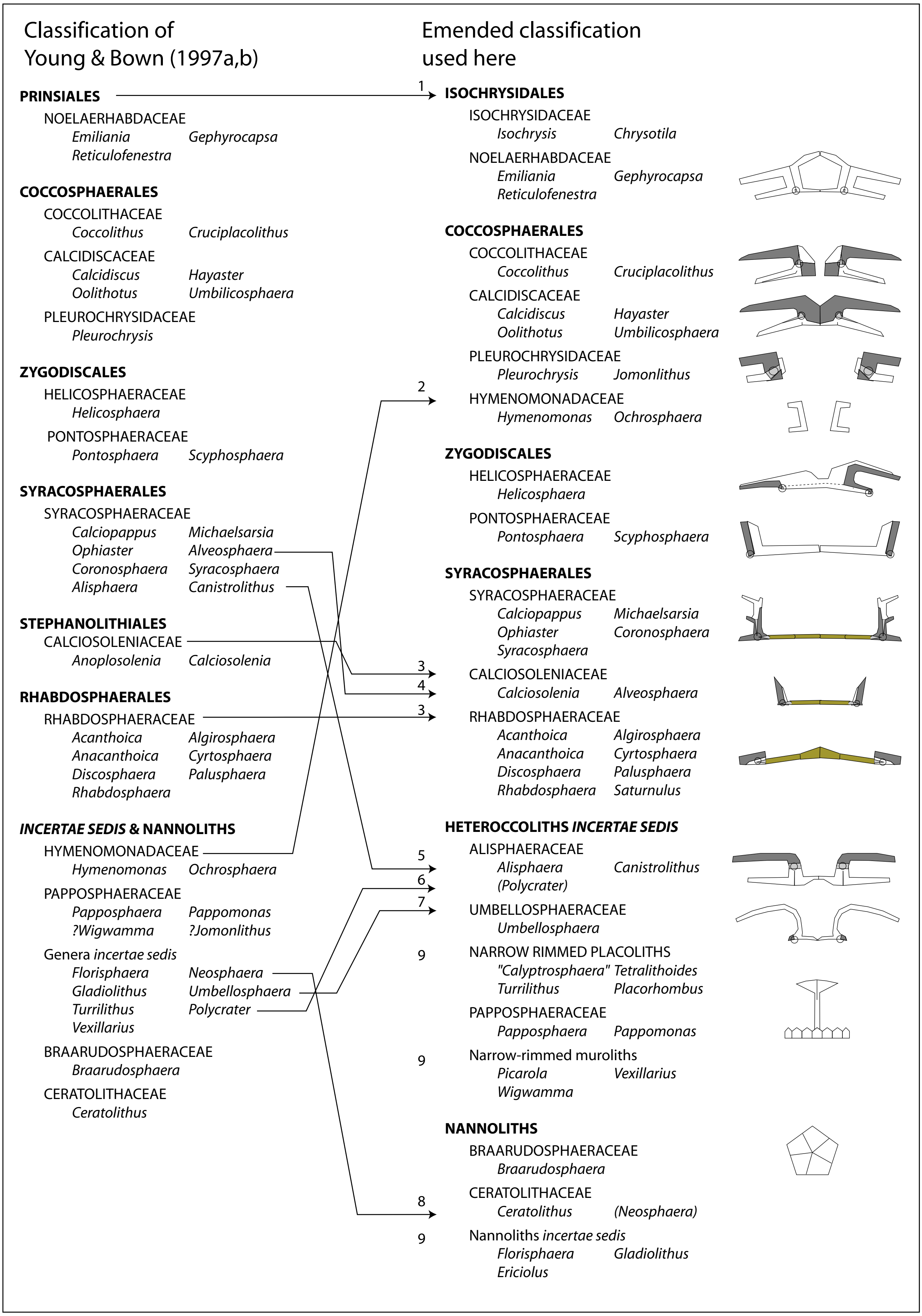


Figure 3 - Comparison of classification adopted here with that of Young & Bown (1997)

1. Major heterococcolith groups, except Syracosphaerales

1.1 Isochrysidales (Noelaerhabdaceae)

Order ISOCHRYSIDALES Pascher 1910

Taxa included: Noelaerhabdaceae (see below) plus the extinct family Prinsiaceae (see Young & Bown 1997a,b) and the extant family of non-calcifying haptophytes Isochrysidaceae (Edvardsen et al. 2000). As noted in the introduction the order Isochrysidales is used instead of Prinsiales Young & Bown 1997. Grouping of the Isochrysidaceae and Noelaerhabdaceae is based on flagellar characters (haptonema vestigial) and is supported by biochemical characters (production of alkenones) and molecular genetics (Edvardsen et al. 2000, Fujiwara et al. 2001, Sáez et al. in press). Grouping of Prinsiaceae and Noelaerhabdaceae is based on coccolith structure and stratophenetic data (Young et al. 1992, Young & Bown 1997).

Family **NOELAERHABDACEAE** Jerkovic 1970 emend. Young & Bown 1997

Life-cycles and culture studies: *Emiliania huxleyi* and *Gephyrocapsa oceanica* have been cultured extensively and their life-cycle is well worked out (Klaveness 1972, Green et al 1996, Houdan et al. in press). The dominant phase is diploid, non-motile and usually heterococcolith-bearing (= C-cells), although naked mutants often occur in culture (= N-cells). The alternate phase is haploid, scale-bearing and motile (= S-cells). There is no holococcolith stage.

Coccolith structure: Coccoliths are placoliths with *Emiliania*-type structure, i.e. V-unit vestigial, R-unit forms proximal shield, distal shield, inner and outer tube-cycles, grill and any central-area structures; strongly birefringent. In the SEM characteristic features include; grill in central area, anti-clockwise imbrication of inner tube elements, and monocyclic proximal shield. References: Young (1989), Young et al. (1994).

SYNONYM: Gephyrocapsaceae Black, 1971.

1.1.1 *Emiliania*

Emiliania Hay & Mohler *in* Hay et al. 1967

Slits between all distal shield, and some proximal shield, elements. TYPE: *Emiliania huxleyi*.

Emiliania huxleyi (Lohmann 1902) Hay & Mohler, in Hay et al. 1967 var. *huxleyi* [*Pontosphaera*]

Ubiquitous species, often forming blooms. Coccospheres often with multiple layers of coccoliths.

Well-established morphotypes:

Young & Westbroek (1991) distinguished three types based on heterococcolith morphology, see also van Bleijswijk et al. (1991) and Young (1994). Medlin et al. (1996) consider these types should be regarded as separate varieties, their recommended names are given in brackets, (). It should be noted that additional, non-genotypic, variation is seen in degree of calcification, leading to variable central area closure and slitting of proximal shield.

Type A (*huxleyi*): liths medium -sized (3-4 μm), distal shield elements robust, central *area* elements curved.

Type B (*pujosiae*): liths large (3.5-5 μm), distal shield elements delicate, central area elements irregular laths. Proximal shield often wider than distal shield.

Type C (*kleijneae*): liths small (2.5-3.5 μm), distal shield elements delicate, central area open or covered by thin plate.

Additional morphotypes:

Recent work suggests the following should also be distinguished:

Type B/C: liths medium-sized, (3-4 μm), distal shield elements delicate, i.e. similar in morphology to types B & C, but intermediate in size. This form often dominates assemblages in the Southern Ocean (Hockfield 2000; Findlay & Giraudeau 2000, referred to as type C),

Type R: Form similar to type A but with heavily calcified shield elements, indeed slits often closed giving a *Reticulofenestra*-like appearance (hence designation as type R). Several specimens of this form have been isolated from the S.W. Pacific and they have maintained their distinctive morphology for several years indicating that this stable genotypic variation (Probert, Young unpubl. obs). Similar morphotypes were observed in the same area by Nishida (1979) and Burns (1977).

Emiliania huxleyi var. *corona* (Okada & McIntyre 1977) Jordan & Young 1990

Like *E. huxleyi* type A but with inner tube cycle forming discontinuous elevated crown around central area.

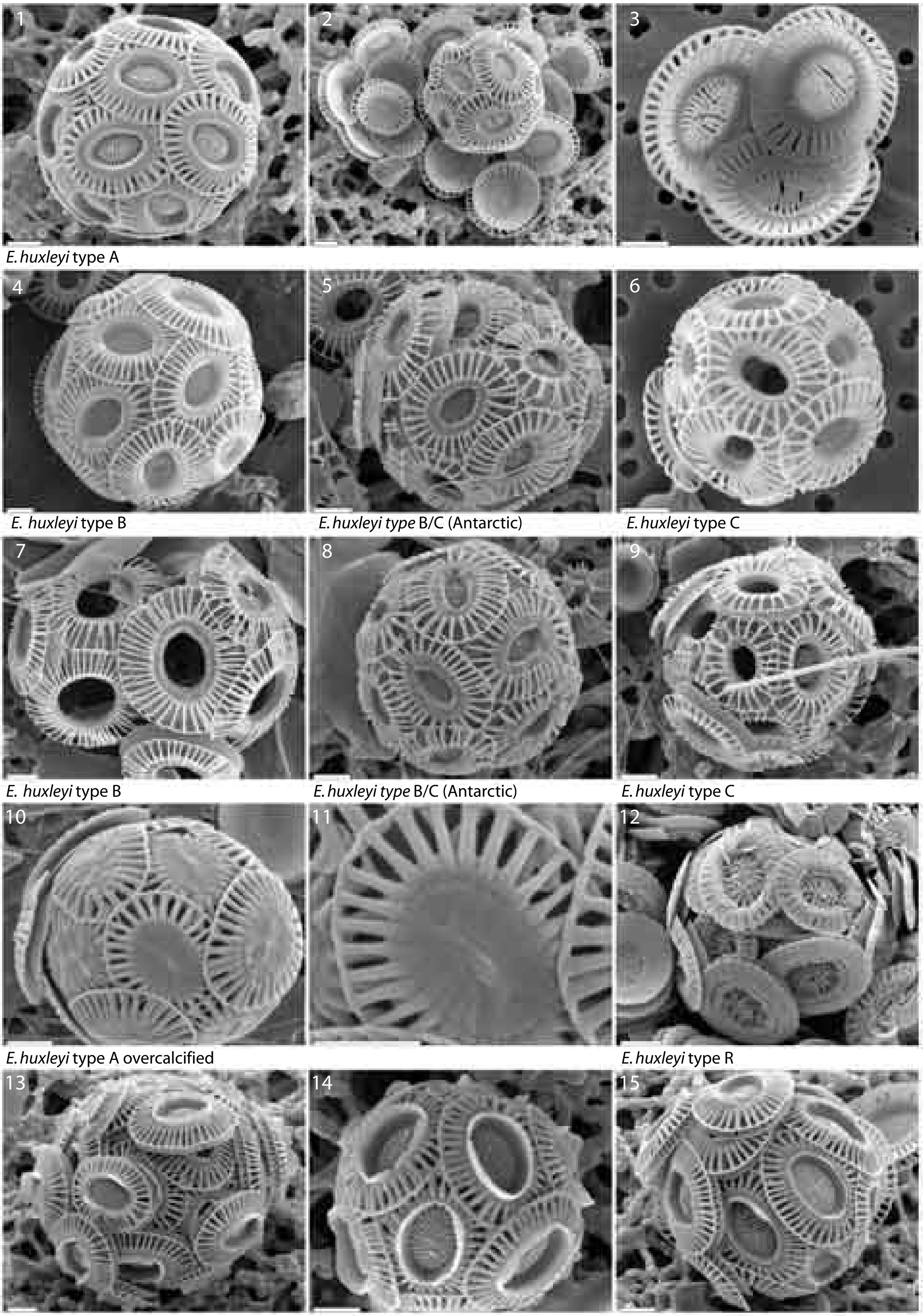


Plate 1 - Noelaerhabdaceae: *Emiliania*

1.1.2 *Gephyrocapsa*

Gephyrocapsa Kamptner 1943

Structure similar to *Emiliania* but with conjunct bridge, formed from inner tube-elements spanning central area; shields usually solid, i.e. without slits between the elements. Key references: Samtleben (1980), Bollmann (1997). TYPE: *G. oceanica*.

Conventional species: numerous species of *Gephyrocapsa* have been described. The following are commonly used, but species concepts applied by authors have varied:

Gephyrocapsa oceanica Kamptner 1943

Large, with bridge at high angle to long axis, inner tube protrudes to form collar around central area. Coccospheres often occur in clusters.
Coccospheres, 6 to 10 μm; coccoliths, 3.5 to 6 μm long.

Gephyrocapsa muellerae Bréhéret 1978

Intermediate size, bridge at low angle to long axis, central area rather small. In older literature often named *G. caribbeanica*.
Coccospheres, 5 to 9 μm; coccoliths, 3 to 4 μm long.

Gephyrocapsa caribbeanica Boudreaux & Hay, in Hay et al. 1967 *(not figured)*

Large, bridge at intermediate angle to long axis, central area almost closed. An important species in the Late Quaternary but not consistently recorded in modern nannoflora.

Species smaller than 2.5 μm (coccolith length)**:** Very small *Gephyrocapsa* specimens are highly variable in morphology and it is possible that several species occur. The following species fall in this category.

Gephyrocapsa ericsonii McIntyre & Bé 1967

Very small, low to intermediate angle bridge, wide central area, thin bridge. Specimens often show slits between distal shield elements. These morphotypes have sometimes been referred to as separate species, *G. protohuxleyi* (McIntyre 1970*)*, but they intergrade with normal *G. ericsonii*.
Coccospheres, 3 to 5 μm; coccoliths, 1.4 to 2.3 μm long.

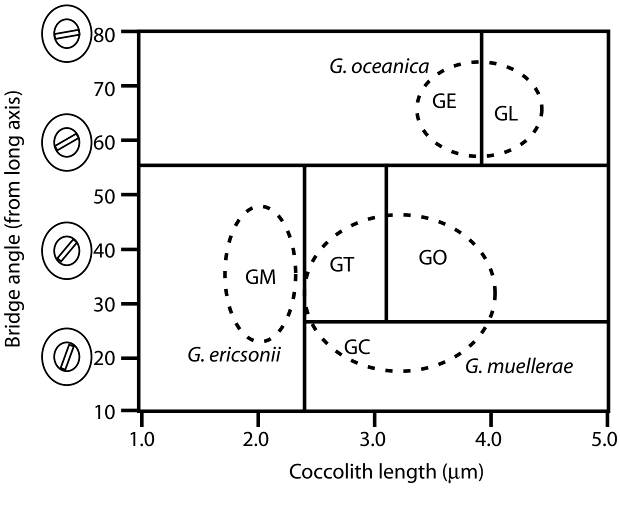
Gephyrocapsa ornata Heimdal 1973

Similar to *G. ericsonii* but with teeth around tube, much higher bridge, and consistently low bridge angle (within 10-20° of long axis).

G*ephyrocapsa crassipons* Okada & McIntyre 1977 *(not figured)*

Similar to *G. ericsonii* but more heavily calcified; central area nearly closed by inner tube cycle; broad, low bridge. Possibly an ecomorphotype of *G. ericsonii* rather than a true species (Okada pers comm., 2000). Characteristic of high fertility areas of the Equatorial Pacific (Hagino & Okada 2001).

Morphotypes: Bollmann (1997), conducted a global survey of Holocene *Gephyrocapsa* coccoliths and identified the following morphotypes which he interpreted as genotypically distinct taxa with variable ecological preferences. NB ba = bridge angle, measured from *long* axis of coccolith. SST = mean annual sea surface temperature.
GL (larger); mean ba >56°; mean length >3.9 μm. Occurs in eutrophic temperate regions with SSTs of 18-23°C.
GE (equatorial); mean ba >56°; mean length 3.1-3.9 μm. Occurs in equatorial regions, with SST of 25-30C.
GO (oligotrophic); mean ba 27-56°; mean length >3.1 μm. Occurs in oligotrophic gyre regions with SSTs of 22-25°C.
GT (transitional); mean ba 27-56°; mean length 2.4-3.1 μm. Occurs in regions with SSTs of 19-20°C.
GC (cold); mean ba <27°; mean length >2.4-3.5 μm. Occurs in temperate to sub-arctic regions with SSTs of <21°C.
GM (minute); mean ba 20-50°; mean length <2.4 μm. Widespread, may include several species.
As indicated on the figure *G. oceanica* as conventionally used includes two morphotypes, which based on Bollmann's analysis are probably ecologically and genotypically distinct. Similarly, *G. muellerae* appears to comprise three morphotypes.



Gephyrocapsa morphotypes in terms of size and bridge angle. Redrawn form Bollmann (1997). The positions of the letters GE etc. indicate the frequency maxima of the respective morphotypes. The ellipses are added here to indicate the conventional species concepts.

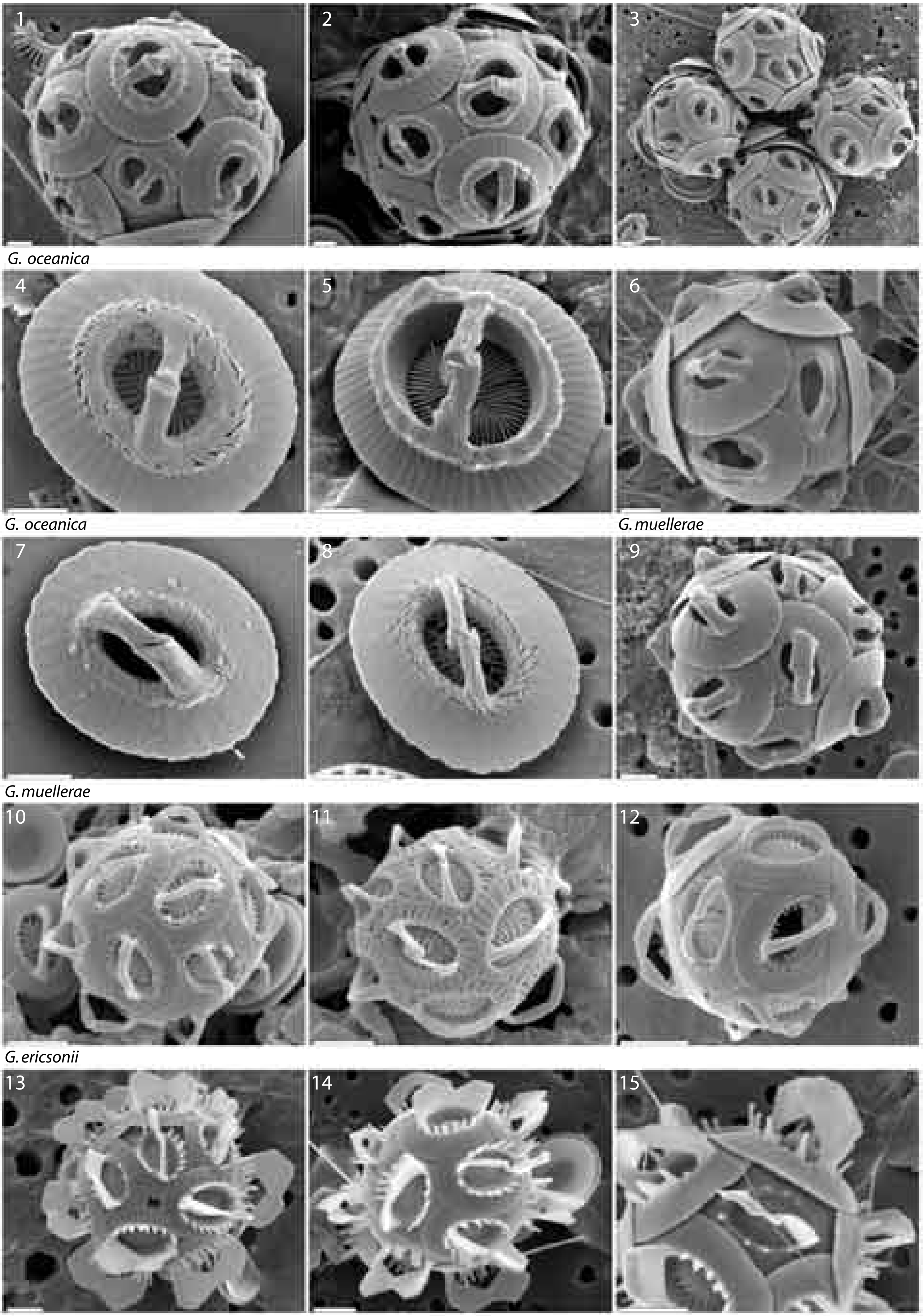


Plate 2 - Noelaerhabdaceae: *Gephyrocapsa*

?*Gephyrocapsa*

?*Gephyrocapsa* with elevated bridge

A range of rare forms occur in which the bridge appears as two high paddle-like plates. These have been illustrated by Nishida (1979; gen. & sp. indet., pl. 4., fig. 4), Winter et al. (1979; *Crenalithus*? sp. pl. 1 fig. 1; sp cf. *G. ornata* pl. 1, fig. 10), Heimdal & Gaarder (1981, pl. 4 fig. 22), and Kleijne (1993; *Gephyrocapsa*? sp. type A pl. 2 fig. 3). They are variable and may represent more than one species, alternatively they may be extreme forms of *R. maceria,* or malformations produced by various species.

1.1.3 *Reticulofenestra*

Reticulofenestra Hay, Mohler & Wade 1966

Coccoliths with typical reticulofenestrid structure but without bridge or slitting between shield elements. Central-area may be partially closed by extensions of the inner tube-elements. There are numerous fossil species, including many large forms (see e.g. Young 1998). However, the genus is defined by absence of distinguishing features, it is certainly paraphyletic, and probably polyphyletic. The extant species are all small and may be more closely related to *Gephyrocapsa* and *Emiliania* than to typical fossil species; the best reference for them is Okada & McIntyre (1977). NB Apart from *R. sessilis* all of these species were described from the Pacific Ocean and appear to be much more common there than in the Atlantic. TYPE: *R. caucasica* Hay, Mohler & Wade 1966. SYNONYM: *Crenalithus* - the genus *Crenalithus* has often been used as a synonym of small *Reticulofenestra* in modern and Quaternary studies. However, the holotype of the type species, *Coccolithus doronicoides* Black & Barnes 1961 is a proximal view of *Gephyrocapsa oceanica* (see Young 1998, Jordan & Young 1990).

Reticulofenestra parvula (Okada & McIntyre 1977) Biekart 1989 [*Crenalithus*]

Very small species, rather similar to *G. ericsonii* and often co-occurring with it, but in samples with the two species they are quite distinct.

Variant: *R. parvula* var. *tecticentrum* (Okada & McIntyre 1977) Jordan & Young 1990 - overcalcified form in which inner tube cycle closes the central area ("*Dictyococcites*" morphology). As with *E. huxleyi* intergrades to normal forms occur and this is probably an ecomorphotype.

Coccospheres 3-4 μm; liths 1.2-2 μm.

Reticulofenestra punctata (Okada & McIntyre 1977) Jordan & Young 1990 [*Crenalithus*] *(not figured)*

Form with narrow shield, holes in central area. Possibly a non-genotypic variant of *R. parvula*.

Coccospheres 3-4 μm; liths 1-1.5 μm.

Reticulofenestra maceria (Okada & McIntyre 1977) Young n. comb [*Umbilicosphaera*] *(not figured)*

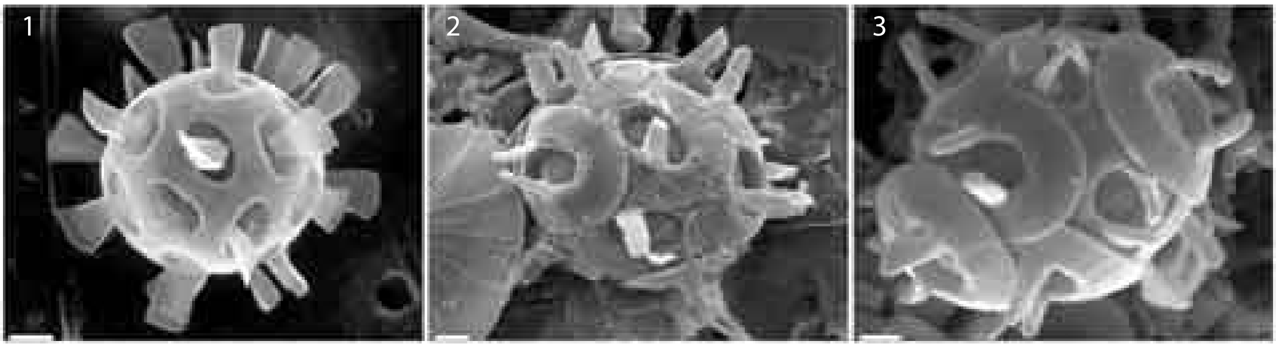
Narrow shield, open central area; inner wall protrudes as discontinuous crown surrounding central area (cf. *E. huxleyi* var. *corona*). Possibly related to ?*Gephyrocapsa* with elevated bridge. Combined here in *Reticulofenestra* since holotype clearly shows reticulofenestrid rim structure. SYNONYM: *Emiliania coronata* Martini 1993.

Coccospheres 10 μm; liths 4.5 μm.

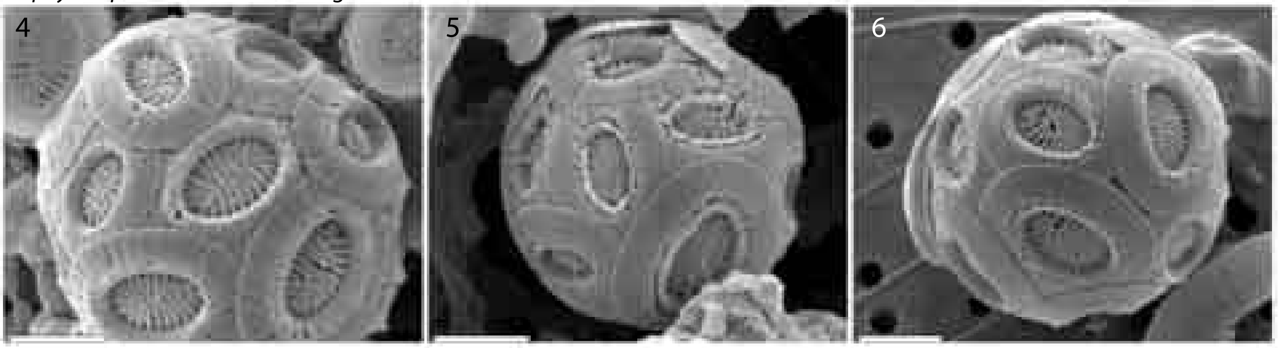
Reticulofenestra sessilis (Lohmann 1912) Jordan & Young 1990 [*Pontosphaera*]

Closed central area. Rather heavily calcified giving irregular form, strongly crenulate margin. Occurs almost exclusively in symbiotic? associations with the centric diatom *Thalassiosira*. Deep photic.

Coccospheres 6-10 μm; liths 2.5-4 μm.

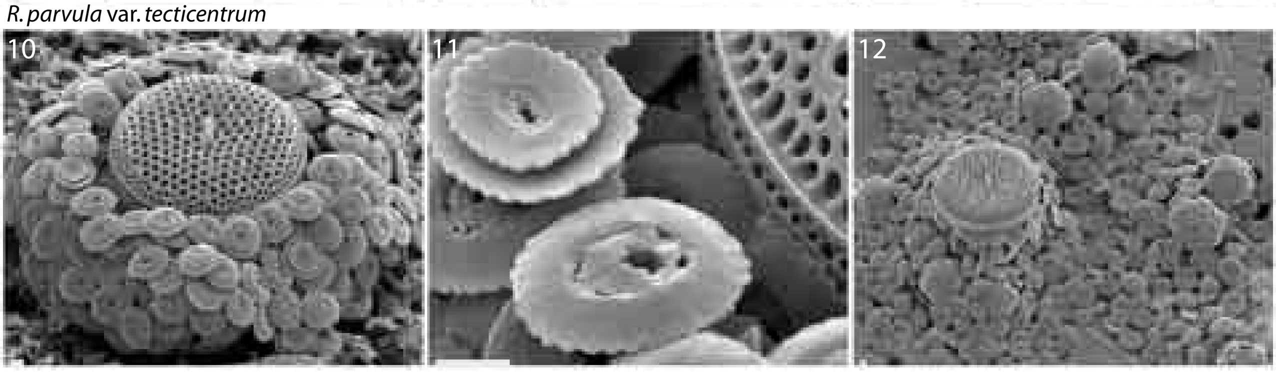


Gephyrocapsa with elevated bridge

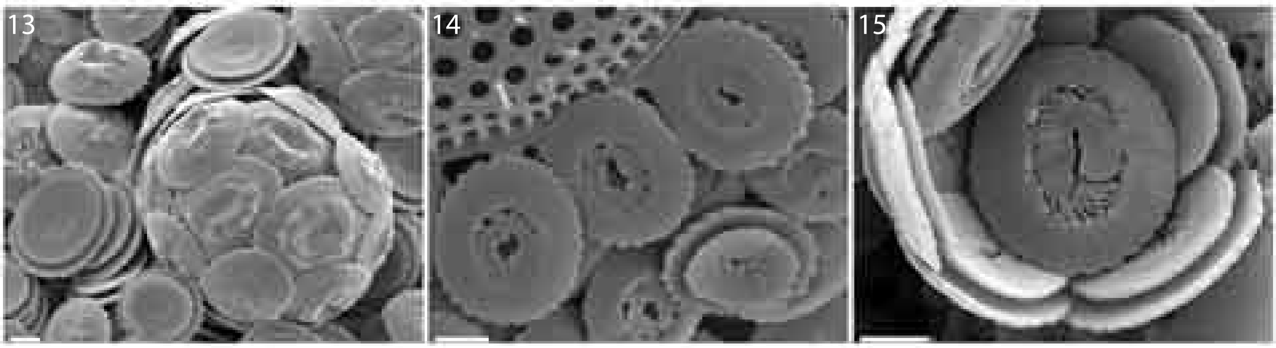


R. parvula

R. parvula var. *tecticentrum*



R. sessilis



R. sessilis

Plate 3 - Noelaerhabdaceae: *Reticulofenestra*

1.2 Coccosphaerales - oceanic (Coccolithaceae & Calcidiscaceae)

Order COCCOSPHAERALES **Haeckel 1894 emend. Young & Bown 1997**

Taxa included: The family Coccolithaceae has often been used for all placoliths not placed in the Noelaerhabdaceae (e.g. Jordan & Kleijne 1994; Jordan & Green 1994). Young & Bown (1997) noted that two major structural types occurred in this group and divided it into two families, the Coccolithaceae and Calcidiscaceae which they then included in their revised order Coccosphaerales. The family Pleurochrysidaceae was also tentatively included in this order on the grounds of coccolith structure. This grouping has subsequently been supported by molecular genetic studies (Edvardsen et al. 2000, Fujiwara et al. 2001, Sáez et al. 2003, Sáez et al. in press) and further studies of the structure of *Pleurochrysis* coccoliths (Marsh 1999). In addition the Hymenomonadaceae are included here, since numerous cytological and life-cycle characters indicate that they are closely related to the Pleurochrysidaceae (e.g. Gayral 1971, Gayral & Fresnel 1983, Fresnel & Billard 1991, Fresnel & Probert subm.) even though their coccolith structure is not obviously similar. This placement is also supported by molecular genetics (Sáez et al., in press).

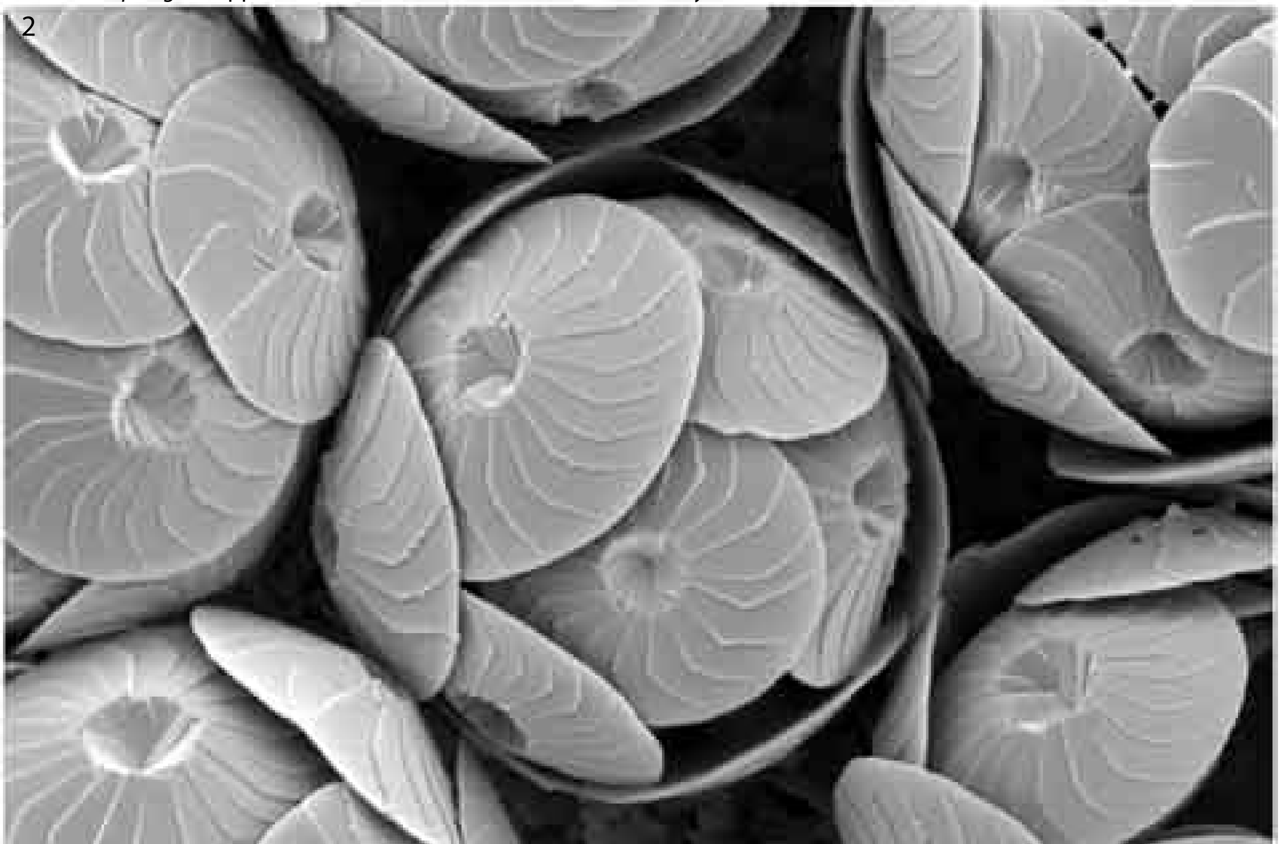
Coccolith structure: The Coccolithaceae, Calcidiscaceae and Pleurochrysidaceae all form placolith coccoliths, i.e. coccoliths formed of two shields separated by a tube. Common structural features are:

1. Growth occurs downward as well as upward from the proto-coccolith ring, which consequently becomes embedded within the rim. Hence, on intact specimens, there is no obvious belt of alternating V- and R-elements, but such a belt is seen on specimens where the proximal shield has been partially detached (Young et al. in press).
2. The V-units form the distal shield and most of the tube whilst the R-units form the proximal shield and in some cases part of the tube. In consequence the distal shield is dark in cross-polarised light whilst the proximal shield is bright.

It is also noteworthy that the coccospheres in all cases are monomorphic, this applies even to the motile genera of the Pleurochrysidaceae and Hymenomonadaceae, and to the known holococcolith stages of the Coccolithaceae and Calcidiscaceae.

Life-cycles and culture studies: Heteromorphic life-cycles have been documented from culture studies of the Coccolithaceae, Pleurochrysidaceae and Hymenomonadaceae and inferred from observations of combination coccospheres of Calcidiscaceae (Parke & Adams 1960, Rowson et al. 1986, Fresnel & Billard 1991, Kleijne 1991, Fresnel 1994, Cortes 2000, Renaud & Klaas 2001, Geisen et al. 2002, Billard & Inouye in press, Houdan et al. subm.). In the Coccolithaceae and Calcidiscaceae non-motile diploid heterococcolith-bearing stages alternate with motile haploid holococcolith-bearing stages. In the Pleurochrysidaceae and Hymenomonadaceae motile diploid heterococcolith-bearing stages alternate with motile and benthic haploid non-calcifying stages.

Coccolithus pelagicus spp. *braarudii* fosssil bloom from Late Quaternary of Cariaco Basin, ODP Site 1002C



Calcidiscus leptoporus spp. *leptoporus* - laboratory culture

Plate 4 - Coccosphaerales

1.2.1 Coccolithaceae

Family **COCCOLITHACEAE** Poche 1913 emend. Young & Bown 1997

Dominant phase of life-cycle non-motile with placolith heterococcoliths. These have the *Coccolithus*-type rim-structure, as described in Young (1992) and Young et al. (in press). The V-unit forms both the distal shield and the proximal layer of the inner tube (= centro-proximal cycle). The R-unit forms the proximal shield and the distal layer of the inner tube (= centro-distal cycle). The proximal shield itself is bicyclic with distinct upper and lower layers but these are both formed from the R-unit. The central-area is often spanned by disjunct structures and these are used to define various fossil genera (see e.g. Perch-Nielsen 1985b, Young & Bown 1997).

Coccolithus Schwartz 1894

Central-area open or with a disjunct transverse bar. TYPE: *C. oceanicus* Schwartz 1894 (j. syn. of *C. pelagicus*). SYNONYMS: *Coccosphaera* Wallich 1877; *Cyclolithus* Kamptner 1948.

Coccolithus pelagicus (Wallich 1877) Schiller 1930 [*Coccosphaera*]

The only extant species. The subdivision into two sub-species is supported by a wealth of morphological, biogeographic and culture data (Geisen et al. subm.). It is paralleled by slight morphological differentiation of the associated holococcoliths (Geisen et al. 2002).

Coccolithus pelagicus (Wallich 1877) Schiller 1930 ssp. *pelagicus*

Arctic form, liths 6-10 μm, central opening small and bar rudimentary, absent or becoming cross-like and filling opening. Occurs in waters <10°C. NB Wallich (1877) based his description of *C. pelagicus* on sediment samples from south of Iceland containing exclusively this morphotype (Young et al. in prep.).

HOL - planar with continuous cover of crystallites in rhombohedral array (formerly called *Crystallolithus hyalinus* Gaarder & Markali 1957).

Coccolithus pelagicus ssp. *braarudii* (Gaarder 1962) Geisen et al. 2002

Temperate form, liths 9-15 μm, central opening wide, usually spanned by well-formed bar that extends to the edge of the central area. Occurs in waters ca. 14-18°C.

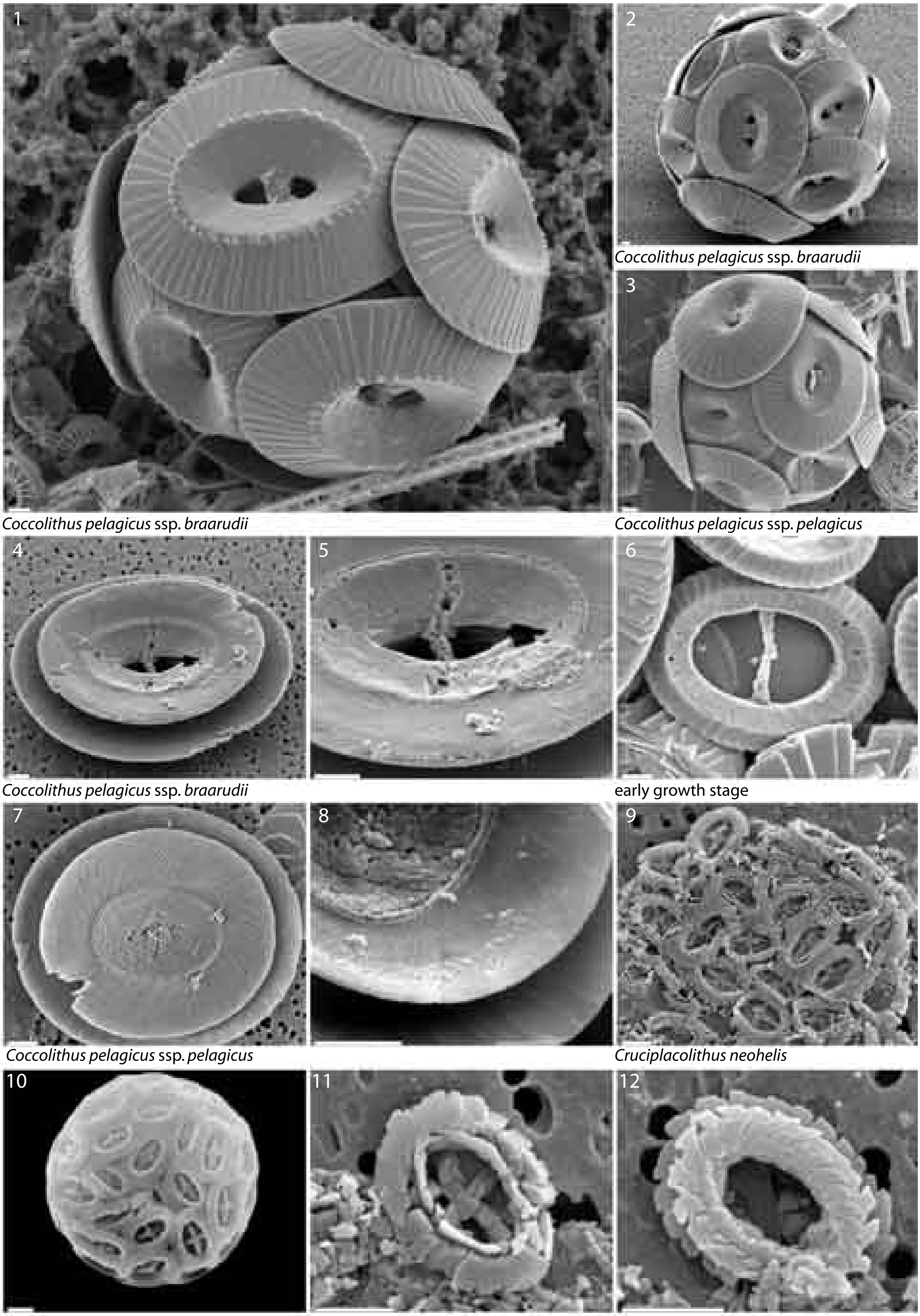
HOL - planar with incomplete cover of crystallites arranged in radial strings extending from a central ellipse (formerly called *Crystallolithus braarudii* Gaarder 1962).

Cruciplacolithus Hay & Mohler *in* Hay et al. 1967

Coccolith structure similar to that of *Coccolithus,* but central area spanned by disjunct axial cross. TYPE: *Cruciplacolithus tenuis* (Stradner 1961).

Cruciplacolithus neohelis (McIntyre & Bé 1967) Reinhardt 1972 [*Coccolithus*]

Neritic species rarely found in oceanic samples. Coccoliths small (2.2-3.2 μm) with cross in central-area, and a few additional laths on baseplate (see Fresnel 1986). Coccospheres 7.5-9 μm. Two generic assignments have been used for this species; *Cruciplacolithus* on the basic of central area morphology, with the implication that it is directly descended from this Palaeogene genus; or *Coccolithus*, with the implication that it is an unrelated homoeomorph of the Palaeogene descended from *Coccolithus pelagicus*. Molecular genetic data (Sáez et al., in press) indicates a deep divergence from *Coccolithus* and so supports assignment to *Cruciplacolithus*. Cytology described by West (1969), Fresnel (1986), Inouye & Kawachi (1994).



1: *Coccolithus pelagicus* ssp. *braarudii*

2: *Coccolithus pelagicus* ssp. *braarudii*

3: *Coccolithus pelagicus* ssp. *pelagicus*

4–5: *Coccolithus pelagicus* ssp. *braarudii*

6: early growth stage

7–8: *Coccolithus pelagicus* ssp. *pelagicus*

9: *Cruciplacolithus neohelis*

10–12: *Cruciplacolithus neohelis*

Plate 5 - Coccolithaceae: *Coccolithus* & *Cruciplacolithus*

1.2.2-1.2.3 Calcidiscaceae

Family **CALCIDISCACEAE** Young & Bown 1997

Dominant phase of life-cycle non-motile with placolith heterococcoliths. V-unit forms the distal shield and tube, extending to the proximal surface. R-unit forms the proximal shield. As in the Coccolithaceae, growth occurs downward from the proto-coccolith ring which becomes embedded within the structure so that alternating V- and R-units are only visible on specimens where the proximal shield has broken off. Distal shield sutures often show laevogyral curvature. The proximal shield is usually formed of a single layer of elements with sub-radial sutures; sometimes a lower layer is developed, with elements showing strong dextral obliquity (in proximal view). The connection between the proximal and distal shields is weak and they frequently separate.

These genera have previously been included within the Coccolithaceae but the distinctively different structure, appears to warrant classification in a separate family (Young & Bown 1997). The grouping is supported by molecular genetic data (Sáez et al., in press). Key references: Inouye & Pienaar (1984) - cytology of *Umbilicosphaera*; Kleijne (1993) - detailed description of species; Young et al. (in press) - coccolith structure.

1.2.2 *Calcidiscus* & *Oolithotus*

Calcidiscus Kamptner 1950

Coccoliths (sub)-circular, central-area closed or with narrow opening. Distal shield elements with laevogyral sutures. Proximal shield elements often kinked (sometimes bicyclic in fossil specimens). TYPE: *C. quadriforatus* (subj. j. syn. of *C. leptoporus*). Synonyms: *Cyclococcolithus, Cyclococcolithina, Cycloplacolithella, Cycloplacolithus*.

Calcidiscus leptoporus (Murray & Blackman 1898) Loeblich & Tappan 1978 [*Coccosphaera*]

The only extant species. Subdivision into three morphotypes or sub-species was first proposed by Kleijne (1993). It has been supported by extensive subsequent work on their biogeography, morphology, stability in culture, associated holococcoliths, and molecular genetics (Knappertsbusch 1997, Baumann & Sprengel 2000, Renaud & Klaas 2001, Renaud et al. 2002, Geisen et al. 2002, Sáez et al. in press, Quinn et al in press). We follow Geisen et al. (2002) in treating them as sub-species.

Calcidiscus leptoporus (Murray & Blackman 1898) Loeblich & Tappan 1978 ssp. *leptoporus*

Coccoliths intermediate sized, 5-8 μm, with 15-30 elements; distal shield sutures smoothly curved. The most common form.

HOL = planar holococcolith with crystallites in hexagonal array (formerly called *Crystallolithus rigidus*). Association documented by Kleijne (1993), Cortes (2000), Renaud & Klaas (2001), Geisen et al. (2002).

Calcidiscus leptoporus ssp. *quadriperforatus* (Kamptner 1937) Geisen et al. 2002

Coccoliths large sized, 7-11 μm, with 20-35 elements; distal shield sutures smoothly curved. Usually there is a zone of etching(?) and obscured sutures around crest of tube.

HOL = open tube with internal septa (formerly called *Syracolithus quadriperforatus*). Association is based on a single, unambiguous, combination coccosphere (Geisen et al. 2002, and plate 47).

Calcidiscus leptoporus small type

Coccoliths small, 3-5 μm, with 10-20 elements; distal shield sutures usually angular and serrated (Kleijne 1993). Can resemble *U. foliosa* but has closed central area and fewer elements. This is almost certainly a discrete sub-species, but it has not been cultured and the holococcolith phase is not known. If the holococcolith has been described previously it will provide the sub-species name.

Oolithotus Reinhardt *in* Cohen & Reinhardt 1968

Cells non-motile, but coccosphere asymmetrical with opening. Coccoliths also asymmetrical, otherwise very like *Calcidiscus*. Predominantly deep-photic. TYPE: *O. antillarum*.

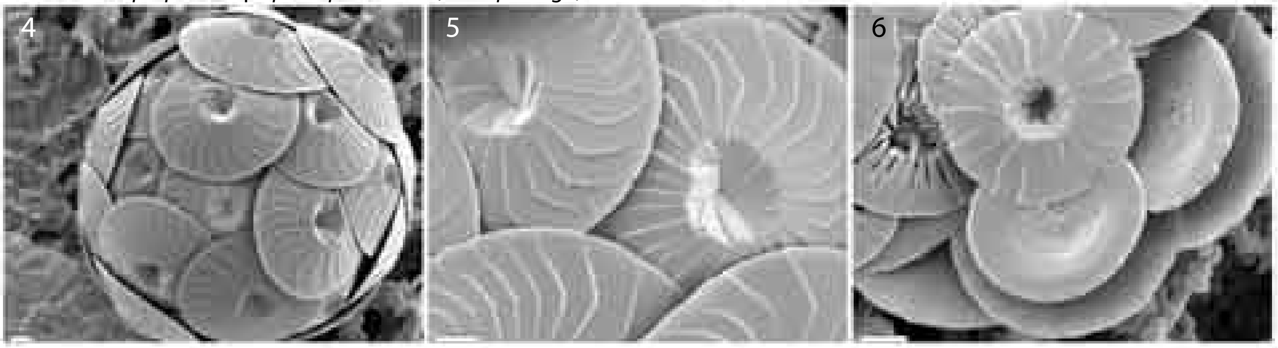
Oolithotus antillarum (Cohen 1964) Reinhardt, in Cohen & Reinhardt 1968 [*Discolithus*]

Small form, coccoliths 3-6µm; strongly asymmetric; proximal shield much smaller than distal, sutures complexly kinked becoming pseudo-bicyclic; usually with deep, narrow depression on distal surface. SYNONYM: *O. fragilis* var. *cavum* (Okada & McIntyre 1977) Jordan & Young 1990 [*O. fragilis* ssp. *cavum*] - see Kleijne (1993) for discussion, although our observations indicate wider size range.

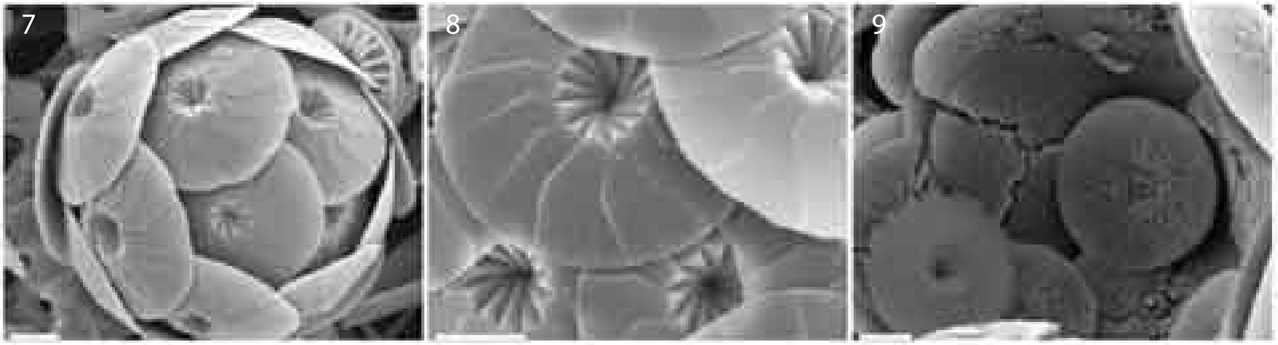
Oolithotus fragilis (Lohmann 1912) Martini & Müller 1972 [*Coccolithophora*]

Large form, coccoliths 5-9µm; weakly asymmetric; proximal shield only slightly smaller than distal, sutures jagged; broad depression on distal surface, distal sutures often kinked. Easily confused with *C. leptoporus* in LM. One combination coccosphere, with holococcoliths observed in LM, but holococcoliths could not be determined (Geisen & Broerse unpubl. obs.).

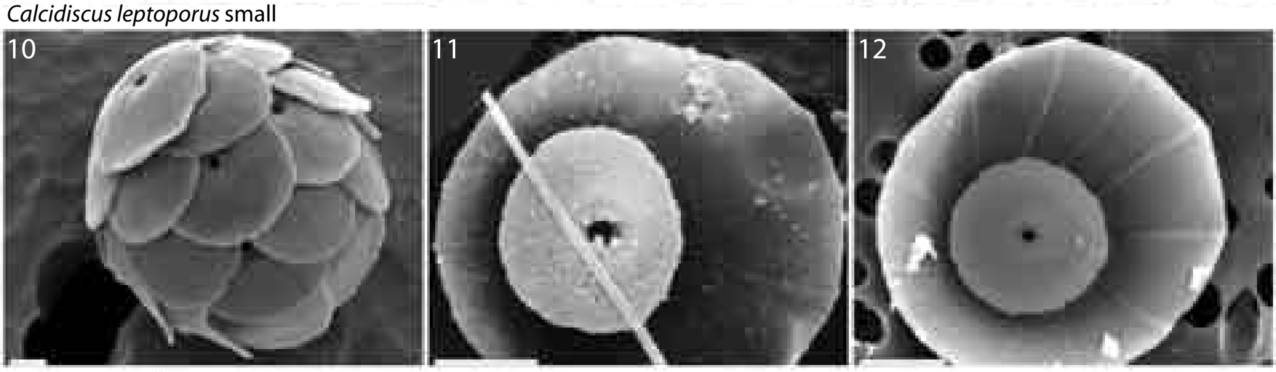
Calcidiscus leptoporus ssp. *quadriperforatus* (= *C. lept.* large)



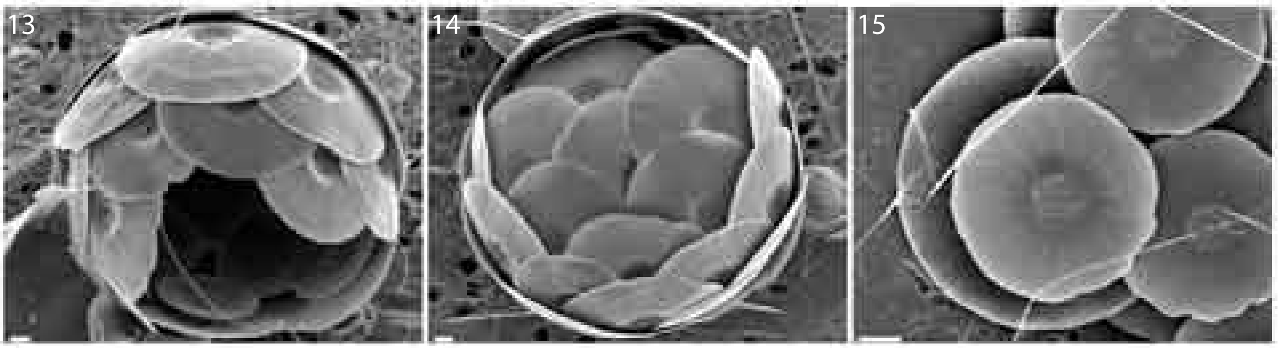
Calcidiscus leptoprus ssp. *leptoporus* intermediate



Calcidiscus leptoporus small



Oolithotus antillarum



Oolithotus fragilis

Plate 6 - Calcidiscaceae: *Calcidiscus* & *Oolithotus*

1.2.3 *Hayaster*

Hayaster Bukry 1973

Coccoliths with diminutive proximal shield; distal shield with straight radial sutures and blunt ray ends, non-imbricate, 9-13 elements. TYPE: *H. perplexus*.

Hayaster perplexus (Bramlette & Riedel 1954) Bukry 1973 [*Discoaster*]

The only described species, with the characters of the genus. Coccoliths show considerable variation in size and in relative size of the two shields, so it is possible that more than one species is present.

1.2.4 *Umbilicosphaera*

Umbilicosphaera Lohmann 1902

Coccoliths circular or elliptical, with *Calcidiscus* structure but central area open, distal shield elements usually show complex kinked sutures. Proximal shield monocyclic or bicyclic. TYPE: *U. mirabilis* Lohmann 1902 (j. syn. of *U. sibogae*).

Umbilicosphaera sibogae (Weber-van Bosse 1901) Gaarder 1970 [*Coccosphaera*]

Coccospheres large (20-30 μm) usually containing 2-4 cells. Liths circular, 3-7 μm; central opening broad; proximal shield monocyclic, flat, wider than distal shield. SYNONYM: *U. mirabilis* Lohmann 1902. NB The type specimen of *U. mirabilis* is a typical *U. sibogae* but many authors applied the name to *U. foliosa*.

Umbilicosphaera anulus (Lecal 1967) Young & Geisen n. comb. [*Cyclolithus*]

Coccoliths broadly elliptical with narrow rim and broad, open, central-area. Included here in *Umbilicosphaera,* on grounds of coccolith morphology and structure, which is similar to that of *U. sibogae*. [NB The genus *Cyclolithus* is based on a very poorly described large late Miocene coccolith, *Cyclolithus inflexus* Kamptner 1948 which is most likely a junior synonym of *Coccolithus pelagicus,* so the generic name *Cyclolithus* should not be used]. SYNONYMS: *Cyclolithella ferrazae* Sanchez-Suarez 1990; *U. calvata* Steinmetz 1991; *U. scituloma* Steinmetz 1991 (see also Kleijne 1993, for discussion of separation from *U. hulburtiana*).

Umbilicosphaera foliosa (Kamptner 1963, ex Kleijne 1993) Geisen in Sáez et al. 2003. [*Cycloplacolithus*]

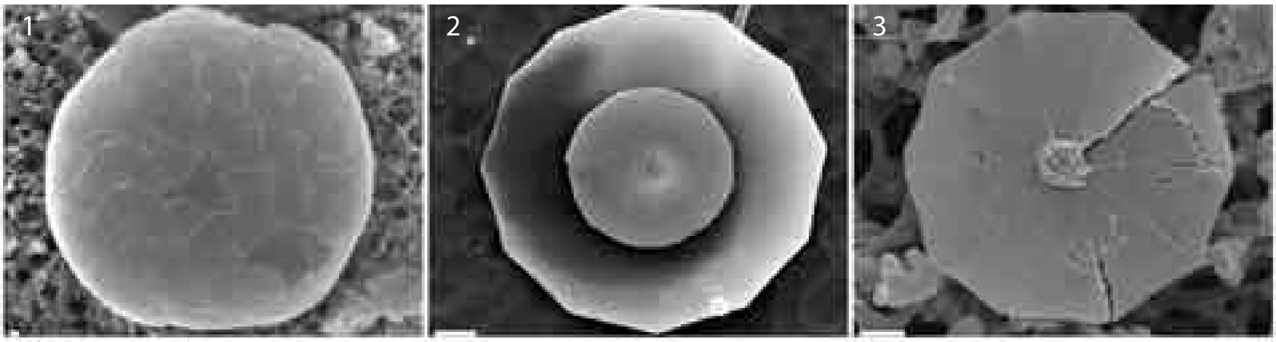
Central opening narrow; usually with hook-shaped protrusions. Proximal shield bicyclic, concave, smaller than distal shield. Conventionally regarded as a variety of *U. sibogae* (*U. sibogae* var. *foliosa*) but there are strong morphological differences between *U. sibogae* and *U. foliosa* and cultures of the two species maintain their respective morphologies (Geisen et al. in press). Molecular genetic data indicates that they are sibling species and suggests a divergence in the Miocene (Sáez et al. 2003).

Umbilicosphaera hulburtiana Gaarder 1970

Coccoliths elliptical and may have nodes around crest of distal shield, otherwise similar to *U. foliosa*, including bicyclic proximal shield.

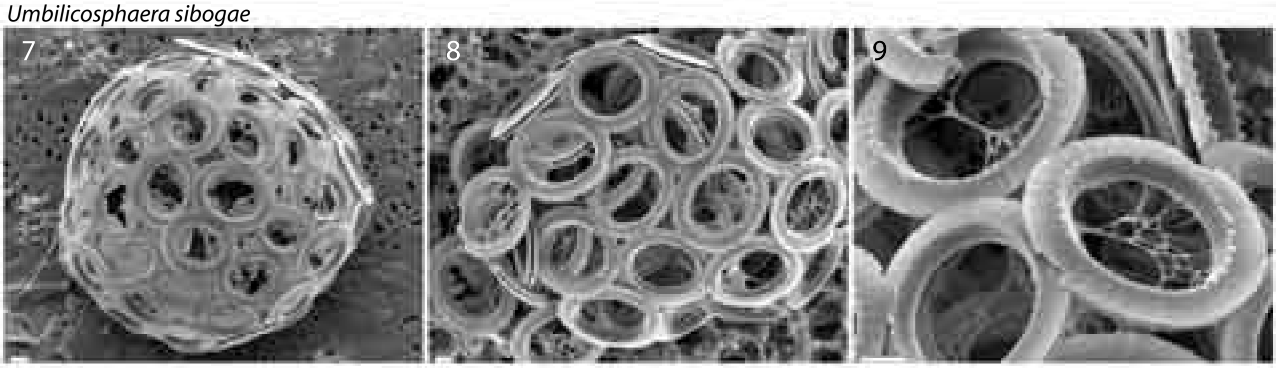
[*Umbilicosphaera angustiforamen* Okada & McIntyre 1977 - form with narrow rim and open central area. Not recorded since description, the illustrated specimens do not closely resemble typical *Umbilicosphaera*, but have possible affinity with *Tetralithoides*]

[*Umbilicosphaera maceria* Okada & McIntyre 1977 -> recombined here in *Reticulofenestra*]

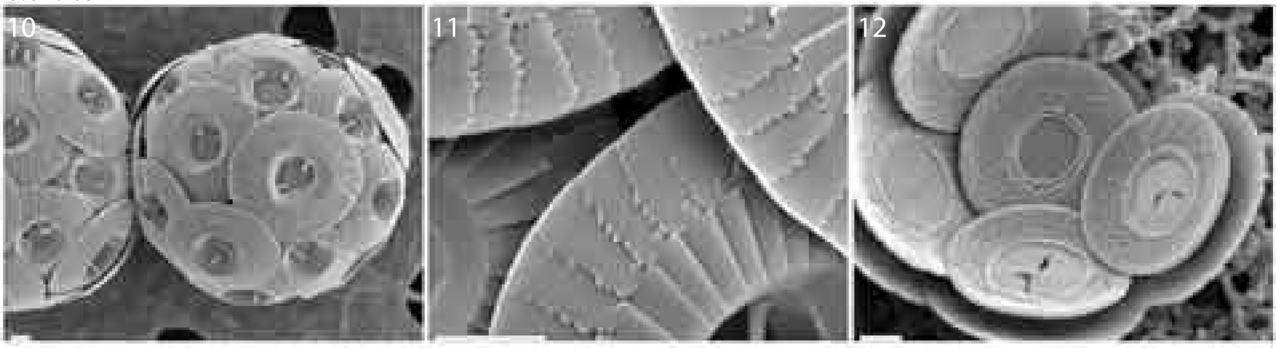


Hayaster perplexa

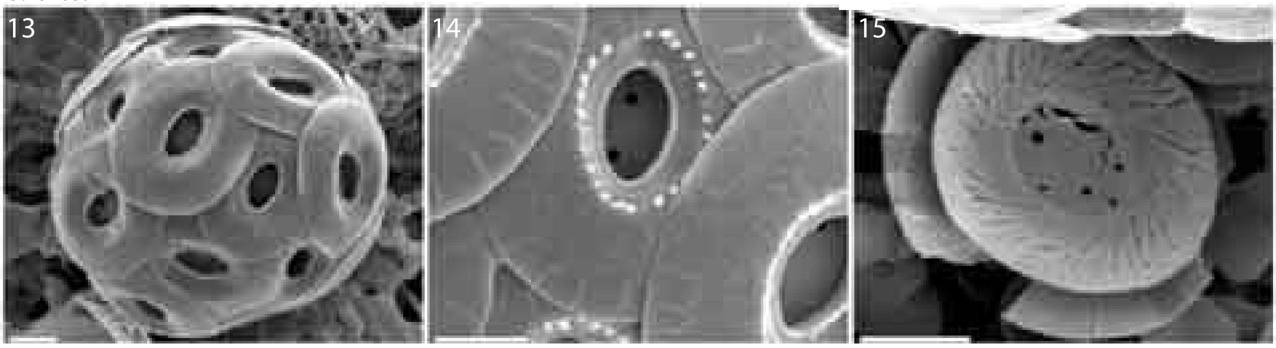
Umbilicosphaera sibogae



U. anulus



U. foliosa



U. hulburtiana

Plate 7 - Calcidiscaceae: *Hayaster* & *Umbilicosphaera*

1.3 Coccosphaerales - littoral (Pleurochrysidaceae & Hymenomonadaceae)

Family **PLEUROCHRYSIDACEAE** Fresnel & Billard 1991

Taxa included: This family was included in the Coccosphaerales by Young & Bown (1997) since the rim structure appears to be a simplified version of that of the Coccolithaceae. This is supported by the detailed analysis of coccolith structure of Marsh (1999) and molecular genetic data, (Edvardsen et al., 2000; Fujiwara et al., 2001; Sáez et al. in prep.). At one time species were assigned to either *Cricosphaera* or *Pleurochrysis* on the basis of their life-cycles. Following revisions of Jordan et al. (1993) the family is now monogeneric.

Life-cycles and culture studies: These species are neritic and easily isolated and maintained in culture., hence taxonomy is based on cultures. Diploid phase is motile and heterococcolith-bearing, haploid phase is non-calcifying, flagellate or benthic.

Coccolith structure: Coccoliths are formed of two cycles of tightly interlocked anvil-shaped crystal-units. V-unit forms distal shield and tube. R-unit forms proximal shield and small element on inside of tube (Marsh et al., 1999). Central area open. Coccoliths with this structure have been termed cricoliths.

Key references: Gayral & Fresnel (1983) - life-cycle; van der Wal et al. (1983) - cytology; Fresnel & Billard (1991) - species overview; Marsh et al. (1999) - coccolith ultrastructure. TYPE: *P. scherfellii* (NB *P. carterae* was type of *Cricosphaera*).

Pleurochrysis Pringsheim 1955 (= *Cricosphaera* Braarud 1960)

Coccolithophore motile, neritic; coccosphere monomorphic. Coccoliths are elliptical narrow-shielded placoliths with structure described above.

1.3.1 Smooth *Pleurochrysis*

The following taxa have more or less smooth distal surfaces, without nodes or projections:

Pleurochrysis carterae (Braarud & Fagerland 1946) Christensen 1978 var. *carterae* [*Syracosphaera*]

Typical form, liths 2-3 μm long. SYNONYMS: *Pleurochrysis scherfellii* Pringsheim 1955 - has slightly different benthic stage; *Pleurochrysis elongata* (Droop 1955) Jordan et al. 1993 [*Syracosphaera*] - described from light microscopy, and distinguished from *P. carterae* by having more elongate coccosphere, the coccoliths, however, are very similar to those of typical *P. carterae*. The specimen in plate 8 fig. 4 is from the type strain of "*P. elongata*".

Pleurochrysis gayraliae (Beuffe 1978) Jordan et al. 1993 [Cricosphaera]

Coccoliths 2-3 μm long, broadly elliptical; placolith-like, with broad flanges.

Pleurochrysis placolithoides Fresnel & Billard 1991

Coccoliths placolith-like, i.e. with broad flanges. Large, coccoliths 2-4 μm long, distal shield nearly twice as wide as in any other *Pleurochrysis* species. Coccospheres ca. 15 μm.

1.3.2 Ornate *Pleurochrysis*

The following taxa have nodes or projections on the distal surface:

Pleurochrysis carterae var. *dentata* Johansen & Doucette *in* Johansen et al. 1988

Variety (but maybe better considered as a separate species) with tooth-like projections forming an irregular collar around the tube.

Pleurochrysis roscoffensis (Dangeard 1934) Fresnel & Billard 1991 [*Syracolithus*]

Nodes on both distal shield and tube inner wall. SYNONYM: *P. haptonemofera* Inouye & Chihara 1979.

Pleurochrysis pseudoroscoffensis Gayral & Fresnel 1983

Nodes on tube inner wall but not on distal shield. Intermediates to *P. roscoffensis* occur so the distinction may be artificial (Probert unpubl. obs.).

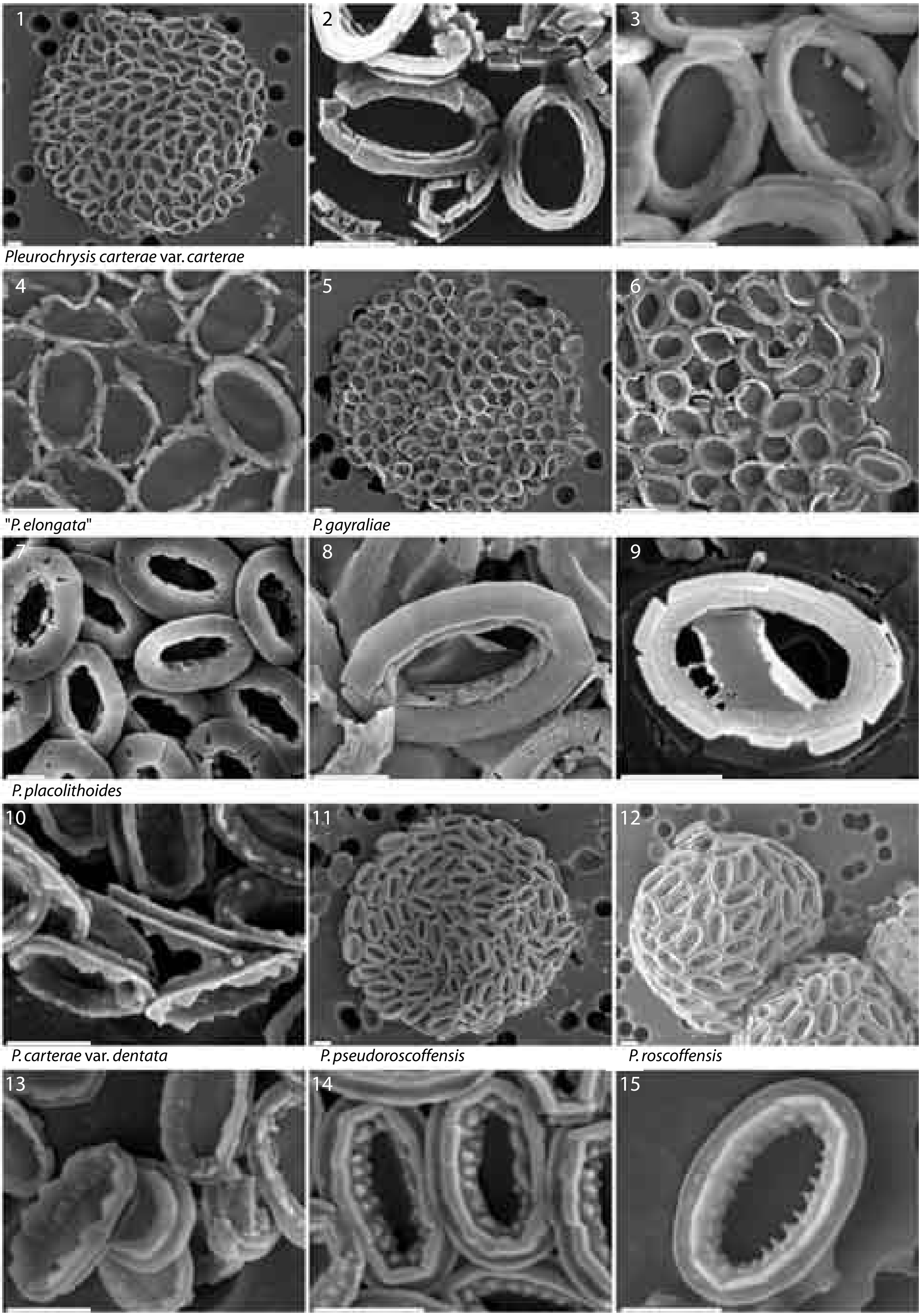


Plate 8 - Pleurochrysidaceae: *Pleurochrysis*

1.3.3 - 1.3.4 Hymenomonadaceae

Family **HYMENOMONADACEAE** Senn 1900

Small littoral and fresh-water coccolithophores. As with Pleurochrysidaceae, almost all observations and species concepts are based on culture studies. Life-cycle consists of diploid phase with coccoliths and body-scales, haploid phase with organic scales only. Coccoliths are goblet-shaped muroliths with open central-area, well-developed proximal flange, and a narrow distal flange or flaring end, entirely formed of a single cycle of <20 crystal-units (tremaliths). In *Ochrosphaera*, crystal-units have sub-vertical orientations. They differ from *Pleurochrysidaceae* by the absence of a second cycle of units (*i.e*. R-units). Affinity of this family is not obvious from coccolith morphology, but the life-cycle and cytological characters strongly indicate affinity with the Pleurochrysidaceae.

Key references: Braarud (1954), Manton & Peterfi (1969), Fresnel (1994), Fresnel & Probert (subm.).

1.3.3 *Hymenomonas*

Hymenomonas Stein 1878

Freshwater and marine species; cells with long flagella, haptonema vestigial or absent; coccoliths broadly elliptical. Formed of 14-16 non-imbricate elements; formed of basal flange, vertical tube and flaring distal funnel; elements have pointed ends. Species reviewed by Gayral & Fresnel (1979). TYPE: *H. roseola*.

Hymenomonas coronata Mills 1975

Cells 14-16 μm; tube only, with denticulate margin but no funnel.

Hymenomonas globosa (Magne 1954) Gayral & Fresnel 1976

Cells 14-16 μm; tube ca. 0.5 μm high, funnel ca. 0.5 μm.

Hymenomonas lacuna Pienaar 1976

Cells 25-30 μm; tube ca. 0.8 μm high, funnel ca. 0.4 μm - i.e. tube better developed and coccolith higher than in *H. globosa*.

Hymenomonas roseola Stein 1878 *(not figured)*

Freshwater. Coccoliths +/- identical to *H. globosa*. This is the only definite freshwater coccolithophore, see Braarud (1954), Manton & Peterfi (1969), Preisig (2002). SYNONYMS: *Pontosphaera stagnicola* Chodat & Rosillo 1925, *H. coccolithophora* Conrad, *H. danubiensis* Kamptner, *H. flava* Stokes, *H. scherfellii* Conrad, according to Schiller (1930), Braarud (1954) and Preisig (2002). NB *H. prenantii* Lecal 1965 is now considered to be a synonym of *Gyromitus disomatus* Skuja and so not a coccolithophore, see Preisig (2002).

1.3.4 *Ochrosphaera*

Ochrosphaera Schussnig 1930

Littoral, predominantly non-motile; coccoliths vari-monomorphic some are vase-shaped with proximal flange and simple distal margin, others with variably developed distal flange. Key references: Gayral & Fresnel-Morange (1971), Inouye & Chihara (1986), Fresnel & Probert (subm.). TYPE: *O. neapolitana*.

Ochrosphaera neapolitana Schussnig 1930

SYNONYM: *O. verrucosa* Schussnig 1940. NB The name *O. verrucosa* has often been applied to coccoliths with distal flanges whereas the archetypal *O. neapolitana* morphotype has been regarded as lacking the distal flange. However, both coccolith morphotypes occur on most cells, and in all cultures studied (Fresnel & Probert, subm.).

In old cultures calcite overgrowths can occur on the live coccospheres and may proceed to form massively overcalcified pseudo-cysts (Fresnel & Probert, subm.).

1.3.5 Genus *incertae sedis Jomonlithus*

The genus *Jomonlithus* was described from a similar coastal environment to the Pleurochrysidaceae and Hymenomonadaceae and it is similar in basic morphology although the coccolith structure seems different. Hence, it is placed here as a genus *incertae sedis* associated with these families. This is supported by molecular genetics data (Sáez et al., in press).

Jomonlithus Inouye & Chihara 1983

Murolith coccoliths with apparently rather simple rim, partially calcified specimens show beaded ultrastructure. No central-area structures. TYPE: *J. littoralis*.

Jomonlithus littoralis Inouye & Chihara 1983

Type species, showing characters of the genus.

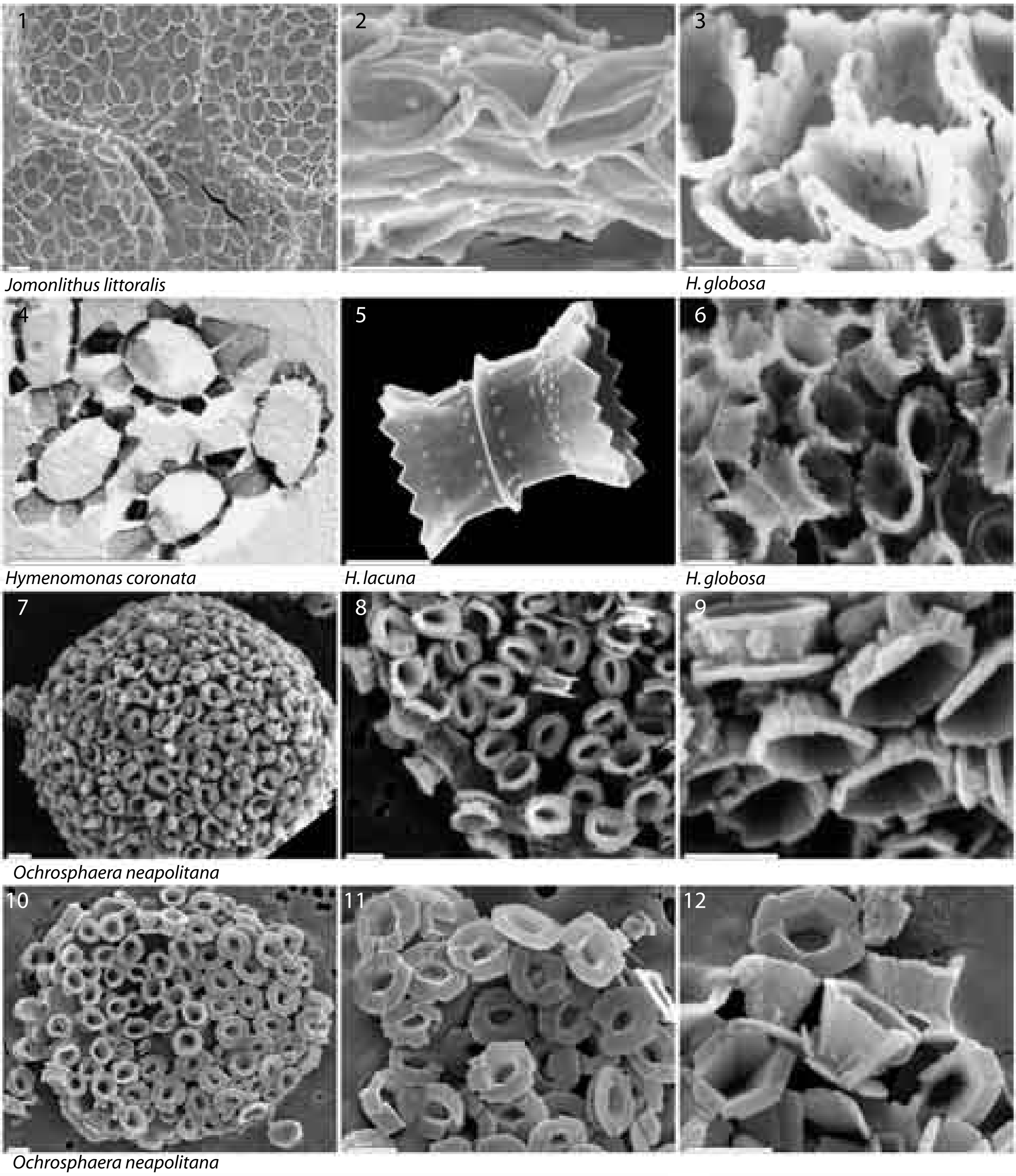


Plate 9 - *Jomonlithus* and Hymenomonadaceae: *Hymenomonas & Ochrosphaera*

1.4 Zygodiscales (Helicosphaeraceae & Pontosphaeraceae)

Order ZYGODISCALES **Young & Bown 1997**

Taxa included: The extant families Helicosphaeraceae and Pontosphaeraceae and extinct family Zygodiscaceae. These show highly variable shape but similar structure and there is strong palaeontological evidence for their evolutionary connections (Romein 1979; Aubry 1989).

Coccolith structure: V-units form outer rim, in Pontosphaeraceae this is a narrow cycle of anticlockwise imbricating elements, in the Helicosphaeraceae a helical flange. The R-units form a proximal plate of rather regular inward-growing elements and a distal blanket, which typically appears as a mass of minute tangentially elongated crystallites. Growth does not occur downwards from the proto-coccolith ring and so the alternating belt of V-R nuclei remains clearly visible on the proximal surface (e.g. plate 10 fig. 3).

Life-cycles and culture studies: *Helicosphaera carteri* has been cultured repeatedly (Inouye pers. comm., Probert unpubl. data) and *Scyphosphaera apsteinii* once (Probert unpubl. data). No life-cycle transitions have been observed in these cultures, but combination coccospheres have been observed for *Helicosphaera* (Cros et al. 2000, Geisen et al. 2002). These indicate that the haploid phase forms holococcoliths with distinctive rhomboid-array ultrastructure - *Syracolithus* (see section 4.5.3).

Family **HELICOSPHAERACEAE** Black 1971

Coccospheres ellipsoidal with a prominent flagellar opening. Coccoliths arranged spirally round the coccosphere and usually vary in size and shape from the antapex to the flagellar pole, toward the flagellar opening the coccoliths become larger and have more prominent flanges. Outer rim (V-units) of the coccolith is modified into a helical flange, ending in a wing or spike. R-units form the baseplate and extend to form a blanket of small elements (Young et al. in press).

1.4.1 *Helicosphaera*

Helicosphaera Kamptner 1954 (= *Helicopontosphaera* Hay & Mohler 1967)

Coccoliths with helical flange, numerous fossil species have been recognised based on presence/absence of a disjunct bar, bar orientation, flange shape, etc. (see e.g. Theodoridis 1984, Perch-Nielsen 1985b, Aubry 1990, Young 1998). TYPE: *H. carteri*.

Species concepts: *H. hyalina* and *H. wallichii* have often been regarded as varieties of *H. carteri* (e.g. Jordan & Young 1990, Jordan & Green 1994, Cros & Fortuño 2002), since they are similar in size and coccospheres bearing more than one morphotype have been illustrated (e.g. Nishida 1979). However cultures observations and molecular genetic data indicates that they are distinct species (Sáez et al. 2003, Geisen et al. in press).

Helicosphaera carteri (Wallich 1877) Kamptner 1954 [*Coccosphaera*]

Medium to large size (liths 6-12 μm), blanket extends beyond central area to cover most of the flange, flange ends in wing; central-area with two inline slits or sometimes a single long slit, slits may be reduced to small round pores.

HOL - "*Syracolithus catilliferus*" and "*S. confusus"* (see Cros et al. 2000, Geisen et al. 2002).

SYNONYM: *H. kamptneri* (Hay and Mohler in Hay et al. 1967) Locker 1973 [*Helicopontosphaera*].

Helicosphaera hyalina Gaarder 1970

Like *H. carteri* but coccoliths with closed central area (i.e. no pores) and usually smaller; also blanket is confined to central area leaving a broader rim of exposed flange elements than in *H. carteri*. The broad exposed rim is the most reliable criterion for distinguishing this species, since *H. carteri* coccospheres occasionally bear coccoliths without pores.

Helicosphaera wallichii (Lohmann 1902) Okada & McIntyre 1977 [*Coccolithophora*]

Like *H. carteri* but: central-area with oblique twisted slits; bridge typically better developed; and liths perhaps slightly larger.

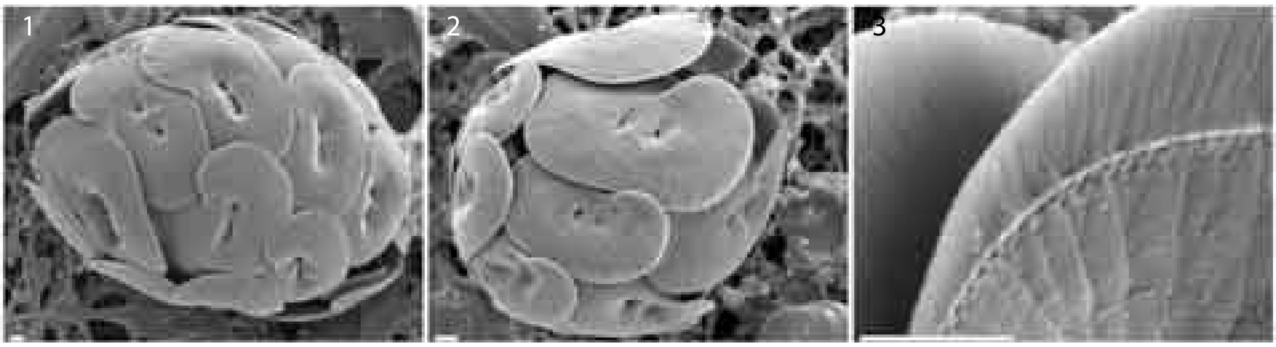
NB Slits obliquity: In distal view the slits are rotated about 10-20° clockwise (and so away from the wing), this is the "normal" sense of obliquity in *Helicosphaera*, as shown by many fossil species. The Pleistocene species *H. inversa* is similar but shows the opposite sense of obliquity.

HOL - unknown but *H. wallichii* often co-occurs with *Syracolithus dalmaticus* in our samples (Geisen et al., in press).

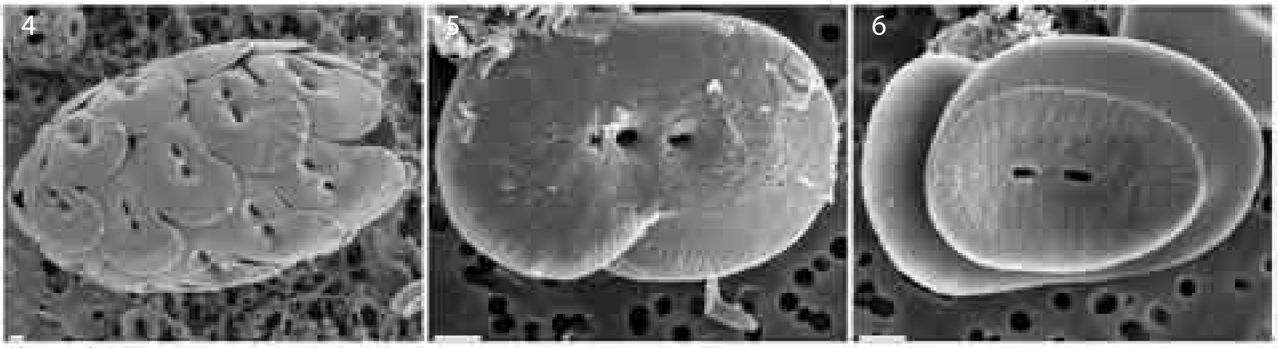
Helicosphaera pavimentum Okada & McIntyre 1977

Smaller than *H. carteri*, narrow flange, small wing; central area closed or with two small inline pores; blanket elements confined to central area and a weak ridge often surrounds them. Coccospheres 10-13μm, liths 4-5 μm.

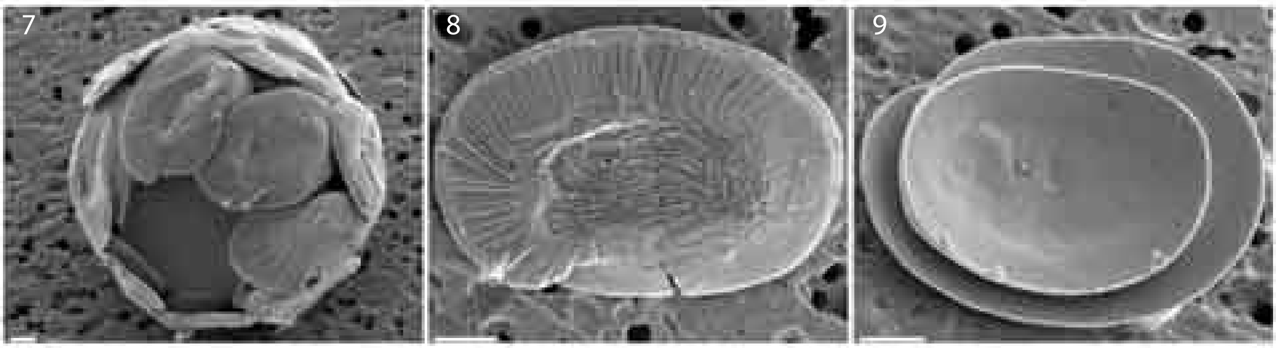
HOL - unknown, but Geisen et al. (in press) speculate that *S. ponticuliferus* is a likely candidate.



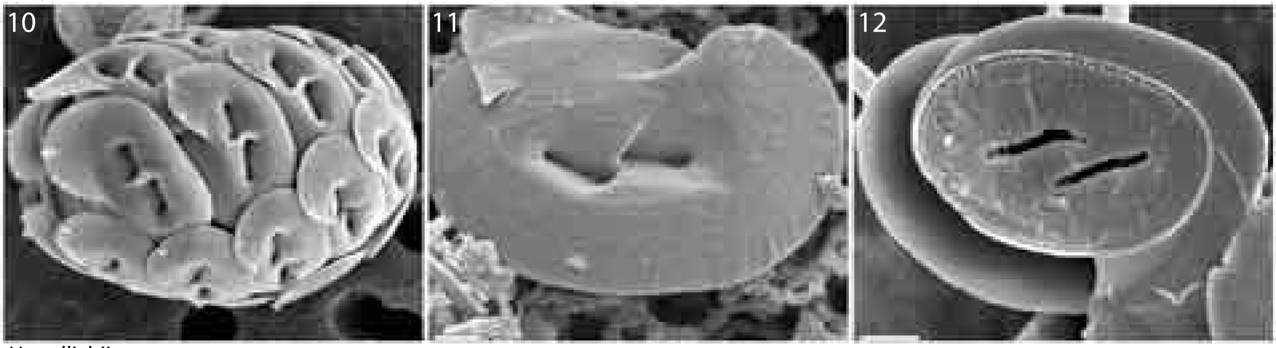
H. carteri



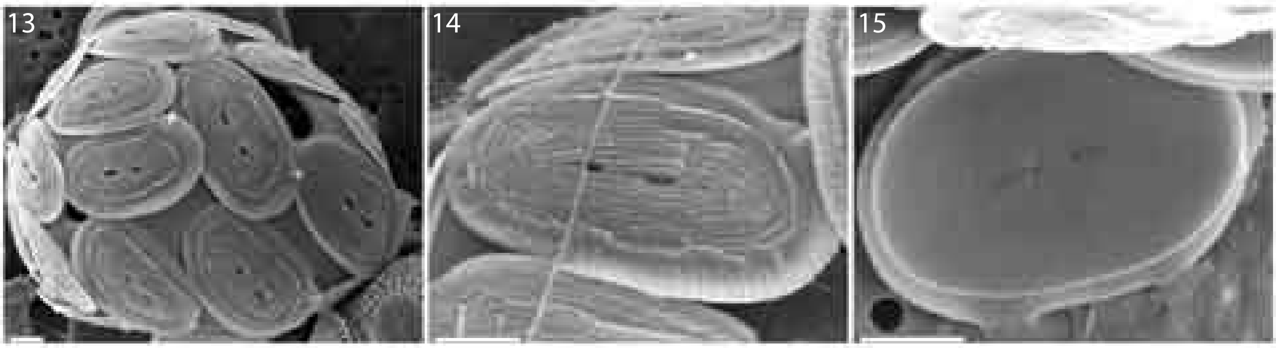
H. carteri



H. hyalina



H. wallichii



H. pavimentum

Plate 10 - Helicosphaeraceae: *Helicosphaera*

1.4.2-1.4.3 Pontosphaeraceae

Family **PONTOSPHAERACEAE** Lemmermann 1908

Coccospheres sub-spherical, non-motile. Monomorphic (*Pontosphaera*) or dimorphic with strongly-modified equatorial coccoliths (*Scyphosphaera*). Coccoliths are muroliths, central area with variable number of perforations. V-units form narrow outer rim-cycle with anti-clockwise imbrication. R-units form inner rim, with clockwise imbrication, baseplate and blanket.

1.4.2 *Pontosphaera*

Pontosphaera Lohmann 1902

Monomorphic - muroliths only. Species level taxonomy is poorly worked out. Coccolith structure and species reviewed by Aubry (1990). TYPE: *P. syracusana*. SYNONYMS: *Discolithina* Loeblich & Tappan 1963; *Discolithus* Huxley 1868.

Pontosphaera discopora Schiller 1925

Rim elevated above central area, three or more irregular cycles of small (0.1-0.2 μm) pores. Very similar to *Scyphosphaera apsteinii* BCs, but usually thicker.

Pontosphaera japonica (Takayama 1967) Nishida 1971 [*Discolithina*]

Rim flush with central-area, broad; pores very small (ca. 0.05µm), not visible in LM, in semi-regular array with ca. 10-15 rows of pores on each side of the coccolith. Coccospheres 17-21 μm. SYNONYM: *Discolithus millepuncta* Gartner 1967.

Pontosphaera multipora (Kamptner 1948) Roth 1970 [*Discolithus*]

Three or more cycles of large pores (0.3-0.5 μm), pores in outermost cycle usually elongated radially, inner cycles rather irregular; rim highly variable in width and may obscure outer pores. SYNONYM: *Pontosphaera turgida* Muller *in* Muller et al. 1974 - form with very broad rim (similar to plate 11 fig. 5), described from Late Quaternary, falls within variation observed in modern *P. multipora*.

[*Pontosphaera stagnicola* Chodat & Rosillo 1925. - Freshwater, probably a j. syn. of *Hymenomonas roseola* according to Manton & Peterfi (1969)]

Pontosphaera syracusana Lohmann 1902

Rim strongly elevated, narrow, flaring outward; central-area covered by a thin plate with numerous small (ca. 0.05 μm) pores.

1.4.3 *Scyphosphaera*

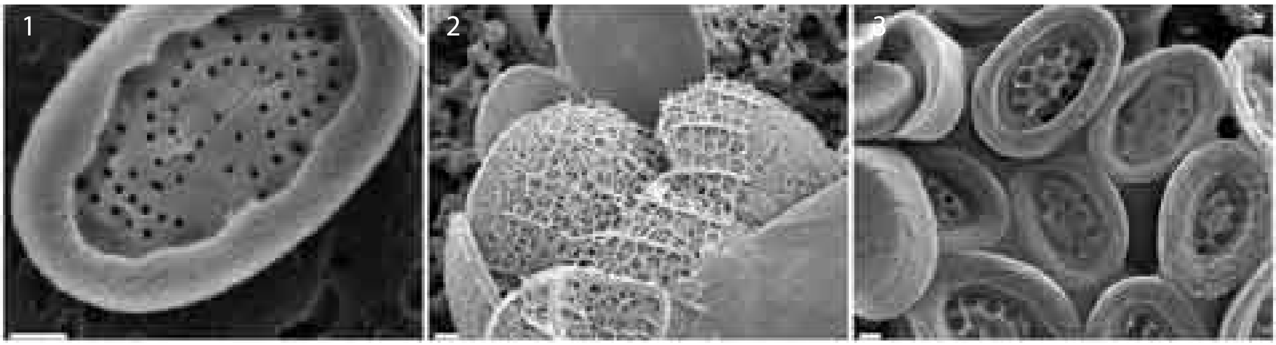
Scyphosphaera Lohmann 1902

Like *Pontosphaera* but dimorphic, with elevated equatorial coccoliths - lopadoliths. Numerous fossil species, see reviews of Perch-Nielsen (1985b), Aubry (1990), Young (1998), Siesser (1998). TYPE: *S. apsteinii*.

Scyphosphaera apsteinii Lohmann 1902

Equatorial coccoliths typically have simple convex outward profile, but may be somewhat constricted at base, or flare to wide opening ("*dilatata*"morphotype). BCs similar to those of *P. discopora* in plan view, but usually much thinner; rim width highly variable even on one coccosphere.

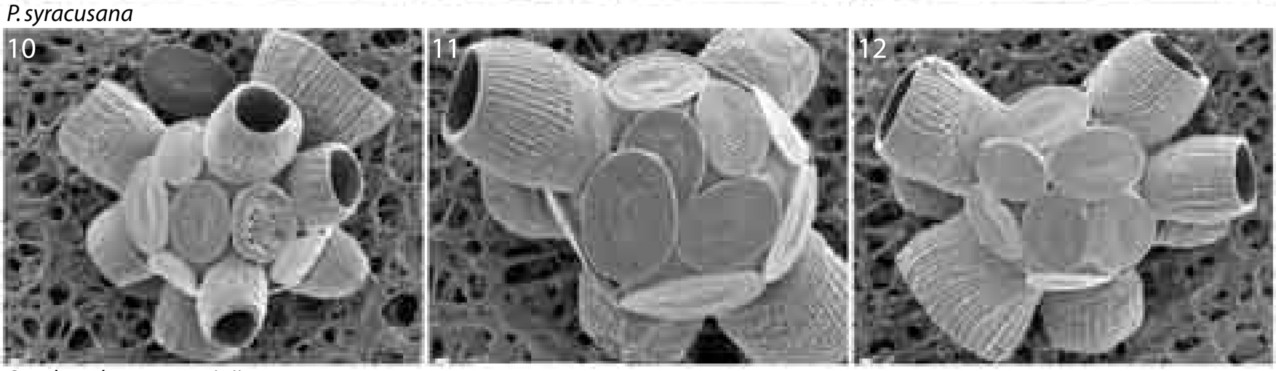
SYNONYM *Scyphosphaera apsteinii* f. *dilatata* Gaarder 1970. Like *apsteinii* but some lopadoliths with wide opening. Our observations on a culture strain show that this is an intraspecific variant. Hence, we agree with Gaarder (1970) that this is not a discrete species and we do not follow Siesser (1998), who regarded *S. apsteinii* f. *dilatata* as a synonym of the Neogene species *S. cohenii*.



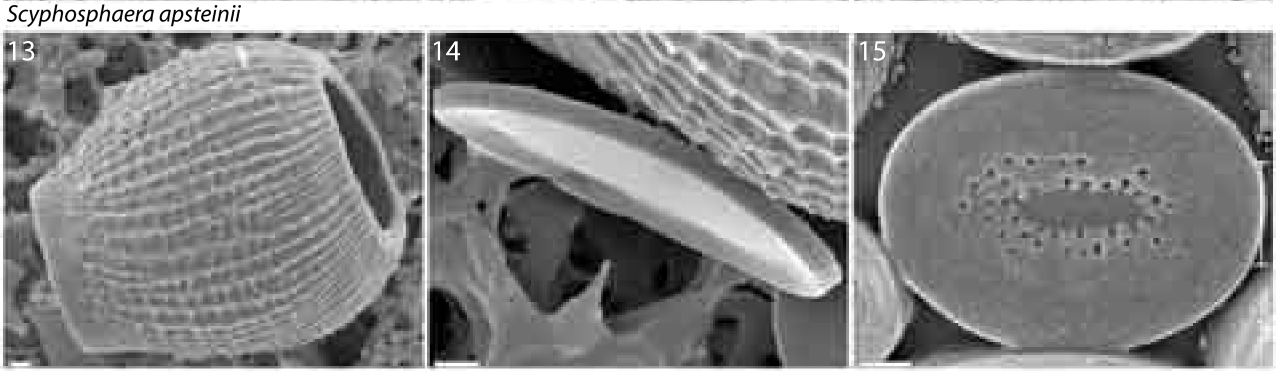
Pontosphaera discopora *P. japonica* (+ diatom debris) *P. multipora*

P. multipora

P. syracusana



Scyphosphaera apsteinii



Scyphosphaera apsteinii

Plate 11 - Pontosphaeraceae: *Pontosphaera* & *Scyphosphaera*

2. Syracosphaerales (Syracosphaeraceae, Calciosoleniaceae & Rhabdosphaeraceae)

Order SYRACOSPHAERALES **Hay 1977 emend.**

Taxa included: Families Syracosphaeraceae, Rhabdosphaeraceae and Calciosoleniaceae, plus the genus *incertae sedis Coronosphaera*. The families are united here on the basis of V/R/T coccolith structure (see below). The order is also characterised by polymorphism, oceanic ecology, motility of the heterococcolith phase and holococcolith formation in the alternate phase, although none of these are unique to the group or universal within it.

Coccolith structure: Coccoliths are unusually complex consisting typically of three components

1. A *rim* showing normal V/R structure, but with the proto-coccolith ring embedded within the rim;
2. A *radial lath cycle* with openings between the laths, outer ends interdigitate with rim elements. In some species the laths are composite, formed of two or more elements;
3. An *axial structure* in the centre of the coccolith. This may be a low mound, flat plaque, elevated ridge or spine and may be formed from the radial lath elements and/or from additional, disjunct, elements.

The radial lath cycle is especially distinctive, these elements interdigitate with the rim elements, in the case of *S. pulchra* the laths have tangential c-axis orientations (Young et al. in press) and we hypothesise that this is a general pattern. Hence, it appears likely that the proto-coccolith ring consists of three repeating nuclei types (V/R/T), rather than the usual V/R alternation. This distinctive structure makes it likely that this grouping is monophyletic in origin. The lath cycle is absent in some Rhabdosphaeraceae, probably as a result of secondary loss.

Coccolith types: Typically members of this order show more than one coccolith type (plate 12 fig. 1), the main types which can be developed are:

1. Body coccoliths (BCs), the main coccolith type forming inner layer (endotheca) of coccosphere, always present.
2. Circum-flagellar coccoliths (CFCs); modified coccoliths occurring around the flagellar opening, typically they are similar to the body coccoliths but modified by e.g. presence of a spine or smaller size. Seen on numerous species.
3. Antapical coccoliths (AACs); modified coccoliths occurring at opposite end of the coccosphere to the flagellar opening, typically similar to the body coccoliths but modified by e.g. presence of a spine or smaller size. Seen on limited number of species.
4. Exothecal coccoliths (XCs); modified coccoliths forming outer layer (exotheca) of coccosphere. Usually show the same basic structure as body coccoliths but morphology may be highly modified. Seen on most *Syracosphaera* species, but often missing on individual specimens.

Life-cycles and culture studies: The only species which have been cultured from this very diverse order are *Syracosphaera pulchra* (Inouye & Pienaar 1998; Geisen et al. 2002), *Algirosphaera robusta* (Probert et al. in prep.) and *Coronosphaera mediterranea* (Geisen et al. 2002). Of these,, single strains of *C. mediterranea* and *S. pulchra* have undergone phase changes, producing holococcoliths of respectively *Zygosphaera hellenica* and *Calyptrosphaera pirus* (Geisen et al. 2002, Houdan et al. in press). Numerous other species of the Syracosphaeraceae and two species of Rhabdosphaeraceae (*Acanthoica quattrospina, Algirosphaera robusta*) have been observed to form combination coccospheres with holococcoliths (Cros et al. 2000, and refs. therein, Cros & Fortuño 2002, Triantaphyllou & Dimiza 2003). This suggests that heteromorphic life-cycles are a common feature of the order.

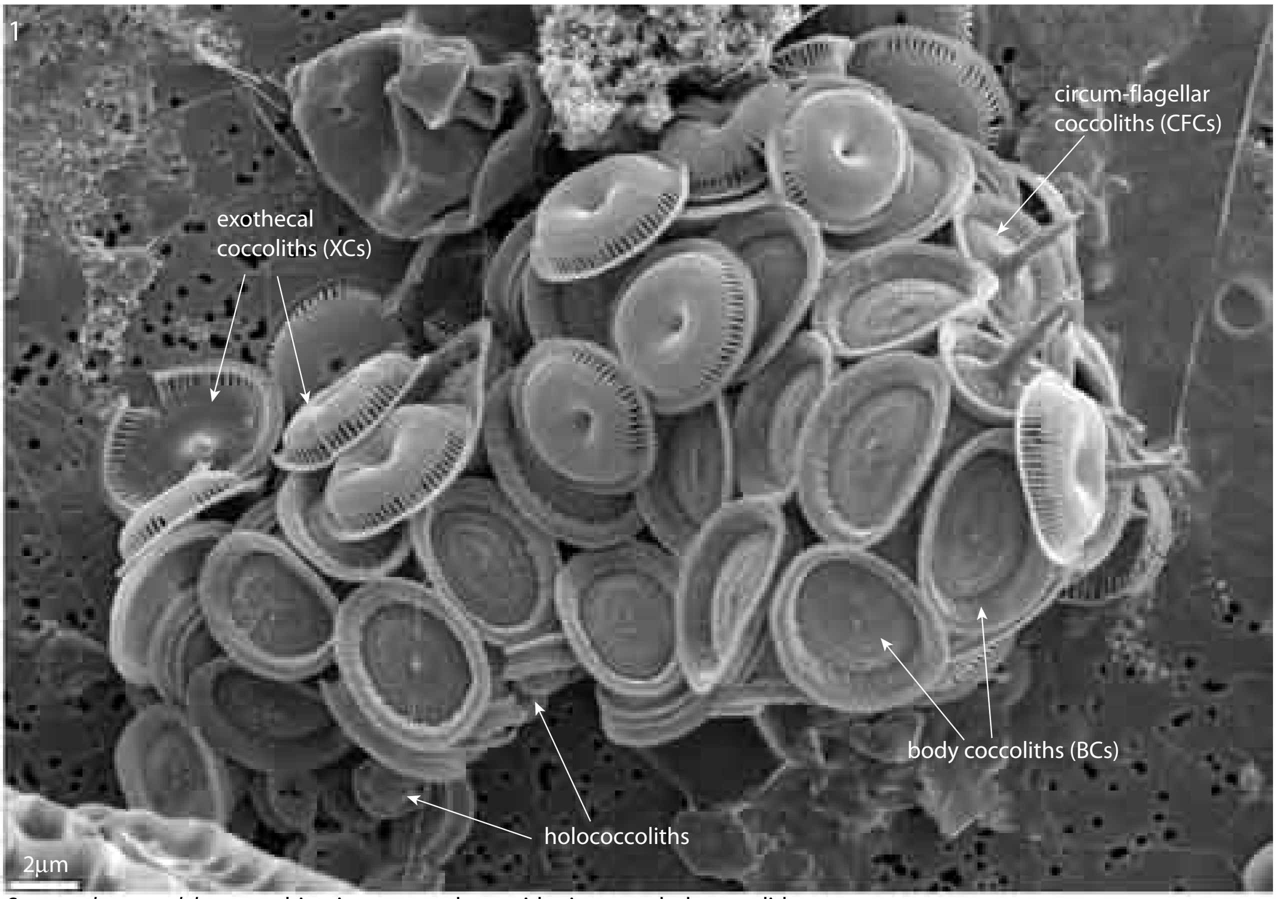
Family **SYRACOSPHAERACEAE** (Lohmann 1902) Lemmerman 1903

Motile, coccospheres typically elaborate, often showing dithecatism (development of distinct inner and outer layers of coccoliths) and/or modified polar coccoliths. The endothecal (inner layer) coccoliths are normally relatively conservative in form, typically muroliths with a well-developed central-area lath-cycle and variable inner central-area (coccoliths with this structure have been termed caneoliths). Exothecal coccoliths are much more variable, including planolith, murolith and dome-shaped forms (the planoliths have been termed cyrtoliths).

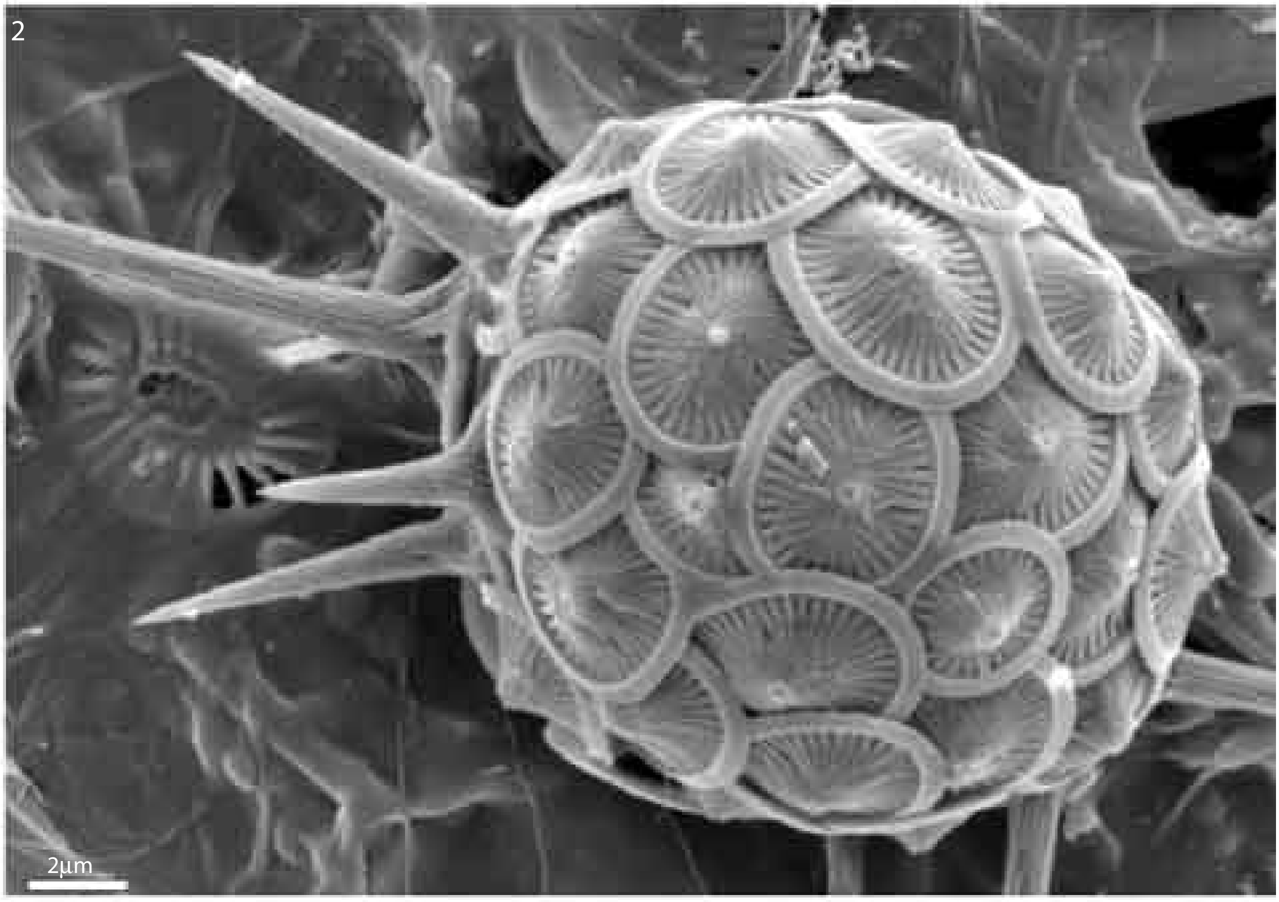
These coccoliths are typically delicate and only rarely preserved. The recent tendency, following Jordan & Young (1990), has been to include most species forms in the single genus *Syracosphaera*. The main exception is a set of genera with highly modified circum-flagellar and/or antapical coccoliths forming appendages, instead of exothecal coccoliths.

The fossil record of the family is poor but extends back into the Paleogene; fossil specimens are normally assigned to *Syracosphaera*.

Key references: Okada & McIntyre (1977) - many new spp.; Gaarder & Heimdal (1977) - detailed descriptions of several species; Inouye & Pienaar (1988) - detailed description of *S. pulchra* cytology and coccolith structure; Kleijne (1993) - illustration and notes on most spp. and many undescribed forms; Cros (2000) - analysis of exothecal coccoliths; Cros et al (2000) - holococcolith-heterococcolith combinations; Cros & Fortuño (2002) - detailed description of most species.



Syracosphaera pulchra - combination coccosphere with *pirus*-type holococcoliths



Acanthoica quattrospina - a typical Rhabdosphaeraceae

Plate 12 - Syracosphaerales - typical Syracosphaerceae and Rhabdosphaeracea

2.1 Genera with appendages

The genera *Calciopappus, Michaelsarsia* and *Ophiaster* have a set of appendages formed from highly modified coccoliths around either the flagellar or the antapical pole. They are all considered monothecate and the body coccoliths are muroliths with a single, weak, proximal flange, low rim and usually a disjunct axial structure. This grouping is convenient although possibly artificial. Key references: Heimdal & Gaarder (1981), Manton & Oates (1983), Manton et al. (1984).

2.1.1 *Calciopappus*

Calciopappus Gaarder & Ramsfjell 1954 emend. Manton & Oates 1983

Circum-flagellar coccoliths modified into elongate spines. Manton & Oates (1983) observed spine coccoliths developing inside cell, with the spine tip near the antapical end of the coccosphere. TYPE: *C. caudatus*. Lith types:

1. BCs - muroliths, +/- oblong, with low narrow rim; axial structure is plaque formed of two rectangular laths, overlapped by ends of radial laths.
2. CFC - a single coccolith with a moderate length spine sometimes occurs, with the spine protruding through the ring of whorl coccoliths (e.g. plate 13/10-11). Not present in all specimens.
3. Whorl coccoliths - asymmetric ring-shaped planoliths. These surround flagellar pole, forming foundation for the spines.
4. Spine coccoliths - arcuate base supports two struts that merge into very long slightly curved spine, with bayonet tip. Manton & Oates (1983) interpret entire spine as a modified coccolith rim, so homologous with link coccoliths of *Ophiaster* and *Michaelsarsia*.

Calciopappus caudatus Gaarder & Ramsfjell 1954

BCs - 1.5-2 μm, parallel sided, oblong, with laths showing strong sinistral obliquity, inner wall usually visible.

Whorl coccoliths - D-shaped, without projection. No CFC. Higher latitude form.

Calciopappus rigidus Heimdal *in* Heimdal & Gaarder 1981

BCs - irregular elliptical with laths oriented nearly radially, inner wall very low.

Whorl coccoliths - with thumb-like projection opposite spines.

CFC - a single spine-bearing CFC sometimes present.

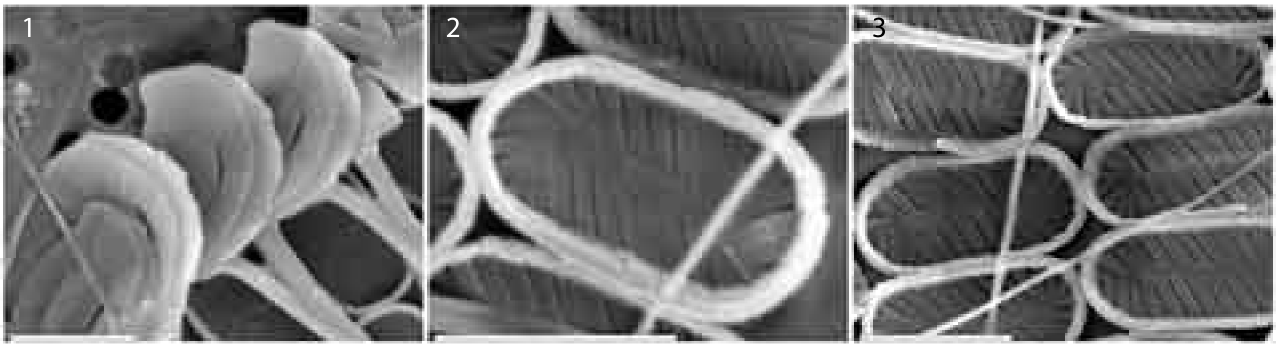
Calciopappus sp. of Cros & Fortuño (2002)

Small lightly calcified form.

BCs - with open central area.

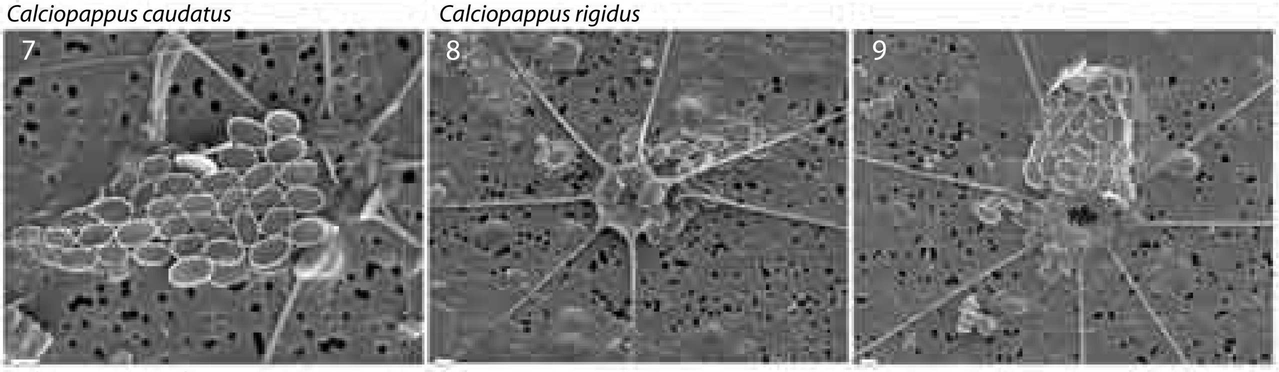
Whorl coccoliths - with two short spike-like projections; spines thin and distinctly curved.

Described by Cros & Fortuño (2002) from W. Mediterranean, also found off Naples (A. Houdan, pers. comm.) and Vietnam (Doan Nhu Hai, pers. comm.).

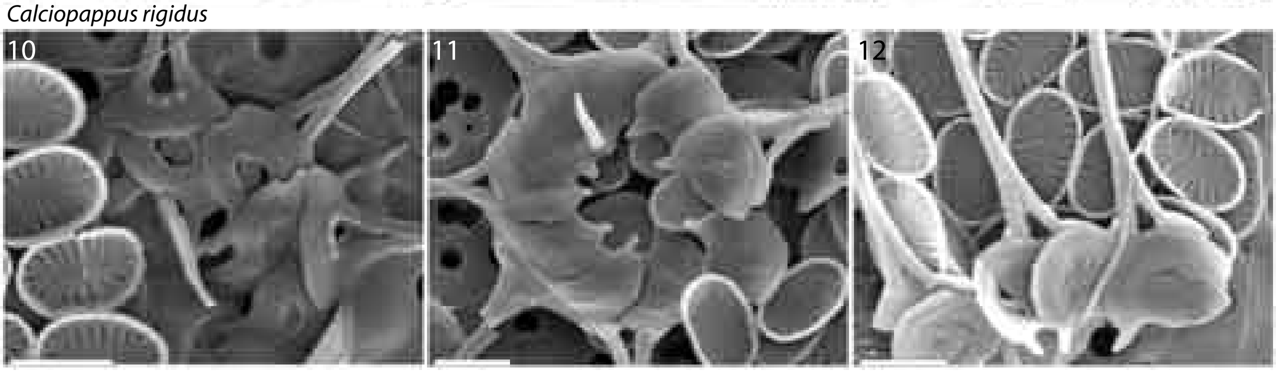


Calciopappus caudatus

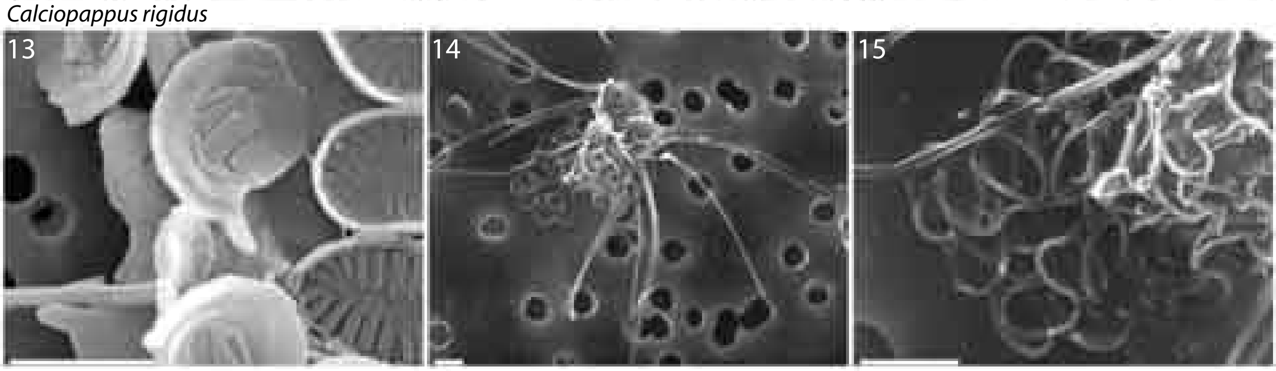
Calciopappus caudatus *Calciopappus rigidus*



Calciopappus rigidus



Calciopappus rigidus



Calciopappus rigidus *Calciopappus* sp.

Plate 13 - Syracosphaeraceae: *Calciopappus*

2.1.2 *Michaelsarsia*

Michaelsarsia Gran, *in* Murray & Hjort 1912 emend. Manton et al. 1984 (= *Halopappus* Lohmann 1912)

Apical appendages formed from string of three highly-modified coccoliths (osteoliths). TYPE: *M. elegans*. Lith types:

1. BCs - well calcified; broad rims with proximal flange; axial structure disjunct, formed of numerous small elements; laths bipartite (each formed of two elements with slight offset).
2. CFCs - small, lenticular (nearly rhombic), with low spines.
3. Whorl coccoliths - planoliths with circular central opening (often with organic cover) and asymmetric rim.
4. Link coccoliths (osteoliths) - elongate, symmetrical, convex sided with spoon-shaped ends.

Michaelsarsia adriaticus (Schiller 1914) Manton et al. 1984 [*Halopappus*]

BCs - oblong (sides sub-parallel), elongate; rim narrow; axial structure is low ridge of numerous small elements.
CFCs - spine with broad central canal.
Whorl coccoliths - with narrow opening.
Link coccoliths - narrow, sides almost touching.

Michaelsarsia elegans Gran 1912 emend. Manton et al. 1984

BCs - long elliptical; rim broad; axial structure is prominent mound, about 1/3 width of coccolith.
CFCs - spine solid or with narrow central canal.
Whorl coccoliths - with wide opening.
Link coccoliths - broad, sides well separated.

2.1.3 *Ophiaster*

Ophiaster Gran 1912 emend. Manton & Oates. 1983

Appendages formed from strings of highly modified antapical coccoliths (osteoliths). The appendages have some similarity to those of *Michaelsarsia* but are formed antapically rather than apically, there are no whorl coccoliths and the body coccoliths are smaller and simpler. TYPE: *O. formosus*. Lith types:

1. BCs - elliptical weakly calcified muroliths; rim narrow with weak proximal flange.
2. CFCs - like BCs but with spines.
3. Antapical link coccoliths (osteoliths) - form a ring of usually 4-7 arms. Elongate with spoon-like and tongue-like ends. Slightly curved in plan view, rim elements short along concave side and longer on convex side, sometimes extended into thorn-like processes. First link is differentiated from the others, typically having broader end where it attaches to the coccosphere.

Ophiaster hydroideus (Lohmann 1903) Lohmann 1913 emend. Manton & Oates 1983

BCs with central plaque formed of a few laths. Link coccoliths elongate.

Ophiaster formosus Gran 1912 emend Manton & Oates 1983

Similar to *O. hydroideus,* but with broader link coccoliths. This distinction seems tenuous and is not followed by many authors, but in light of the experience from *Syracosphaera,* it may prove valid on further research.

[*Ophiaster formosus* var. *inversus* Manton & Oates 1983]

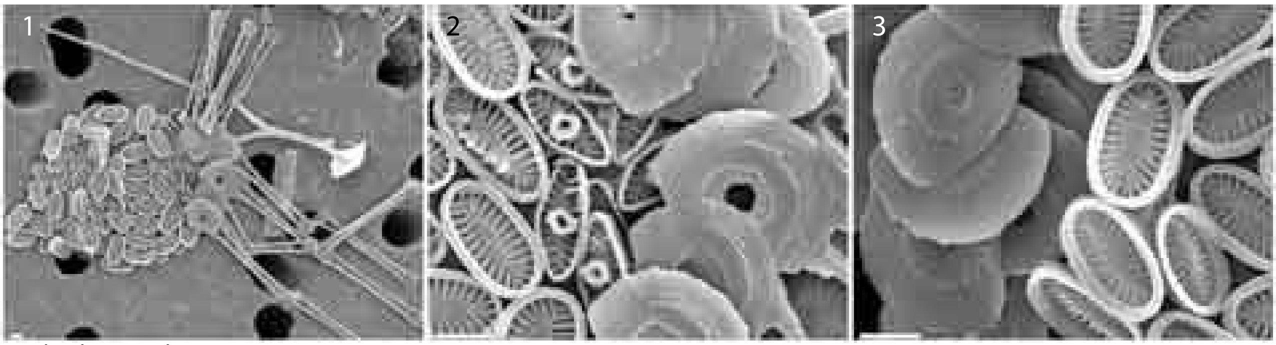
Variant of *O. formosus* with first link showing opposite taper to usual - i.e. narrow end attached to coccosphere. Specimens have not been illustrated since the original description and possibly these were artefacts.

Ophiaster minimus Manton & Oates 1983 *(not figured)*

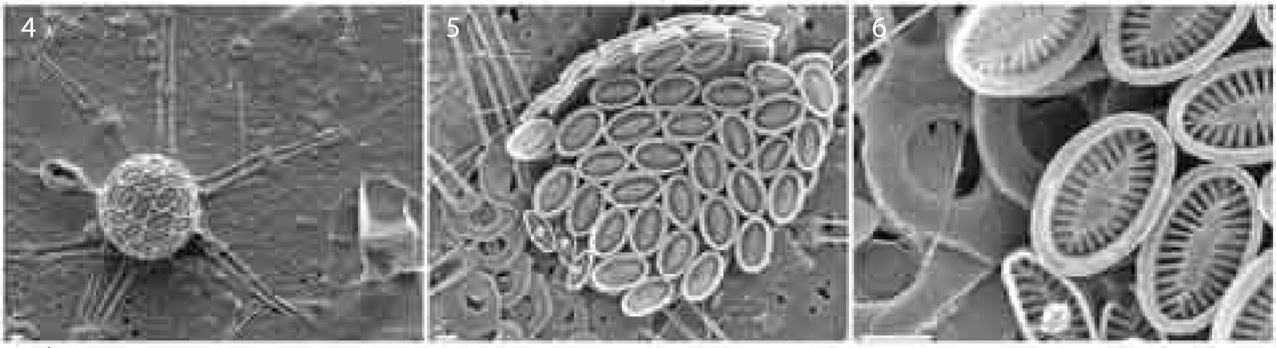
Very small (coccosphere ca. 3.5 μm). BCs without central structures. Proximal link liths distinctive.

Ophiaster reductus Manton & Oates 1983

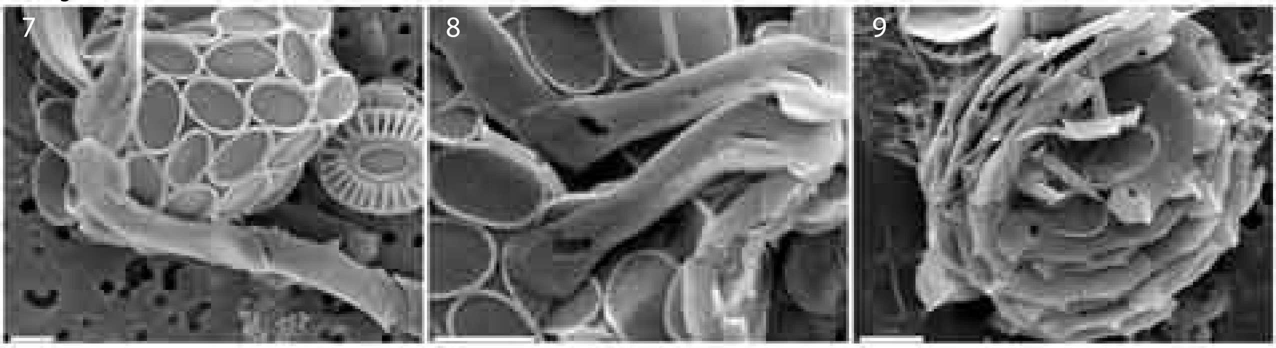
BCs - lack central plaques. Cycle of small antapical BCs with open central area surrounds whorl.



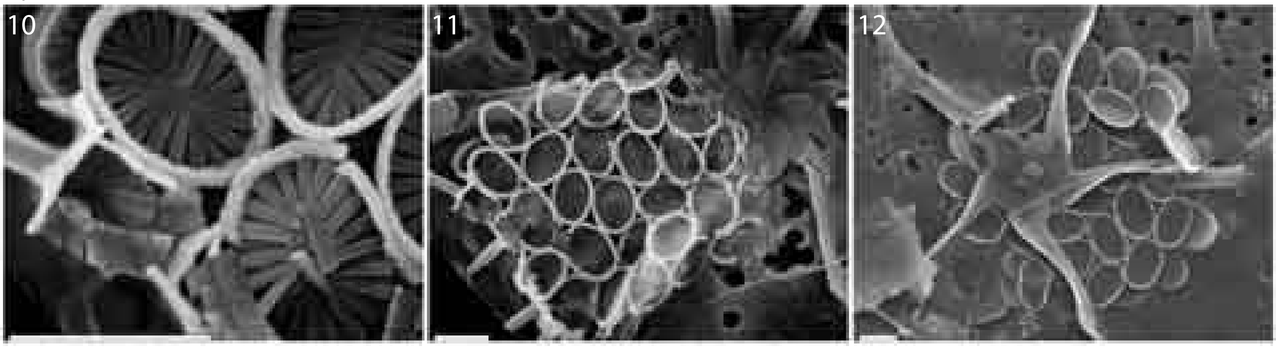
Michaelsarsia adriaticus



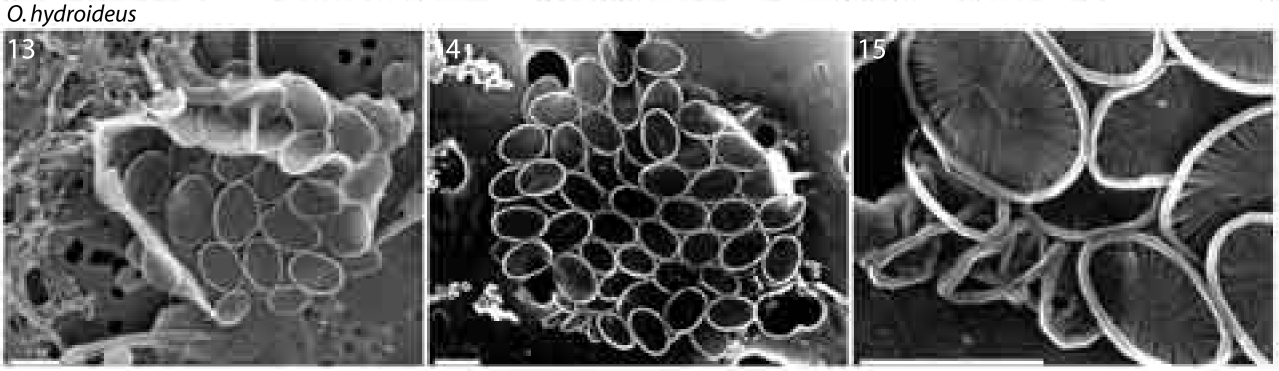
M. elegans



Ophiaster formosus



O. hydroideus



O. hydroideus *O. reductus*

Plate 14 - Syracosphaeraceae: *Michaelsarsia* & *Ophiaster*

2.2 - 2.4 *Syracosphaera*

Syracosphaera Lohmann 1902

Usually dithecate, Exothecal coccoliths (XCs) highly variable. Endothecal coccoliths are muroliths with 1, 2 or 3 flanges, the forms with 2 flanges are often placolith-like, these are often differentiated into body coccoliths (BCs), circum-flagellar coccoliths (CFCs) and antapical coccoliths (AACs).

TYPE: *S. pulchra*. SYNONYMS: *Caneosphaera* Gaarder *in* Gaarder & Heimdal 1977; *Deutschlandia* Lohmann 1912; *Gaarderia* Kleijne 1993. NB *Caneosphaera* and *Deutschlandia* are usually considered synonyms of *Syracosphaera* following Jordan & Young (1990), *Gaarderia* is recombined in *Syracosphaera* here.

Exothecal coccolith structure: As argued by Inouye & Pienaar (1988) and Cros (2000) exothecal coccoliths appear to be modified versions of the endothecal coccoliths, and are composed of the same set of components - rim, radial lath cycle and axial structure. However, the morphology of the coccoliths is highly variable and often radically different to that of the body coccoliths.

Classification: Since there are numerous species of *Syracosphaera* a classification is needed. The scheme adopted is based on a combination of body coccolith morphology, especially number of flanges and exothecal coccolith form. It is likely to be in part artificial but its main purpose is to facilitate identification. For an outline of the scheme, see the classification overview (Fig. 4).

2.2 *S. nodosa* group - BCs muroliths with proximal flange only, XCs flat planoliths

2.2.1 *S. nodosa* type

XCs planoliths, circular to elliptical, radial cycle variably developed, form complete exotheca. BCs muroliths with proximal flange; wall slightly flaring; no spines; sharp radial laths. CFCs with spines (except *Syracosphaera* sp. type L).

Syracosphaera nodosa Kamptner 1941

XCs - circular, wheel-like, (2.5-3.5 μm); flat; broad rim; radial cycle well-developed, showing sinistral obliquity in distal view; central plate +/- square, formed of two overlapping elements. (NB *S. rotula* XCs are superficially similar, but with a narrower rim, longer laths, and a marginal wall).

BCs - elliptical (1.5-2.5 μm) wall flaring, with characteristic vertical ribs on outer surface, flat-topped (non-corrugated); low mound in centre. CFCs with strong spine, ca. 1.3 μm high.

HOL ?= *Helladosphaera cornifera,* see Cros et al (2000).

Variation: three types of *S. nodosa* can be distinguished, primarily on XC morphology. The XC types do not co-occur on single coccospheres and probably are indicative of separate (sub-)species:

Type A - XC rim smooth, no slits; the most common form.

Type B - XCs with dentate periphery and wide central plate, BCs delicate, lacking central mound. Distinguished as *Syracosphaera* sp. type B by Kleijne (1993).

Type C - XC with broad rim, elements slits occurring between each element. BCs apparently with higher rim than in type 1. Distinguished as *Syracosphaera* sp. aff. *nodosa* by Cros & Fortuño 2002.

Syracosphaera sp. type L of Kleijne 1993

Coccosphere spherical (6-9 μm).

BCs - broadly -elliptical (1.7-2.5 μm), with thin, low, wall; central-area, broad, slightly vaulted, with low axial mound formed of lath tips and disjunct plates.

XCs - circular (1.6-2.0 μm), very thin, with central cycle of dextrally oblique radial elements and rim of wide elements. (XC structure is similar to that of *S. nana*).

Syracosphaera nana (Kamptner 1941) Okada & McIntyre 1977 (= *S.* sp. type A of Kleijne 1991, 1993)

Coccosphere consistently ovoid / egg-shaped (5-7 μm).

XCs - broadly elliptical (1.8-2.2 μm); broad rim; slightly vaulted central part formed of laths showing dextral obliquity. Delicate, not easily seen.

BCs - long elliptical to oblong (1-2 μm); wall flat topped, not strongly flaring; central area vaulted into whaleback, radial cycle only; axial structure - weak ridge formed by fusion of lath tips.

CFCs - with low spines (0.1-0.2 μm high).

NB The name *S. nana* has been applied to many different *Syracosphaera* species in the literature, however, this seems to be the form described by Kamptner (1941), see also Cros & Fortuño (2002). Under ICBN rules, the combination of Okada & McIntyre (1977) is valid even though the specimen they illustrate is of a different species (*S.* sp. type J).

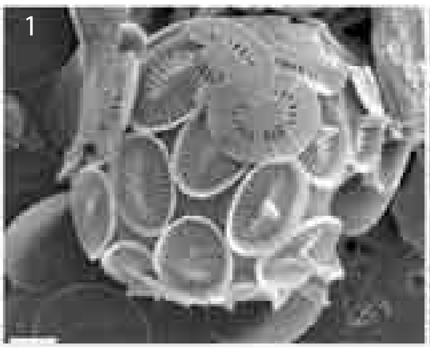
HOL - planar form (see plate 41), never described as a separate species (Kleijne 1991; Cros et al 2000).

Syracosphaera sp. aff. *nana* of Cros (2000)

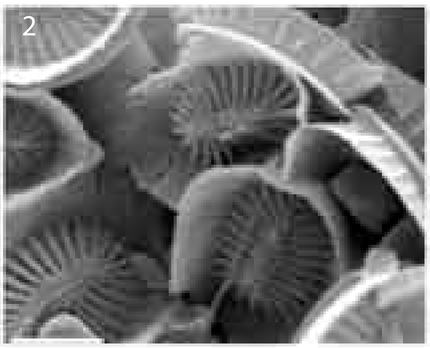
XCs - oval slightly larger than BCs, similar to those of *S. nana*.

BCs - very small (1-1.5 μm); wall low, with slightly beaded top; radial cycle shows distinctive sinistral obliquity, no central structure.

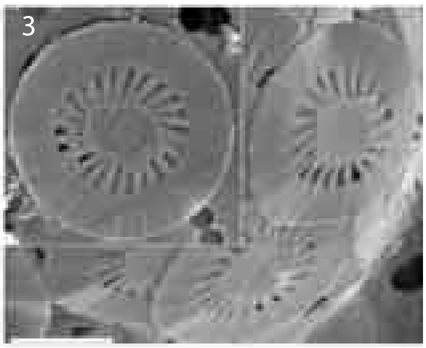
CFCs - with low spine.



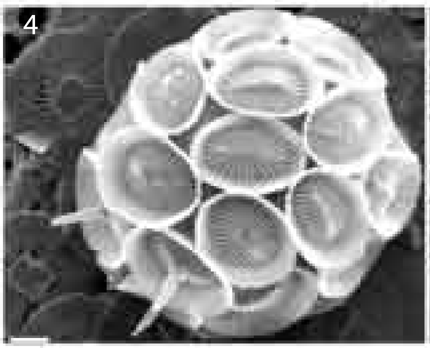
S. nodosa type A



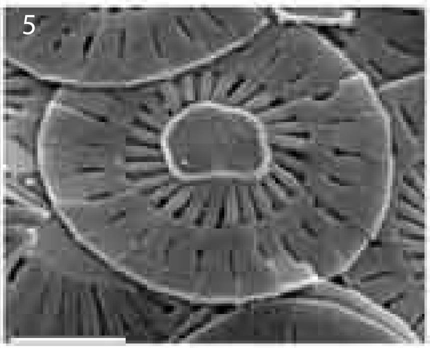
S. nodosa type A



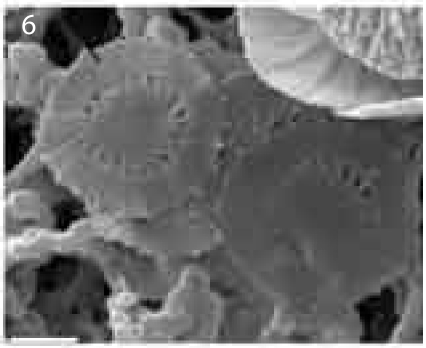
S. nodosa type A XCs (proximal & distal)



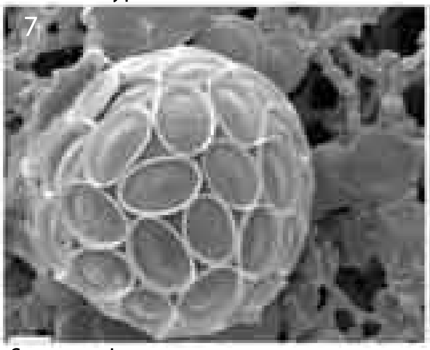
S. nodosa type C



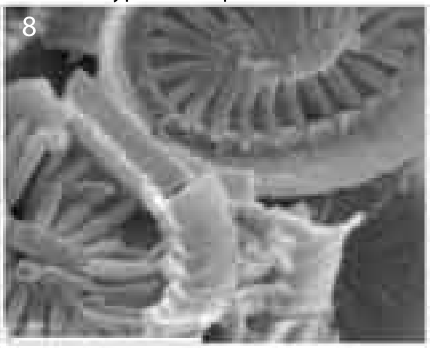
S. nodosa type C XCs (proximal)



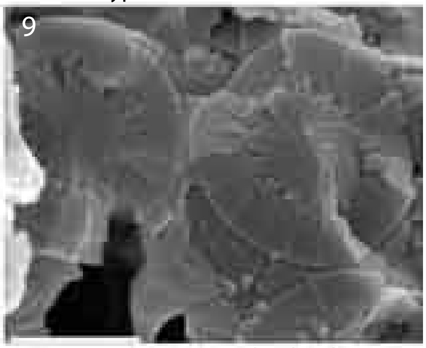
S. nodosa type B XCs (distal)



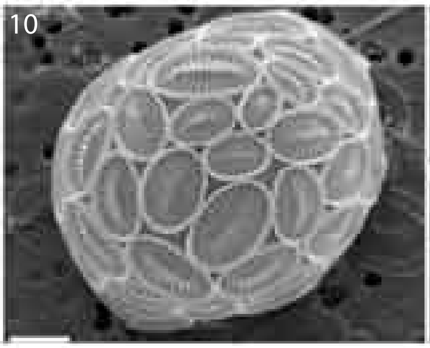
S. sp. type L



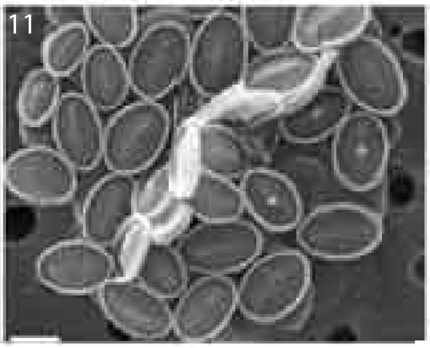
S. sp. type L



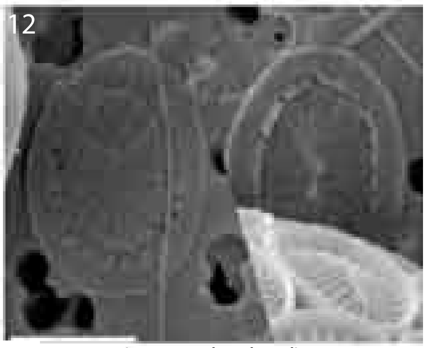
S. sp. type L XCs (proximal & distal)



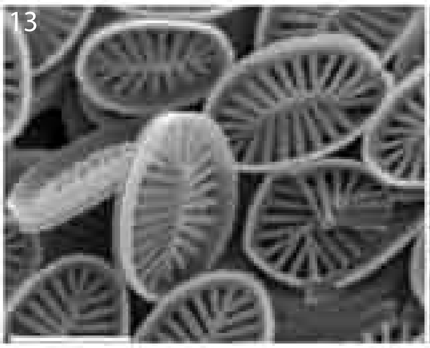
S. nana



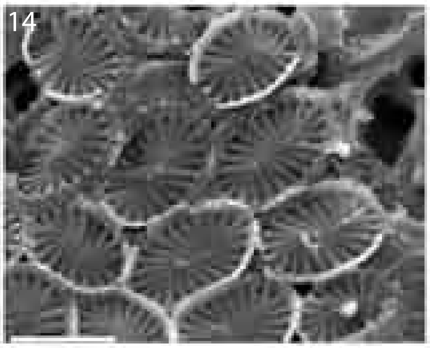
S. nana



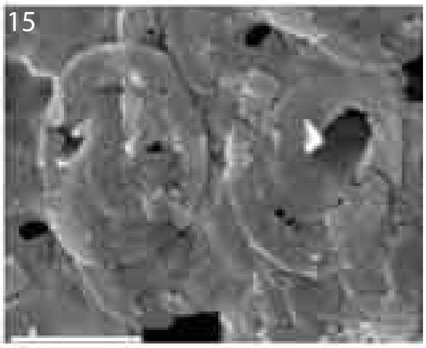
S. nana XCs (proximal & distal)



S. nana



S. sp. cf. *nana*



S. sp. cf. *nana* XCs (proximal & distal)

Plate 15 - Syracosphaeraceae: *Syracosphaera nodosa* group, *S. nodosa* type

2.2.2 *S. anthos* type

Similar to *S. nodosa* type but XCs robust with broad rim, curved sutures and conical central structure.

Syracosphaera anthos (Lohmann 1912) Janin 1987 [*Deutschlandia*]

XCs - circular with very broad rim, elements large with kinked sutures. Central structure is small cone often with slits in base. Complete exotheca are often developed, with coccoliths showing imbricated arrangement.

BCs - long elliptical; central area vaulted, laths bipartite with step-like join forming a ring between plaque and rim; axial structure is broad plaque.

CFCs - with prominent spine ca. 1 μm high, often hidden by XCs.

Coccospheres 10-15 μm; BCs 2-2.5 μm; XCs 3-5.5 μm.

HOL = *Periphyllophora mirabilis,* see Cros et al (2000).

2.2.3 *S. lamina* type

Similar to *S. nodosa* type, but XCs large and rather weakly calcified with only narrow radial cycle.

BCs thin-walled with corrugated top. No spines on CFCs so endotheca monomorphic. The three forms included show many similarities and possible intermediates occur.

Syracosphaera lamina Lecal-Schlauder 1951

XCs - (sub-)circular (ca. 3.5 μm), flat, broad rim, narrow radial cycle, quadrate central plate formed of two elements; delicate and rarely seen.

BCs - long elliptical (3-4 μm); wall flaring with corrugated top. Central area flat bottomed, laths show sharp edges in proximal view. Axial structure is an elevated longitudinal ridge, on proximal side this is formed from a couple of elongate laths.

CFCs - without spines / not differentiated.

Syracosphaera tumularis Sánchez-Suárez 1990 (= *S.* sp. type C of Kleijne 1993)

XCs - sub-circular (3.8-4.6 μm); like *S. lamina,* but axial structure more rounded, formed of complex polygonal plates.

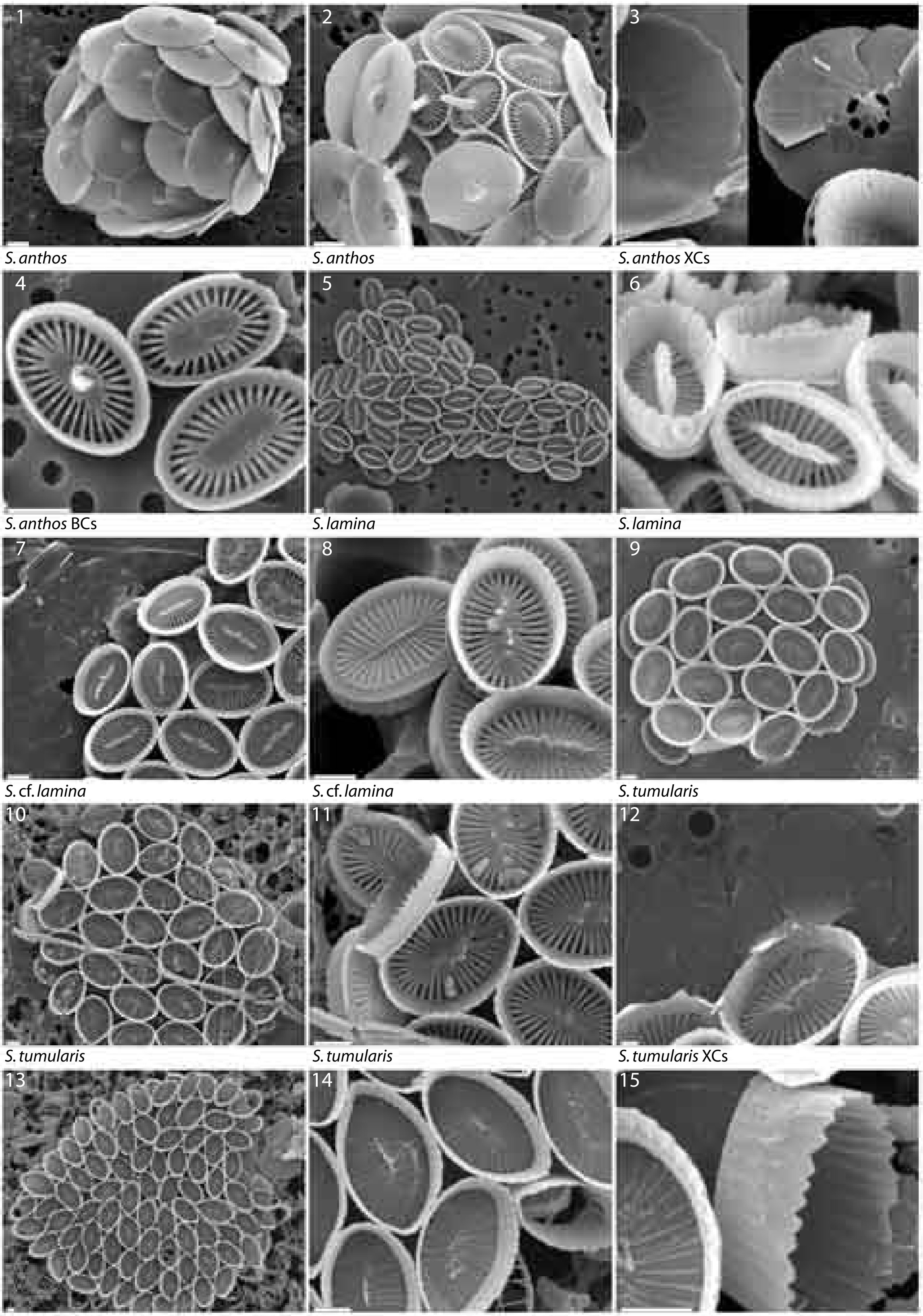
BCs - elliptical (3.3-4.2 μm); similar to *S. lamina,* but broadly elliptical, rim low and axial ridge, low or absent. If ridge is absent, laths meet in a few clusters along mid-line. In proximal view, two elongate elements are prominent along the long axis.

This is a common species, but has usually been recorded in open nomenclature.

Syracosphaera sp. cf. *tumularis* (= *Pontosphaera* sp. T of Reid 1980)

XCs - not observed.

BCs - like *S. tumularis* but larger (3-4 μm vs. 2.5-3.5 μm), walls much higher, top only weakly corrugated. NB We have observed several specimens of this morphotype in Gulf of Mexico samples (JRY, V. Pariente) and it seems likely to be a discrete species.



1 *S. anthos*
2 *S. anthos*
3 *S. anthos* XCs
4 *S. anthos* BCs
5 *S. lamina*
6 *S. lamina*
7 *S.* cf. *lamina*
8 *S.* cf. *lamina*
9 *S. tumularis*
10 *S. tumularis*
11 *S. tumularis*
12 *S. tumularis* XCs
13 *S.* sp. cf. *tumularis*
14 *S.* sp. cf. *tumularis*
15 *S.* sp. cf. *tumularis*

Plate 16 - Syracosphaeraceae: *Syracosphaera, S. nodosa* group

2.2.4 *S. bannockii* type

XCs are irregular planoliths, asymmetric rim, narrow medial cycle, often occurring in a ribbon-like arrangement, which may wrap around the coccosphere or extend beyond it.
BCs muroliths with proximal flange; wall low; radial laths rather broad and flat.
CFCs have spines, with simple rounded tips.
The described species are very similar and it is possible that they may prove to represent intraspecific variation within a single species, alternatively it may prove to be a plexus including several closely related species.

Syracosphaera bannockii (Borsetti & Cati 1976) Cros et al. 2000
XCs - narrowly elliptical, rim asymmetric wing at one end, blunt ended clockwise helical appearance (cf. *H. orientalis*); central area slightly vaulted; narrow medial cycle; central mass formed of single irregular cycle of elements.
BCs - elliptical; rim broad, with inner cycle; central area weakly vaulted, radial laths fuse toward centre but no discrete central mass.
CFCs - with spines, sometimes slightly curved.
HOL = *Corisphaera* sp. type A of Kleijne (1991) and *Zygosphaera bannockii*, see Cros et al. (2000), Geisen et al (2002).

Syracosphaera delicata Cros et al. 2000
XCs - elliptical to oblong, rim asymmetric, helical appearance in distal view with ridge along one edge; central area slightly vaulted; narrow medial cycle; central mass formed of single irregular cycle of elements.
BCs - broadly elliptical; rim delicate, with no inner cycle; central area flat, openings between laths small, and plaque of irregular elements.
CFCs - with very small and delicate spines.
Similar to *S. bannockii* but BCs more delicate, lacking inner wall and XCs with distal ridge.

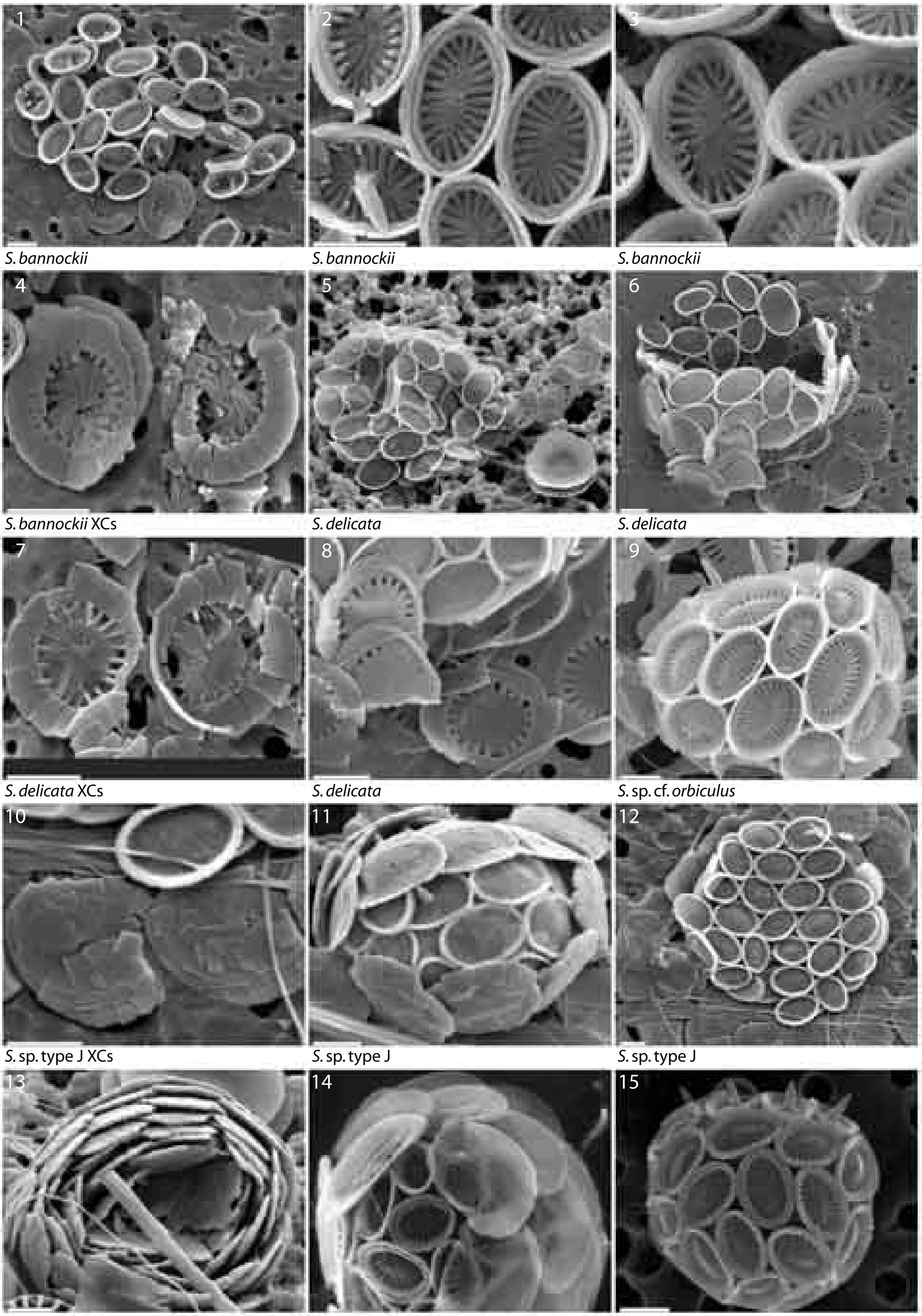
Syracosphaera orbiculus Okada & McIntyre 1977
Like *S. delicata* but BCs more robust; CFCs with better developed spines; XCs larger and ?without ridge. Cros & Fortuño (2002) illustrate two possibly separate species with affinities to *S. orbiculus*.
Coccospheres 6-9 μm; BCs 1.5-2.5 μm; XCs 3-4 μm.

2.2.5 Laminated type

XCs consist partly or entirely of several layers of superposed elements. These are not obviously *Syracosphaera* coccoliths and can even be mistaken for *Florisphaera* (e.g. Reid 1980).

Syracosphaera sp. type J of Kleijne 1993 (= *S. nana* of Okada & McInytre 1977, figs 7-8, not 9)
XCs - rounded trigonal planoliths (2.5-3.5 μm).; proximal face flat, hint of circular central area; distal face with mass of laminae, one margin denticulate.
BCs - elliptical, small (1.5-2.5 μm); low flaring rim, proximal flange only, radial cycle defines ring of marginal pores.
Coccospheres 6-8 μm.
NB Cros & Fortuño (2002) recognise a variant '*Syracosphaera* sp.' of this morphotype and Kleijne & Cros (in prep.) subdivide it into two species, varying in rim width.

Syracosphaera sp. type K of Kleijne 1993
XCs - asymetrical planoliths (ca. 2.5 μm). laminated wing extends around half width, other half of lith with narrow rim and openings between radial elements.
BCs - elliptical; rim broad with clear inner cycle; central area with well separated radial laths, weak central body (1.4-1.7 μm).
Coccospheres 6 μm.
NB Rather similar to *S. bannockii*, but BCs have more clearly separated inner and outer walls, and XCs have wing-like extension to margin.



1 *S. bannockii*
2 *S. bannockii*
3 *S. bannockii*
4 *S. bannockii* XCs
5 *S. delicata*
6 *S. delicata*
7 *S. delicata* XCs
8 *S. delicata*
9 *S.* sp. cf. *orbiculus*
10 *S.* sp. type J XCs
11 *S.* sp. type J
12 *S.* sp. type J
13 *S.* sp. type J
14 *S.* sp. type K
15 *S.* sp. type K

Plate 17 - Syracosphaeraceae: *Syracosphaera, S. nodosa* group

2.3 *S. pulchra* group - BCs with 3 flanges and/or spines, XCs muroliths or domal

XCs - dome-shaped (*S. pulchra, S. histrica*) or muroliths (only slightly modified versions of BCs).
Coccospheres often pyriform to elongated.
BCs - with distal, mid-wall and basal flanges (except *S. noroitica* type), and/or with low spines (except *S. pulchra* and *S. dilatata* type).
CFCs - spine-bearing (except *S. corolla*), with bifurcate spine-tip (except *S. dilatata* and *S.* sp. type D).
NB We have included in this group all *Syracosphaera* species which have body coccoliths with three flanges and/or spines, and these species also have exothecal coccoliths which are either muroliths or dome-shaped. However, only a few species (*S. histrica, S. pirus, S. prolongata*) show all of these characters so the group is more heterogeneous and perhaps more artificial than the *S. nodosa* and *S. molischii* groups. It is, however, very convenient for identification of species.

2.3.1 *S. pulchra* type

BCs with 3 flanges, CFCs spine-bearing, with notched tip. XCs dome-shaped.

Syracosphaera pulchra Lohmann 1902
BCs - large (4.5-8 μm); mid-wall flange prominent; inner wall-cycle well developed; central area with three concentric cycles of thin radial laths, occasionally incipient spine in centre.
CFCs - similar to BCs but with robust bifurcate-tipped spine.
XCs - dome-shaped, rim sub-horizontal, flange-like. Radial cycle forms vertical part of wall, numerous elements with wide slits. Central part formed of several cycles of laths; with a central conical depression.
Coccospheres 15-25 μm.
HOL = *Calyptrosphaera oblonga* and *Calyptrosphaera pirus,* see Cros et al. (2000), Geisen et al. (2002), Saugestad & Heimdal (2002). Since the *oblonga*-type and *pirus*-type holococcoliths are well differentiated we suspect that *S. pulchra* consists of two species which are only differentiable in the holococcolithophore life-cycle stage (Geisen et al. 2002, in press).

Syracosphaera histrica Kamptner 1941
XCs - similar to *S. pulchra* but flatter and with rib-like slits in the central part.
BCs - elliptical (2.5-4.5 μm); mid wall flange beaded; central area with two concentric cycles of radial laths, inner one usually fused to form plate; low spine in centre.
CFCs - similar with well-developed spine, ca 1.5 μm high.
Coccospheres 11-20 μm.
HOL ?= *Calyptrolithophora papillifera,* only one specimen recorded so association is unproven (Cros et al. 2000).

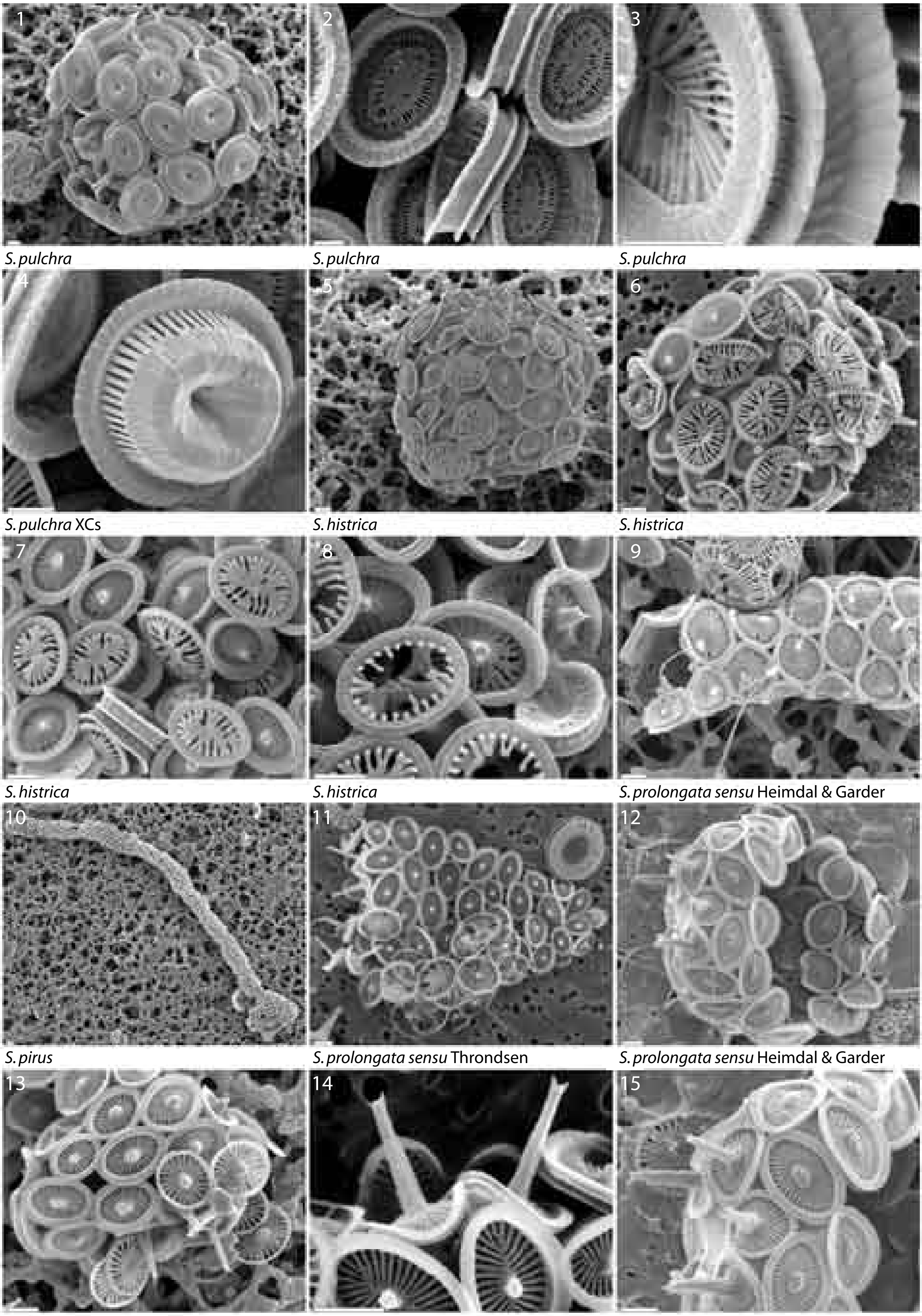
2.3.2 *S. prolongata* type

BCs with 3 flanges and spines or bosses, CFCs spine-bearing, with bifurcate tip. XCs muroliths with spines. The three forms are very similar and possible intergrades occur, they may yet prove to be varieties of a single morphologically variable species.

Syracosphaera pirus Halldal & Markali 1955
Coccosphere shape variable - spherical to pyriform to spectacularly elongate.
XCs - sub-circular muroliths.
BCs - small (1.5-2.5 μm) elliptical to lenticular, with large central boss.
CFCs with large spines.

Syracosphaera prolongata Gran 1912, *ex* Lohmann 1913 type 1/sensu Throndsen 1972
Very like *S. pirus,* but BCs and XCs with small central spine instead of boss and more delicately calcified.
XCs - sub-circular muroliths; rim forms narrow vertical wall with narrow distal flange and proximal beading where radial laths join it. Radial laths delicate, well separated; central hollow spines.

Syracosphaera prolongata Gran 1912, *ex* Lohmann 1913 type 2/sensu Heimdal & Gaarder 1981
Similar to type 1 but with broad central boss with twisted elements, instead of central spines, in both BCs and XCs. BCs slightly larger (2.2-3 μm).



1 *S. pulchra*; 2 *S. pulchra*; 3 *S. pulchra*

4 *S. pulchra* XCs; 5 *S. histrica*; 6 *S. histrica*

7 *S. histrica*; 8 *S. histrica*; 9 *S. prolongata sensu* Heimdal & Garder

10 *S. pirus*; 11 *S. prolongata sensu* Throndsen; 12 *S. prolongata sensu* Heimdal & Garder

13 *S. pirus*; 14 *S. prolongata sensu* Throndsen; 15 *S. prolongata sensu* Heimdal & Garder

Plate 18 - Syracosphaeraceae: *Syracosphaera, S. pulchra* group

2.3.3 *S. noroitica* type

BCs with proximal flange only, weakly developed inner wall. Coccospheres are highly varimorphic, the apical BCs have a robust central structure, this decreases toward the antapical area where there are BCs without a central structure. CFCs spine-bearing, with bifurcate tip. XCs muroliths.

Syracosphaera noroitica Knappertsbusch 1993 (= *S*. sp. type E of Kleijne 1993)
XCs - muroliths, larger than BCs; radial cycle forms a beaded proximal flange; slender spine.
BCs - elliptical (ca. 2.5 μm); varimorphic low spine or small boss in centre; elliptical; rim high, proximal flange only, inner wall cycle clear; central area flat, formed from bicyclic radial cycle
CFCs - circular small (ca. 1μm); , with tall delicate, bifurcate spines (ca. 1 μm).
AACs - smaller than BCs with lateral spines, formed from radial laths.
Coccospheres 6-10 μm.

Syracosphaera florida Sánchez-Suárez 1990 (= *S*. sp. type F of Kleijne 1993)
Similar to *S. noroitica*, but BCs have low wall with crenulate distal margin; CFCs elliptical.

Syracosphaera sp. type G of Kleijne 1993
Similar to *S. noroitica,* but BCs have low wall with crenulate distal margin and very large elongate bosses. Coccospheres not known; BCs 1.1-2.1 μm; XCs 1.8 μm.

Syracosphaera sp. A of Winter et al. 1979 *(not figured)*
XCs - cup-shaped, lath cycle extended to form conical lower part of lith. See Winter et al. (1979) plate 4 fig. 9; also illustrated on the EMIDAS database (www.emidas.ethz.ch), as *Syracosphaera* sp.

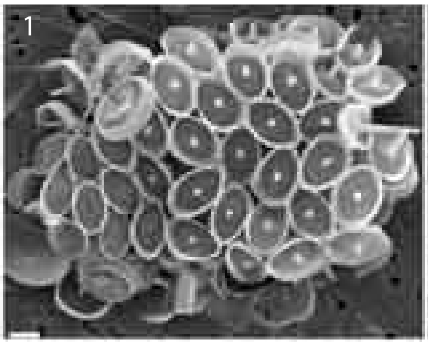
2.3.4 *S. dilatata* type

BCs with 3 flanges, but mid-wall flange weakly developed, as ring bead-like nodes; XCs muroliths, similar to BCs.

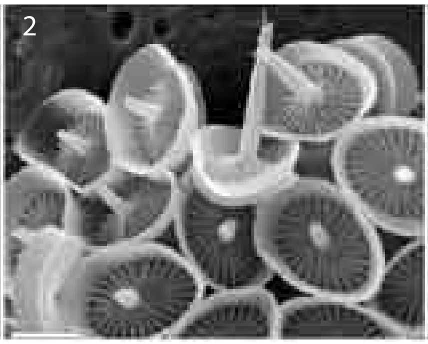
Syracosphaera dilatata Jordan et al. 1993 [ex *Caneosphaera halldallii* f. *dilatata* Heimdal & Gaarder 1981]
BCs - irregularly oblong; rim high, vertical, with proximal, beaded mid-wall and serrated distal flanges. Two serrations per element on distal flange. Radial laths well separated, meet at central mound underlain by single longitudinal lath.
CFCs - slightly smaller and less elongate than BCs; with smooth tipped spine, prominent beaded mid-wall flange.
XCs - muroliths essentially similar to the BCs, but larger and more slender, with higher wall, more oblong shape, weaker central area structure. Weakly developed beaded mid wall flange.
NB This form is variable and may require subdivision into two or three (sub-)species, alternatively it may prove that type D and *dilatata* are variants of a single species.

Syracosphaera sp. type D of Kleijne 1993
Very similar to *S. dilatata*, main differences:
BCs - mid-wall flange continuous, not beaded (and rather weak), distal flange broader.
XCs - mid-wall flange very weak or missing.
NB CFCs in both type D and *dilatata* show beaded mid-wall flange.
Coccospheres 8-12 μm; BCs 2.1-3.1 μm; XCs 3.1-3.8 μm.
HOL ?= *Homozygosphaera arethusae,* see Cros et al. (2000).

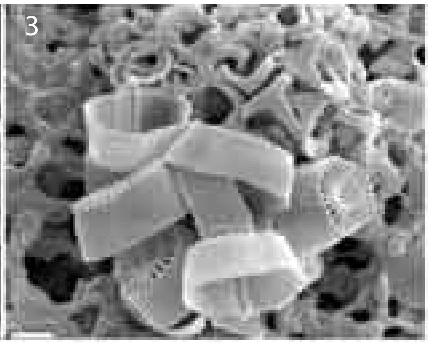
Syracosphaera corolla Lecal 1966
BCs - mid wall flange beaded; distal flange shows chirality (anticlockwise obliquity).
CFCs - not differentiated.
XCs - with broad distal flange showing chirality.
NB Kleijne (1993) removed this species to a separate genus, *Gaarderia*. However, in the light of recognition of exothecal muroliths in other *Syracosphaera* species (Cros 2000) this separation seems inconsistent so we prefer to revert to the older combination *S. corolla*.



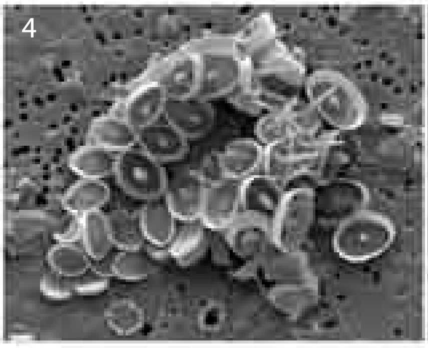
S. noroitica



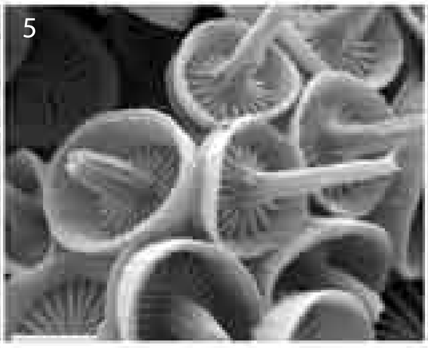
S. noroitica



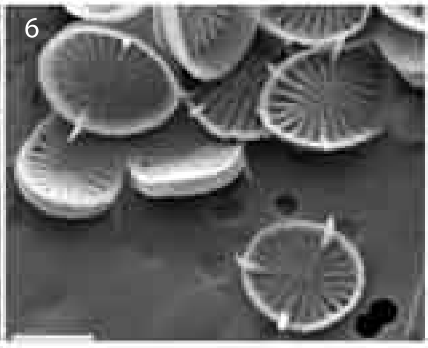
S. noroitica XCs



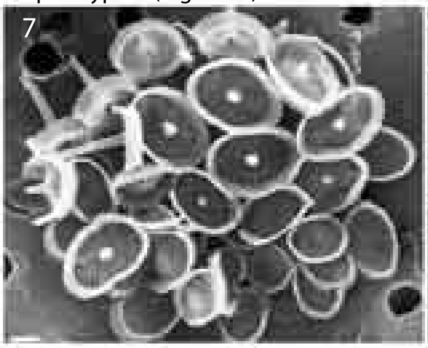
S. sp. cf. type G (high wall)



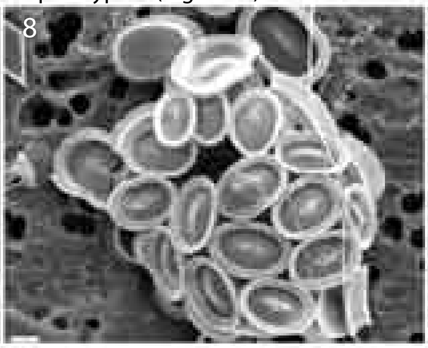
S. sp. cf. type G (high wall)



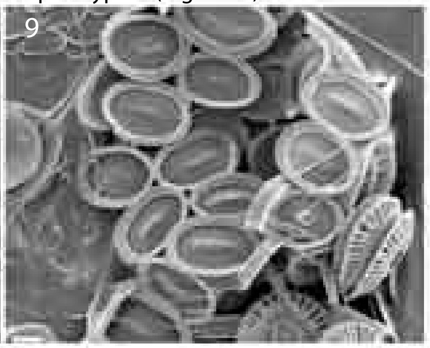
S. sp. cf. type G (high wall) AACs



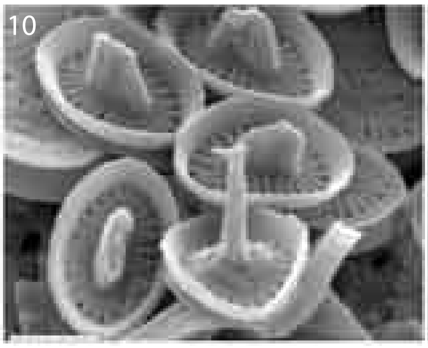
S. florida



S. dilatata

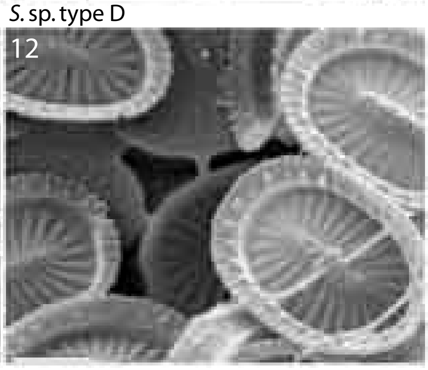


S. sp. type D

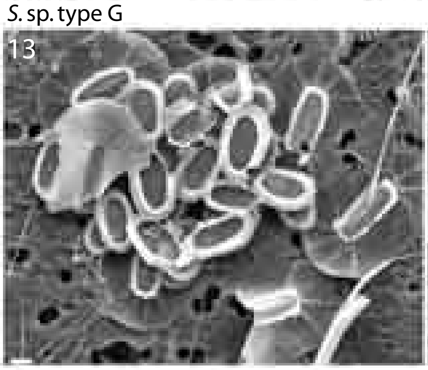


S. sp. type G

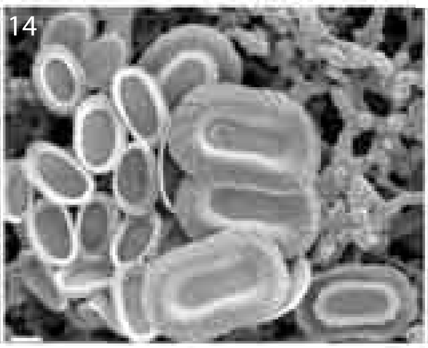
S. dilatata



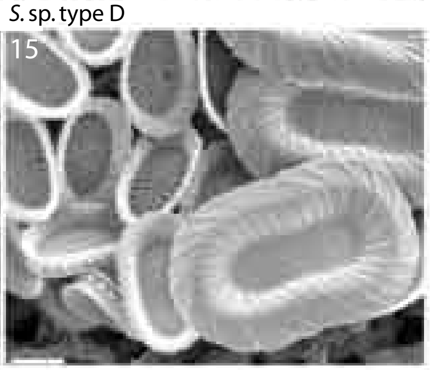
S. sp. type D



S. corolla



S. corolla



S. corolla

Plate 19 - Syracosphaeraceae: *Syracosphaera, S. pulchra* group

2.4 *S. molischii* group - placolith-like BCs

BCs with proximal and distal flanges, placolith-like, often with ridges and irregular central area calcification, no spines, no distinct inner wall cycle; laths rather broad. XCs variable.

2.4.1 *S. molischii* type - undulating XCs

XCs "undulating" planoliths, confined to imbricate circlet around flagellar pole, formed of:

1. Asymmetric flange with variably-developed wing like extensions (directed toward and away from apical pole of coccosphere).
2. Conical central area (concave on distal side, convex on proximal side), with horseshoe shaped slits at either end.

CFCs with spines showing calyx with 4-fold symmetry, AACs usually present.

Syracosphaera molischii Schiller 1925

BCs - large (2-4 μm), distal flange broad; variably ornamented - usually heavily ribbed, sometimes with teeth protruding into central area; tube low; proximal flange, narrow, smooth. Laths broad with weak axial ridge. Central structure - irregular ridge and/or ring formed by growth upward from the laths.
CFCs - with prominent spine, smaller and less ornamented than BCs.
AAC - one BC type coccolith with a stubby spine often occurs near the antapical pole.
XCs - large; flange ribbed on distal side, expands clockwise into wing (directed apically) about twice as wide as rest of flange. One or two nodes usually present near centre of the proximal surface.
SYNONYMS: *S. corrugis* Okada & McIntyre 1977 and *S. elatensis* Winter *in* Winter et al. 1979 see Heimdal & Gaarder (1981), Kleijne (1993).
HOL ?= *Anthosphaera fragaria*, see Cros et al. (2000). This association is based on a single specimen and is certainly not proven.

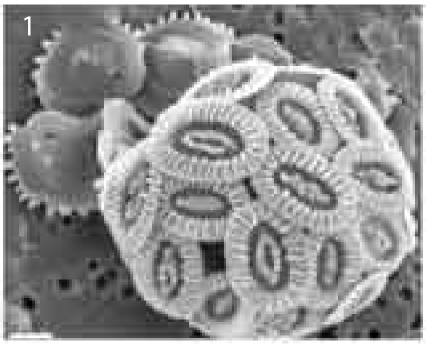
Variation: *S. molischii* shows very variable ornamentation and the following types can be distinguished based on distal flange ornamentation, possibly these are discrete species, in which case the names *S. elatensis* and *S. corrugis* should be reinstated. It should be noted, however, that other aspects of morphology (e.g. central area ornamentation, XC ornament) seem to show independent variation:
Type 1 - Outer part of distal flange with low ridges, inner part fewer high ridges.
Type 2 - Outer part of distal flange with low ridges, inner part formed of tooth-like projections (= *S. elatensis*).
Type 3 - Outer part of distal flange with low ridges, inner part smooth (= *S. corrugis*).
Type 4 - Outer part of flange smooth, inner part formed of tooth-like projections.

Syracosphaera sp. II cf. *epigrosa* Okada & McIntyre 1977 of Kleijne 1993

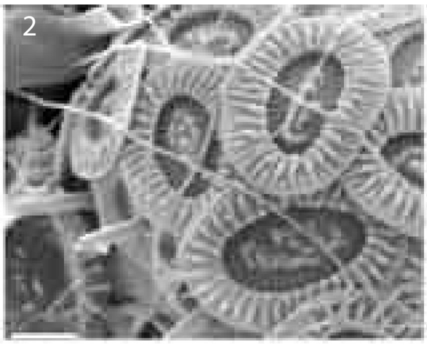
Although it has not been formally described this is certainly a discrete species, an extended description is given by Cros & Fortuño(2002), as *Syracosphaera* sp. (slender).
BCs - flanges smooth and narrow; no distinct axial structure.
CFCs - distal flange very narrow; tall (ca. 2 μm) spines with calyx of four triangular plates.
AACs - one or two usually present, similar to CFCs but rim higher and calyx larger.
XCs - with broad smooth flange extended into wings; central part conical.
Coccospheres 6-10 μm; BCs 1.3-2.2 μm; XCs 2.3-3.1 μm.

Syracosphaera marginaporata Knappertsbusch 1993 (= *S.* sp. H of Kleijne 1993)

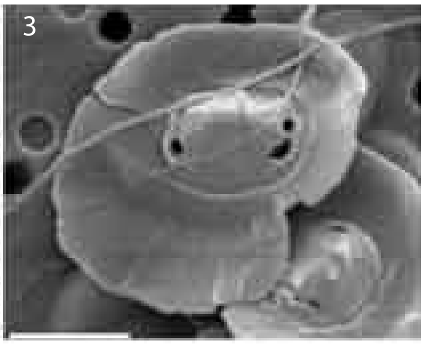
BCs - small (ca. 1.5 μm), rim narrow, smooth; laths narrow initially defining ring of pores, then usually merge to form broad, smooth central mass.
CFCs - narrow tall spine; distal flange, delicate, usually absent (illustrated by Cros 2000 pl. 5/3, Knappertsbusch 1993 pl. 2/3). AAC not observed.
XCs - irregular, delicately calcified; flange smooth, flat, broad, weak wing development.



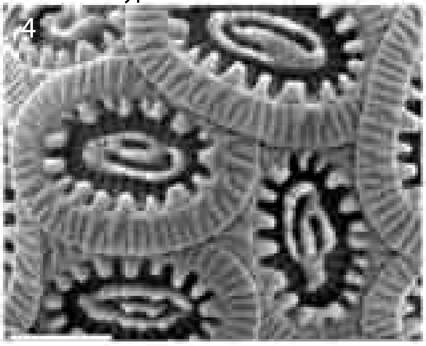
S. molischii type 1



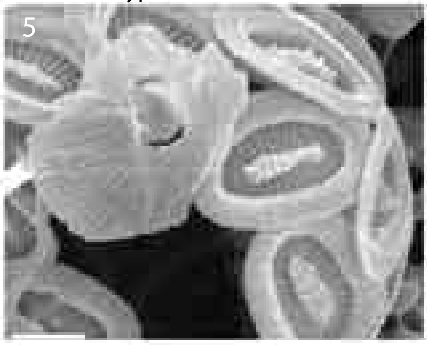
S. molischii type 1



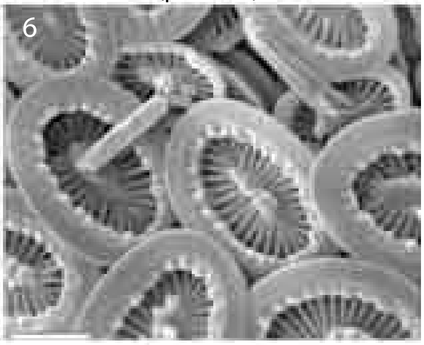
S. molischii XCs (proximal)



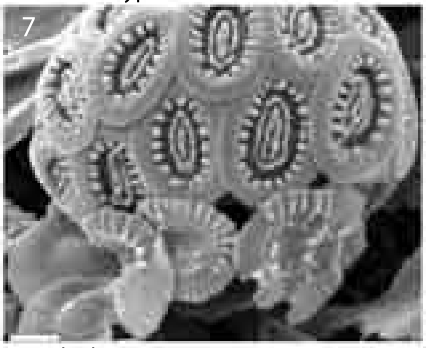
S. molischii type 2



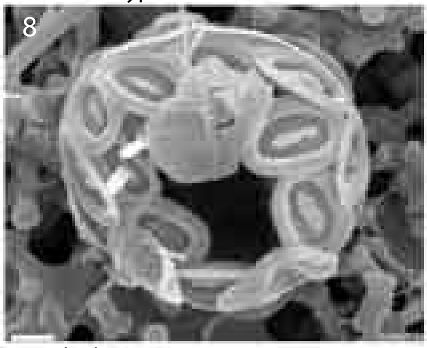
S. molischii type 3



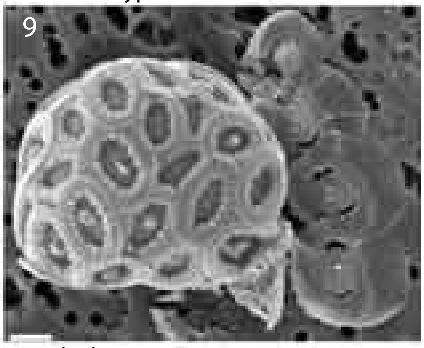
S. molischii type 4



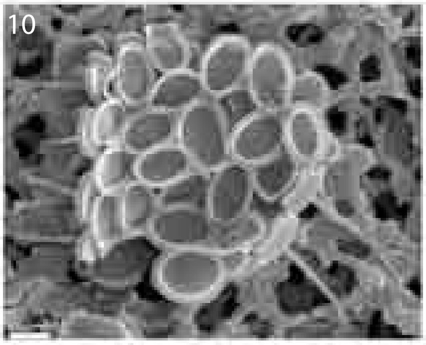
S. molischii type 2



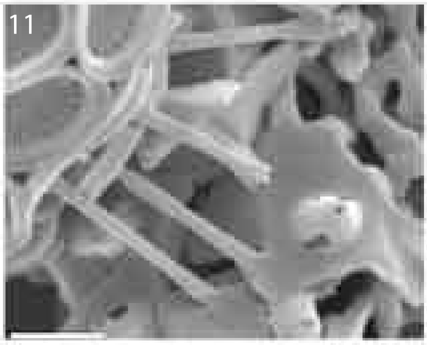
S. molischii type 3



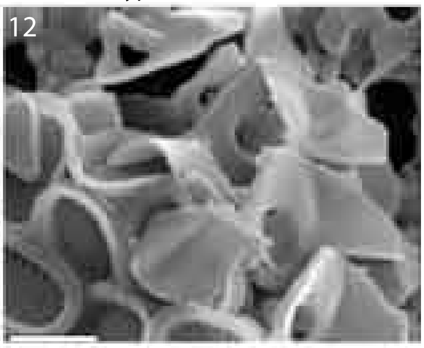
S. molischii type 4



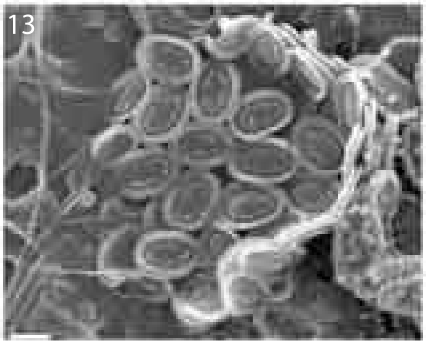
S. sp. II cf. *epigrosa*



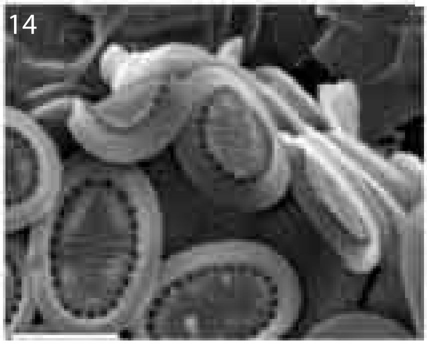
S. sp. II cf. *epigrosa*



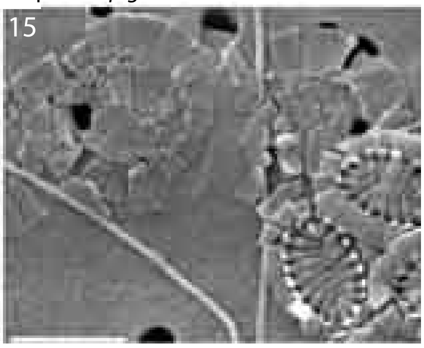
S. sp. II cf. *epigrosa* XCs



S. marginaporata



S. marginaporata



S. marginaporata XCs

Plate 20 - Syracosphaeraceae: *Syracosphaera, S. molischii* group

Syracosphaera ossa (Lecal 1966) Loeblich & Tappan 1968 [*Syracolithus*]

BCs - placolith like with broad smooth distal flange. Ridge-like central mass often present and can almost fill central area. BCs usually vary greatly in size on coccosphere.

CFCs - smaller than BCs and rim narrower; spine well developed (ca. 1.5 μm tall), formed of four blades (cruciform in cross section), typically with blades parallel to long axis extended to form wide flat spine.

AAC - One BC type lith with a quadrate spine often present (stem narrower than CFCs).

XCs - rim smooth, flange expanded into broad apically directed wing and long antapically directed wing.

Variation: Two sub-types are present and seem to be consistently differentiable (our obs.):

Type 1 - BCs without axial structure, XCs with long flange extensions. (This form corresponds to the holotype of Lecal 1966).

Type 2 - most BCs with axial ridge, XCs with moderate length flange extensions.

Syracosphaera epigrosa Okada & McIntyre 1977

This is a poorly known form with only a few definite specimens illustrated, and no observations on XCs or CFCs. The BCs are similar to those of *S. ossa* but with a central ring of high nodes formed by growth up from laths. We suspect that it will prove to have CFCs and XCs similar to those of *S. ossa* and may even prove to be an ornamented variety of *S. ossa* rather than a discrete species. Coccospheres 8-13 μm; BCs 1-3 μm.

2.4.2 *S. borealis* type - elliptical XCs

XCs elliptical discs, with a narrow rim, central part convex rather than concave. CFCs not differentiated.

Syracosphaera borealis Okada & McIntyre 1977

BCs - with moderate breadth, slightly flaring, distal flange, with low sutural ridges; axial structure - prominent irregular ridge formed by upgrowth from laths.

XCs - small, folded into saddle-shape; rim, narrow, symmetrical (no wing development). Usually only a few observed.

Coccospheres 6-8 μm /BCs 1.5-2.5 μm.

Variation: two forms seem to be differentiable.

Type 1 - axial structure prominent irregular ridge or ring. This form corresponds to the holotype and is common in the sub-Arctic.

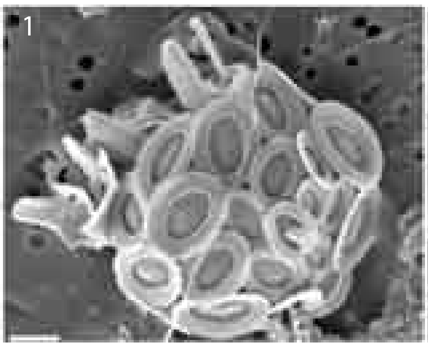
Type 2 - no real axial structure but irregular ring of isolated nodes. This form was referred to as *Syracosphaera* sp. I cf. *epigrosa* by Kleijne (1993), it appears to be a temperate water and Mediterranean form.

Syracosphaera exigua Okada & McIntyre 1977

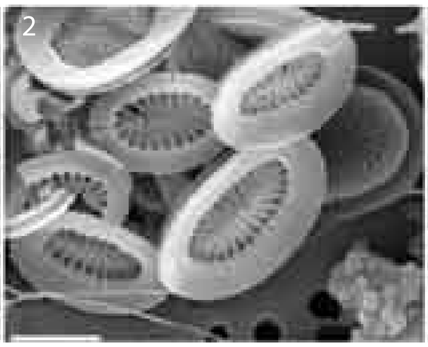
BCs - distal flange narrow, ornamented with nodes on inner margin from each of which two ridges radiate to outer margin; distinct connecting ring; axial structure - irregular central ridge formed by limited upgrowth from laths. (NB Heimdal & Gaarder 1980 illustrate very different BCs as *S. exigua* - but these are *S. dilatata* or *S.* sp. D).

XCs - elliptical, slightly asymmetric, vaulted; rim narrow; no clear lath cycle; central field of about 10 plates with ridge-like sutures. Can form a complete exotheca.

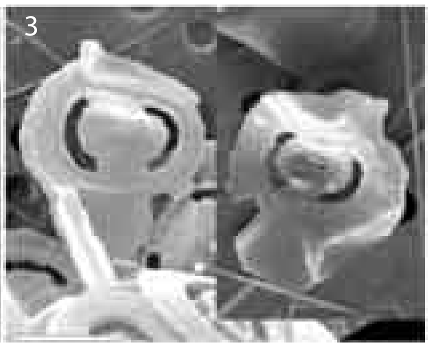
Coccospheres 7-12 μm; BCs 2-4 μm.



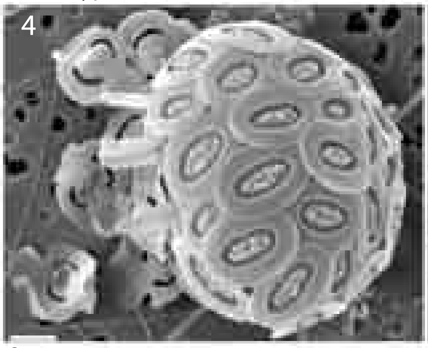
S. ossa type 1



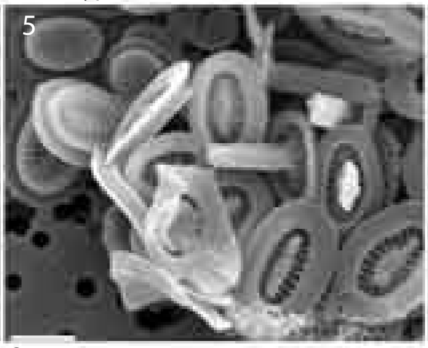
S. ossa type 1 BCs



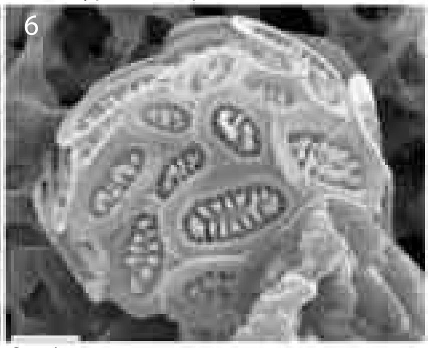
S. ossa type 2 XCs (proximal & distal)



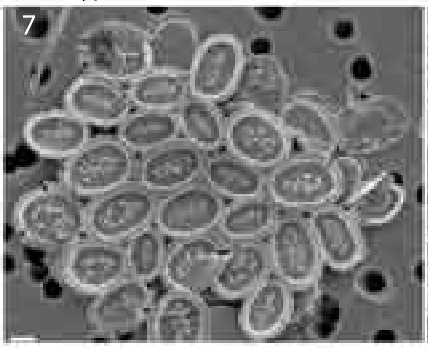
S. ossa type 2



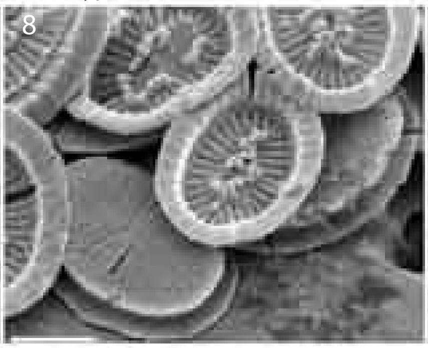
S. ossa type 2



S. epigrosa

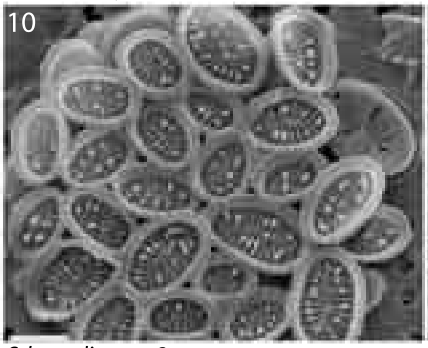


S. borealis type 1

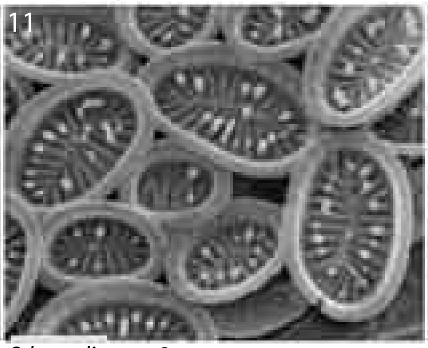


S. borealis type 1

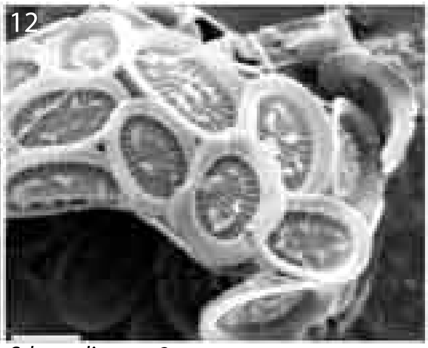
S. borealis type 1 XCs



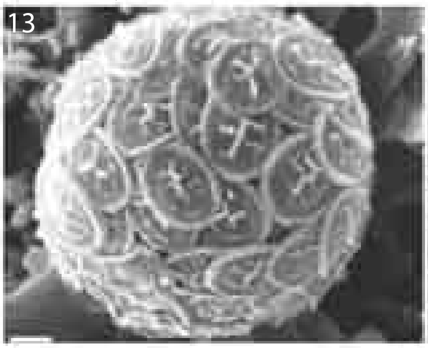
S. borealis type 2



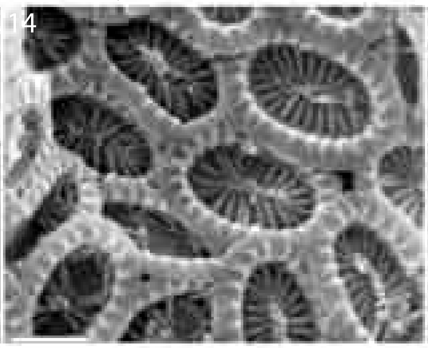
S. borealis type 2



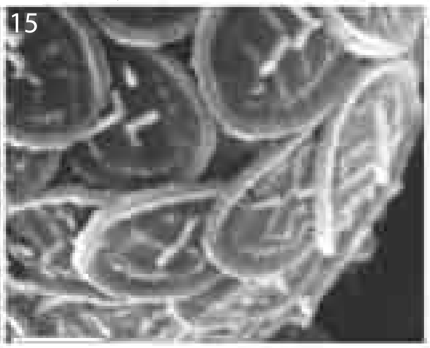
S. borealis type 2



S. exigua



S. exigua BCs



S. exigua XCs

Plate 21 - Syracosphaeraceae: *Syracosphaera, S. molischii* group

2.4.3 *S. rotula* type - wheel-like XC*s*

XCs wheel-like, with radial laths well-separated, spoke-like. BCs and XCs both show distinct chirality. CFCs not differentiated. The grouping of these two species was suggested by the new discovery of XCs on *S. ampliora*, it is supported by the absence of CFCs on these two species and their rather similar BCs.

Syracosphaera rotula Okada & McIntyre 1977

BCs - distal flange narrow, with weak sutural ridges showing clockwise obliquity; laths broad, restricted at outer ends forming ring of pseudo-pores; axial structure - weak ridge formed from fusion of lath tips, without upgrowths.
CFCs - not differentiated.
XCs - conical (but usually flattened); rim elements L-shaped forming a proximally-directed wall. Broad lath cycle with sinistral obliquity (i.e. anti-clockwise in distal view). Central plate quadrate, formed of two large elements.
Coccospheres 5-7 μm; BCs 3-3.5 μm; XCs 1-2.5 μm

Syracosphaera ampliora Okada & McIntyre 1977

BCs - rim smooth, sutures slightly elevated, kinked showing distinct anticlockwise obliquity in outer part; radial laths often with median bulge, which may produce double cycle of perforations; axial structure - prominent rounded mound formed by fusion of laths.
CFCs - not differentiated.
XCs - usually absent, but two specimens of ours show single XCs; smaller than BCs, broadly elliptical, rim flat (without proximally-directed wall), radial laths stubby showing distinct obliquity, central plate quadrate.
NB This species is similar to *S. ossa* (and was illustrated as *S.* aff. *ossa* by Borsetti & Cati 1972, and Gaarder & Heimdal 1977) but BCs have narrower rim with prominent sutures, and their size and shape is less variable, also XCs wheel-like rather than undulating.
Coccospheres 6-10 μm; BCs 2-3 μm.

2.4.4 *S. halldalii* type - no XCs

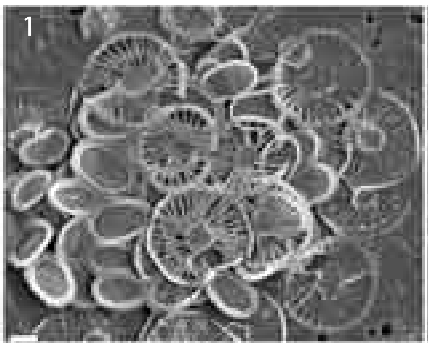
Monothecate - no XCs. These are common species, which have been very widely observed so it seems unlikely that exothecal coccoliths have been overlooked. BCs with horizontal flanges and vertical tubes.

Syracosphaera halldalii Gaarder, *in* Gaarder & Hasle 1971 ex Jordan & Green 1994

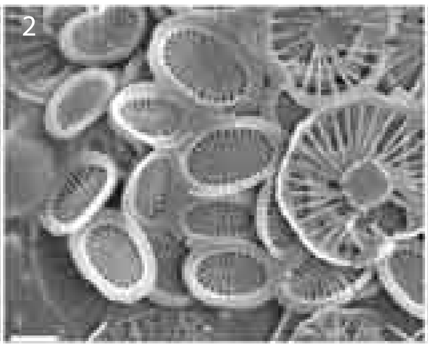
BCs - with narrow distal flange; flanges well-separated by vertical sided tube; laths well-separated; low axial ridge formed of one or two laths. Short teeth protruding over central area from distal flange occur in some specimens.
CFCs - with tall spine, quadrate section, blunt end.
Coccospheres 5-20 μm; BCs 2-4 μm.
NB This is the type species of *Caneosphaera* Gaarder *in* Gaarder & Heimdal 1977, it is normally combined in *Syracosphaera* following Jordan & Young (1990), but the consistent absence of XCs means reinstatement of the genus *Caneosphaera* may be justified.

Syracosphaera protrudens Okada & McIntyre 1977

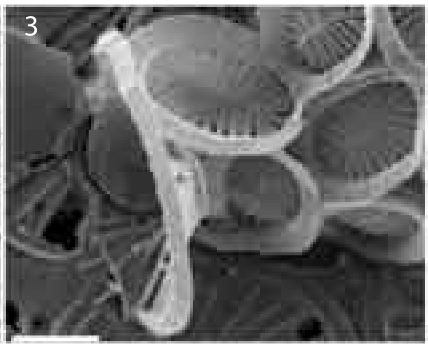
Very similar to *S. halldalii* but with narrower distal flange with sutural ridges (showing weak clockwise obliquity) and long teeth protruding over central area from distal flange. Often included in *S. halldalii* but separation of the two morphotypes is clear and consistent.



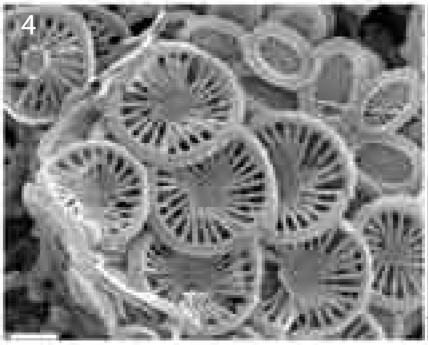
S. rotula



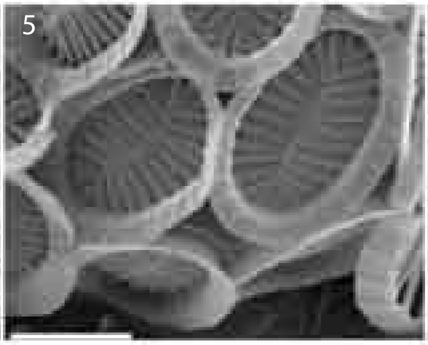
S. rotula



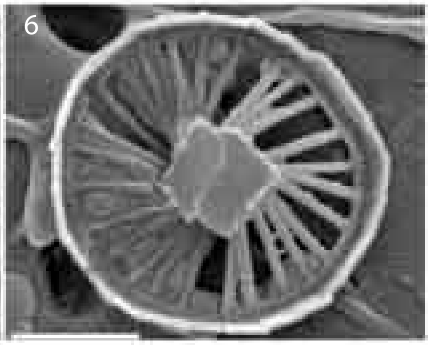
S. rotula XCs



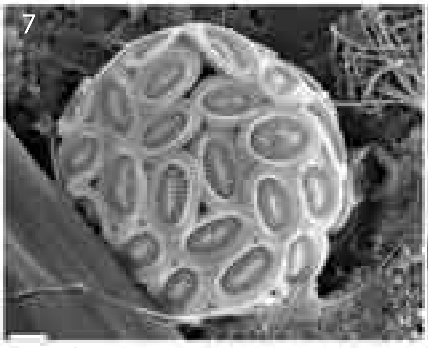
S. rotula



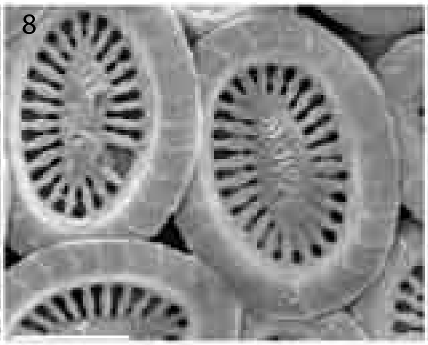
S. rotula



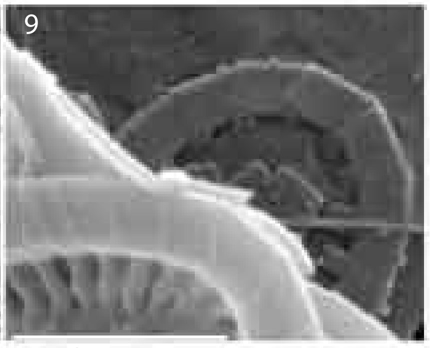
S. rotula XC (proximal)



S. ampliora

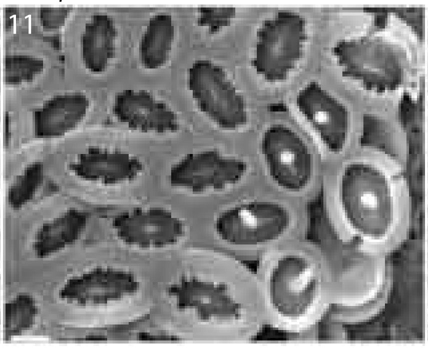


S. ampliora

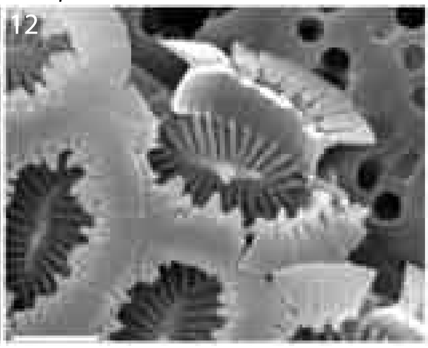


S. ampliora XC

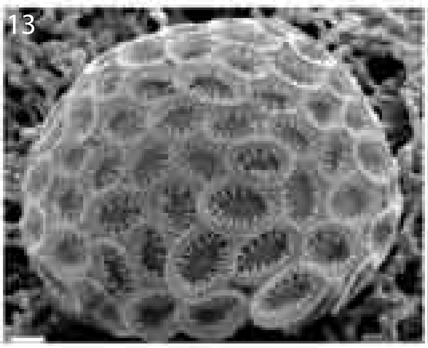
S. halldalii



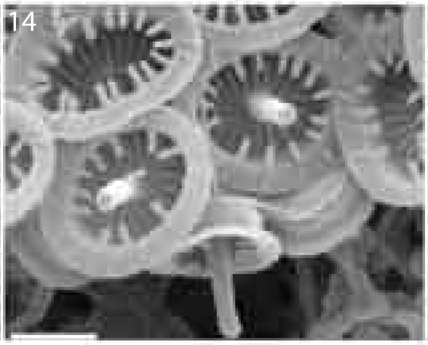
S. halldalii



S. halldalii



S. protrudens



S. protrudens

S. protrudens

Plate 22 - Syracosphaeraceae: *Syracosphaera, S. molischii* group

2.5 Syracosphaerales - Genus *incertae sedis Coronosphaera*

Coronosphaera Gaarder *in* Gaarder & Heimdal 1977

Monothecate, dimorphic, motile. BCs flangeless muroliths; rims formed of an outer cycle of strongly imbricate (anticlockwise) elements and an inner cycle of vertical elements. Two radial laths per rim element. CFCs similar but slightly smaller, with low spine. *Coronosphaera* is usually placed in the family Syracosphaeraceae. However, both the strong imbrication of the rim elements and the occurrence of two laths per rim are anomalous, so it is considered here to be a genus *incertae sedis* within the order Syracosphaerales. References: Gaarder & Heimdal (1977) - morphology; Geisen et al. (2002) - holococcolith associations; Houdan et al. (subm.) - culture observations. TYPE: *C. mediterranea*.

Coronosphaera mediterranea (Lohmann 1902) Gaarder, *in* Gaarder & Heimdal 1977 [*Syracosphaera*]

Coccospheres (sub-)spherical 12-20 μm. BCs elliptical (3-4 μm); low central mound formed of two irregular elements joined by transverse suture. Inner rim cycle lower than outer, forming shelf inside the lith.

Holococcolith associations (see also plate 50): three different holococcolith morphotypes have been shown to be associated with *C. mediterranea*.

1. *Calyptrolithina wettsteinii* - combination coccospheres figured in Kamptner (1941) and Cros et al. (2000).
2. *Calyptrolithophora hasleana* - combination coccospheres figured in Cortes & Bollmann (2002).
3. *Zygosphaera hellenica* - developed in culture isolate, Geisen et al. (2002).

The range of holococcolith morphologies developed suggests that *C. mediterranea* may comprise at least three species which cannot, yet, be differentiated on the basis of heterococcolith morphology (Geisen et al. 2002). NB Although the three holococcolith types have been placed in different genera they have common features, in particular they are all dimorphic with flat-topped BCs and zygolith CFCs.

Coronosphaera binodata (Kamptner 1927) Gaarder *in* Gaarder & Heimdal 1977 [*Syracosphaera*]

Like *C. mediterranea* but BCs with central mound divided into two nodes; rims broader.

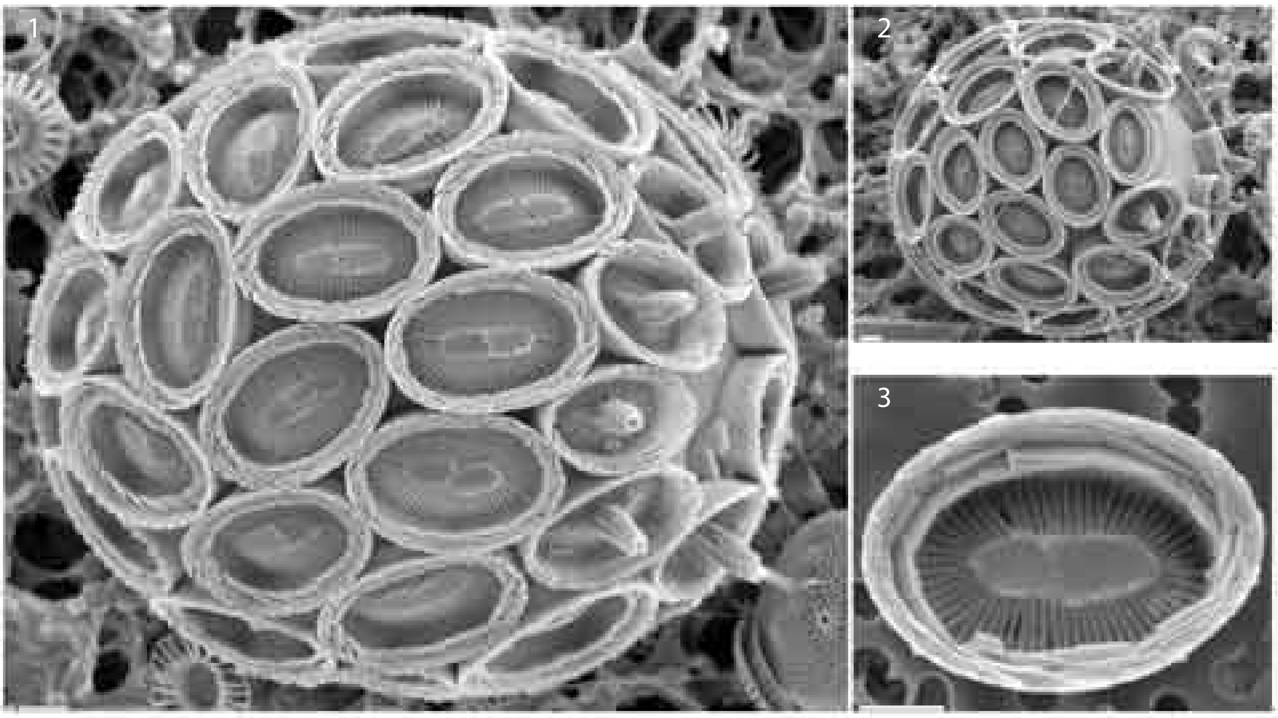
Coronosphaera maxima (Halldal & Markali 1955) Gaarder, *in* Gaarder & Heimdal 1977 [*Syracosphaera*]

Like *C. mediterranea* but larger coccospheres (25-40 μm) and BCs (3-6 μm); CFCs more elliptical. Very good specimen illustrated in Reid (1980, pl. 5/1-3). This is one of the largest extant coccolithophores.

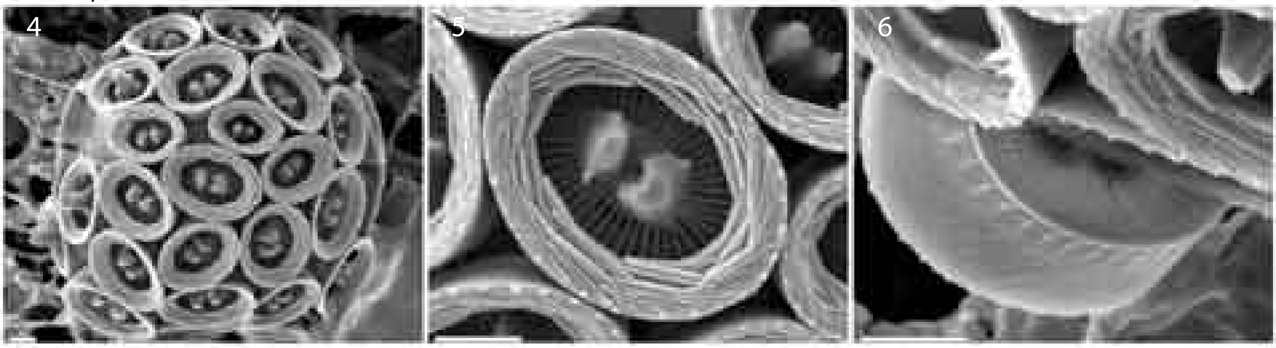
Coronosphaera sp.

Similar to *C. mediterranea* but wall is narrower and higher, lacking clear inner cycle and with small central spine. Figured by Kleijne (1993, pl. 3:3) as *C. mediterranea*, and by Winter et al. (1979, pl. IV fig. 2), as *C. mediterranea*.

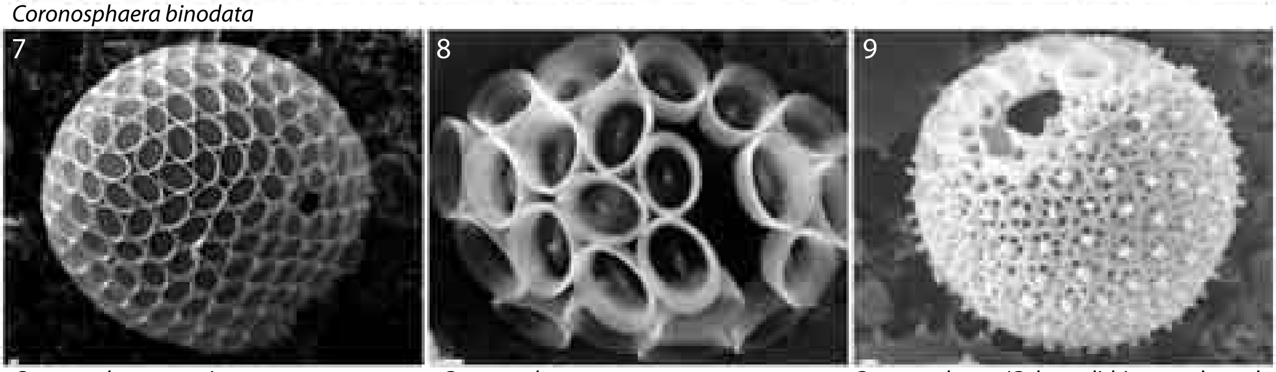
HOL ?= *Calyptrolithina* cf. *multipora*. A single combination coccosphere, illustrated here (plate 23, figs 9, 12) was found by Vita Pariente in the Gulf of Mexico. Definitive identification is not possible but it appears to consist of the same *Coronosphaera* species and a holococcolith similar to *Calyptrolithina multipora*, although with less pores than is usual.



Coronosphaera mediterranea



Coronosphaera binodata



Coronosphaera maxima *Coronosphaera* sp. *Coronosphaera/Calyptrolithina* comb. csph.

Coronosphaera maxima *Coronosphaera* sp. *Coronosphaera/Calyptrolithina* comb. csph.

Plate 23 - Syracosphaerales, genus incertae sedis: *Coronosphaera*

2.6 Calciosoleniaceae

Family **CALCIOSOLENIACEAE** Kamptner 1927

Motile with elongate, monothecate, fusiform coccospheres. Coccoliths are muroliths without flanges, usually termed scapholiths (synonym rhomboliths). The rim is predominantly formed of V-units, with small R-units at the base/inner margin (our obs.). The central-area has a single lath-cycle; pairs of laths from opposite sides of coccolith meet, forming transverse bars. Reference: Manton & Oates (1985) - coccolith structure.

This family is not recognised in some classifications of the extant coccolithophores, with the genera instead being included in the Syracosphaeraceae, mainly due to similarities between central-area structures. We prefer to maintain it as a separate family since the rim structure is not like that of typical Syracosphaeraceae. The group ranges back into the Mesozoic and may have evolved from the Stephanolithiaceae (see e.g. Perch-Nielsen 1985a, Bown & Young 1997).

There is a non-calcifying haptophyte *Navisolenia* Lecal 1965, which has an elongate test, covered in rhombic scales. As discussed by Leadbeater & Morton (1973) and Manton & Oates (1985) it is strikingly similar to *Calciosolenia*. These similarities include, in addition to basic form, the patterning of the base-plate scale and sense of asymmetry of the scales. Hence, it was included in the Calciosoleniaceae by Jordan and Green (1994). However, rhombic plates are clearly an efficient way to cover an elongate test and this basic morphology has almost certainly evolved separately in the genus *Placorhombus* (see below).

Calciosolenia Gran 1912 emend.

Coccosphere with rhombic muroliths (scapholiths); monomorphic or dimorphic. TYPE: *C. murrayi*. SYNONYMS: *Acanthosolenia* Bernard 1939; *Anoplosolenia* Deflandre 1952; *Scapholithus* Deflandre 1954. NB The monomorphic species *C. brasiliensis* is usually placed in a separate genus, *Anoplosolenia*, leaving the dimorphic species *C. murrayi* in *Calciosolenia*. We prefer to include both species in a single genus, since the coccolith structure of the two species is identical and their affinity is not in dispute. Including the two species in one genus makes this affinity clearer, reduces the number of monospecific genera, and avoids the problem of having generic concepts which cannot be applied to isolated coccoliths in the fossil record. As a result, the artificial genus *Scapholithus,* which is often used by palaeontologists for isolated scapholiths, becomes redundant, all such specimens can be included in *Calciosolenia*.

Calciosolenia murrayi Gran 1912

Coccosphere dimorphic, broad, tapering rather abruptly at ends with only a few elongate liths. Terminal liths have one end extended into spine. Bars not very regular and often merge into continuous sheet.
Liths 2-4 μm long, spines up to 25 μm, coccospheres up to 30 μm.

Calciosolenia brasiliensis (Lohmann 1919) Young n. comb. [*Cylindrotheca*]

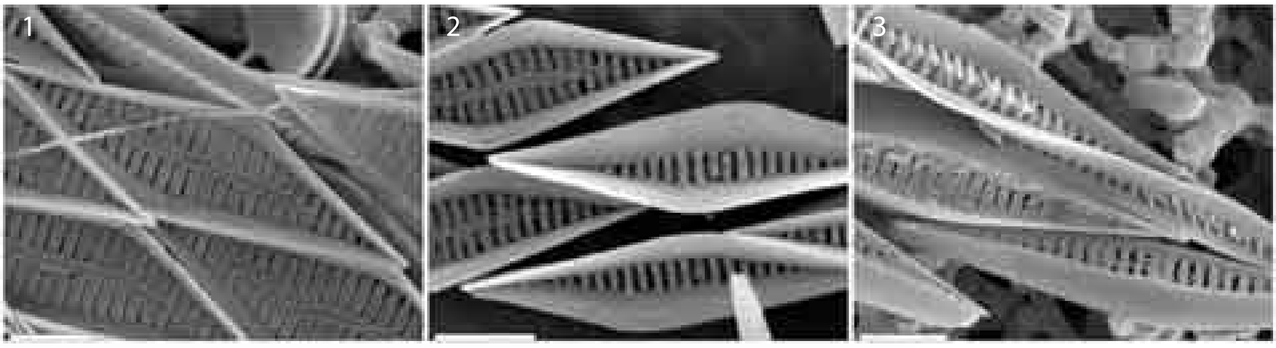
Coccosphere monomorphic, slender; ends tapered with many very elongate liths, but no spines. Liths have very regular bars, which offset neatly to form median ridge.
Liths typically larger than those of *C. murrayi*, 3-7 μm long.
Usually recorded as *Anoplosolenia brasiliensis*, see discussion of genus.

Alveosphaera Jordan & Young 1990

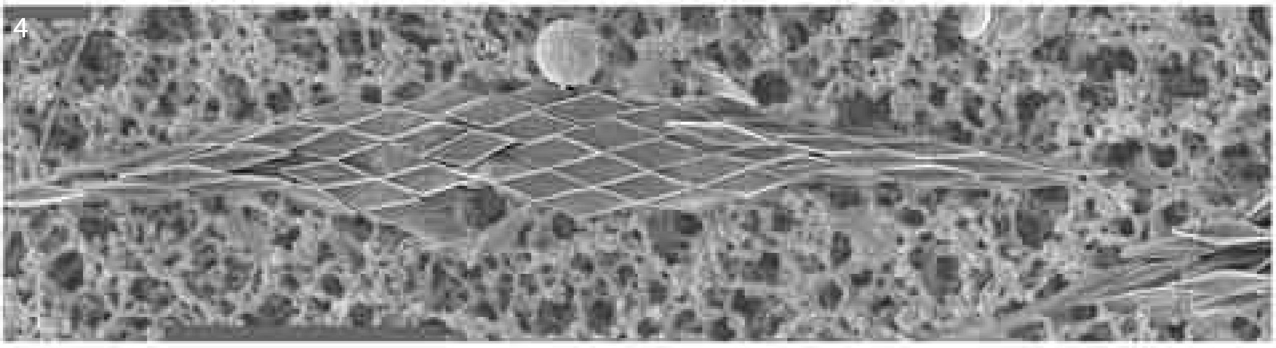
Monomorphic, coccoliths are elongate oblong muroliths, scapholith-like. TYPE: *A. bimurata*.

Alveosphaera bimurata (Okada & McIntyre 1977) Jordan & Young 1990 [*Calciosolenia*?]

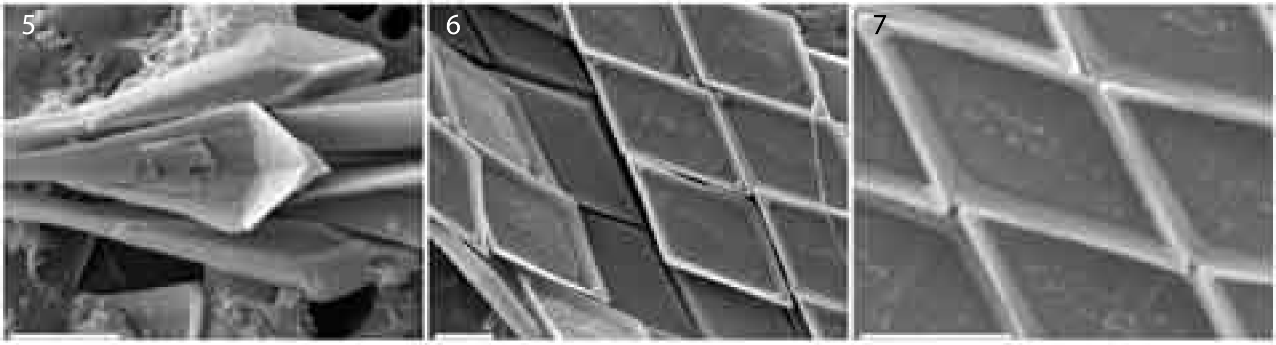
Coccosphere spindle-shaped. Rim relatively high, radial laths very delicate.



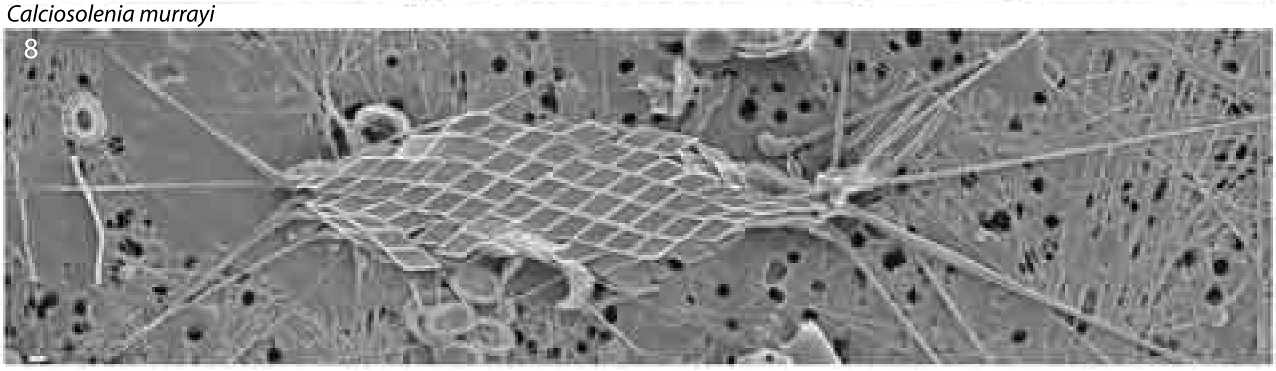
Calciosolenia brasiliensis



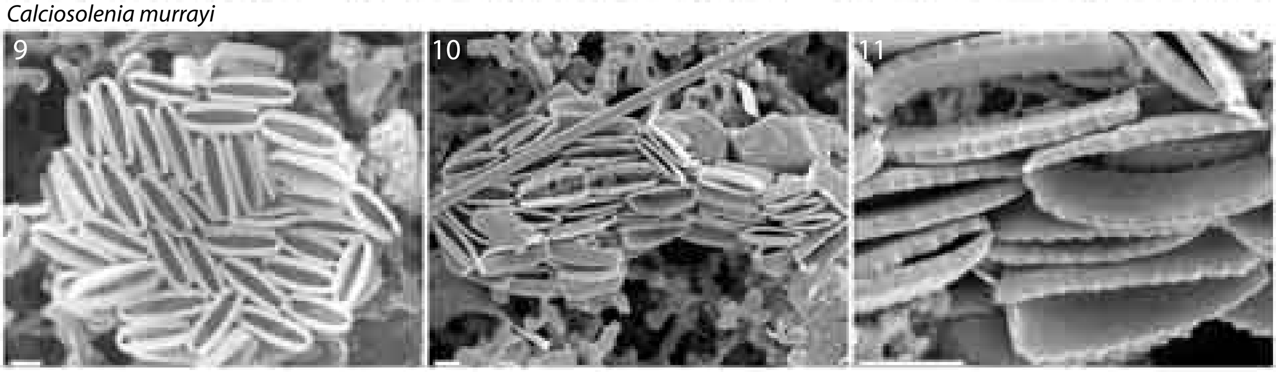
Calciosolenia brasiliensis



Calciosolenia murrayi



Calciosolenia murrayi



Alveosphaera bimurata

Plate 24 - Calciosoleniaceae: *Calciosolenia* & *Alveosphaera*

2.7 Rhabdosphaeraceae

Family **RHABDOSPHAERACEAE** Haeckel 1894

Motile or non-motile, typically with spine-bearing and non-spine-bearing coccoliths with similar shields, but polymorphic, varimorphic and monomorphic genera also occur. The spine-bearing coccoliths may be confined to the poles or distributed around the coccosphere, greatly increasing its outer diameter.

The coccoliths are typically disc-shaped (planoliths) and formed of three components.

1. Rim: narrow; slightly elevated; formed of two cycles of elements.
   Upper/outer rim cycle of simple non-imbricate elements (Kleijne 1992), these are V-units (our LM obs.).
   Lower/inner rim cycle showing strong obliquity. Crystallographic orientation uncertain.
2. Radial cycle - joins rim to central lamellar cycle; radial laths, of equal number to rim units; slits often present between the laths (absent in *Rhabdosphaera* and *Saturnulus*).
3. Lamellar cycle(s) - lamellar elements showing clockwise imbrication, often multiple cycles with inner cycles more elongate, inclined and in helical arrangement forming spine or protrusion. May end in a “cuneate cycle” of a few well-formed elements.

References: Extant species are reviewed by Norris (1984), Kleijne (1992), Aubry (1999), Cros & Fortuño (2002). Rhabdosphaeraceae are rare in the Neogene, but form a diverse and abundant group in the Eocene (Perch-Nielsen 1985b; Varol 1989; Shafik 1989; Aubry 1999).

2.7.1 *Rhabdosphaera* & *Palusphaera*

Rhabdosphaera Haeckel 1894

Dimorphic (arguably dithecate) with inner spine-bearing and outer non spine-bearing coccoliths, distributed around coccosphere. Radial cycle absent, lamellar cycle fills central area and forms spine. TYPE: *R. clavigera*. SYNONYM: *Rhabdolithus* Kamptner ex Deflandre in Grassé 1952.

Rhabdosphaera clavigera Murray & Blackman 1898

Spines robust, formed of five clockwise-spiral sets of elements with pentameral terminal papilla. Lith bases elliptical/oblong, 3-3.5 μm. Spine-bearing liths with wider rim than non spine-bearing liths.

SYNONYM: *R. stylifera* Lohmann 1902. Forms with club-shaped (*clavigera*) and narrower parallel-sided (*stylifera*) spines are often separated as varieties of *R. clavigera*. However the two types intergrade and both can be found on single coccospheres, so this is evidently an example of degree of calcification variation rather than genotypic variation. Hence, taxonomic names should not be used for the different morphotypes, although it may be useful to informally differentiate them for ecological studies.

HOL ?= *Sphaerocalyptra quadridentata*, see Cros & Fortuño (2002).

Rhabdosphaera xiphos (Deflandre & Fert 1954) Norris 1984 [*Rhabdolithus*]

Ordinary liths broadly elliptical. About 9 relatively large, imbricate, plates of lamellar cycle, produce a distinctive star pattern on the distal surface. Spine-bearing liths circular, spines long (6-7 μm) delicate and tapering, with collar near base.

[*Rhabdosphaera longistylis* Schiller 1925]

This is probably not a coccolithophore, see Norris (1984).

Palusphaera Lecal 1965 emend. Norris 1984

Monomorphic, all liths have long spines. Radial cycle absent. TYPE: *P. vandelii*.

Palusphaera vandelii Lecal 1965 emend. Norris 1984

Long (>10 μm) delicate tapering spines without collar. Basal disk circular, with broad rim on distal side.

Palusphaera sp. 1 of Cros & Fortuño (2002)

Form with robust spines and maximum spine thickness approximately 1/3 up spine. As noted by Cros & Fortuño (2002), this is probably a separate species, but may prove to be merely a more calcified version of *P. vandelii*.

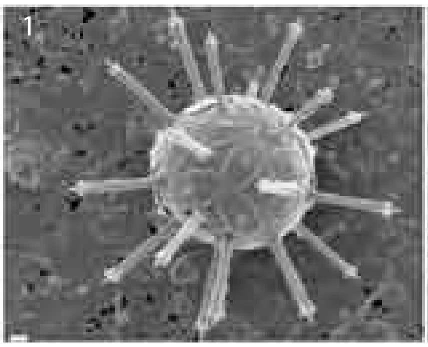
2.7.2 *Discosphaera*

Discosphaera Haeckel 1894

Monomorphic, with trumpet-like (salpingiform) spines. Coccolith bases broadly elliptical, with normal rim, radial and lamellar cycles. Spine circular, weakly attached above narrow pore in centre of the base, by organic (?) thread. TYPE: *D. thomsonii* Ostenfeld 1899 (j. syn of *D. tubifera*).

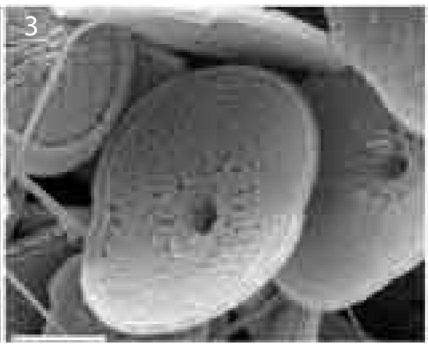
Discosphaera tubifera (Murray & Blackman 1898) Ostenfeld 1900 [*Rhabdosphaera*]

The only described species, see generic description. Common in oligotrophic surface waters.

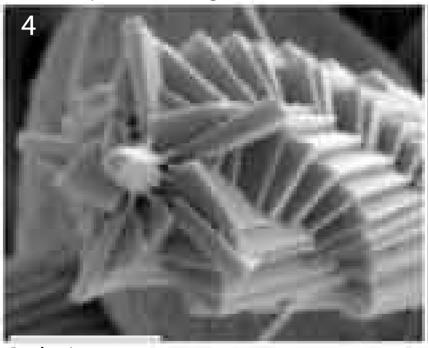


Rhabdosphaera clavigera

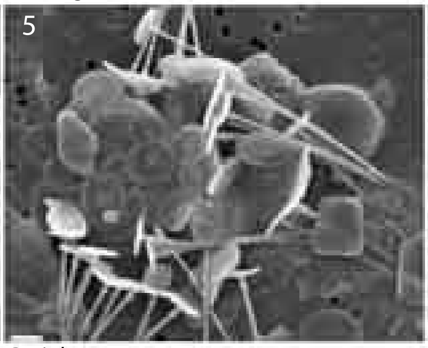
R. clavigera



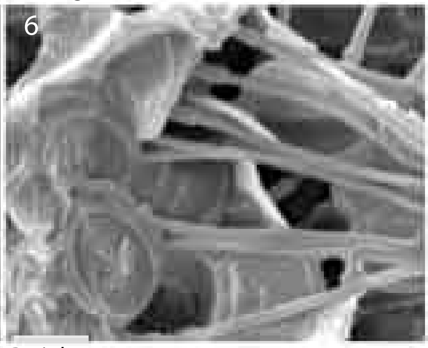
R. clavigera



R. clavigera

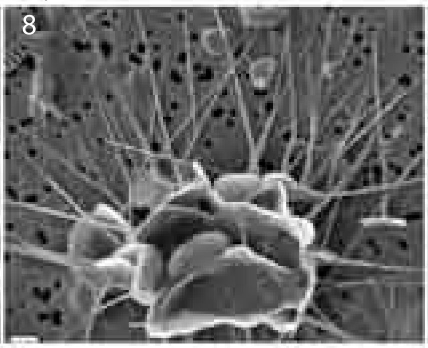


R. xiphos

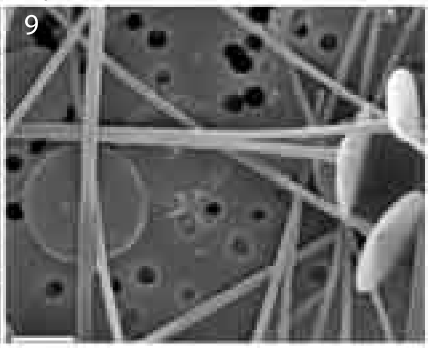


R. xiphos

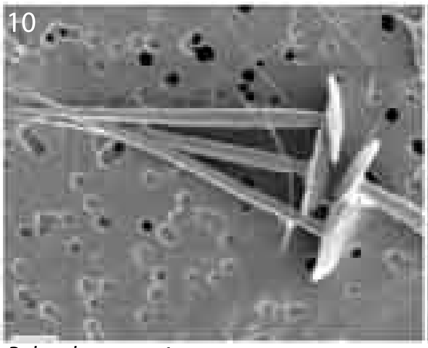
R. xiphos



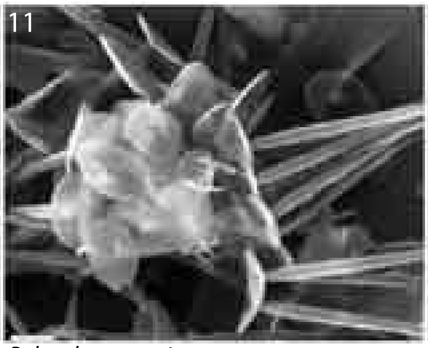
Palusphaera vandelii



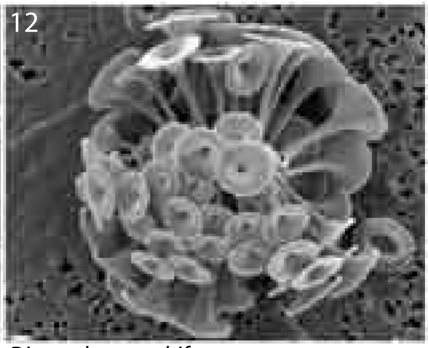
P. vandelii



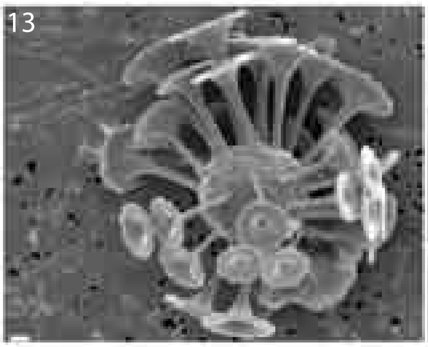
Palusphaera sp. 1



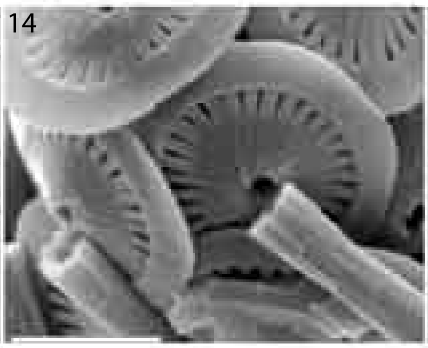
Palusphaera sp. 1



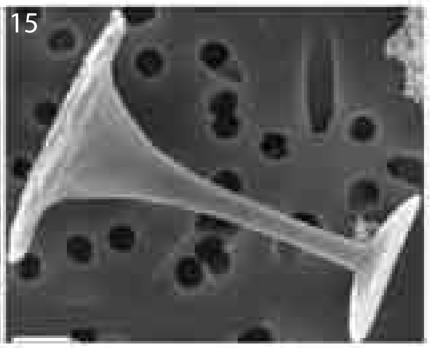
Discosphaera tubifera



Discosphaera tubifera



D. tubifera



D. tubifera

Plate 25 - Rhabdosphaeraceae: *Rhabdosphaera, Palusphaera* & *Discosphaera*

2.7.3 *Acanthoica*

Acanthoica Lohmann 1903 emend. Schiller 1913 and Kleijne 1992

Polymorphic with characteristic set of apical and antapical spines shown by all species, though some individual specimens may depart from standard pattern. TYPE: *A. quattrospina*. The following coccolith types occur:

1. Body coccoliths; well-developed radial cycle, usually with openings; lamellar cycle forms low solid cone or hollow protrusion.
2. Four circum flagellar coccoliths, with spine formed by lamellar cycles. 3 with short spines, 1 with long spine.
3. Two antapical coccoliths; very long spines, basal disk folded with broad rim but no radial cycle.

Acanthoica quattrospina Lohmann 1903

Most common species. Body coccoliths sub-circular, (1.5-2.5 μm), with slits between radial cycle elements, lamellar cycle makes low cone. Long spines on polar coccoliths (one or both ends). SYNONYM: *Acanthoica coronata* Lohmann (1903) spines at one end only, but this is probably a result of incomplete coccosphere formation.
HOL = form with affinities to *Sphaerocalyptra*, not separately described (Cros et al. 2000).

Acanthoica janchenii Schiller 1925

Like *A. quattrospina,* but with no gaps between radial cycle elements. This is an uncertain distinction, since intermediates and coccospheres with both types occur.

Acanthoica acanthifera Lohmann 1912 ex Lohmann 1913

Like *A. quattrospina* but lamellar cycle forms hollow protrusion.

Acanthoica biscayensis Kleijne 1992

Like *A. quattrospina* but liths larger (2.5-3 μm), oblong, no gaps between radial cycle elements.

Acanthoica maxima Heimdal *in* Heimdal & Gaarder 1981

Like *A. quattrospina* but liths larger (3.5-4 μm), elongate oblong, with gaps between radial cycle elements.

[*Acanthoica ornata* Conrad 1928 - freshwater, no modern records]

[*Acanthoica schilleri* Conrad 1928 - freshwater, no modern records]

2.7.4 *Anacanthoica* & *Cyrtosphaera*

These genera have similar body coccoliths to those of *Acanthoica,* but lack the specialised apical coccoliths.

Anacanthoica Deflandre 1952

Monomorphic, no spines, otherwise similar to *Acanthoica*. TYPE: *A. acanthos*.

Anacanthoica acanthos (Schiller 1925) Deflandre 1952 [*Acanthoica*]

Coccoliths with broad rim, 24-35 laths, low conical protrusion.

Anacanthoica cidaris (Schlauder 1945) Kleijne 1992 [*Acanthoica*]

Coccoliths with narrow rim, broadly elliptical with slight inflection on sides; 44-60 laths; sharp conical “witches’ hat” protrusion. NB Differs from *Cyrtosphaera aculeata* in being monomorphic and protrusions do not end terminal papillae.

Cyrtosphaera Kleijne 1992

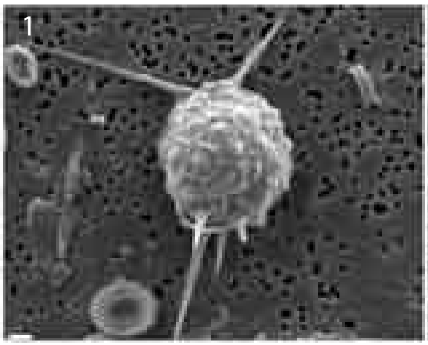
Vari-monomorphic, with protrusions on all coccoliths, higher toward the flagellar pole. TYPE: *C. aculeata*.

Cyrtosphaera aculeata (Kamptner 1941) Kleijne 1992 [*Acanthoica*]

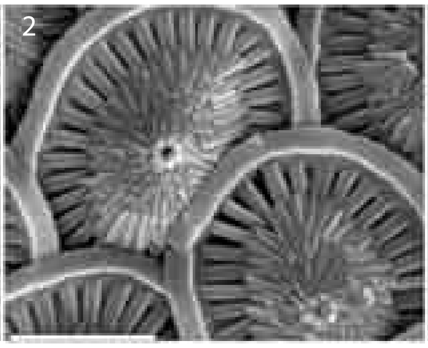
Coccoliths like *A. cidaris,* but protrusion ends in papilla; protrusion modified into spine in apical liths. 26-38 laths, 1.8-2.5 μm.

Cyrtosphaera lecaliae Kleijne 1992

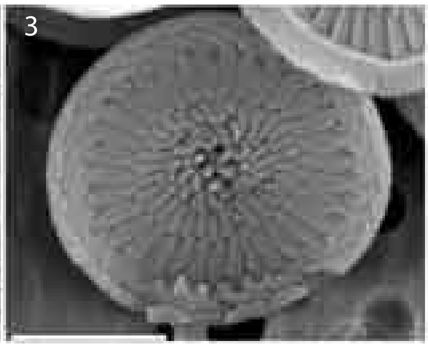
Like *C. aculeata*, but coccoliths larger, CFC spines better developed, BC papillae less prominent, 42-52 laths, 2.5-3.5 μm.



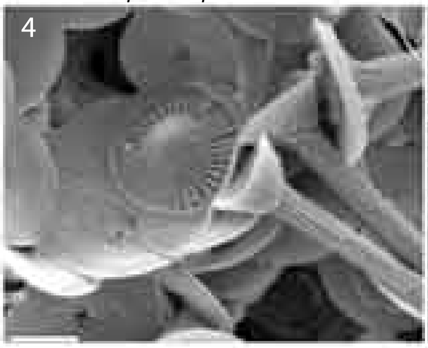
Acanthoica quattrospina



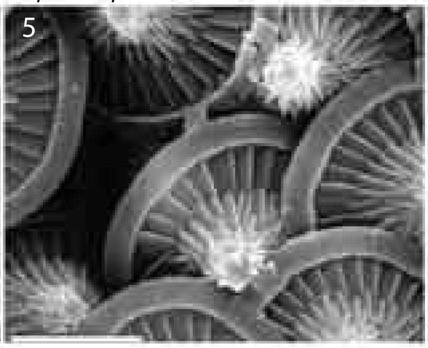
A. quattrospina



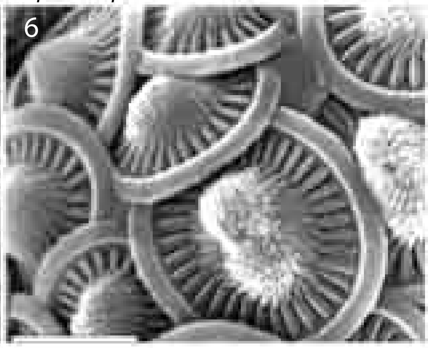
A. quattrospina



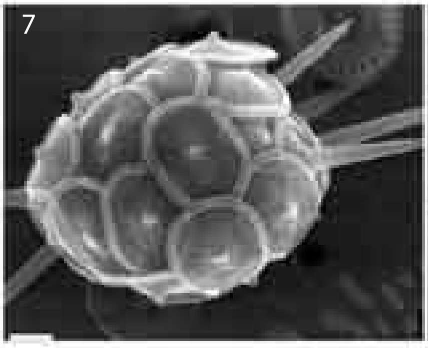
A. quattrospina



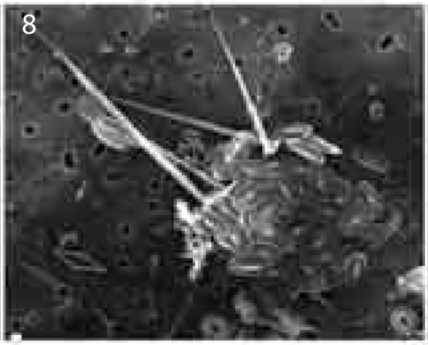
A. janchenii



A. acanthifera

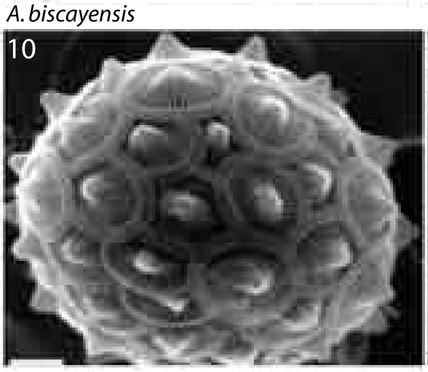


A. biscayensis



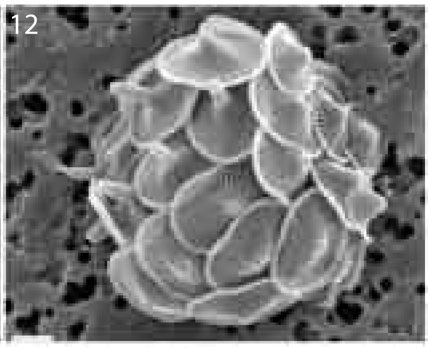
A. maxima

Anacanthoica cidaris

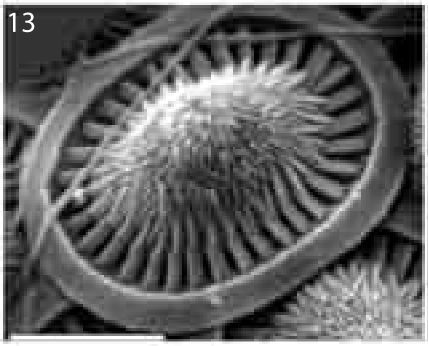


Anacanthoica acanthos

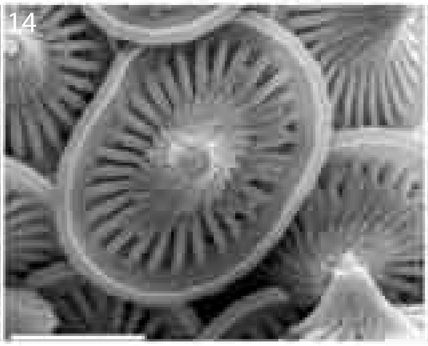
Cyrtosphaera aculeata



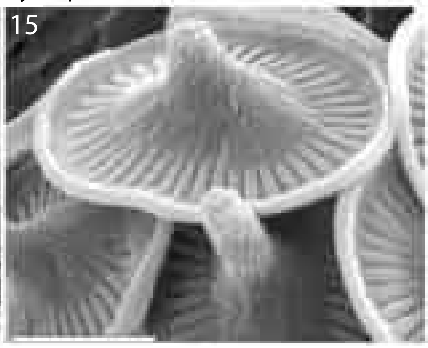
Cyrtosphaera lecaliae



Anacanthoica acanthos



Cyrtosphaera aculeata



Cyrtosphaera lecaliae

Plate 26 - Rhabdosphaeraceae: *Acanthoica, Anacanthoica* & *Cyrtosphaera*

2.7.5 *Algirosphaera*

Algirosphaera Schlauder 1945 emend. Norris 1984

Lamellar cycle modified into/replaced by elongate domal or double-lipped (labiatiform) protrusion, rim and radial cycle normal. The species were often placed in *Anthosphaera* in the older literature (see Aubry 1999 for full discussion). TYPE: *A. oryza* (subj. j. syn of *A. robusta*).

Algirosphaera robusta (Lohmann 1902) Norris 1984 [*Syracosphaera*]

Coccosphere dimorphic. Prominent flagellar opening surrounded by 3 CFCs with higher and wider protrusion. Cycle of irregular laths cover proximal face of central area.

SYNONYMS: *A. oryza* Schlauder 1945; *A. quadricornu* (Schiller 1914) Norris 1984 [*Syracosphaera*]; *A. aurea* (Bernard & Lecal 1960) [*Anthosphaera*]; *Anthosphaera bicornu* Schlauder 1945; and others, see Kleijne (1992). Subdivisions on nature of circum-flagellar coccoliths, coccosphere shape, and shape of body coccoliths have been suggested but do not seem meaningful (Kleijne 1992, Probert et al., in prep.).

HOL - combination coccospheres with *Sphaerocalyptra quadridentata* have been illustrated by Kamptner (1941) and Triantaphyllou & Dimiza (2003).

Algirosphaera cucullata (Lecal-Schlauder 1951) Young, Probert & Kleijne n. comb. [*Acanthoica*]

Coccosphere weakly varimorphic (protrusions rather higher toward apical pole). Liths with domal protrusion, “bowler hat” shaped. Like *Algirosphaera robusta* but lacks discrete polar coccoliths; liths are less elongate; and protrusion is covered by elongate needle-like elements, rather than tile-like elements. Placed in *Cyrtosphaera* by Kleijne 1992 on the basis of varimorphism but the coccolith structure is closer to *A. robusta* than to *C. aculeata*.

Algirosphaera meteora (Muller 1972) Norris 1984 [*Anthosphaera*]

Coccosphere monomorphic. Coccoliths broadly elliptical, with constriction around base of the spine; proximal surface lacks central irregular cycle.

2.6.6 “Saturnulus”

n. gen. “Saturnulus” (Østergaard et al. *in* prep.)

Very small polymorphic forms with protrusion-bearing equatorial coccoliths, (coccospheres ca 5 μm, liths 1-1.5 μm). Deep-photic zone, rare.

Equatorial coccoliths have protrusion reminiscent of that of *Algirosphaera*, which is the main grounds for tentative inclusion here in the Rhabdosphaeraceae - the bases do not show obvious *Rhabdosphaera* structure. Body coccoliths simpler disks in most species, usually two body coccolith types present. These forms are comprehensively described in Østergaard et al. (in prep.), but since this paper has not been published yet the manuscript names given in it have no current validity and so are given in inverted commas and are not italicised.

n. gen. sp. 1 (“S. emidasius” *in* Østergaard et al. in prep.)

Trimorphic. (a) Equatorial coccoliths with sub-rectangular protrusions and quadrate base. (b) Weakly calcified (?) elliptical body coccoliths without protrusions; (c) A few heavily calcified body coccoliths.

n. gen. sp. 2 (“S. blagnacensis” Bollmann *in* Østergaard et al. in prep.)

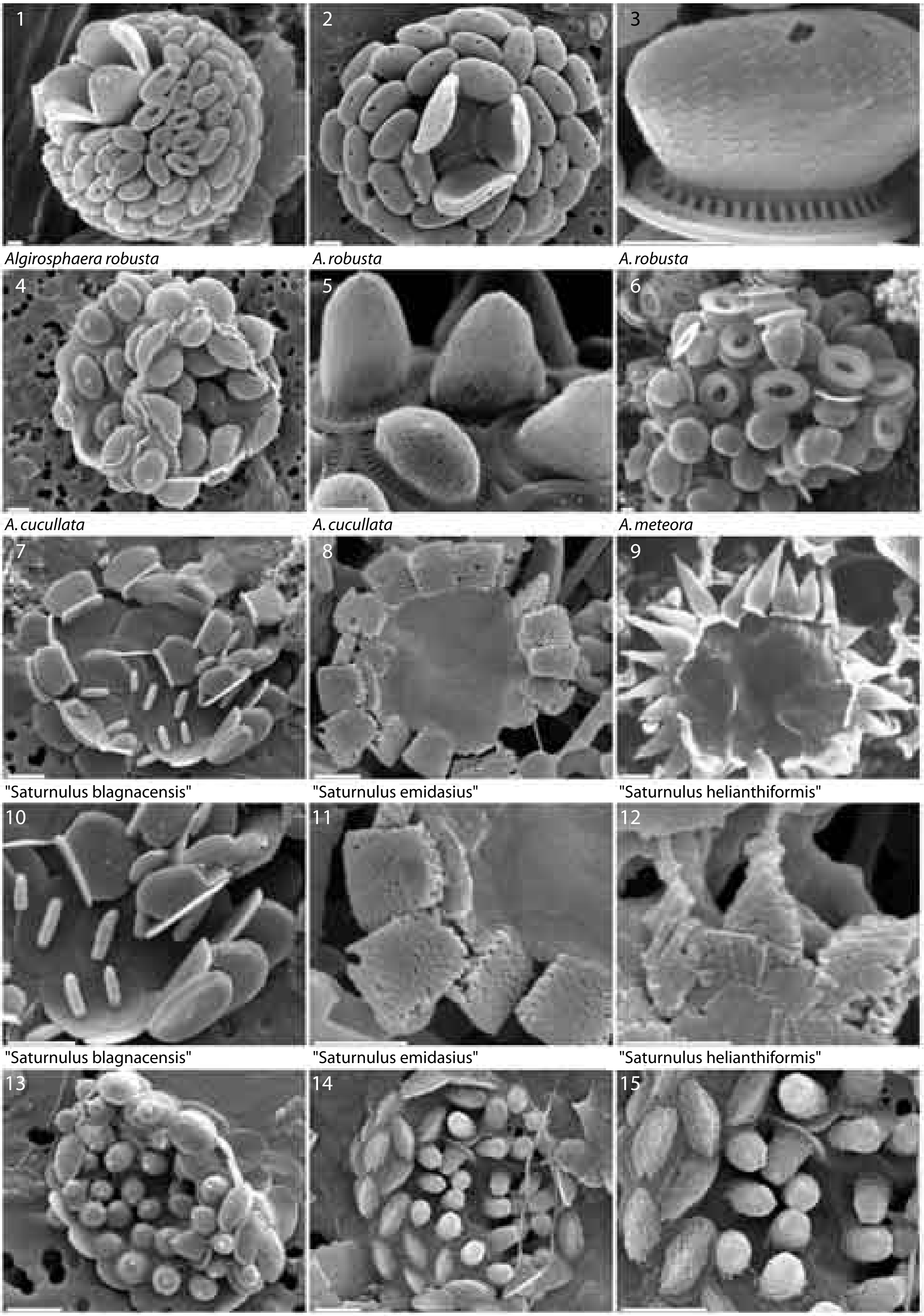
Trimorphic. (a) Equatorial coccoliths with rounded protrusions; (b) Body coccoliths with smaller rounded protrusions; (c) Body coccoliths without protrusions. (NB The two body coccolith types appear to occur on opposite sides of the coccosphere).

n. gen. sp. 3 (“S. helianthiformis” *in* Østergaard et al. in prep.)

Trimorphic. (a) Equatorial coccoliths with elongate triangular-shaped, slightly twisted, protrusions and quadrate bases. (b) Weakly calcified elliptical body coccoliths without protrusions. (c) A few heavily calcified body coccoliths.

n. gen. sp. 4 = Coccolithophore sp. 1 of Cros & Fortuño (2002, p. 70, fig. 110 C-D)

Trimorphic. (a) ?Equatorial coccoliths with elongate hump-backed protrusions and elliptical bases. (b) circular body coccoliths with tower-like protrusions; (c) broadly elliptical coccoliths with low protrusions.



1 *Algirosphaera robusta*; 2 *A. robusta*; 3 *A. robusta*

4 *A. cucullata*; 5 *A. cucullata*; 6 *A. meteora*

7 "Saturnulus blagnacensis"; 8 "Saturnulus emidasius"; 9 "Saturnulus helianthiformis"

10 "Saturnulus blagnacensis"; 11 "Saturnulus emidasius"; 12 "Saturnulus helianthiformis"

13 "Saturnulus" sp.; 14 "Saturnulus" sp.; 15 "Saturnulus" sp.

Plate 27 - Rhabdosphaeraceae: *Algirosphaera* & "Saturnulus"

3 Heterococcolith families and genera *incertae sedis*

This diverse set of taxa all show basic heterococcolith features, but do not show clear affinities to any of the order level groups. More precisely, we predict that all these forms will prove to be diploid phase coccolithophores, but we are unable to predict where they will fall within the phylogeny of the coccolithophores. Future culture studies or molecular genetic work should resolve this uncertainty.

3.1 Alisphaeraceae - *Alisphaera* and *Canistrolithus*

Family **ALISPHAERACEAE** new family. Young, Kleijne & Cros

Diagnosis: Coccolithophores, dominant stage of life-cycle typically: motile, bearing heterococcoliths arranged in meridional rows. Coccoliths asymmetrical with edge directed toward flagellar opening extended into a flange or protrusion. Entire coccolith formed of rim units; proto-coccolith ring locus within tube; V-units form upper tube and distal flange; R-units form two-layered lower tube and proximal structures, sometimes with distal extension.

Alternate life-cycle phase typically: motile, bearing quadrate, aragonitic, nannoliths. Nannoliths with conical upper part and cruciform base.

NB The Latin diagnosis is given in an appendix.

Type genus: *Alisphaera* Heimdal 1973.

Taxa included: The genera *Alisphaera*, and *Canistrolithus* are combined in this family on the grounds of very similar, and distinctive coccolith structure. *Polycrater* is included following observation of combination coccospheres (Cros & Fortuño 2002). This is an aragonitic nannolith (Manton & Oates 1980, Young et al. 1999) and strongly supports the family-level separation of this group.

Life-cycles and culture studies: None of these species have been cultured yet. Observations of combination coccospheres of *Alisphaera* with *Polycrater* and of *Canistrolithus* with *Polycrater* suggest that these are alternate phases (Cros et al. 2000a, Cros & Fortuño 2002). By analogy with other taxa, we predict that the heterococcolith phase (*Alisphaera*/*Canistrolithus*) is diploid and that the nannolith phase (*Polycrater*) is haploid.

Heterococcolith structure: As discussed by Kleijne et al. (2002),, the proto-coccolith ring is located approximately halfway up the tube. Our LM observations indicate that the upper unit (D-unit of Kleijne et al. 2002) is the V-unit, this forms the distal flange and upper tube. The R-unit forms the inner and outer layers of the lower tube (with slightly different imbrication directions), and in *Alisphaera* the proximal flange and irregular central area grill.

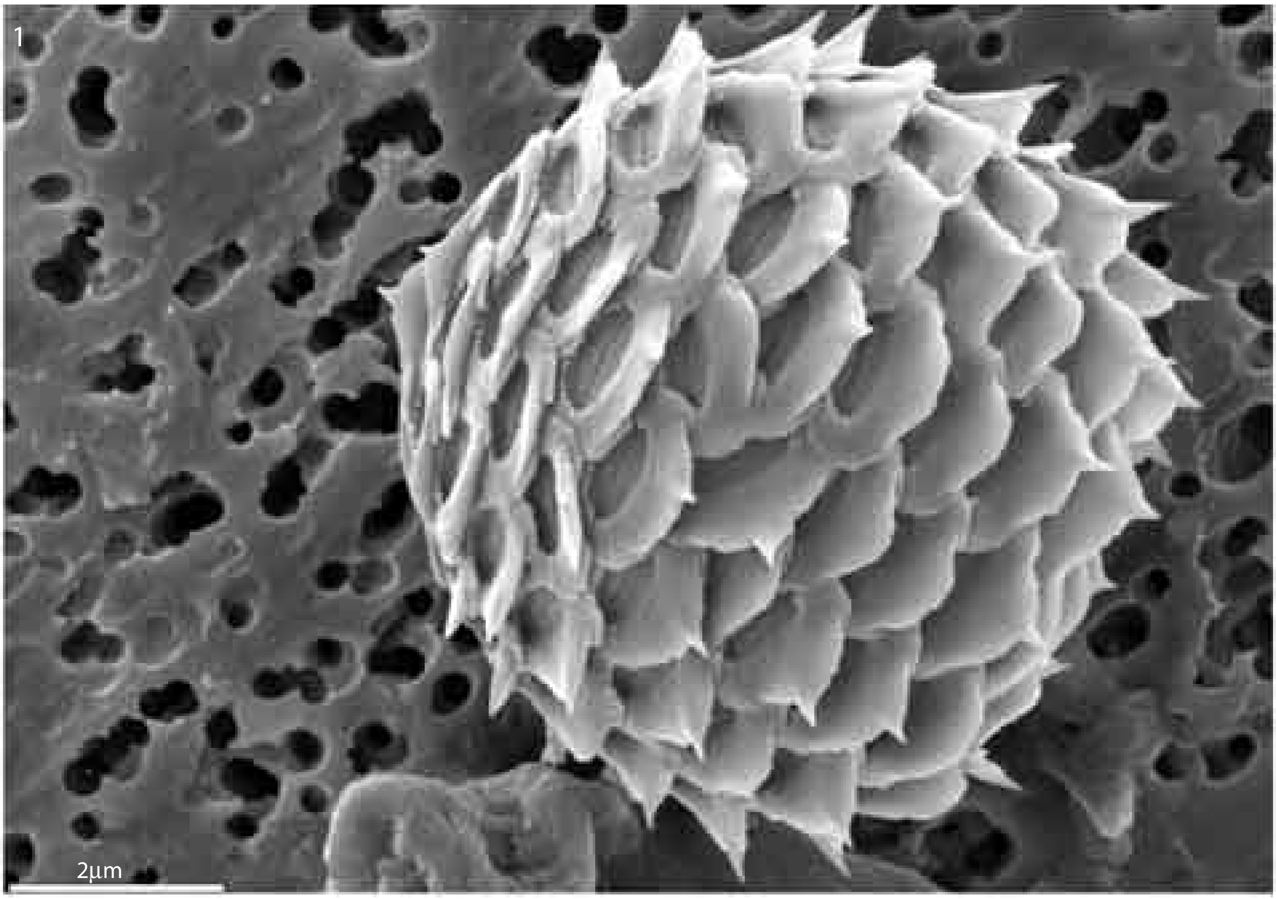
Alisphaera Heimdal 1973

Coccosphere monothecate, ellipsoidal with apical opening. Coccoliths arranged on coccosphere with long axis aligned equatorially and broader flange directed toward apical opening.

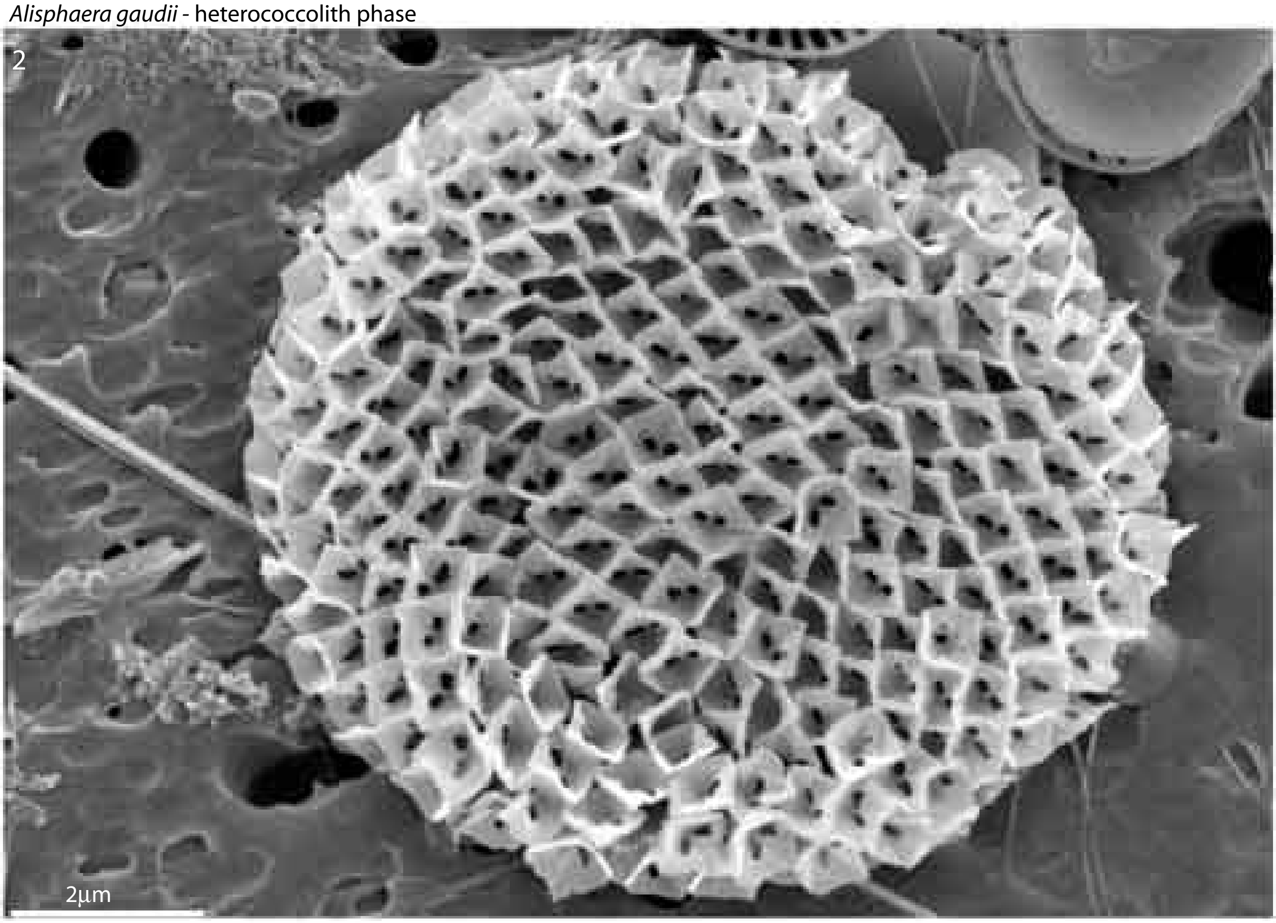
Coccoliths placolith-like, with asymmetrical distal flange, one side broader with a variable extension, other side narrow and in many species with 8-10 teeth projecting into central area. Plate in central area formed by extension of tube elements inward, usually with irregular central fissure. No discrete CFCs. Combination cells of *Polycrater* sp. and *Alisphaera gaudii* have been observed (Cros et al. 2000a, Cros & Fortuño 2002). TYPE: *A. ordinata*.

The species-level taxonomy of the genus was reviewed by Jordan & Chamberlain (1993) and by Kleijne et al. (2002). NB As well as describing new species Kleijne et al (2002) significantly revised the taxonomic concepts of *A. unicornis* and *A. spatula*. Essentially *A. unicornis* sensu Jordan & Chamberlain (1993) corresponds to *A. gaudii* whilst *A. spatula* sensu Jordan & Chamberlain (1993) corresponds to *A. unicornis* sensu Kleijne et al. (2002). The confusion stems from the fact that Okada & McIntyre (1977) illustrated two rather different specimens as *A. unicornis*, See Kleijne et al. (2002) for detailed synonymies.

The notes below are based on Kleijne et al. (2002), but with the species arranged in three groups for clarity. Some of the species are based on very few specimens and further research may result either in differentiation of more species, or some lumping.



Alisphaera gaudii - heterococcolith phase



Alisphaera gaudii - polycrater phase

Plate 28 - Alisphaeraceae

3.1.1 *Alisphaera unicornis* group; distal flange with spike-like protrusion formed from a single element, or smooth

Alisphaera unicornis Okada & McIntyre 1977
Most coccoliths with well-developed horn-like spine on broad margin of flange. Inner margin of distal flange smooth, without teeth. The most commonly recorded species.
Liths 2-3 μm long.

Alisphaera spatula Steinmetz 1991 *(not figured)*
Similar to *A. unicornis*, and poorly differentiated from it, but spine flatter and broader, coccolith smaller and bearing teeth.

Alisphaera pinnigera Kleijne et al. 2002
Dimorphic, most coccoliths with no protrusion, a few with a sharp spike-like protrusion. Coccoliths also smaller and smoother than those of *A. unicornis* with narrower central area and well-developed teeth (but often hidden on the coccosphere by the overlapping flange of the adjacent coccolith).
Liths 1.3-2.0 μm long.

Alisphaera uncinata Kleijne et al. 2002 *(not figured)*
Similar to *A. pinnigera* but protrusion hook-like and only present on a few (ca. 4) coccoliths.
Liths 1.5-1.7 μm long.

3.1.2 *Alisphaera capulata* group; distal flange with sub-vertical extension

Alisphaera capulata Heimdal *in* Heimdal & Gaarder 1981
Flange extension sub-vertical, L-shaped. Central area elements short, leaving wide central opening instead of narrow fissure (but organic scale often present in central area).
Coccoliths 1.4-1.7 μm long.

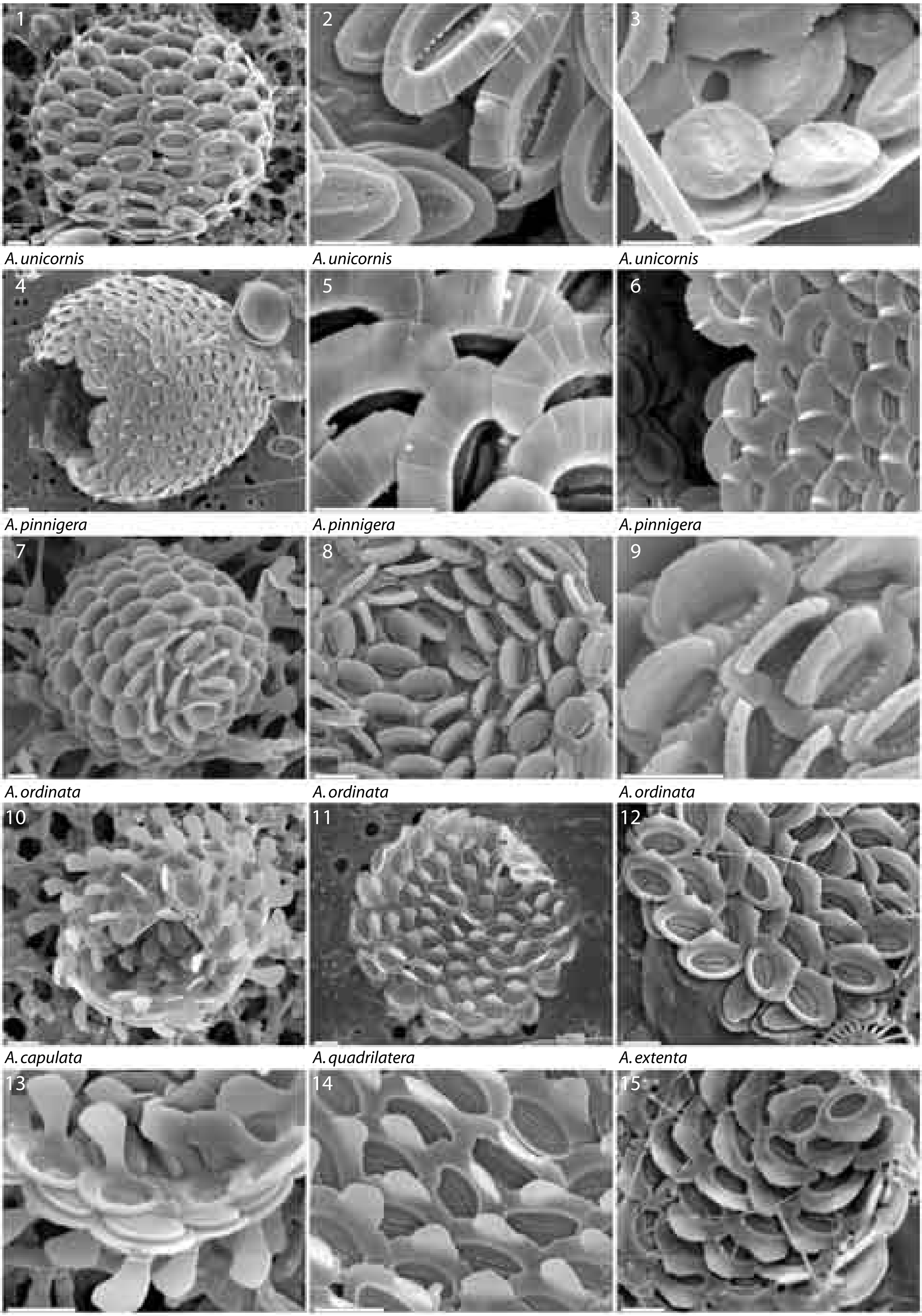
Alisphaera ordinata (Kamptner 1941) Heimdal 1973 [*Acanthoica*]
Flange extension a rounded sub-vertical wing extending the full length of the central area. Teeth well-developed.
Liths 1.1-2.3 μm long.

Alisphaera quadrilatera Kleijne et al. 2002
Flange extension sub-vertical, angular with sub-parallel sides and pointed end. Similar to *A. capulata* but with distinct central fissure and flange extension simpler.
Liths 1.4-1.8 μm long.

3.1.3 *Alisphaera extenta* group; distal flange with wing-like extension

Alisphaera extenta Kleijne et al. 2002
Broad side of flange extended into pointed wing. In oblique and side views it can be seen that the wing flares upwards and ends in sub-vertical wall. Teeth absent.
Liths 1.1-2.3 μm long.

Alisphaera gaudii Kleijne et al. 2002 *(figured on plates 28 & 30)*
Similar to *A. extenta* but more ornate and varimorphic, wing extended into a sharply pointed spur in some specimens. Teeth well developed. Combination coccospheres with "*Polycrater*" coccoliths observed (Cros & Fortuño 2002).
Liths 1.6-2.0 μm long.



1 *A. unicornis*
2 *A. unicornis*
3 *A. unicornis*
4 *A. pinnigera*
5 *A. pinnigera*
6 *A. pinnigera*
7 *A. ordinata*
8 *A. ordinata*
9 *A. ordinata*
10 *A. capulata*
11 *A. quadrilatera*
12 *A. extenta*
13 *A. capulata*
14 *A. quadrilatera*
15 *A. extenta*

Plate 29 - Alisphaeraceae: *Alisphaera*

3.1.4 *Canistrolithus*

Canistrolithus Jordan & Chamberlain 1993

Monothecate, coccoliths are elongate, oblong, muroliths with an asymmetric distal flange. Outer tube wall elements show weakly anticlockwise imbrication; inner tube wall elements vertical. In Comparison To Alisphaera, there is no proximal flange or grill and the tube is higher, but basic structure appears similar (Kleijne et al. 2002). TYPE: *C. valliformis*.

Canistrolithus valliformis Jordan & Chamberlain 1993 *(not figured)*

Dimorphic - some coccoliths have distally directed spine on one side of coccolith. Row of peg-like nodules around central opening. Central area open.

Canistrolithus sp. 1 of Cros & Fortuño (2002)

Dimorphic; no peg-like nodules around central opening; special coccoliths with spine asymmetrically placed on one end of coccolith. Combination coccospheres with "*Polycrater*" coccoliths observed.

3.1.5 *Polycrater* phase

Polycrater Manton & Oates 1980

Coccoliths are aragonitic; quadrate in plan view, hour-glass shaped in profile; *ca.* 1 μm across; formed of upper cone and a cross-shaped base of four feet. Very numerous coccoliths on each coccosphere, spirally arranged. TYPE: *P. galapagensis*.

Cros & Fortuño (2002) have shown that *Polycrater* forms combination coccospheres with *Alisphaera* and *Canistrolithus*. They also showed that a range of different morphotypes can be recognised, including forms with holes, skeletal forms, and forms with tubercles ("dots"). These morphotypes are mostly based on rather few specimens, so it is conceivable that they intergrade. However, since there are numerous *Alisphaera* spp., we suspect that most of them will prove to be discrete forms each forming part of the life-cycle of a different *Alisphaera* or *Canistrolithus* species.

By analogy with holococcoliths, where associations are demonstrated it will be appropriate to refer to these forms as polycrater (POL) phases of the respective heterococcolith species (e.g. *Alisphaera gaudii* POL). However, forms that have not yet been associated with a heterococcolith phase can most conveniently be referred to as species of *Polycrater* (i.e. *Polycrater galapagensis* or *Polycrater* sp.).

Polycrater galapagensis Manton & Oates 1980

Typical form, coccoliths are simple cones without holes, notches or extensions.

Canistrolithus sp. 1 POL phase

Form very similar to typical *Polycrater* but with tubercles (or "dots") on one half of distal surface of cone.

Alisphaera gaudii POL phase

Form with two lenticular openings on one half of distal surface of cone. NB The name is based on the similarity of the form to the architectural motifs of Gaudi.

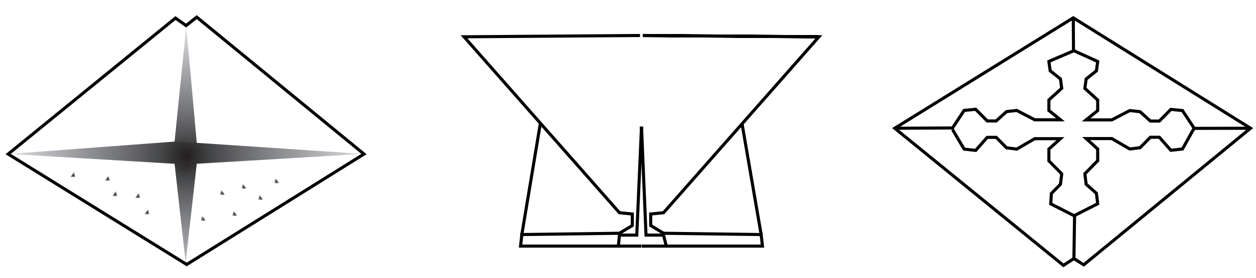
Life-cycle association with *Alisphaera gaudii* HET demonstrated by Cros & Fortuño (2002).

Polycrater sp. ladle-like coccoliths of Cros & Fortuño 2002

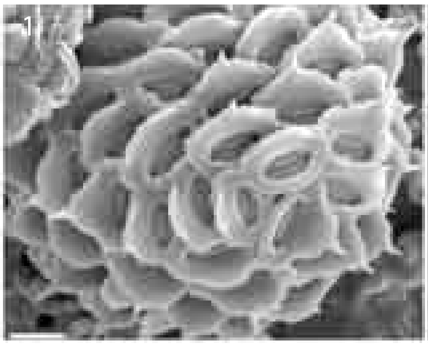
Form with one half of cone reduced to a spine, the other half broad, so coccolith has ladle-like appearance. Feet elaborately fluted. The specimens illustrated by Cros & Fortuño (2002) have longer spines and narrower bowl than those figured here but are otherwise similar.

Additional forms described and illustrated by Cros & Fortuño (2002), not illustrated here.

Polycrater sp. with slit; notch-like slit developed on one edge of cone.
Polycrater sp. with lip-like borders; cone has broad lip-like borders.
Polycrater sp. minimum; with minute coccoliths (<0.5 μm across vs. ca. 1 μm across in other species).
Polycrater sp. very modified; cone reduced to a single spine.

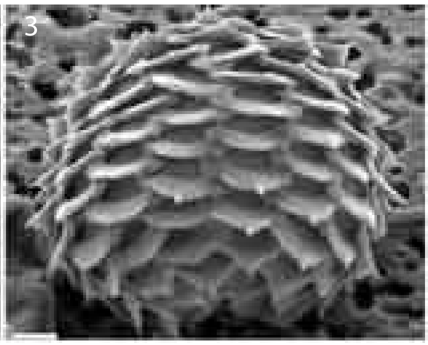


A polycrater nannolith in distal sid e and proximal view, based on *Canistrolithus* sp. 1 POL

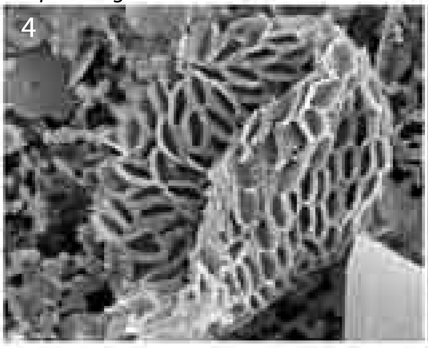


Alisphaera gaudii

Alisphaera gaudii

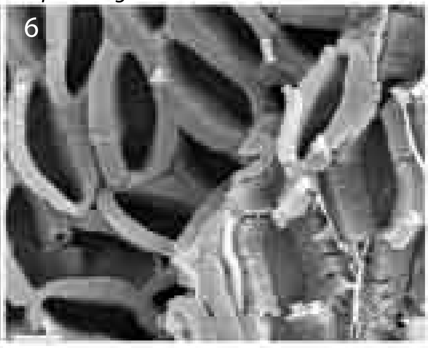


Alisphaera gaudii

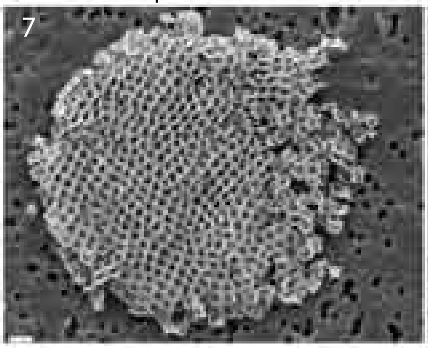


Canistrolithus sp. 1 HET

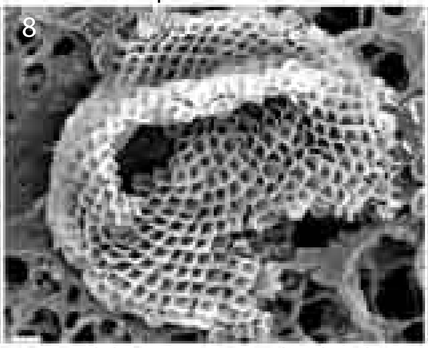
Canistrolithus sp. 1 HET



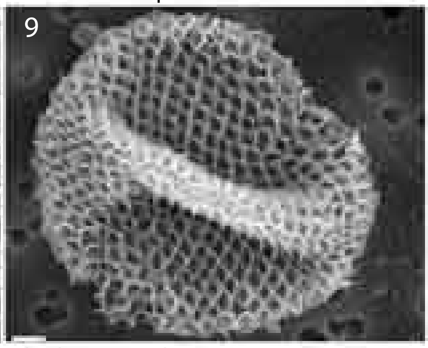
Canistrolithus sp. 1 HET



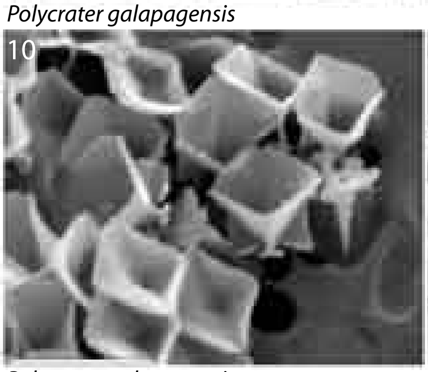
Polycrater galapagensis



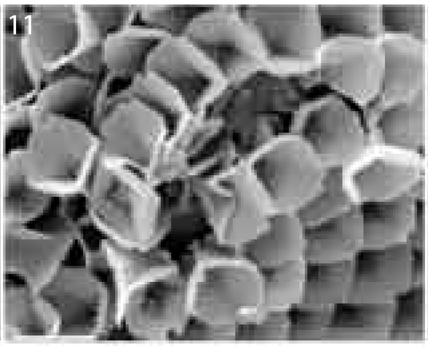
Canistrolithus sp. 1 POL (with tubercles)



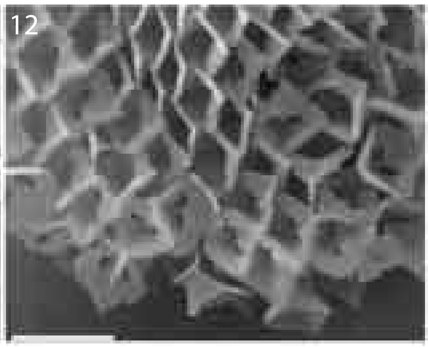
Alisphaera gaudii POL



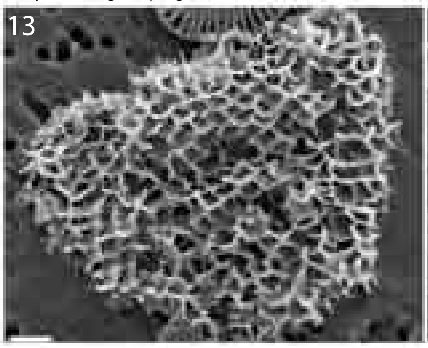
Polycrater galapagensis



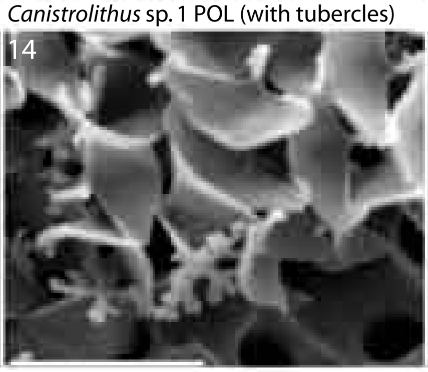
Canistrolithus sp. 1 POL (with tubercles)



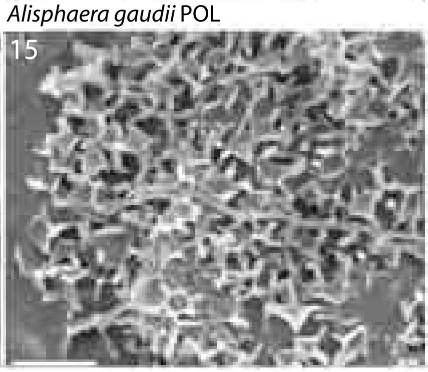
Alisphaera gaudii POL



Polycrater sp. ladle-like



Polycrater sp. ladle-like



Polycrater sp. ladle-like

Plate 30 - Alisphaeraceae: *Alisphaera, Canistrolithus* & *Polycrater*

3.2 Umbellosphaeraceae

Family **UMBELLOSPHAERACEAE** new family Young & Kleijne

Description: Coccosphere dimorphic; coccoliths consist of a funnel-shaped distal part on a flat base. The funnel elements are continuous with the basal plate elements of the central area; a flange may be present around the basal plate, formed by a separate cycle of elements. Coccoliths are variable in size.

Type genus and species: *Umbellosphaera tenuis*.

Remarks: Kleijne (1993) described a sub-family, the Umbellosphaeroideae, within the Syracosphaeraceae, including *Umbellosphaera* and *Gaarderia*. With higher resolution SEM observations and better understanding of *Syracosphaera* coccolith morphology it is now clear that *Gaarderia corolla* should be recombined into *Syracosphaera*, but that *Umbellosphaera* is not associated with the Syracosphaerales. For consistency of taxonomic usage, we have raised the taxon from sub-family to family status.

Umbellosphaera Paasche *in* Markali & Paasche 1955

Description: Coccospheres sub-spherical without obvious flagellar opening. Flagella have, however, been observed by Markali & Paasche (1955). Liths placolith-like with distal shield greatly extended. R-unit forms central-area, tube and distal shield. Very narrow proximal shield is possibly formed from separate crystal-units. Distal shield is thin, except in some *U. tenuis* morphotypes, and so shows low birefringence; tube highly birefringent. TYPE: *U. tenuis* (by subsequent designation, Loeblich & Tappan 1963). SYNONYM: *Ellipsodiscoaster* Boudreaux & Hay 1969.

Ecology: Sub-tropical, often dominate oligotrophic coccolithophore communities.

Affinities: The coccoliths are clearly heterococcoliths, but show no obvious affinities to any of the major groups. The absence of a well developed V-unit cycle makes affinity with the Coccosphaerales or Zygodiscales unlikely and the absence of T-unit radial laths separates them from the Syracosphaerales. An alternative possibility suggested by the dominant development of the R-units is that they are highly modified Noelaerhabdaceae. This is weakly supported by the rare occurrence of malformed *E. huxleyi* specimens, which resemble Umbellosphaera, and by the general similarity of the cross-polarised light interference figure of *Umbellosphaera* coccoliths to those of Noelaerhabdaceaen coccoliths.

Coccolith types: (NB These are somewhat intergradational, see Kleijne 1993 for longer discussion):

1. Macrococcoliths: large liths with broad rims, forming outer surface of coccosphere; central area sub-circular.
2. Micrococcoliths: small liths with narrow rims, only visible on broken coccospheres; Central area elliptical, rims often with less ornament than on the macrococcoliths.

Umbellosphaera irregularis Paasche *in* Markali & Paasche 1955

Liths concave distally, giving the coccosphere an irregular profile (hence the name); distal surface smooth. NB Rarer forms occur with a smooth outline and convex profile (Plate 31/5-6), Kleijne (1993) distinguished these as *U. tenuis* type 0.

SYNONYM: *Ellipsodiscoaster lidzii* Boudreaux & Hay 1969.

Umbellosphaera tenuis (Kamptner 1937) Paasche *in* Markali & Paasche 1955 [*Coccolithus*]

Liths convex distally; distal surface with pattern of ridges; major ridges sub-radial running along sutures; secondary ridges diverge anticlockwise from them.

Variation: The morphology of this species is very variable (plate 31 figs 8-12), in terms of ridge thickness, presence of papillae (nodes) on the ridges, number of secondary ridges, degree of bimodality in ridge thickness. Kleijne (1993) distinguished several types of *U. tenuis*. This work has not been followed up by a detailed study and these types are arguably intergradational. Nonetheless, most specimens are readily assignable to a single type, so it seems possible that they will prove to be discrete (sub) species.

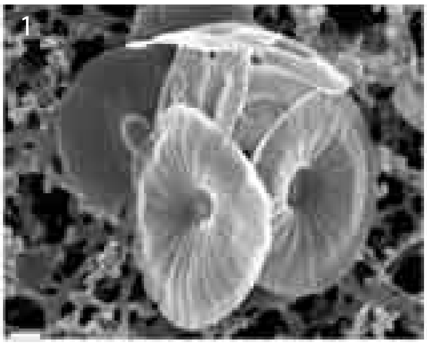
Type I - coccoliths with distinct sutural ridges and numerous finer papillate secondary ridges.

Type II - sutural and secondary ridges papillate.

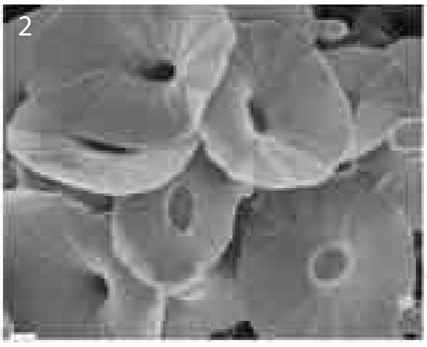
Type IIIa - sutural and secondary ridges heavily calcified and not clearly separable. Central area closed by inward extensions of the sutural rides.

Type IIIb - sutural and secondary ridges heavily calcified but well-separated, 2-4 secondary ridges per element. Central area open.

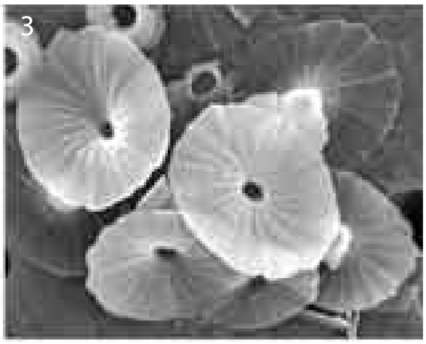
Type IV - sutural ridges well calcified near centre of coccolith, lower toward periphery. Numerous secondary ridges, often anastamosing.



Umbellosphaera irregularis

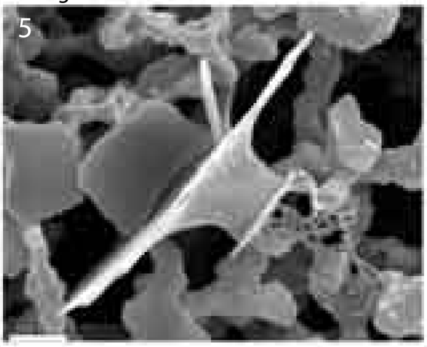


U. irregularis

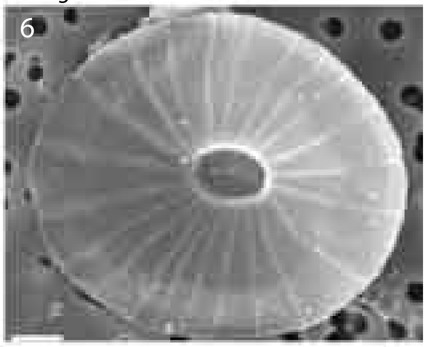


U. irregularis

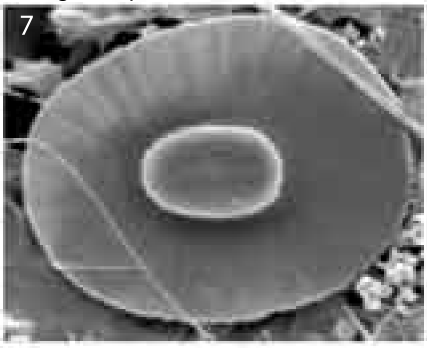
U. irregularis proximal



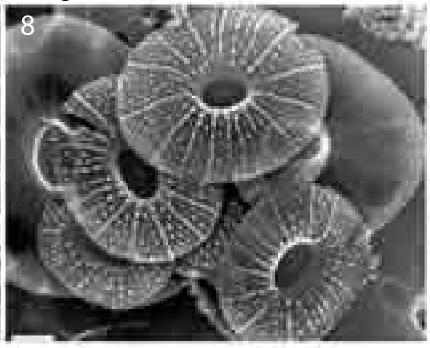
U. irregularis side view



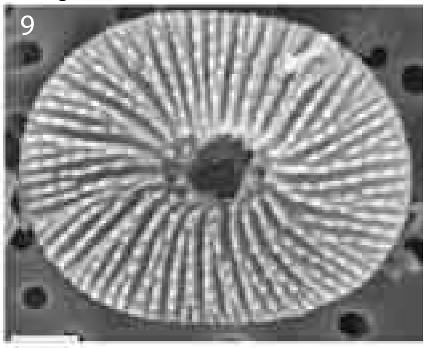
U. irregularis



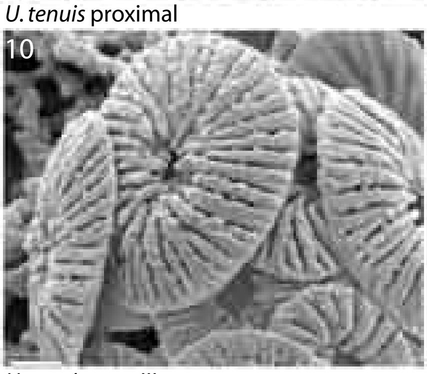
U. tenuis proximal



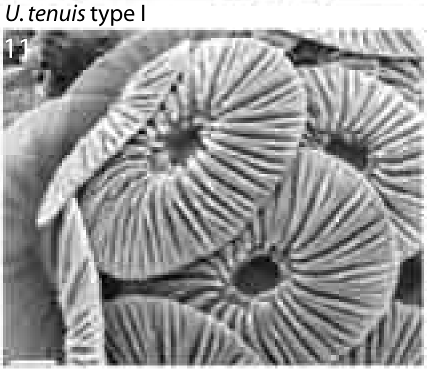
U. tenuis type I



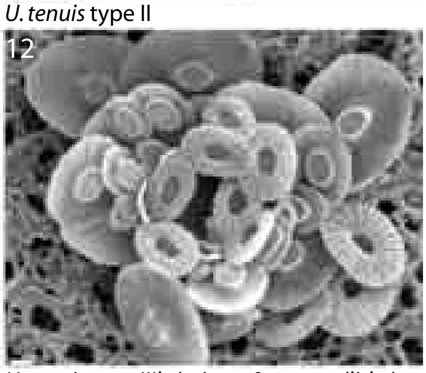
U. tenuis type II



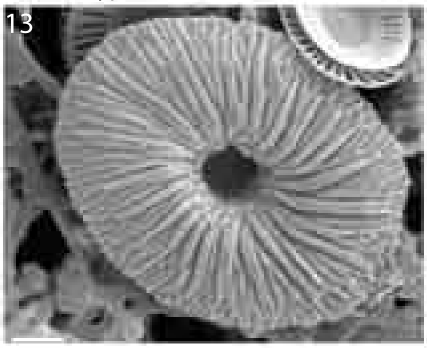
U. tenuis type IIIa



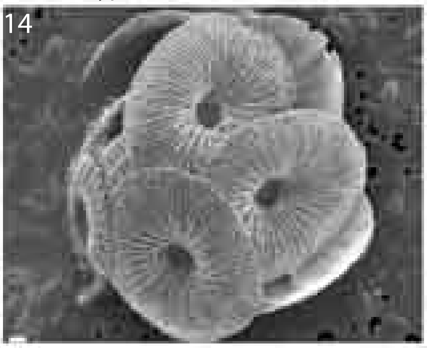
U. tenuis type IIIb



U. tenuis type IIIb (micro- & macroc'liths)



U. tenuis type IV



U. tenuis type IV

U. tenuis type IV (micro- & macroc'liths)

Plate 31 - Umbellosphaeracaea: *Umbellosphaera*

3.3 Narrow-rimmed placoliths

The four monospecific genera included here have coccoliths with narrow placolith rims. These species also all have disjunct central structures formed of platy elements, They are all monomorphic (or in the case of *Placorhombus* weakly dimorphic) and the rim is low, with only a slight separation of the two shields. So, although they have very different shapes, they may prove to be related.

Calyptrosphaera HET/new genus?

The heterococcolith phase of *Calyptrosphaera sphaeroidea* has recently been identified in cultures (Noel et al. in press). This form does not obviously belong to any previously described genus, whilst the genus *Calyptrosphaera* is an objective junior synonym of *Syracosphaera*. As a result, a new genus should probably be described for this form. All details are from Noel et al. (in press).

Calyptrosphaera sphaeroidea HET

Coccospheres non-motile, spherical, ca. 6-10 μm diameter; with ca. 500 coccoliths. Coccoliths minute (0.5-0.8 μm long), elliptical, narrow-rimmed placoliths. Rim apparently formed of single cycle of elements with slightly clockwise-oblique sutures. Central area formed of mass of small angular plates, sometimes slightly convex proximally.

Tetralithoides Theodoridis 1984

TYPE: *T. symeonidesii* Theodoridis 1984 (subj. j. syn of *T. quadrilaminata*, but rim broader cf. Young 1998).

Tetralithoides quadrilaminata (Okada & McIntyre 1977) Jordan, Kleijne & Heimdal 1993 [*Cricosphaera*]

Coccosphere monomorphic, spherical. Coccoliths elliptical with narrow placolith rim surrounding central-area filled by four (rarely three) plates. Liths 4-8 μm long.

Turrilithus Jordan et al. 1991

Monomorphic, coccoliths are placoliths with flaring square-section process. TYPE: *T. latericioides*.

Turrilithus latericioides Jordan et al. 1991

Coccoliths with narrow-rimmed oblong base with two flanges (ca. 1 μm long, 0.15 μm high), square-section flaring process (ca 1.5 m long), partially closed distally and bearing distal spinelets.

Placorhombus new genus Young & Geisen

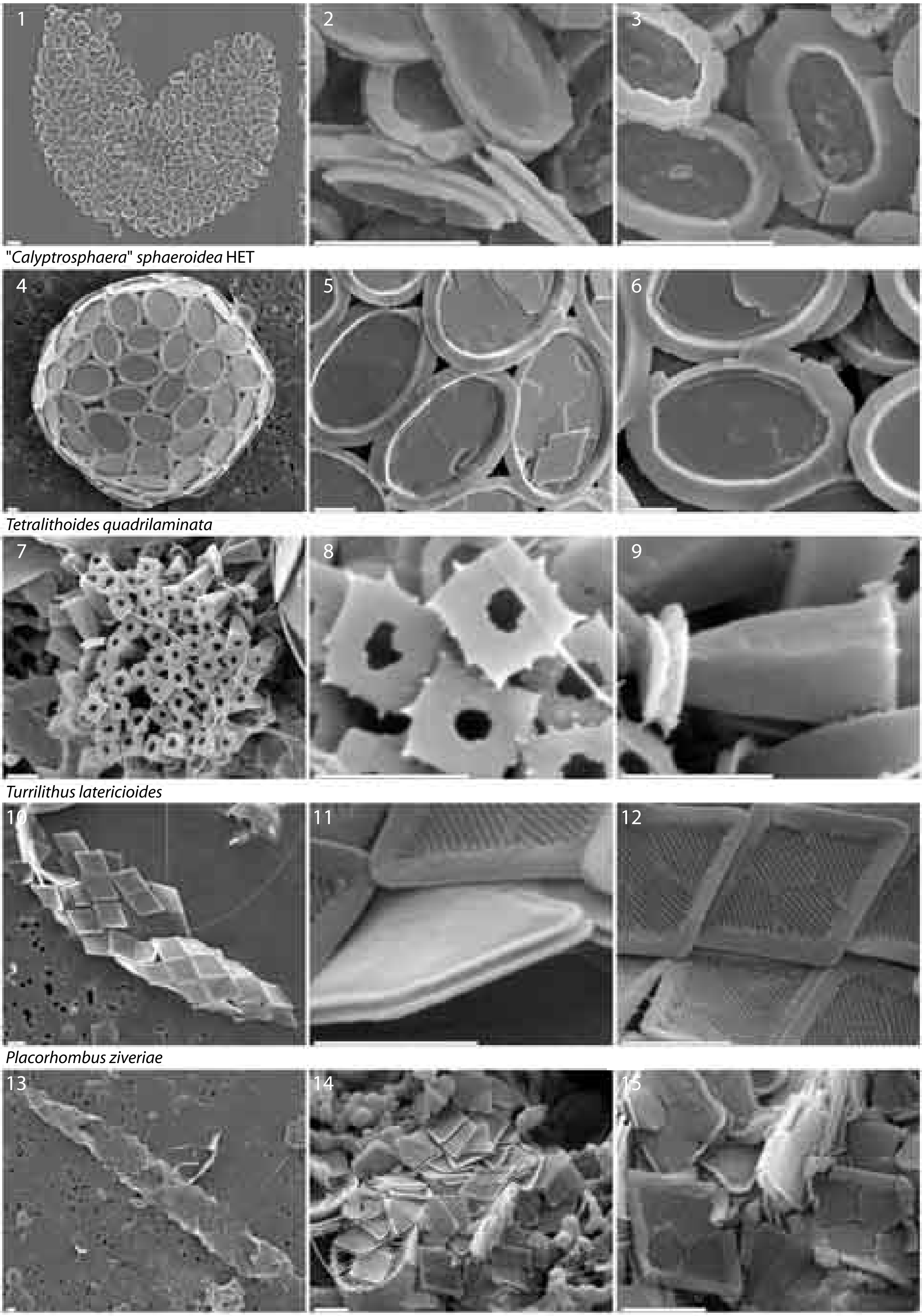
Placorhombus ziveriae new species Young & Geisen

This form has an elongate monomorphic coccosphere with diamond-shaped coccoliths (all four edges of similar length). The coccolith rim is narrow with two flanges; the central area is filled by four plates ornamented with striae on the distal side. Coccolith length 1.9-2.4 μm. N.B *Calciosolenia* has a similar coccolith and coccosphere shape but the coccoliths are muroliths, have laths in the central area and are consistently rhombic rather than diamond shaped.

NB Found by M. Geisen from the Alboran Sea (NW Mediterranean), and by J. Østergaard from the Equatorial Pacific. Formal diagnosis and full description of this species is given in the taxonomic appendix.

Placorhombus sp. cf. *ziveriae*

Similar to *P. ziveriae* but the striae on the end plates are aligned sub-parallel to the long axis of the coccolith and are more closely spaced; also coccoliths smaller (1.6-1.9 μm long). See also taxonomic appendix.



"*Calyptrosphaera*" *sphaeroidea* HET

Tetralithoides quadrilaminata

Turrilithus latericioides

Placorhombus ziveriae

Placorhombus ziveriae *Placorhombus* sp. *Placorhombus* sp.

Plate 32 - Placoliths: *Calyptrosphaera, Tetralithoides, Turrilithus, Placorhombus*

3.4 Papposphaeraceae

Family **PAPPOSPHAERACEAE** Jordan & Young 1990

Minute (cells typically 4-6 μm), lightly-calcified coccolithophores. Mainly recorded from high-latitudes (Arctic and Antarctic), but many additional undescribed low-latitude spp occur (Thomsen & Buck 1998; Østergaard & Thomsen in prep.; Cros & Fortuño 2002; our obs.). Flagella and haptonema usually prominent, much longer than cell.

Taxa included: The family Papposphaeraceae was described for *Pappomonas* and *Papposphaera*. Combination cells indicate that the holococcolithophores *Trigonaspis* and *Turrisphaera* are alternate life-cycle phases of these genera. Several other genera produce rather similar small narrow-rimmed muroliths; *Picarola*, *Vexillarius* and *Wigwamma*. However, these do not show the typical Papposphaeraceae rim structure, so we include them here as a set of possibly related genera *incertae sedis*.

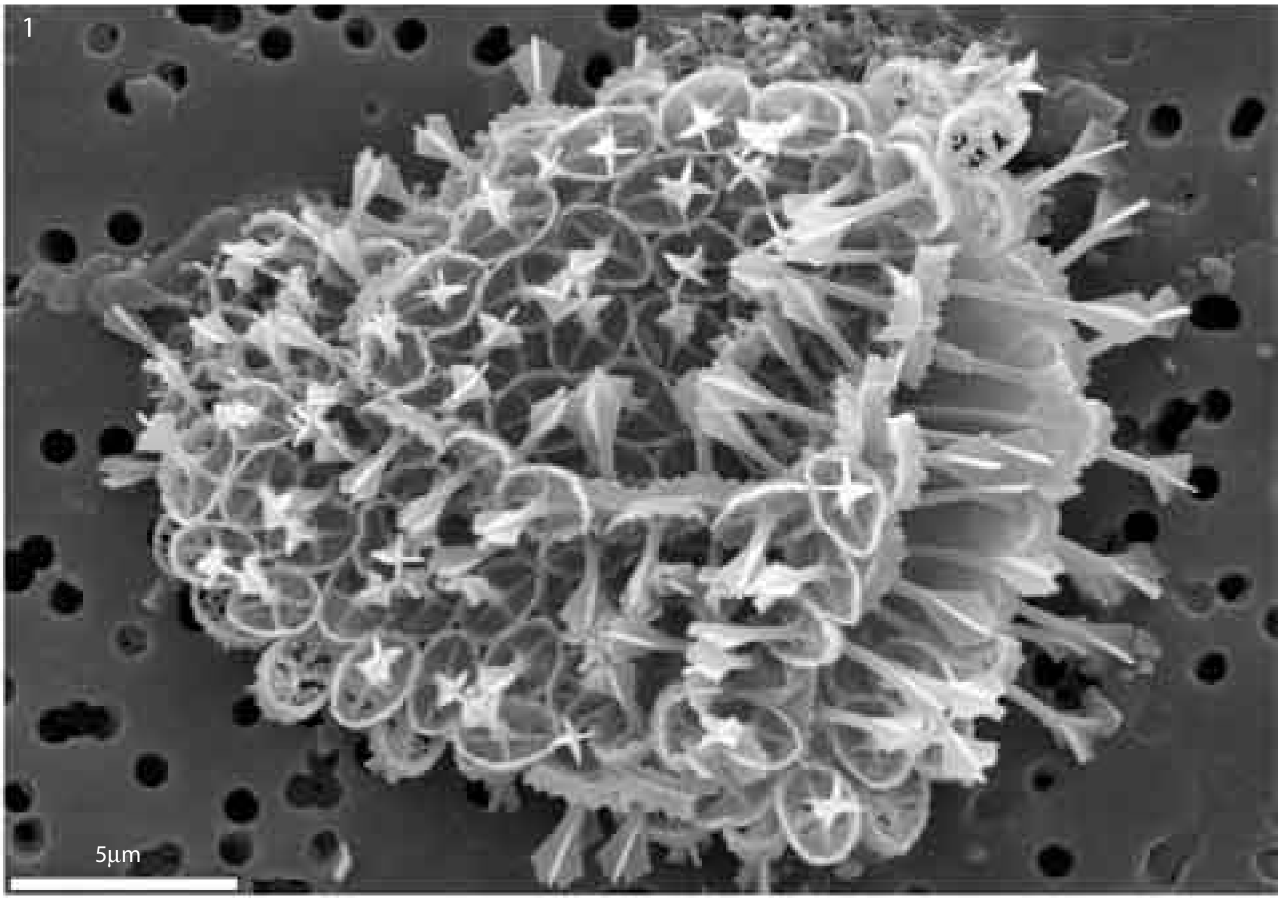
Life-cycles: No species have been cultured, but combination coccospheres with holococcoliths and heterococcoliths have been found for several species (Thomsen *et al*. 1991, Østergaard, unpubl.).

Coccolith structure: Heterococcoliths have a narrow murolith rim; lower/inner rim cycle of elongate elements, upper/outer rim cycle of vertical plate-like elements often slightly separated and angular; central-area with variable structures. Termed pappoliths by Norris (1983).

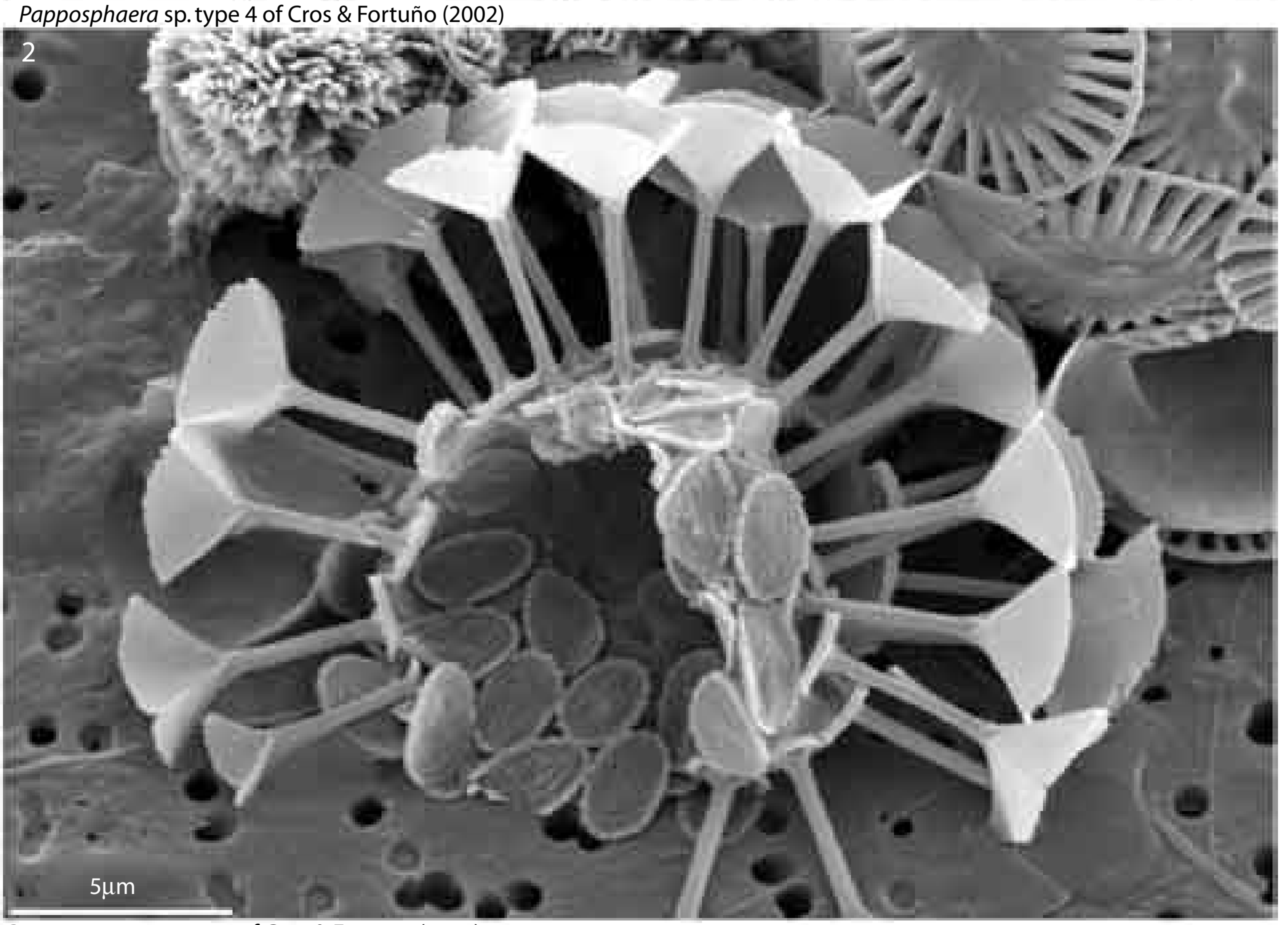
Holococcoliths often tower-like, crystallites arranged in hexagonal or triangular groups (see below section 5.4.2-3, plate 46).

Affinities: The presence of two cycles of elements in the rim strongly suggests V/R mode calcification, although crystallographic orientations are not known. Various authors have speculated that these coccoliths represent an independent calcification event from regular coccolithophores. However, the combination of likely V/R mode calcification in the heterococcoliths and a holo-heterococcolith life-cycle make it much more likely that they are directly descended from regular coccolithophores. Ghost specimens with an organic matrix but no calcification have often been observed (e.g. Manton et al. 1977, Thomsen 1980) but these probably represent decalcification in the water column rather than primary non-calcification (Young et al. 1999). Molecular genetic data will be needed to establish their affinities. We predict they will either fall within the Coccosphaerales or define a separate clade from the other orders.

Key references: Norris (1983) - review; Thomsen (1981) - arctic records; Thomsen et al. (1988) - many new taxa; Thomsen et al. (1991) - life-cycles, including the HOL/HET combinations listed here; Thomsen & Buck (1998) - (sub)tropical records; Findlay & Giraudeau (2000) - Antarctic records; Cros & Fortuño (2002) - W. Mediterranean records, numerous informally described forms.



Papposphaera sp. type 4 of Cros & Fortuño (2002)



Pappomonas sp. type 2 of Cros & Fortuño (2002)

Plate 33 - undescribed Mediterranean Papposphaeraceae

3.4.1 *Papposphaera*

Papposphaera Tangen 1972
Heterococcospheres monomorphic or varimorphic. Coccoliths elliptical; outer rim elements with angular tops, forming serrated margin. Species separated mainly on central area and process structures. The size of the process depends on the location in the periplast. TYPE: *P. lepida*.

Papposphaera arctica (Manton, Sutherland & Oates 1976a) Thomsen et al. 1991
SYNONYM: *P. sarion* Thomsen 1981. HOL = *Turrisphaera arctica*, see Thomsen et al. (1991).
Cell spherical, ca. 7 μm in diameter. Coccoliths, 1.5-2 μm long; central areas with axial cross; process 2-4 μm high ending distally in four sub-parallel crystallites, each ca. 1 μm long (no real calyx).

Papposphaera borealis (Manton, Sutherland & Oates 1976a) Thomsen et al. 1991
SYNONYM: *P. sagittifera* Manton Sutherland & McCully 1976a. HOL = *Turrisphaera borealis*, see Thomsen et al. (1991).
Cell, 4-8 μm. Coccoliths, 1.5-2 μm long; central areas with axial cross and 2-4 additional longitudinal bars; process 2-4 μm high with small calyx of 4 radially diverging blades.

Papposphaera bourrellii Thomsen & Buck 1998
Cell spherical, ca. 4 μm. Coccoliths ca. 0.8 x 0.5 μm, end in a 3.5 μm long process with calyx-like distal appendage.

Papposphaera lepida Tangen 1972
Cell spherical, 4.5-7 μm, diameter of coccosphere 11-16 μm. Coccoliths, 1-1.5 μm long; central areas with axial cross; process 2-4 μm high, tall stem supports flat cone of four large elements, these form an almost continuous outer layer to the coccosphere.

Papposphaera obpyramidalis Thomsen *in* Thomsen et al. 1988
Cell spherical, ca. 5 μm. Coccoliths, ca. 1.5 μm long; central areas with axial cross; process 1.5-2.5 μm high, low stem supports broad cone of four large elements with rounded distal edges, which form almost continuous outer layer to the coccosphere.

Papposphaera simplicissima Thomsen *in* Thomsen et al. 1988
Cell spherical, ca. 4 μm. Coccoliths, ca. 0.5 μm long; central areas open; no process; rim elements separated and so wall is discontinuous. Crystallites of two types occur alternately along the scale periphery.

Papposphaera thomsenii Norris 1983
Coccoliths 1.5-2 μm long; central areas with axial cross; process 5-6 μm high, tall stem supports narrow cone of four elements. Cell and coccosphere dimensions unknown.

Papposphaera sp. type 1 of Cros & Fortuño (2002)
Coccosphere 4-5.6 μm. Coccoliths 0.5-0.8 μm long; central area with axial cross; process ca. 0.5-1.5 μm, robust with narrow conical calyx of four plates. Dimorphic: a few CFCs with tall processes (ca. 1.5 μm); BCs with short processes (<1 μm).

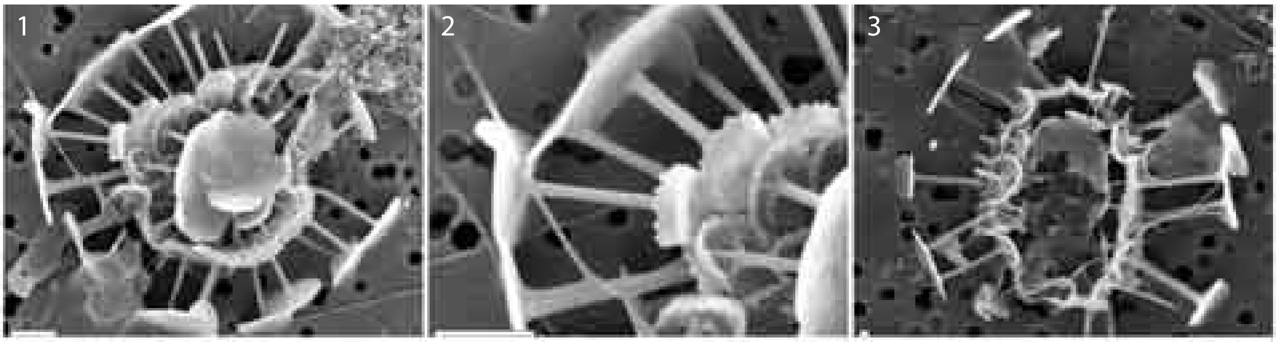
Papposphaera sp. type 2 of Cros & Fortuño (2002)
Coccosphere ca. 5 μm. Coccoliths 0.5-1.0 μm long; central area with diagonal cross; process ca. 0.5-1.5 μm, robust with calyx of three or four rods. Dimorphic: CFCs with tall processes (ca. 1.5 μm) with calyx of 4 (or 3?) rods perpendicular to process. BCs with shorter processes and calyx of 3 diverging rods.

Papposphaera sp. type 3 of Cros & Fortuño (2002)
Coccosphere ca. 10 μm. Coccoliths 0.6-0.8 μm long; central area structure not determined; process ca. 3 μm, delicate with narrow calyx of four plates. Varimorphic: calices vary in width.

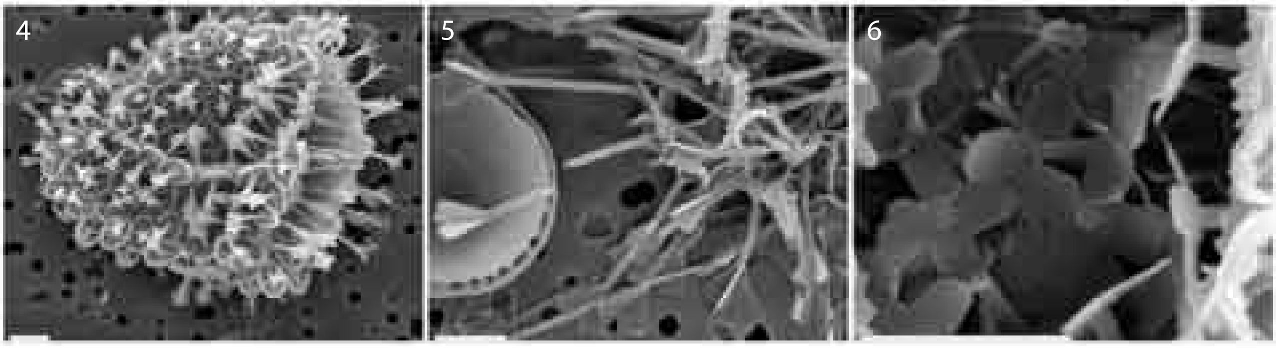
Papposphaera sp. type 4 of Cros & Fortuño (2002)
Coccosphere ca. 6 μm. Coccoliths 0.7-0.8 μm long; central area with axial cross; process ca. 0.5-1.5 μm, robust with radiate calyx of four plates. Varimorphic: process height varies continuously along coccosphere.

?*Papposphaera* sp. type 5 of Cros & Fortuño (2002)
Coccosphere 6-7 μm. Coccoliths ca. 0.7 μm long; central area with axial cross; process ca. 0.5-1.5 μm, with radiate calyx of three plates. Varimorphic: process height varies continuously along coccosphere.

?*Papposphaera* sp. type 6 of Cros & Fortuño (2002)
Coccosphere 5-6 μm. Coccoliths 0.7-1.1 μm long; central area with axial cross; process ca 1.0-2.5 μm, formed of three radiate plates which extend from base to apex without a distinct stem. Varimorphic: process height varies continuously along coccosphere.



1 *Papposphaera lepida* — 2 *Papposphaera lepida* — 3 *Papposphaera* cf. *lepida*



4 *Papposphaera* sp. type 4 — 5 *Papposphaera* sp. type 4 — 6 *Papposphaera* cf. *lepida*

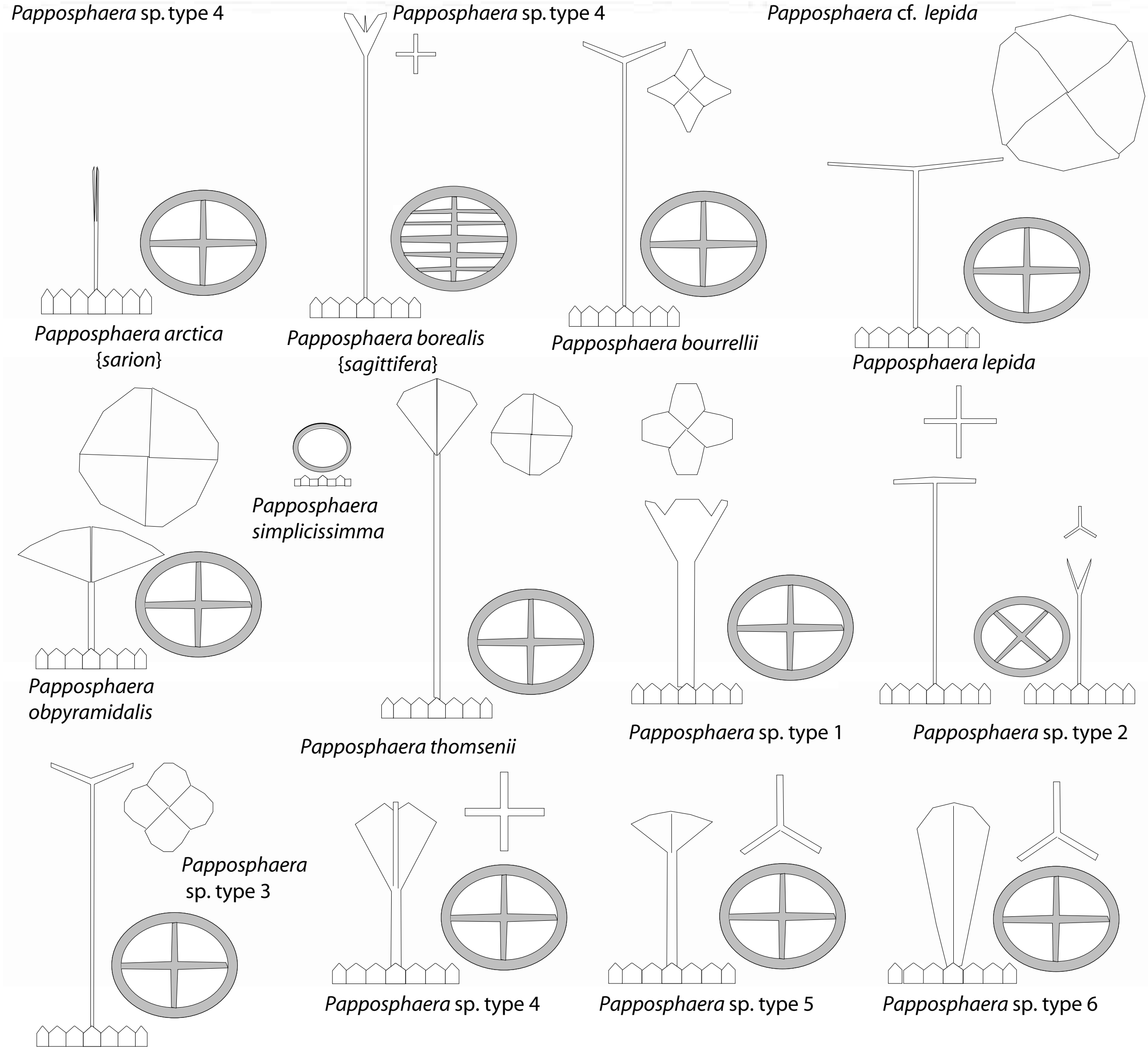


Plate 34 - Papposphaeraceae: *Papposphaera*

3.4.2 *Pappomonas*

Pappomonas Manton & Oates 1975

Heterococcospheres polymorphic, processes present only on some coccoliths, up to three coccolith types (pappoliths):

1. CFCs circular with prominent process.
2. BCs elliptical without spines.
3. AACs similar to CFCs with diminutive version of the process, not observed in all species.

In all liths outer rim elements with angular tops, forming serrated margin, central area and process structures vary between species. TYPE: *P. flabellifera*.

Pappomonas flabellifera Manton & Oates 1975

Cell 4-6 μm. Central area with concentric rings of crystallites; BCs 1-1.5 μm long; CFC process ca. 2 μm high, with long stem supporting two blades.

Variation: Manton et al. (1976) divided the species into two varieties based on form of blades in process and geographical distribution:

Pappomonas flabellifera Manton & Oates 1975 var. *flabellifera* -process Y-shaped, described from S. Africa.

Pappomonas flabellifera var. *borealis* Manton, Sutherland & McCully 1976 - process triangular with serrated end, described from Greenland.

HOL ?= *Trigonaspis diskoensis,* a definite combination cell with *Trigonaspis* was illustrated by Thomsen et al. (1991) but holococcoliths could not be definitively identified as *T. diskoensis*.

Pappomonas virgulosa Manton & Sutherland 1975

Cells ca. 5 μm. Central area with concentric rings of crystallites, rim elements separated and so wall is discontinuous. BCs ca. 1 μm long. CFC process ca. 1.5 μm high, with long stem supporting four (occasionally 2or 3) radiating rods ca. 0.5 μm long.

Pappomonas weddellensis Thomsen *in* Thomsen et al. 1988

Cells 5-6 μm. Central area with axial cross; BCs 1-1.5 μm long; CFC process ca. 2.0-2.5 μm high, with short stem supporting two large fan-like blades, one markedly larger than the other. AACs have much reduced symmetrical central processes without a shaft and smaller distal appendages and may have baseplate calcification of 8 radial bars instead of 4.

Pappomonas sp. type 1 of Cros & Fortuño (2002)

Coccosphere size not determined. Central area with two concentric rings and transverse bar; rim high; BCs ca. 1.2 μm long; CFC process ca. 2.5 μm high tipped by four short radiating rods.

Pappomonas sp. type 2 of Cros & Fortuño (2002)

Coccosphere 6-8 μm. BCs central area with continuous cover of rather irregular plates; 0.5-1.5 μm long; CFC process ca. 2.3 μm high with broad conical calyx of four plates with finely serrated margin, base with cross-bars.

Pappomonas sp. type 3 of Cros & Fortuño (2002)

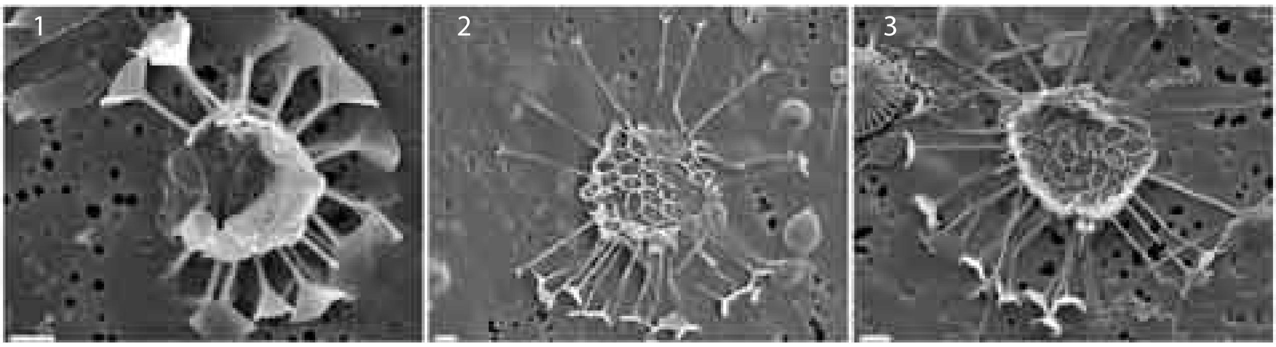
Coccosphere 12-13 μm. Central area with axial cross and low central node; BCs ca.1.0 μm long; CFC process ca 3.5-5.0 μm high, long and slender with narrow conical calyx of four plates. NB The coccoliths of this species are similar to those of *Papposphaera bourrellii,* and *Papposphaera* sp. type 3 of Cros & Fortuño (2002). They differ essentially in having body coccoliths with a central node rather than a spine.

?*Pappomonas* sp. type 4 of Cros & Fortuño (2002)

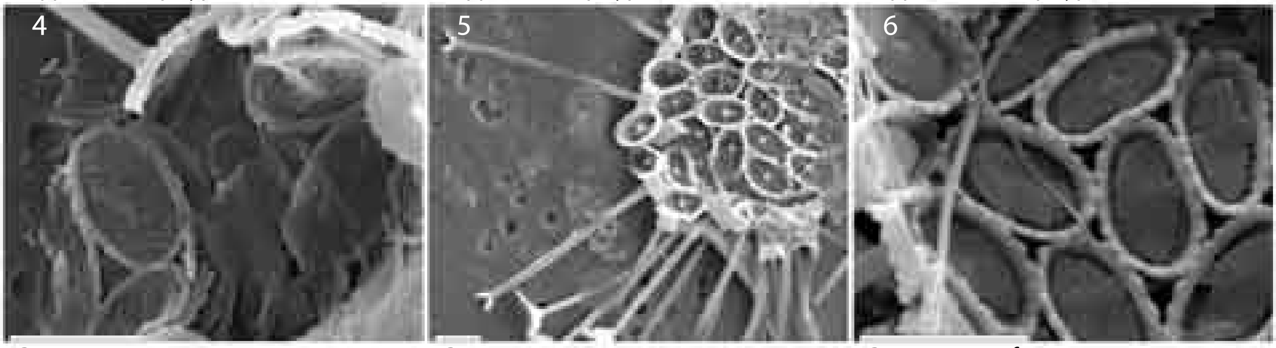
Coccosphere ca. 6 μm. Central area with two concentric rings and transverse bar; BCs 1 μm long; CFC process ca. 2.5 μm high, straight without apical structure, additional ?CFCs have shorter spines (ca. 0.5 μm).

?*Pappomonas* sp. type 5 of Cros & Fortuño (2002)

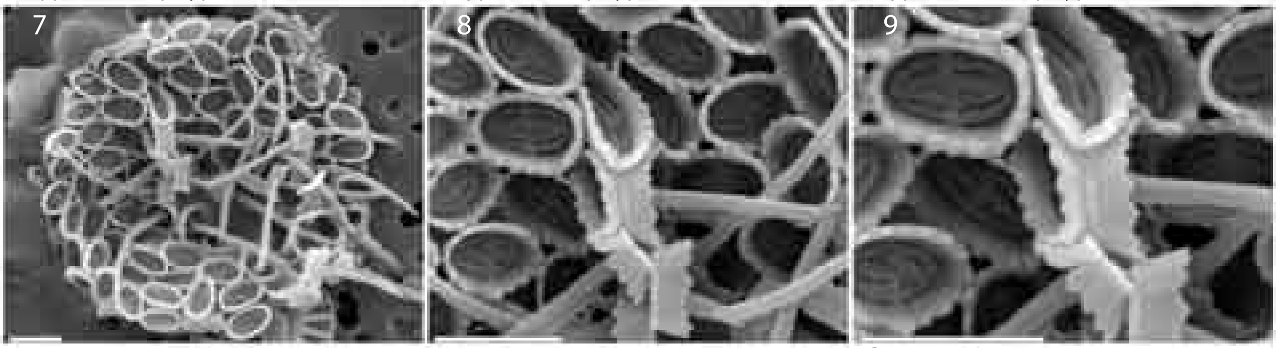
Coccosphere ca. 7 μm. Central area with two concentric rings and transverse bar; BCs 0.5-0.8 μm long; CFC process 2.5-3 μm high, slender square section curved rod without apical structure. AACs, a few present with shorter rod.



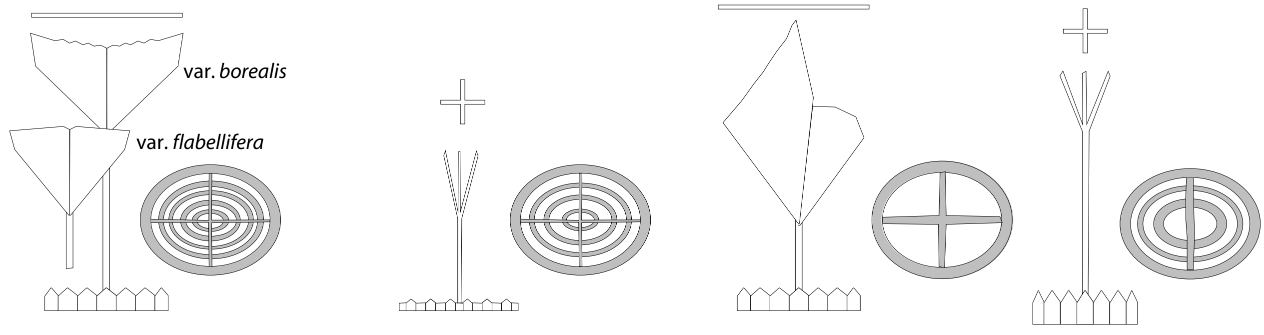
Pappomonas sp. type 2 | *Pappomonas* sp. type 3 | *Pappomonas* cf. sp. type 3



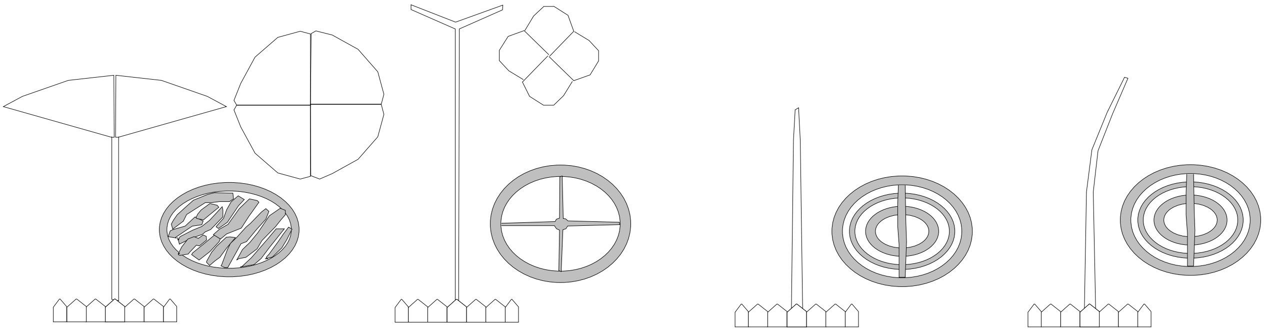
Pappomonas sp. type 2 | *Pappomonas* sp. type 3 | *Pappomonas* cf. sp. type 3



Pappomonas sp. type 5 | *Pappomonas* sp. type 5 | *Pappomonas* sp. type 5



Pappomonas flabellifera | *Pappomonas virgulosa* | *Pappomonas weddellensis* | *Pappomonas* sp. type 1



Pappomonas sp. type 2 | *Pappomonas* sp. type 3 | *Pappomonas* sp. type 4 | *Pappomonas* sp. type 5

Plate 35 - Papposphaeraceae: *Pappomonas*

3.5 Narrow-rimmed muroliths, Genera *incertae sedis* aff. Papposphaeraceae

These genera are all have small murolith coccoliths with narrow rims and elaborate central structures. These characteristics suggest affinity with the Papposphaeraceae but they lack the characteristic serrated distal margin of definite Papposphaeraceae.

3.5.1 Miscellaneous genera

Picarola Cros & Estrada in press (= Genus type A of Cros 2002, plate 48)
Polymorphic. all coccoliths are muroliths with elongate curved quadrate processes. TYPE: *P. margalefii*

Picarola margalefii Cros & Estrada in press
Coccosphere trimorphic, all coccoliths are elliptical muroliths, ca. 1 μm long, with narrow flat topped rim, axial cross and prominent process.
CFCs numerous; large gently-curved, rectangular-section, process 2-3.5 μm long.
BCs numerous; smaller banana-shaped process, 1-2 μm long.
AACs one or two only; rim flaring; moderate sized, nearly straight process, ca. 2 μm long.

Vexillarius Jordan & Chamberlain 1993
Dimorphic, coccoliths are muroliths, equatorial coccoliths have long flaring processes. TYPE: *V. cancellifer.*

Vexillarius cancellifer Jordan & Chamberlain 1993
Body coccoliths are small (ca. 1 μm long) narrowly elliptical muroliths. Equatorial coccoliths have similar bases with long (5-7 μm) square section process, parallel sided in lower half then flaring distally, terminated by a quadrate structure.

Undescribed dimorphic genus and species
This form is only known from one specimen from the Alboran Sea (plate 46/7-9), but is very distinctive. Dimorphic. BCs elliptical ca. 1 μm long; rim narrow and low; diagonal cross bearing low spine. Apical coccoliths elliptical, ca. 2 μm long; rim high and flaring; axial cross, bearing long (>10 μm) spine. NB Cros & Fortuño (2002) illustrate a possibly related form, as unidentified sp. 2 (p.70, fig. 111D).

3.5.2 *Wigwamma*

Wigwamma Manton, Sutherland & Oates 1977
Liths hoop-shaped with narrow rim and "wigwam" of 3 or 4 rods. Rim formed of two concentric cycles of elements. Outer /upper cycle with flat top; rods run from an extended rim element to a common apex., TYPE: *W. arctica*.

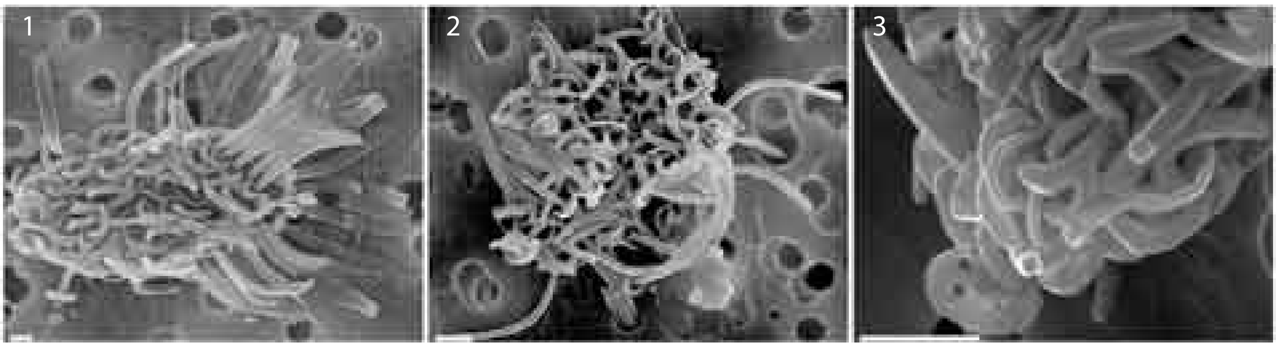
Wigwamma arctica Manton Sutherland & Oates 1977
Cell 4-6 μm. Monomorphic, all liths, ca. 1.5-2 μm with wigwam of 4 rods. In material from the northern hemisphere each wigwam rod is attached to an enlarged crystallite in the rim, as a result the coccoliths have a pentagonal profile. Specimens from the Weddell Sea are triangular in profile since the rim crystallites where each wigwam rod is attached are not enlarged.

Wigwamma triradiata Thomsen *in* Thomsen et al. 1988
Cell oval, 4-6 μm. Dimorphic. BCs have low wigwam of three struts; CFCs high wigwam of two struts each with wing.

Wigwamma annulifera Manton Sutherland & Oates 1977
HOL = *Calciarcus* cf. *alaskensis* Manton Sutherland & Oates 1977, see Thomsen et al. (1991).
Cell ca. 5 μm. Dimorphic. Liths ca. 1-1.5 μm long. BCs simple rings, CFCs with wigwam of 2-4 rods, each with a flange.

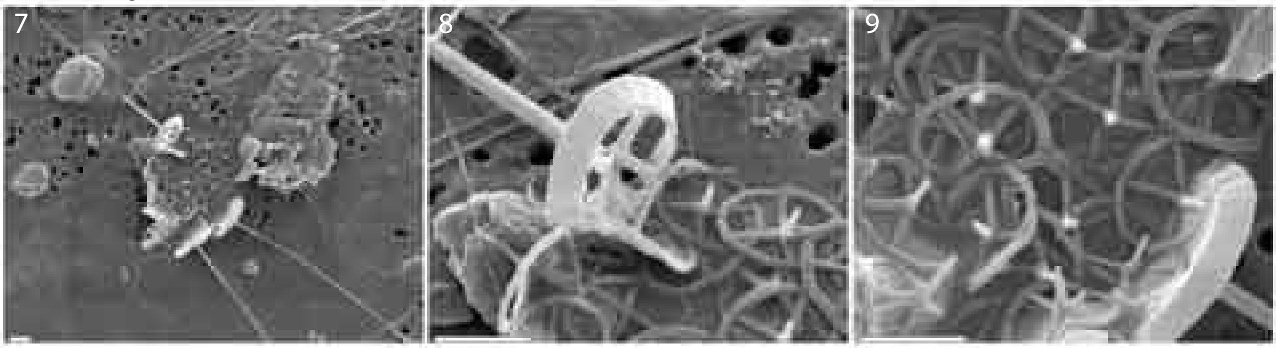
Wigwamma antarctica Thomsen *in* Thomsen et al. 1988
Cell ca. 5 μm in diameter. Dimorphic. BCs simple rings, CFCs with wigwam of 2-4 rods, without flanges, one rod projects as a spine beyond tip of wigwam, poles of two types two broad (wing-like) and two narrow. One or two coccoliths with wigwams of somewhat reduced size may occur at the posterior cell end.

Wigwamma scenozonion Thomsen 1980
Monomorphic, liths are simple only one broadly elliptical ring with one (rarely two) enlarged rim elements, but no wigwam. Cells spherical 4-7 μm; liths ca. 1 μm long.



Picarola margalefii

Picarola margalefii *Vexillarius cancellifer*



Undescribed heterococcolithophore A

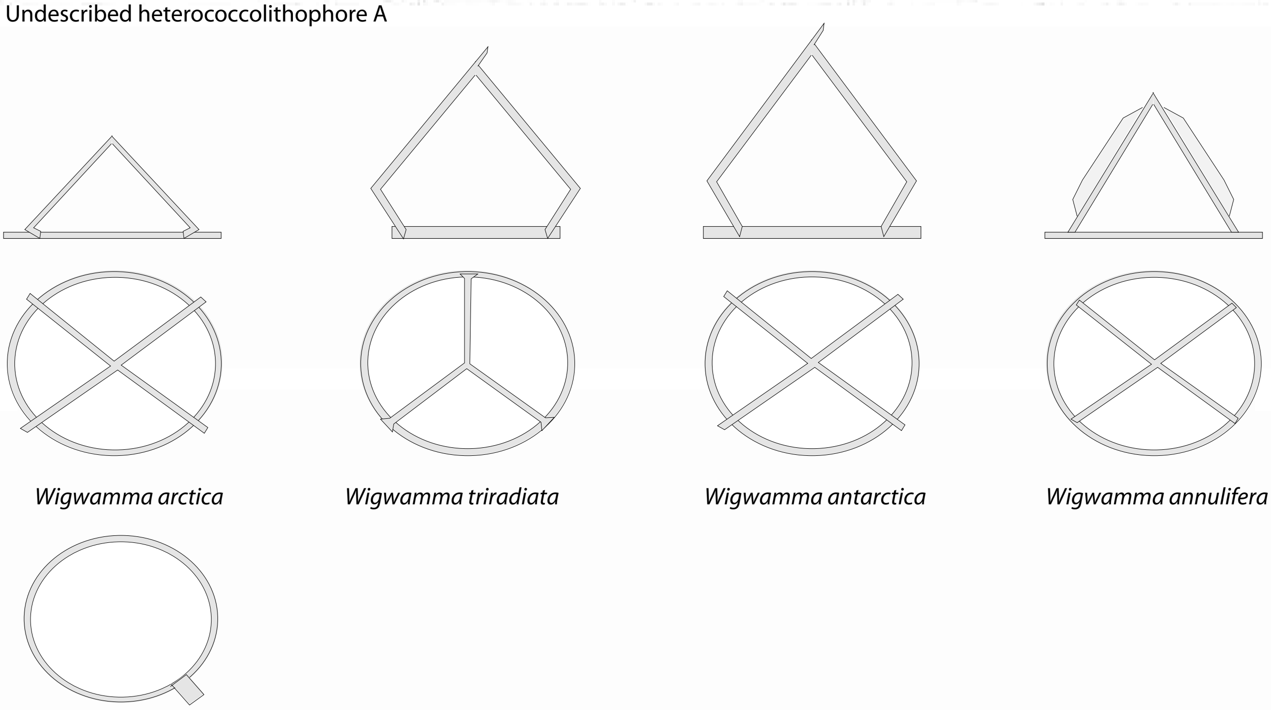


Plate 36 - Genera inc. sed. aff. Papposphaeraceae: *Picarola, Vexillarius* & *Wigwamma*

4. Nannoliths

The term nannolith has been used, especially by palaeontologists as a convenient term for structures about the same size as coccoliths and occurring with coccoliths but lacking definite coccolith affinities. In the modern nannoflora, there are fewer groups of cryptic origins, and the term has been less widely used. However, it is useful for calcareous structures that are thought to be formed by haptophytes but probably by a different biomineralisation process to either heterococcoliths or holococcoliths (Young et al. 1999). NB *Polycrater* is included with the Alisphaeraceae since it has been shown to be a life-cycle phase produced by species of this family.

4.1 Braarudosphaeraceae

Family **BRAARUDOSPHAERACEAE** Deflandre 1947

Group of uncertain affinities. Cells have frequently been isolated but have never grown in culture, they contain visible chloroplasts, so are not cysts or protozoa (Lefort 1972). In addition although *B. bigelowii* is definitely non-motile, Lefort (1972) observed, and illustrated, rare specimens of *B. magnei* with two apically placed, sub-equal flagella. This makes it unlikely that they are dinoflagellates. The combination of highly regulated calcification, two chloroplasts and two sub-equal flagella instead mean that the traditional hypothesis that they are haptophytes is very probable, although it needs to be tested, by molecular genetic or cytological observations.

Cell is enclosed in an exotheca of plates with five-fold symmetry (pentaliths). Pentaliths consist of five segments, each of which behaves as a discrete crystal-unit with c-axis parallel to edge of the pentalith. A lamellar substructure to the segments is consistently present (plate 37, fig 4).

Only two extant species are known and only one of these is well-established, but the family has a geological record back to the Early Cretaceous including several genera and many species (e.g. Perch-Nielsen 1985a,b, Aubry 1989). These include forms with heavily ornamented pentaliths and pentaliths with concave sides. They sometimes occur in enormous abundance in sediments suggesting that *Braarudosphaera* can form massive blooms (see Peleo-Alampay et al. 1999). At present day, *Braarudosphaera* occurs sporadically in shelf environments, usually under conditions of lowered salinity.

Braarudosphaera Deflandre 1947 [*Pontosphaera*]

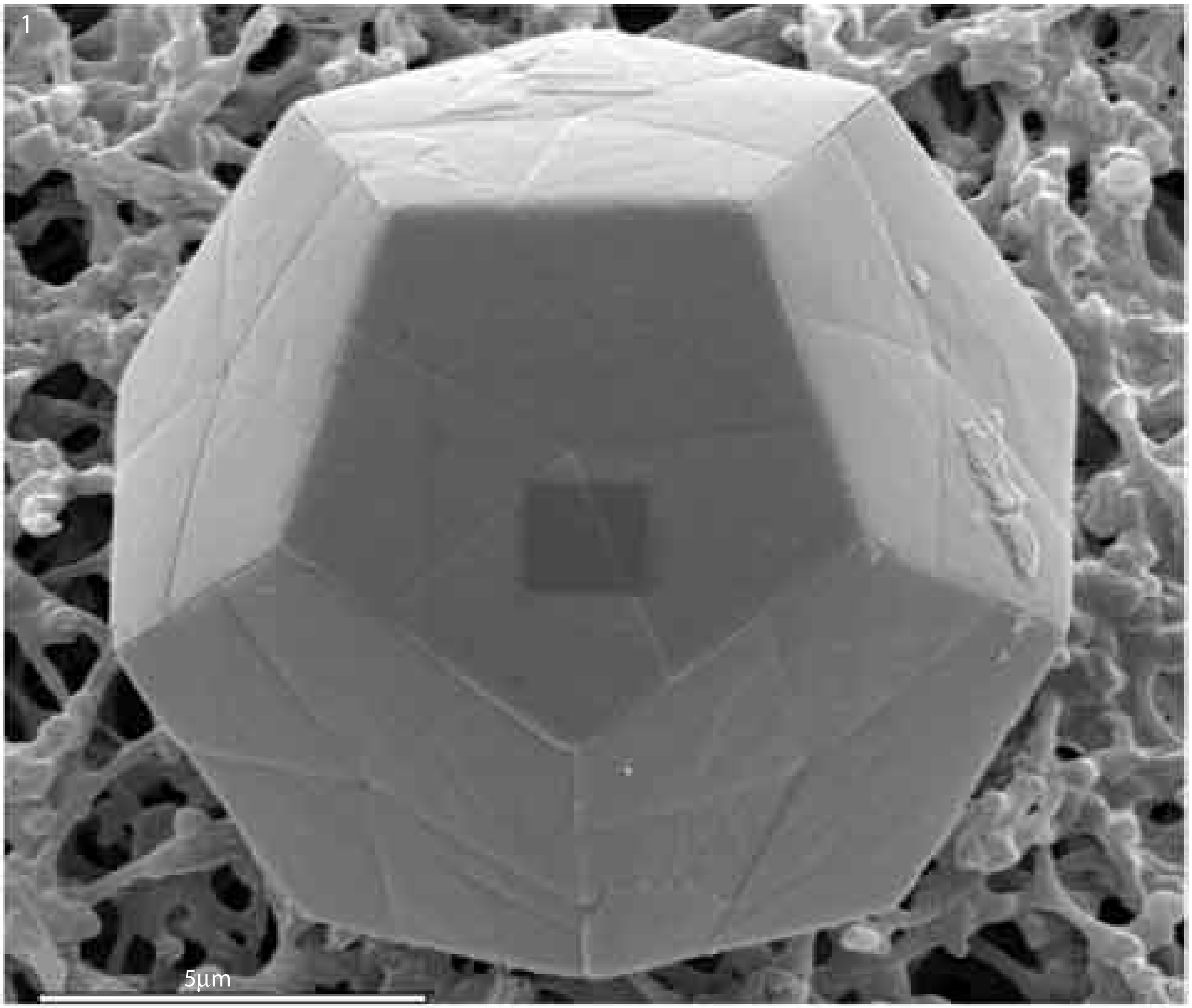
Liths +/-pentagonal, sutures go to edges of pentagon. TYPE: *Pontosphaera bigelowii* Gran & Braarud 1935.

Braarudosphaera bigelowii (Gran & Braarud 1935) Deflandre 1947 [*Pontosphaera*]

Sphere is regular pentagonal dodecahedron with plates closely butting to form a continuous cover. Liths pentagonal, surface smooth, flat or gently concave. Pentalith diameter varies from about 3 to 6 μm but in single samples all pentaliths are usually of very similar size.

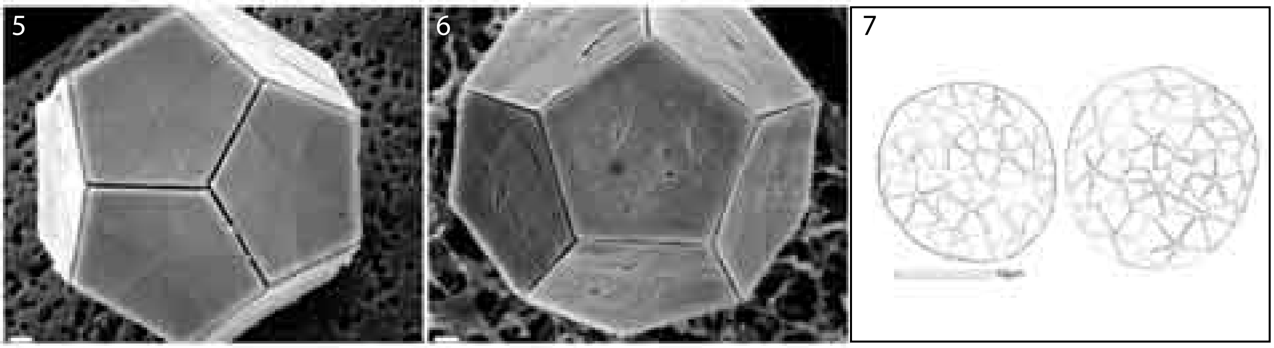
Braarudosphaera magnei Lefort 1972

Pentaliths rounded, and numerous pentaliths occur on coccosphere overlapping irregularly. Not recorded since original description, but it was well-documented, by an experienced phycologist. Cells were observed in live samples and chloroplasts are clearly shown in light micrographs, in addition rare cells bore two sub-equal flagella.



Braarudosphaera bigelowii

Braarudosphaera bigelowii



Braarudosphaera bigelowii *Braarudosphaera magnei*

Plate 37 - Braarudosphaeraceae: *Braarudosphaera*

4.2 Ceratolithaceae

Family **CERATOLITHACEAE** Norris 1965

Characterised by ornate horseshoe-shaped nannoliths, termed ceratoliths. Classic observations of Norris (1971) showed that typically a single ceratolith was wrapped around the cell. Beyond the ceratolith a large coccosphere of hoop-shaped coccoliths sometimes occurs. These large coccospheres can contain up to four cells each with ceratoliths. Alcober & Jordan (1997) observed *C. cristatus* hoop-shaped coccoliths inside coccospheres of "*Neosphaera coccolithomorpha*" planoliths, suggesting that ceratoliths, planoliths and hoop coccoliths may form during alternate phases of a complex life-cycle. These observations have been confirmed by Young et al. (1998), Cros et al. (2000) and Sprengel & Young (2000). The "*Neosphaera*" planoliths show typical heterococcolith features, hence a likely hypothesis is that the ceratolith stage is equivalent to the holococcolith stage in other taxa, and so haploid. Raffi et al. (1999) documented evolutionary relationships between *Ceratolithus* and the fossil genera *Amaurolithus* and *Triquetrorhabdulus*.

Ceratolithus Kamptner 1950

The only extant genus, distinguished from the fossil genus *Amaurolithus* by having the *c*-axis parallel to short axis of the ceratolith rather than perpendicular to the plane of the ceratolith (see e.g. Young 1998).
TYPE: *C. cristatus* Kamptner 1950.

Ceratolithus cristatus Kamptner 1950

The only extant species, but the ceratoliths, planoliths and hoop coccoliths all show significant variation. If consistent associations can be worked out then these may allow formal separation of species or sub-species. In the interim, we prefer to distinguish the types informally - e.g. as *C. cristatus* CER *rostratus* type (see also Young et al. 1998).

Ceratoliths - horseshoe-shaped. Asymmetric, with consistently different ornamentation on the upper and lower surfaces and left and right arms, upper surface with dentate keels, lower surface with smooth keels (see e.g. Kamptner 1950, Young et al. 1997). Morphotypes:

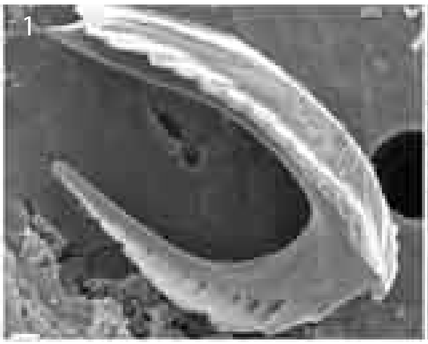
1. *cristatus* type: typical form.
2. *telesmus* type: long arms, curve inwards so tips almost touch [=*C. cristatus* Kamptner 1950 var. *telesmus* (Norris 1965) Jordan & Young 1990, regarded as a separate species by some authors]. *(not figured)*
3. *rostratus* type: with apical beak/rostrum, very often seen with hoop coccoliths. [termed *C. cristatus* forma *rostratus* by Borsetti & Cati (1976) - but without formal description so invalid].

Planoliths - circular heterococcoliths with single shield and tube. Formed of a single cycle of crystal-units with sub-vertical c-axes (Young et al. 1998). [=*Neosphaera* Lecal-Schlauder 1950 (= *Craspedolithus* Kamptner 1963)] Morphotypes:

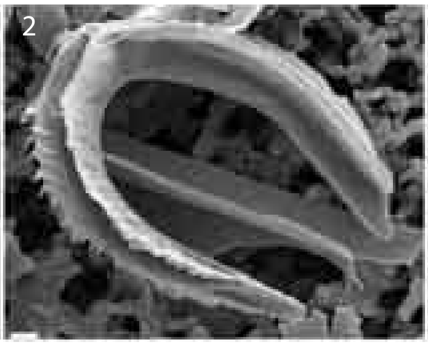
1. large *coccolithomorpha* type: 6-10 μm across, opening 0.4-0.5x total diameter [=*Neosphaera coccolithomorpha* Lecal-Schlauder 1950].
2. small *coccolithomorpha* type: 4-5 μm across, opening 0.35-0.45x total diameter.
3. *nishidae* type: 4-7 μm across, opening 0.15-0.3x total diameter [=*Neosphaera coccolithomorpha* var. *nishidae* Kleijne 1993].

Hoop coccoliths: circular heterococcoliths, simple flat hoop shape, formed of two alternating crystal-unit types. Morphotypes:

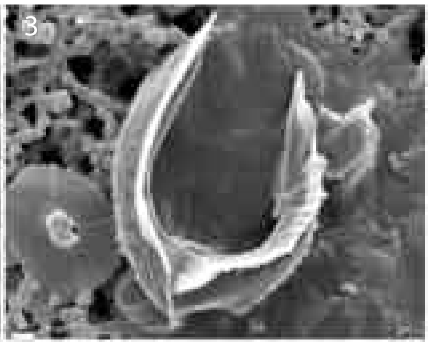
1. robust hoops; 4-5 μm across, rim 0.2-0.4 μm wide. *(not figured)*
2. delicate hoops; 4-6 μm across, rim 0.1-0.2 μm wide.



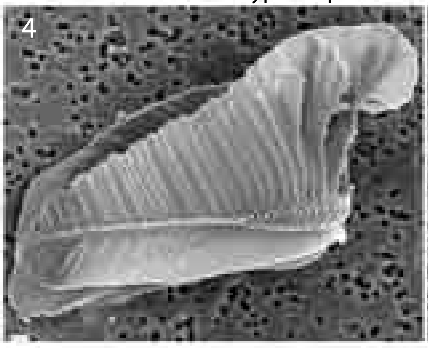
C. cristatus CER *cristatus* type - top



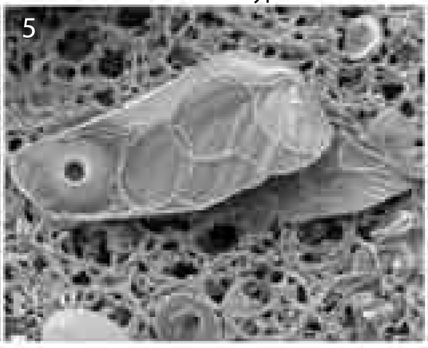
C. cristatus CER *cristatus* type - base



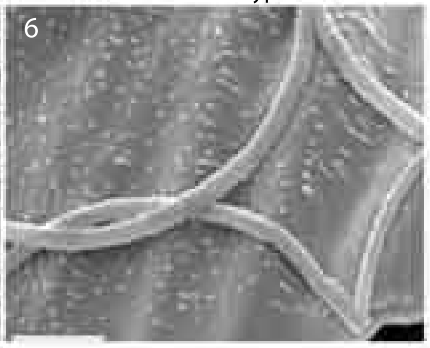
C. cristatus CER *cristatus* type - base



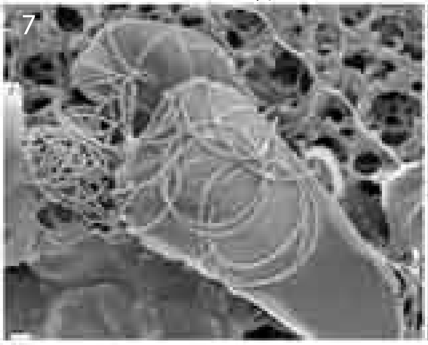
C. cristatus CER *rostratus* type - side



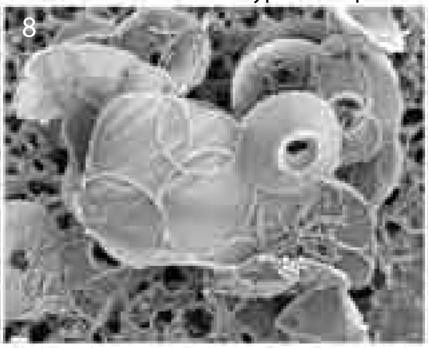
C. cristatus CER *rostratus*type + hoops



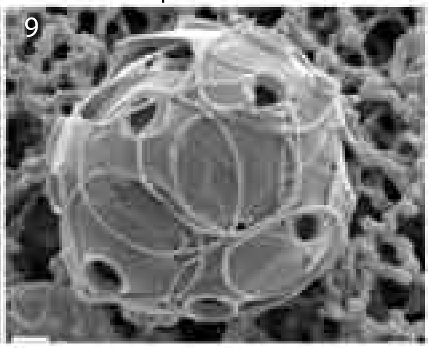
C. cristatus hoops



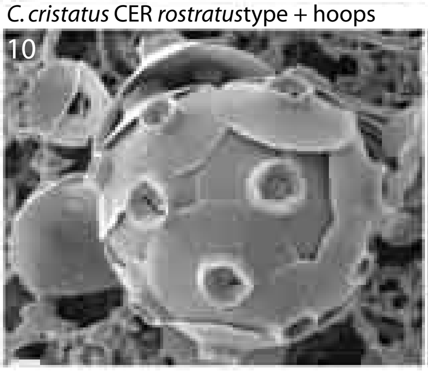
C. cristatus CER *rostratus*type + hoops



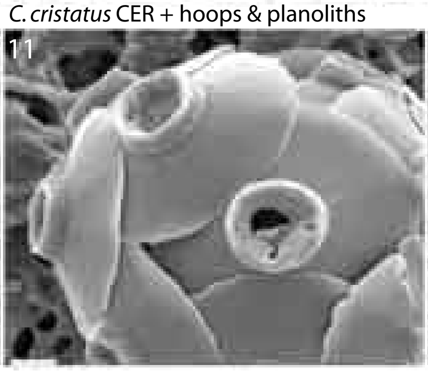
C. cristatus CER + hoops & planoliths



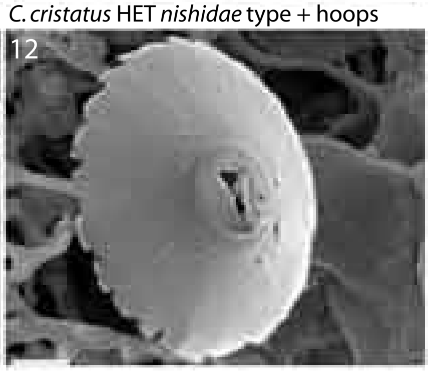
C. cristatus HET *nishidae* type + hoops



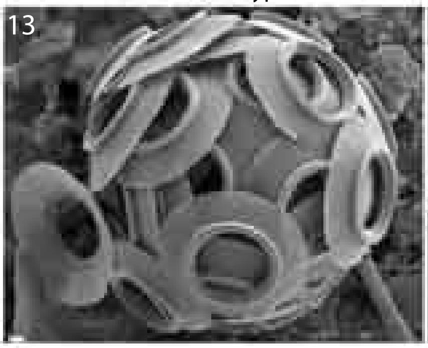
C. cristatus HET *nishidae* type



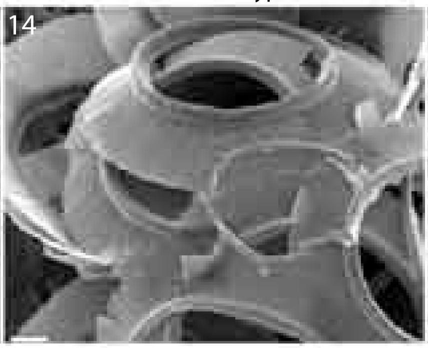
C. cristatus HET *nishidae* type



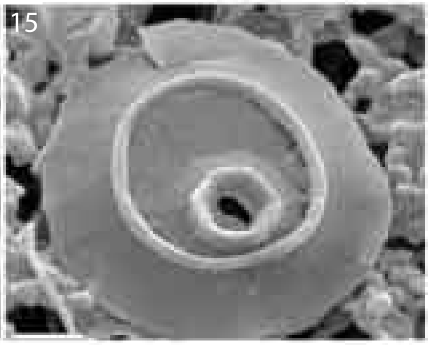
C. cristatus HET *nishidae* type



C. cristatus HET *coccolithomorpha* type



C. cristatus HET *coccolithomorpha* type



C. cristatus HET *coccolithomorpha* type

Plate 38 - Ceratolithaceae: *Ceratolithus*

4.3 Nannoliths *incertae sedis*

The nannolith/heterococcolith divide is subjective. We include here all forms that lack a distinct rim. Since V/R mode calcification has not been identified in any of these taxa we cannot be certain that they are directly related to the coccoliths. However, they share with heterococcoliths the characteristics of being formed from a relatively low number of calcite crystals, each of which has both its crystallographic orientation and morphology strongly regulated.

Florisphaera Okada & Honjo 1973

Liths are small tapering slightly concavo-convex plates, they form artichoke-like coccospheres with a prominent apical opening. *C*-axis parallel to the long axis of the plate but birefringence is low due to small size. A peg-like structure on the base of some specimens may indicate a second crystal-unit. Abundant deep photic species, especially beneath oligotrophic surface waters. TYPE: *F. profunda* Okada & Honjo 1973.

Florisphaera profunda Okada & Honjo 1973 var. *profunda*

Typical form. Liths 1.5-4 μm long. A range of different morphotype are recognisable, including notched, striate and spinosa forms (Quinn et al, subm.), these may prove to be discrete species.

Florisphaera profunda, var. *elongata* Okada & McIntyre 1980

More elongate. A possible morphometric definition might be length 4-6 μm and length > 2x width, but it is not clear that this is really a discrete genotype. NB A holococcolith with a similar shape was observed by Kleijne (1991) and suggested to be a life-cycle stage of this variety.

Gladiolithus Jordan & Chamberlain 1993

Dimorphic deep photic zone coccolithophores. Nannolith types:

A. Tube structures with basal disk supporting a long hexagonal-section spine; in LM isolated spine fragments resemble elongate *Florisphaera profunda* coccoliths.

B. Elliptical plates formed of two elements - "lepidoliths." TYPE: *G. flabellatus*.

Gladiolithus flabellatus (Halldal & Markali 1955) Jordan & Chamberlain 1993 [*Thorosphaera*]

Typical form, no striae on coccoliths.

Gladiolithus striatus Hagino & Okada 1998

Form with striae on distal face of lepidoliths and one side of tube nannoliths, perpendicular to tube length.

Ericiolus Thomsen *in* Thomsen et al. 1995

Monomorphic. Liths are tetrads of spines - "caltrops", with some similarity to the more skeletal *Polycrater* species. Cells monomorphic, saddle-shaped, 3-4 μm across, with long flagella and haptonema. Etymology "little hedgehog". TYPE: *E. spiculiger*.

Ericiolus spiculiger Thomsen *in* Thomsen et al. 1995

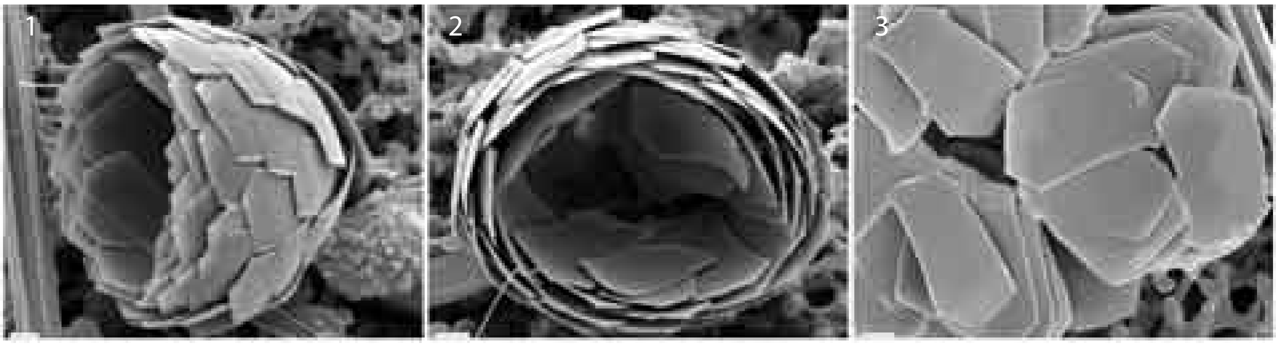
Tetrads consists of three almost coplanar spikes, 0.1-0.2 μm long, forming proximal surface and one longer (0.3-0.4 μm) distally directed spike. Underlain by oval organic baseplate with concentric striations. Described from S. Kattegat, Denmark.

Ericiolus frigidus Thomsen *in* Thomsen et al. 1995

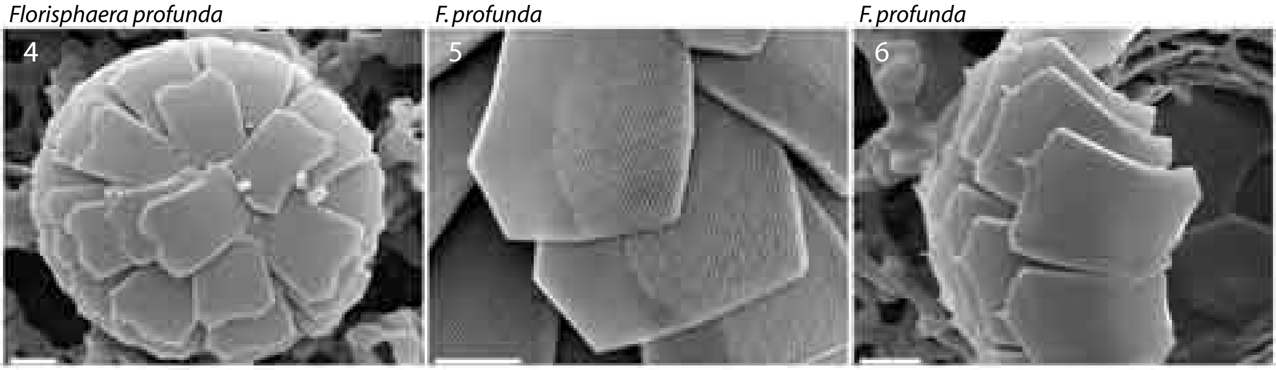
All four spikes of tetrad of similar length (0.2-0.3 μm) and angles between all four are equal. Described from Weddell Sea, Antarctica.

Ericiolus? sp.

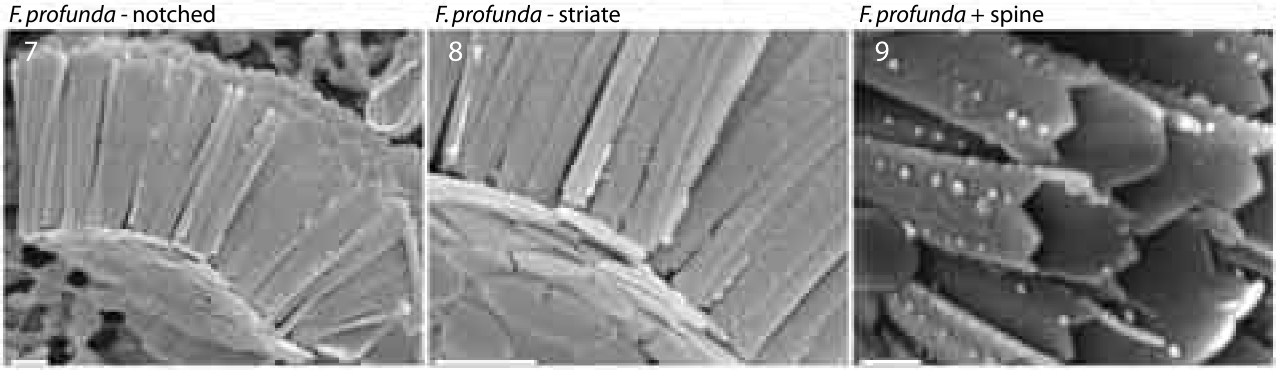
Possibly related form, consisting of three bifurcate rays each with upturned end, and a central spine with terminal knob. Occurs as collapsed coccospheres about 3 μm across, individual nannoliths about 0.4 μm across. Specimens observed in Alboran Sea (W. Mediterranean).



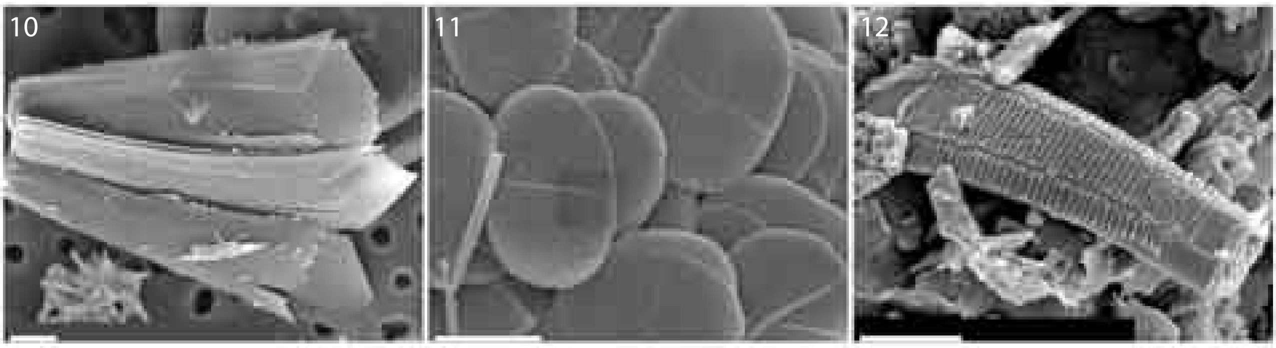
Florisphaera profunda | *F. profunda* | *F. profunda*



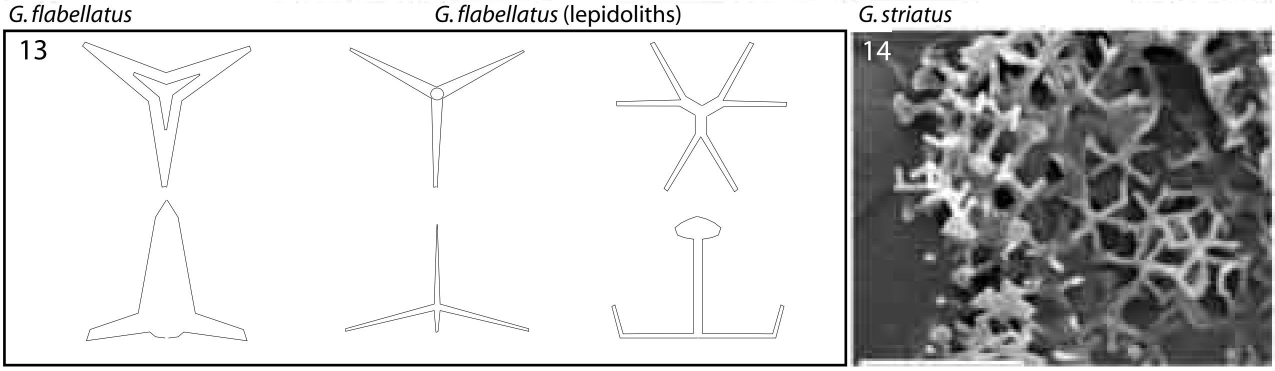
F. profunda - notched | *F. profunda* - striate | *F. profunda* + spine



Gladiolithus flabellatus | *G. flabellatus* | *G. flabellatus* tuberculate



G. flabellatus | *G. flabellatus* (lepidoliths) | *G. striatus*



Ericiolus spiculiger | *Ericiolus frigidus* | *Ericiolus*? sp. | *Ericiolus*? sp.

Plate 39 - Nannoliths: *Florisphaera, Gladiolithus, Ericiolus* & *Braarudosphaera*

5. Holococcoliths [Calyptrosphaeraceae]

Forms included: All holococcoliths are included in this section, irrespective of whether or not they are known to be part of the life-cycle of a heterococcolith bearing species.

Taxonomy: Coccolithophores that are only known from a holococcolith-bearing stage have traditionally been assigned to the family Calyptrosphaeraceae Boudreaux & Hay 1969. However, it seems likely that most and perhaps all holococcolith taxa will prove to have heterococcolith equivalents. Moreover, the type species of the family, *Calyptrosphaera oblonga*, has been shown to be part of the life-cycle of *Syracosphaera pulchra*. As a result, the family Calyptrosphaeraceae is a junior synonym of the family Syracosphaeraceae Lohmann 1902. Since the family has proven an artificial grouping, we do not propose an alternative Linnean name.
For holococcoliths where the associated heterococcolith phase has been identified we use species names based on these associations. For the many other holococcolithophores where there is no information on the associated phase, we have necessarily used the traditional names. This nomenclature has been rather unstable as different criteria have been used to define holococcolithophorid genera. The current nomenclature is essentially that of Kleijne (1991), and since this is a very widely used monograph we give page references to this work. The reassignment of some species to heterococcolith-based species has produced anomalies that we have not attempted to resolve; e.g. we use the combination *Calyptrosphaera dentata* although *Calyptrosphaera* is an objective synonym of *Syracosphaera*. In such cases, proposing new generic names seems counter-productive until life-cycle associations, or molecular genetics, provides evidence of relationships.

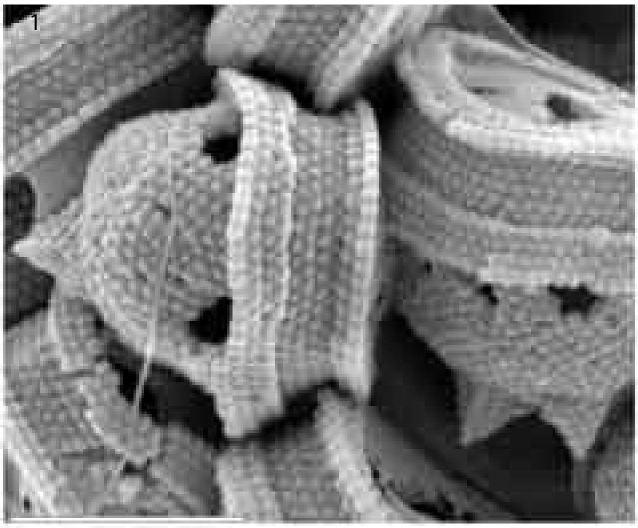
Sub-division of the holococcolithophores: some 86 holococcolithophores are included here so subdivision of them is essential. Several criteria are available for doing this:

1. *Dimorphism*: The presence of distinctive circum flagellar coccoliths (CFCs) is a valuable criterion, especially at generic level and for identification of cells by light microscopy. However, a primary subdivision of all holococcolithophores into monomorphic and dimorphic genera, as used by e.g. Kleijne (1991) and Jordan et al. (1995) separates some very similar forms (e.g. *Zygosphaera* and *Homozygosphaera*). In addition, the division can be subjective, some "monomorphic" species show weak dimorphism (e.g. *Syracosphaera pulchra* HOL). So presence/absence of dimorphism is not used here as the primary basis for holococcolith classification.

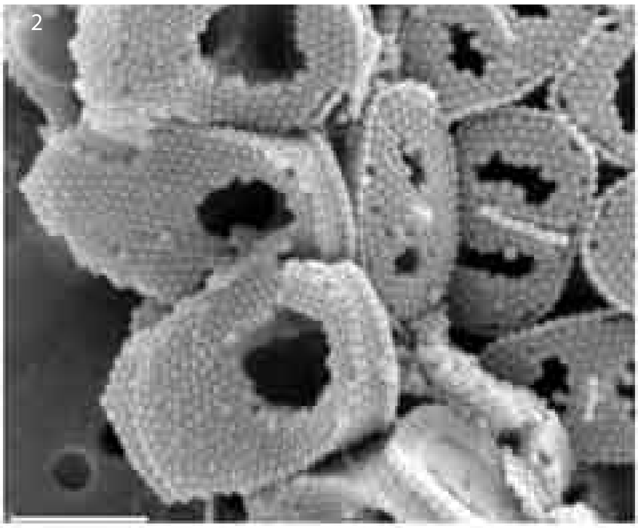
2. *Ultrastructure*: Crystallite arrangement is a useful criterion, but primarily for defining species rather than genera or larger groupings. The most common arrangement is a hexagonal fabric, this may be modified into: (a) hexagonal mesh fabric, in which one in four crystallites are missing giving a sieve-like appearance; (b) tiered fabric, in which the hexagonal arrangement is less obvious, this is common in tube walls; (c) an irregular hexagonal fabric. These fabrics are consistently developed in individual species but do not define larger groupings, and in all cases the crystallographic *c*-axes are perpendicular to the wall surface (our LM observations). Rhombohedral array fabrics are distinctively different, but are only seen in a few species

3. *Coccolith shape*: Basic coccolith shape is inevitably the prime criterion for classification. Most holococcoliths consists of a basal tube with sub-vertical walls, typically about half a micron high. The presence/absence of a tube and the nature of the tube cover in the body coccoliths are used here as the primary basis for classifying holococcolithophores into six groups (see plate 40). These groups are essentially artificial but are convenient for identification.
Numerous distinctive holococcolith shapes have been named, e.g. zygolith, gliscolith, calyptrolith (see Young et al. 1997, or for a more sympathetic review Jordan et al. 1995). However, several of these are so specialised that they only apply to a single genus (e.g. gliscolith, flosculolith). By contrast, calyptrolith, covers such a wide range of morphologies, including conical, flat-topped and convex-covered forms, that it is of limited use. Two of these terms are, however, invaluable - zygolith for holococcoliths with the tube surmounted by a simple bridge and helladolith for similar coccoliths in which the bridge is extended into a flat leaf-like process.

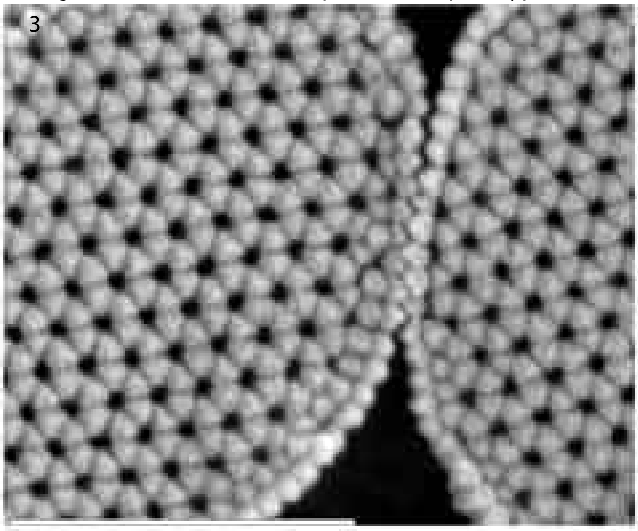
Summary: The system adopted uses the shape of the body coccoliths as the prime criterion, resulting in division of holococcoliths into six groups. These are then each sub-divided into 2 to 6 sub-groups using various criteria including shape of body coccoliths, shape of circum flagellar coccoliths and in a few cases crystallite arrangement. This sub-division is artificial but provides a convenient basis for identification.
Most genera remain in one of the six groups. The main exceptions are (1) *Syracolithus,* which demonstrably contains two separate sets of holococcoliths: flat-topped holococcoliths with rhombohedral crystal fabric associated with *Helicosphaera,* and open-tube-septate holococcoliths associated with *Calcidiscus leptoporus*. (2) *Calyptrosphaera,* which has been used as something of a dustbin genus - for monomorphic calyptrolith bearing species. Here these are divided between the flat-topped and convex-covered categories.



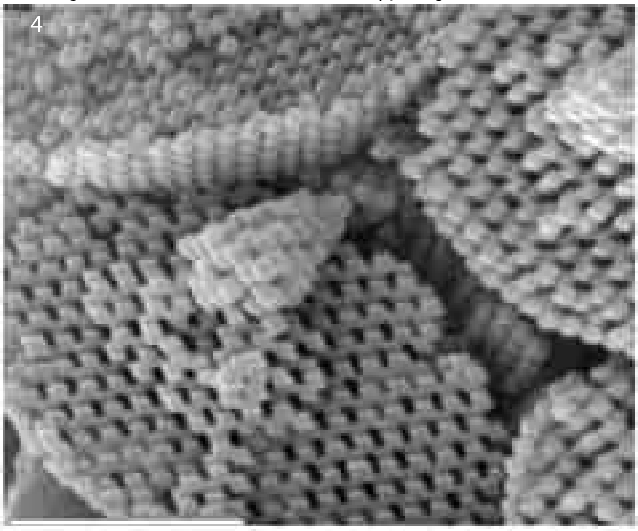
hexagonal and tiered fabrics (*S. pulchra* HOL *pirus* type)



hexagonal and tiered fabrics (*Poricalyptra gaarderiae*)



hexagonal mesh fabric (*Calytrolithophora papillifera*)



rhombohedral crystallite fabric (*Helicosphaera carteri* HOL)

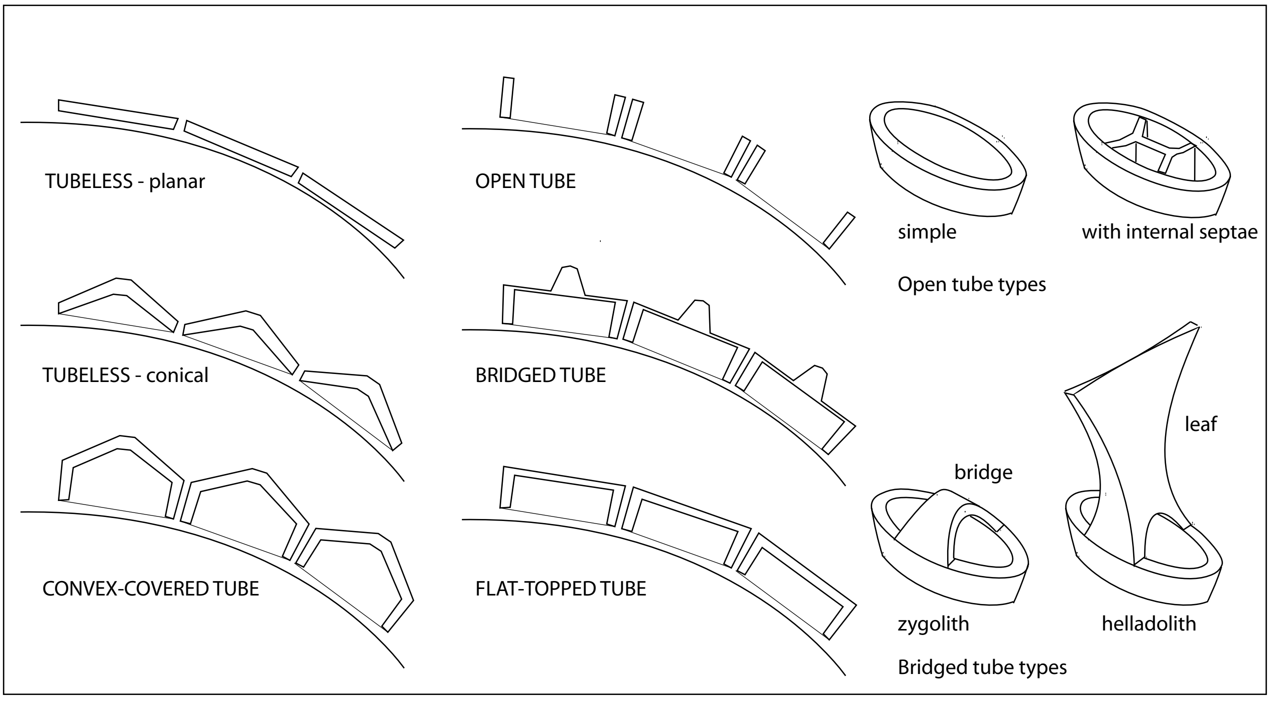


Plate 40 - Holococcoliths: ultrastructure and shape

5.1 Tubeless planar

5.1.1 Planar, monomorphic

{*Crystallolithus* Gaarder & Markali 1956}
Redundant genus, since all species formerly assigned to it are now recognised as being the holococcolith stages of longer established species. Liths are planar disks, variable ultrastructure. Monomorphic.

Coccolithus pelagicus ssp. *pelagicus* HOL {*Crystallolithus hyalinus* Gaarder & Markali 1956}
Liths with single layer of crystallites in rhomboid array (often with incomplete second layer), rim two crystallites high. Reference: Kleijne (1991) p. 17.
Life-cycle association with *C. pelagicus* arctic type is supported by many observations of combination coccospheres and biogeography (Geisen et al. 2002).

Coccolithus pelagicus ssp. *braarudii* HOL {*Crystallolithus braarudii* Gaarder 1962}
Like *hyalinus* but liths with discontinuous cover, central ring of elements connected to rim by spoke-like strings of crystallites; rim two crystallites high. Reference: Kleijne (1991) p. 17, pl. IV (as *hyalinus*).
Life-cycle association with *C. pelagicus* temperate type is supported by culture observations and biogeography (Geisen et al. 2002).

Calcidiscus leptoporus ssp. *leptoporus* HOL {*Crystallolithus rigidus* Gaarder *in* Heimdal & Gaarder 1980}
Liths with double layer of crystallites in hexagonal meshwork array, upper layer often incomplete; rim 3 crystallites high. Reference: Kleijne (1991) p. 17, pl. IV.
Life-cycle combination coccospheres with *Calcidiscus leptoporus* illustrated by Kleijne (1991), Cortes (2000), Renaud & Klaas (2001) and transition seen in culture (Geisen et al. 2002, Houdan et al. subm.).

5.1.2 Planar, dimorphic

Syracosphaera nana (Kamptner 1941) Okada & McIntyre 1977 HOL
BCs solid disk of two layers of crystallites, irregularly arranged except around rim.
CFCs similar to BCs but with elevated transverse ridge. Reference: Kleijne (1991) p. 21, pl. XX. (described as *Syracosphaera* sp. type A, holococcolith stage), see also Cros et al. (2000).

Corisphaera strigilis Gaarder 1962
BCs no tube, solid basal disk, bridge oblique whaleback-shaped, ca. 1 μm long. CFCs similar with bridge extended into leaf. Some similarities to *Anthosphaera*. Reference: Kleijne (1991) p. 52, pl. XIII.

5.1.3 Minute tubeless holococcoliths

Balaniger Thomsen & Oates 1978
Monomorphic. Coccoliths are organic scales with a few pyramidal ?crystallites. TYPE: *B. balticus*.

Balaniger balticus Thomsen & Oates 1978
Cell saddle-shaped, 3-5 μm long; scales irregularly elliptical about 0.5 x 0.3 μm; pyramids 0.1-0.15 μm open triangular cones with faceted or rounded apices, about 10 pyramids per scale.

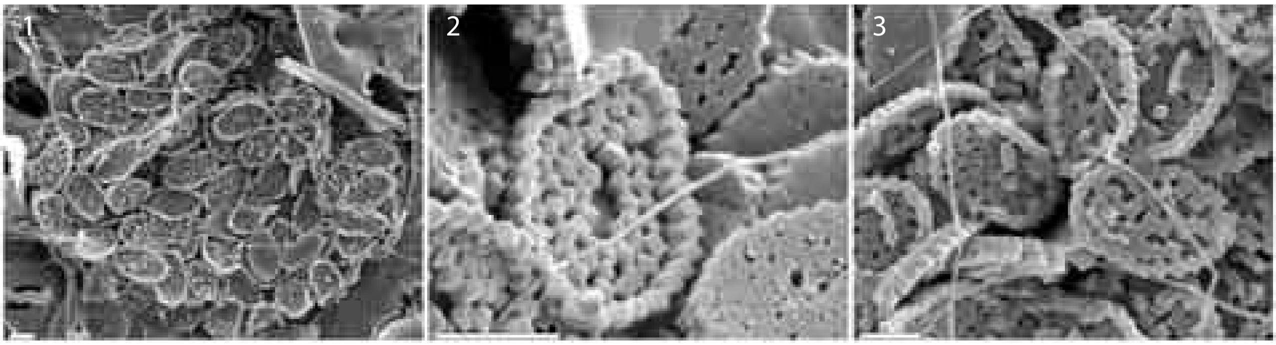
Calciarcus Manton, Sutherland & Oates 1977
Monomorphic. Rhombohedral crystallites forming 3 or 4 radial converging struts attached to a scale with calcareous rim. TYPE: *C. alaskensis*.

Calciarcus alaskensis Manton Sutherland & Oates 1977
Scales ca. 0.5 μm across, with 4 calcified struts.

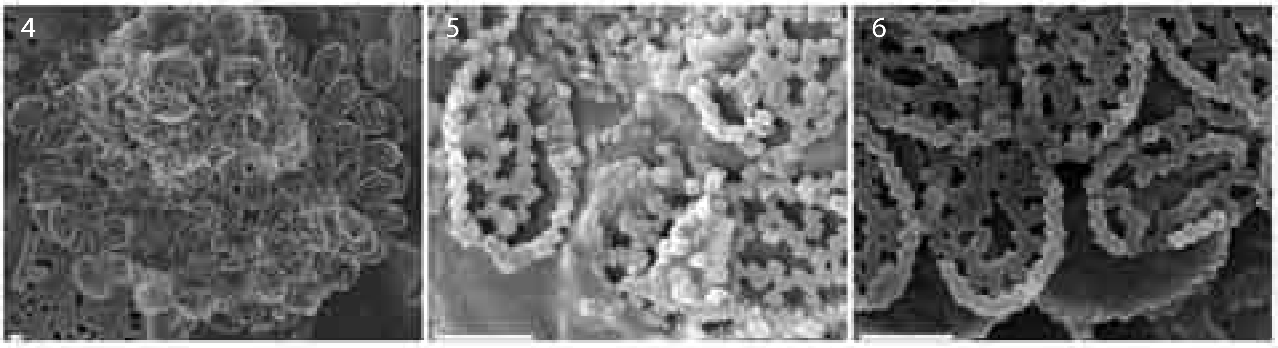
Wigwamma annulifera HOL {=*Calciarcus* cf. *alaskensis* of Thomsen et al. 1981}
Similar to *C. alaskensis* but with 3 struts. This form was illustrated by Thomsen et al. (1981) and was shown to form a combination coccosphere with *W. annulifera* by Thomsen et al. (1991).

Quaternariella Thomsen 1980
Monomorphic. Coccoliths are organic scales with a few rhombohedral crystallites arranged in squares. TYPE: *Q. obscura*.

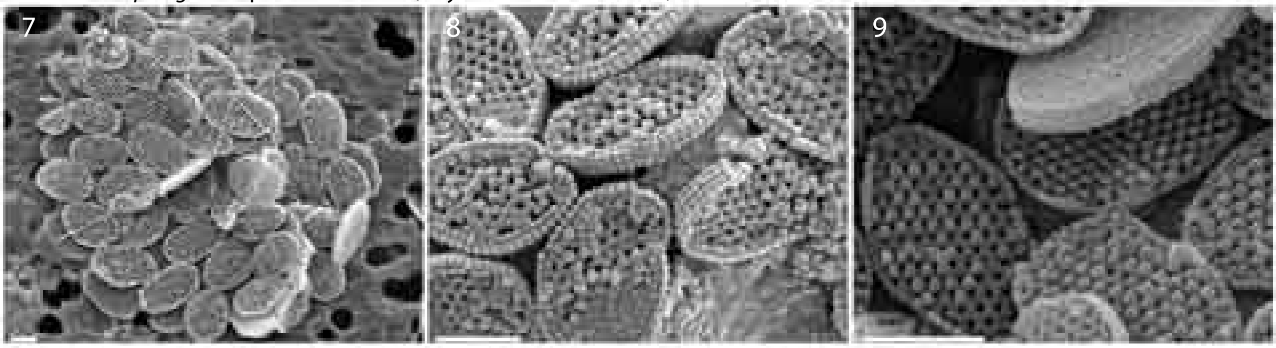
Quaternariella obscura Thomsen 1980
Cell spherical, ca. 3-5 μm wide; scales sub-circular about 0.5 μm across; cluster of four rhombohedral crystallites (0.1-0.15 μm) in centre of each scale.



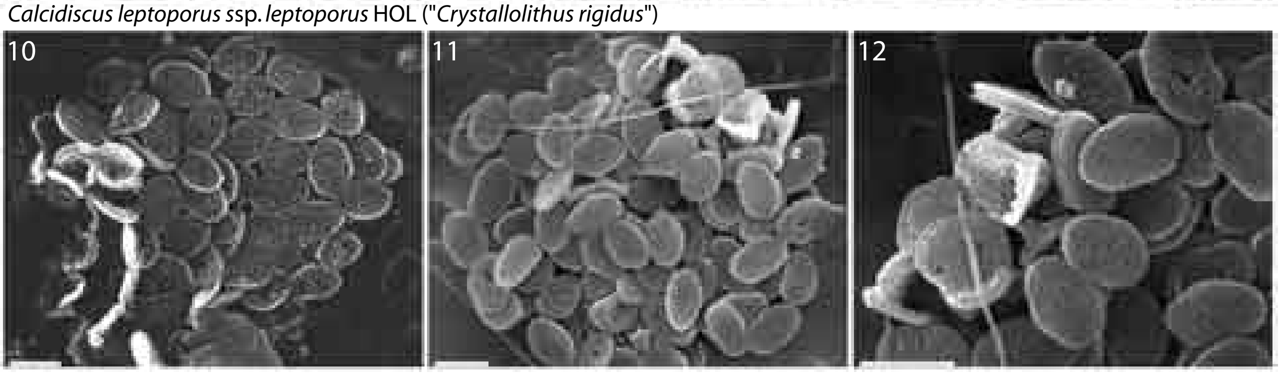
Cocccolithus pelagicus ssp. *pelagicus* HOL ("*Crystallolithus hyalinus*")



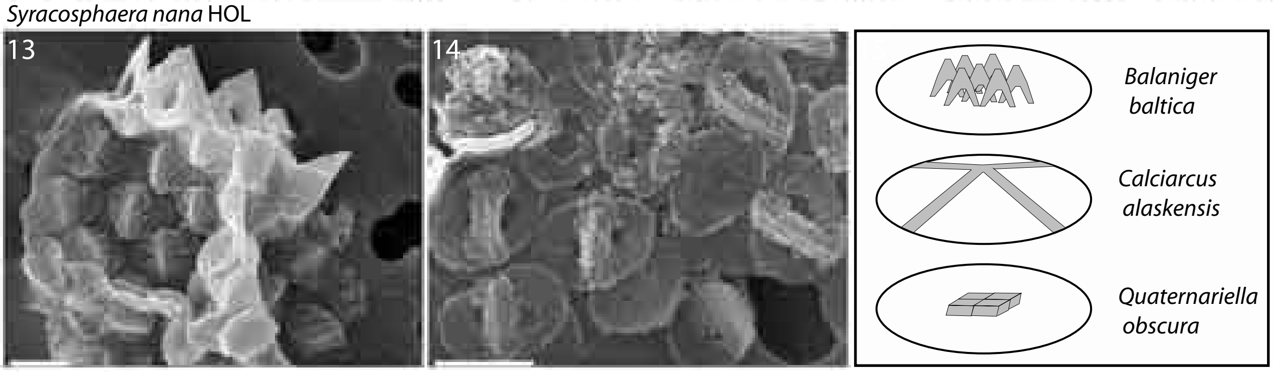
Cocccolithus pelagicus ssp. *braarudii* HOL ("*Crystallolithus braarudii*")



Calcidiscus leptoporus ssp. *leptoporus* HOL ("*Crystallolithus rigidus*")



Syracosphaera nana HOL



Corisphaera strigilis

Plate 41 - Holococcoliths: Tubeless, planar

5.2 Tubeless conical

5.2.1 *Anthosphaera* - fried egg shape, dimorphic

These species all have coccoliths consisting of a simple baseplate with a central more or less conical protrusion, spine or mound of crystallites. Many of these are very small holococcoliths (<1.5 µm).

Anthosphaera Kamptner 1937 emend. Kleijne 1991

BCs low flat domes with flat monolayer basal rim (often described as calyptroliths but rather atypical). Crystallites rather irregular, blocky.

CFCs with basal rim and monolayer leaf-like process (a variant on the helladolith theme, termed fragarioliths). TYPE: *A. fragaria*.

Anthosphaera fragaria Kamptner 1937 emend. Kleijne 1991 - ?= *S. molischii* HOL

BCs with ring of single-crystallite width perforations at base of dome, rim well developed, 1-1.5 µm long. CFCs with high process (2.5-3 µm), lower part with angular crystallites, upper part smooth. Reference: Kleijne (1991) p. 42, pl. VIII.

Anthosphaera lafourcadii (Lecal 1967) Kleijne 1991 [*Helladosphaera*]

Like *A. fragaria*, but BCs smaller (ca. 1 µm), and with less regular crystallites, ring of pores more consistently present, rim narrower; CFCs with low process (<1 µm). Reference: Kleijne (1991) p. 42, pl. IX.

Anthosphaera periperforata Kleijne 1991

Like *A. fragaria*, but BCs with large, anticlockwise-oblique, elongate, pores at base of dome, ca 1.5 µm long. CFCs with medium process (ca 1.5 µm). Reference: Kleijne (1991) p. 42, pl. IX. Cros & Fortuño (2002) distinguish three types.

Type 1 - spines only on AACs, CFCs with flat top

Type 2 - spines on all BCs, CFCs with pointed top.

Type 3 - BCs with large perforations, CFCs with low point. This is almost certainly a distinct species

Anthosphaera sp. type A of Cros & Fortuño (2002) *(not figured)*

Ornate species (origami-like cf. Cros & Fortuño 2002). BCs with flange above the ring perforations, CFCs with multiple spinelets along top.

Anthosphaera sp. type B of Cros & Fortuño (2002) *(not figured)*

Similar to *Anthosphaera* sp. type C but CFCs with broad leaf.

Anthosphaera sp. type C of Cros & Fortuño (2002)

BCs minute (0.5-0.7 µm) only partially calcified, there is an outer ring of rhombohedral crystallites and inner cone of crystallites (usually collapsed), with gap between.

CFCs with high arch ending in point (total height 1.5-2 µm), base similar to that of BCs.

NB A single possible combination coccosphere of this holococcolith with *Syracosphaera marginaporata* was illustrated by Cros & Fortuño (2002, p. 59, fig 112).

5.2.2 *Acanthoica* group - monomorphic, fried egg shape

Acanthoica quattrospina HOL (= sp. aff *Sphaerocalyptra* of Cros et al. 2000)

BCs solid disk one crystallite high, possibly with central opening; conical mound in centre.

CFCs similar to BCs but more elevated, cone-shaped. References; Cros et al. (2000); Cros & Fortuño (2002).

Holococcolithophore sp. aff. *A. quattrospina*

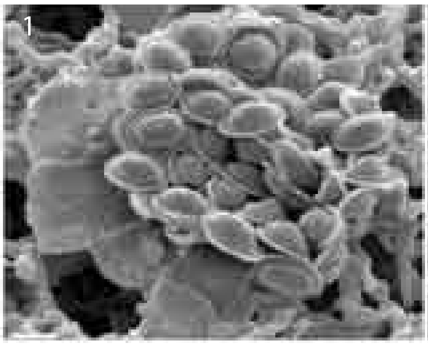
Undescribed species known from one specimen only (plate 42, figs 9, 12). Like *A. quattrospina* sp. HOL solid basal disk with central cone, but cone double and with small perforations around base. CFCs not seen.

Holococcolithophore type A of Kleijne (1991) *(not figured)*

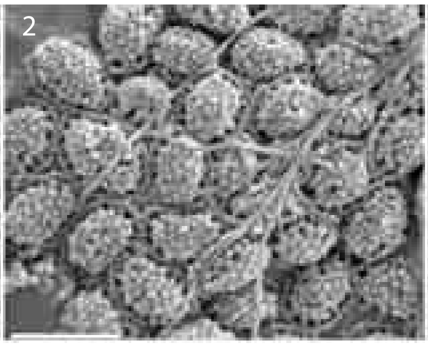
Monomorphic. Wide and flat, monolayer with basal rim of angular crystals; central part of irregularly shaped and arranged microcrystals. Reference: Kleijne (1991) p. 71, pl. XIX.

Holococcolithophore sp. 1 of Cros & Fortuño 2002 *(not figured)*

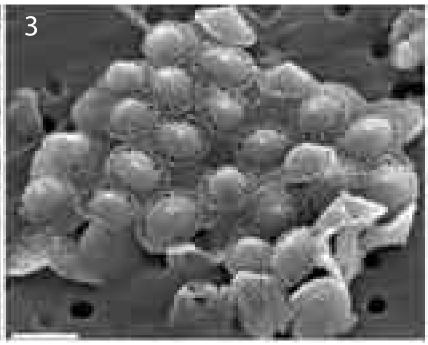
Monomorphic. Wide coccoliths with central mound, often displaced toward one end of coccolith. Two small pores regularly present on proximal side.



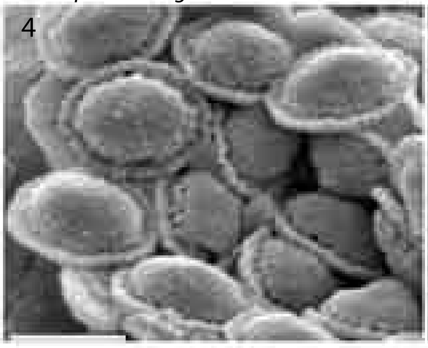
Anthosphaera fragaria



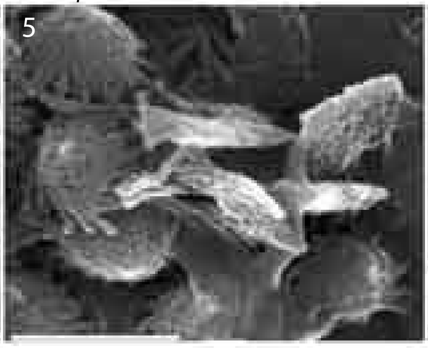
Anthosphaera lafourcadii



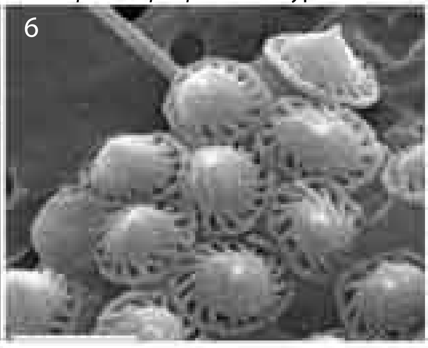
Anthosphaera periperforata type 2



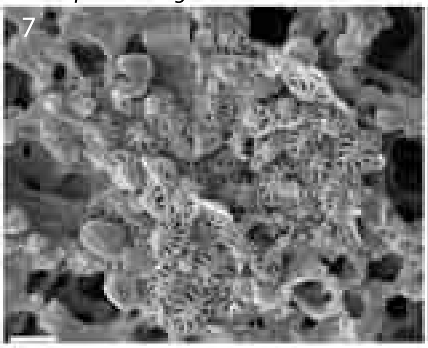
Anthosphaera fragaria



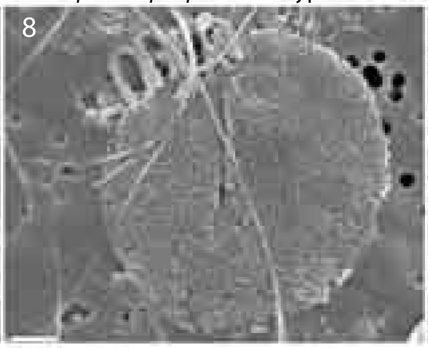
Anthosphaera periperforata type 1



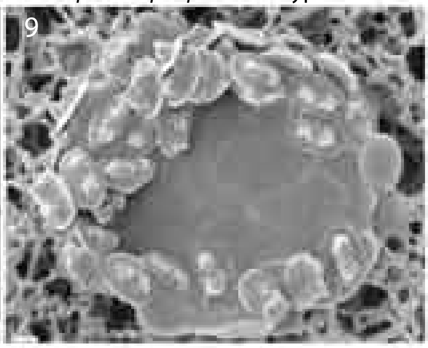
Anthosphaera periperforata type 2



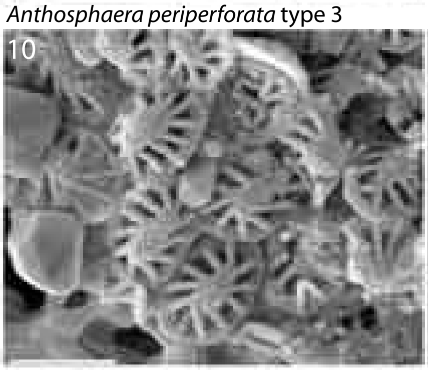
Anthosphaera periperforata type 3



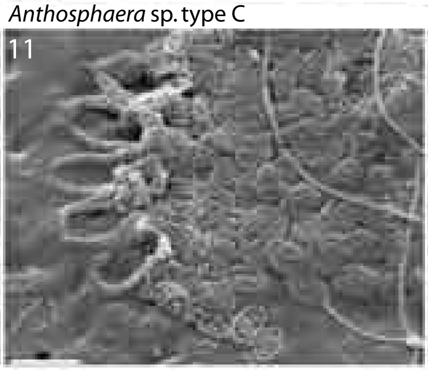
Anthosphaera sp. type C



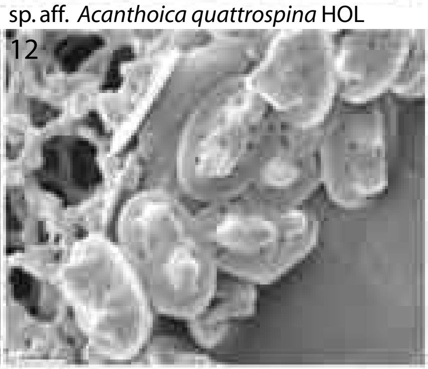
sp. aff. *Acanthoica quattrospina* HOL



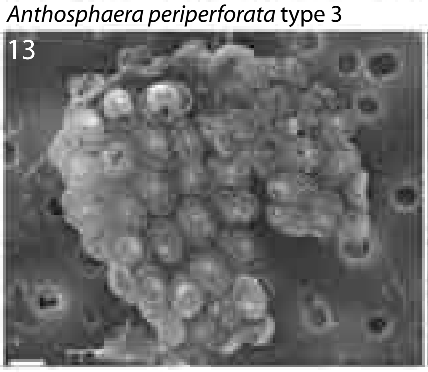
Anthosphaera periperforata type 3



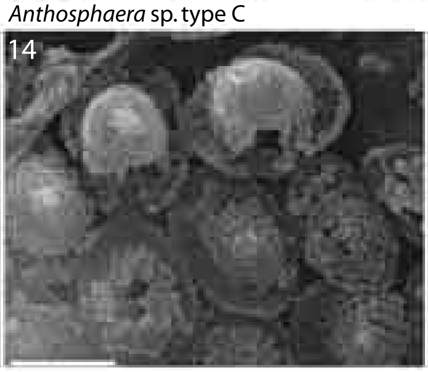
Anthosphaera sp. type C



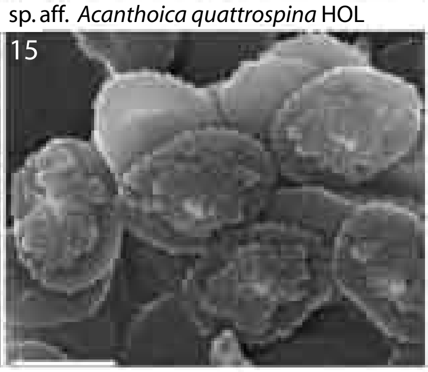
sp. aff. *Acanthoica quattrospina* HOL



Acanthoica quattrospina HOL



Acanthoica quattrospina HOL



Acanthoica quattrospina HOL

Plate 42 - Holococcoliths: Tubeless, fried egg shaped

5.2.3 - 5.2.4 *Sphaerocalyptra* - conical

Sphaerocalyptra Deflandre 1952
Dimorphic, BCs and CFCs conical calyptroliths, without tube. CFCs higher than BCs. TYPE: *S. quadridentata*

5.2.3 *Sphaerocalyptra* species without openings in cone

Sphaerocalyptra quadridentata (Schiller 1913) Deflandre 1952[*Calyptrosphaera*]
BCs conical; with basal flange; walls show irregular perforate fabric; ca 1.8 µm long, 1.2 µm high.
CFCs similar but about 2µm high. Reference: Kleijne (1991) p. 65, pl. XVII.
Life-cycle: *S. quadridentata* has been shown to form combination coccospheres with *Algirosphaera robusta* by Kamptner (1941) and Triantaphyllou & Dimiza (2003). This evidence is quite clear, however, Cros & Fortuño (2002) illustrated two less conclusive combination coccospheres of *S. quadridentata* with *Rhabdosphaera clavigera*. This may be due to: (1) a very conservative holococcolith morphology; or (2) a complex life-cycle with two heterococcolith stages; or (3) that the *R. clavigera* combination coccospheres are artefacts. Given this ambiguity we prefer to retain the traditional name *S. quadridentata*.

Sphaerocalyptra adenensis Kleijne 1991
Similar to *S. quadridentata* but flatter conical shape; no basal flange; walls show non-perforate fabric.
BCs ca. 2 µm long, 1 µm high. Reference: Kleijne (1991) p. 65, pl. XVII.

Sphaerocalyptra cf. *adenensis* Kleijne 1991 of Cros & Fortuño 2002.
Similar to *S. adenensis* but BCs smaller (ca 1.6µm) and with basal flange; CFCs strongly elevated.
BCs ca. 1.6 µm long, 1 µm high.

Sphaerocalyptra sp. 1 of Cros & Fortuño 2002
BCs low but sharp cones; ca. 1.5 µm long. CFCs high cones with distinct base 2 crystallites high.

Sphaerocalyptra sp. 2 of Cros & Fortuño 2002 *(not figured)*
BCs narrow-based steep cones with sharp tip; ca. 0.8 µm long, 0.8 µm high. CFCs high cones with distinct base 2 crystallites high.

5.2.4 *Sphaerocalyptra* species with openings in cone

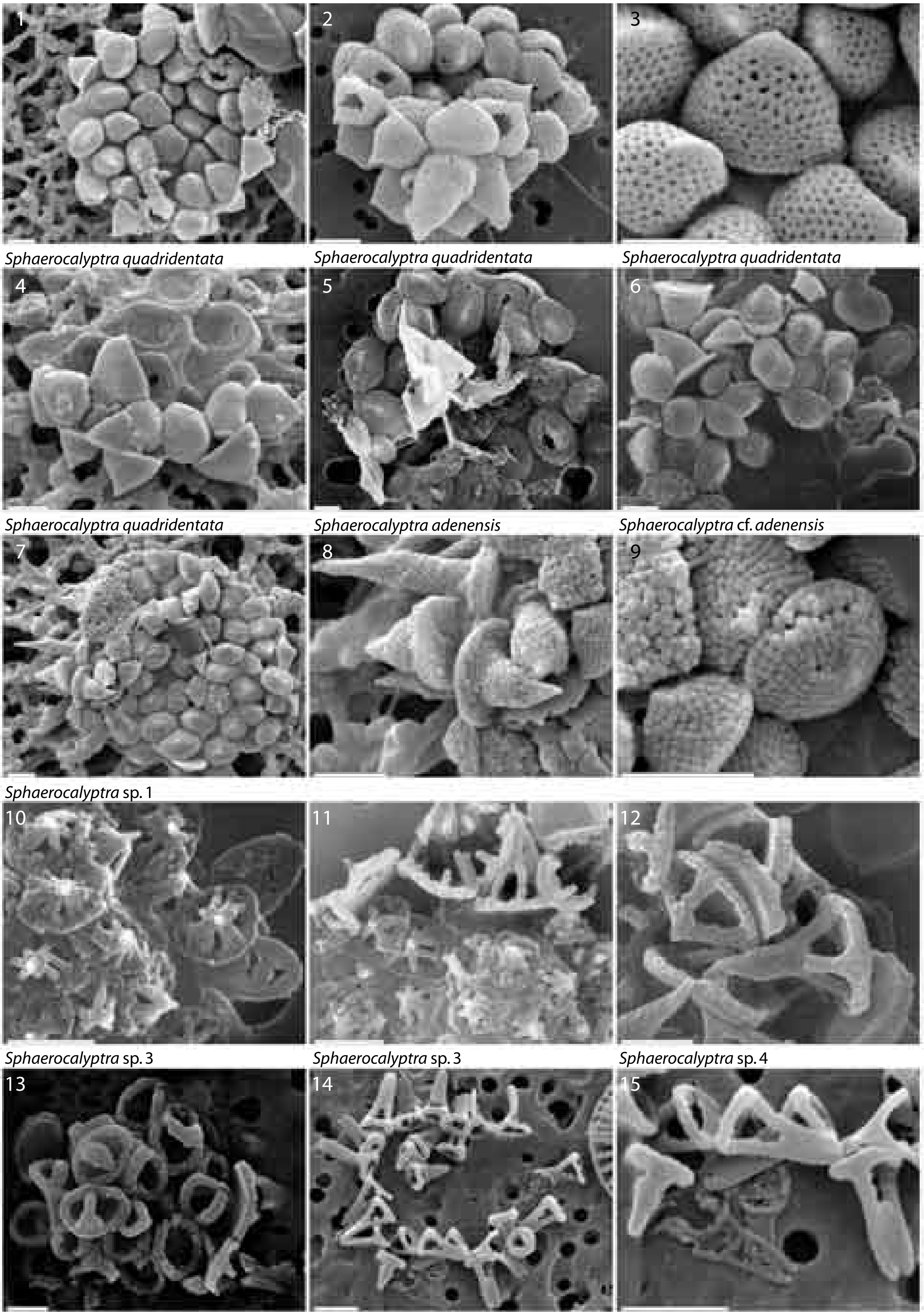
Sphaerocalyptra sp. 3 of Cros & Fortuño 2002
BCs with basal ring 2 crystallites high; surmounted by open cone of 3-4 robust bars; ca. 1.1 µm long. CFCs similar but with spine rising from the cone.

Sphaerocalyptra sp. 4 of Cros & Fortuño 2002
BCs with basal ring 1 crystallite high; surmounted by open cone of 4-6 delicate bars, with apical spine; ca. 1.7 µm long. CFCs similar but with tall spine.

Sphaerocalyptra sp. 5 of Cros & Fortuño 2002
BCs with curved cover with 2-3 openings; ca. 1.6 µm long. CFCs with conical spine supported by a few bars.

Sphaerocalyptra sp. 6 of Cros & Fortuño 2002 *(not figured)*
BCs delicate, ?domal (good specimens not seen); ca. 0.8 µm long. CFCs with long straight spine.

Holococcolithophore sp. cf. *Sphaerocalyptra*
Monomorphic. Coccoliths with small elliptical bases one crystallite high supporting two processes which bend together to form spatulate spine. Base length ca. 0.5 µm), spine height 1-1.5 µm. A very similar form is illustrated by Cros & Fortuño (2002) as "*Papposphaera* holococcolithophore" ("*Turrisphaera*") phase sp. type B. *Papposphaera* affinities do seem possible but are tentative, hence the less definite assignment given here.



1–3: *Sphaerocalyptra quadridentata*

4: *Sphaerocalyptra quadridentata*

5: *Sphaerocalyptra adenensis*

6: *Sphaerocalyptra* cf. *adenensis*

7–9: *Sphaerocalyptra* sp. 1

10–11: *Sphaerocalyptra* sp. 3

12: *Sphaerocalyptra* sp. 4

13: *Sphaerocalyptra* sp. 5

14–15: Holococolithophore sp. cf. *Sphaerocalyptra*

Plate 43 - Holococcoliths: tubeless, conical, *Sphaerocalyptra*

5.3 Convex-covered tube

5.3.1 Convex, regular form

Calyptrosphaera Lohmann 1902

Dome-shaped coccoliths - calyptroliths. Monomorphic (but CFCs may be slightly modified). TYPE: *C. oblonga*. NB Rather variable species have been assigned to *Calyptrosphaera* and the genus is almost certainly polyphyletic. "*Calyptrosphaera*" coccoliths are covered in this guide in three sections: regular species here (*C. oblonga, C. pirus, C. sphaeroidea, C. galea*); elevated species in section 5.3.2 (*C. heimdaliae*, *C. radiata*); flat topped species in section 5.6.4 (*C. dentata, C. cialdii*).

Syracosphaera pulchra HOL *oblonga* type = {*Calyptrosphaera oblonga* Lohmann 1902}

BCs - tube flares initially then curves into convex cover; proximal surface with basal flange and two concentric rings of crystallites, large central opening; hexagonal mesh fabric to tube and cover. CFCs more elevated and with pyramidal central boss.

Liths 2-2.5 μm. References: description - Kleijne (1991) p. 28, pl. III; life-cycle - Cros et al. (2000), Geisen et al. (2002).

Syracosphaera pulchra HOL *pirus* type = {*Calyptrosphaera pirus* Kamptner 1937}

BCs- tube about 10 crystallites high, tiered wall fabric; basal flange; distal cover recessed into tube, domal with ring of 8-10 pores around contact with tube; internal ridges surround pores in at least some specimens. CFCs more elevated and with pyramidal central boss. References: description - Kleijne (1991) p. 28, pl. III-IV; life-cycle - Geisen et al. (2003), Saugestad & Heimdal (2002).

NB Following Norris (1985) this species was usually assigned to *Daktylethra*. However, *Daktylethra* is an Eocene genus (type *D. punctulata* Gartner in Gartner & Bukry 1969) of very different morphology.

Calyptrosphaera sphaeroidea Schiller 1913

Lith shape similar to *C. oblonga* but less regular; irregular wall fabric, crystallites rather larger than in most holococcoliths and with rough surface; CFCs not differentiated. References: description - Kleijne (1991) p. 2 8, pl. II; cytology - Klaveness (1973); life-cycle - Noel et al. (in press).

Noel et al. (subm.) have shown from culture experiments that the alternate life-cycle phase of this species produces narrow-rimmed placoliths (see section 3.3, plate 32). Since the type species of *Calyptrosphaera*, *C. oblonga*, is known to be a life-cycle stage of *Syracosphaera pulchra* a new genus will need to be described for this species.

Calyptrolithina Heimdal 1982

Calyptrolith body coccoliths and apical zygoliths. TYPE: *C. divergens*.

Calyptrolithina divergens (Halldal & Markali 1955) Heimdal 1982 var. *divergens* [*Zygosphaera*]

BC tube flaring, about 5 crystallites high, tiered wall fabric, often with some perforations; basal flange; distal cover conical, recessed within tube, hexagonal mesh fabric. Liths ca. 2 μm long.

CFC similar but distal cover with large pores at each end and extended into bridge.

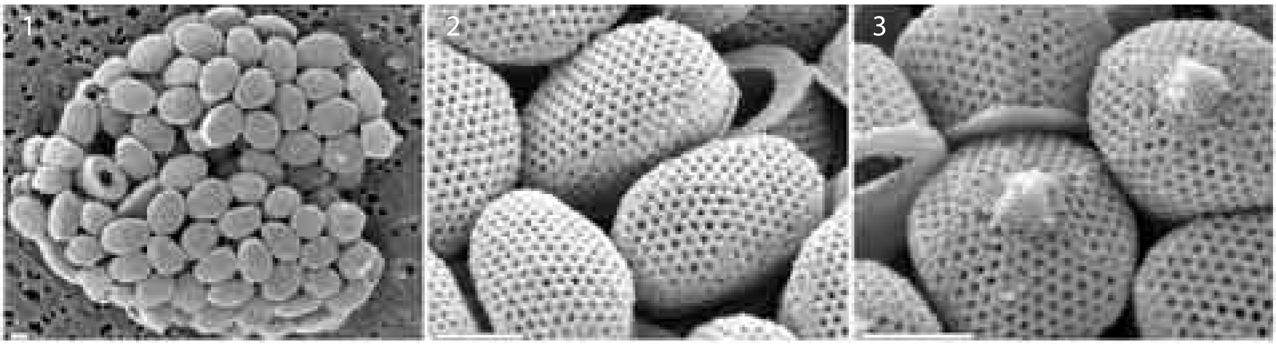
Reference: Kleijne (1991) p. 45, pl. X.

Calyptrolithina divergens var. *tuberosa* (Heimdal 1980) Jordan et al. 1993 [*Zygosphaera*]

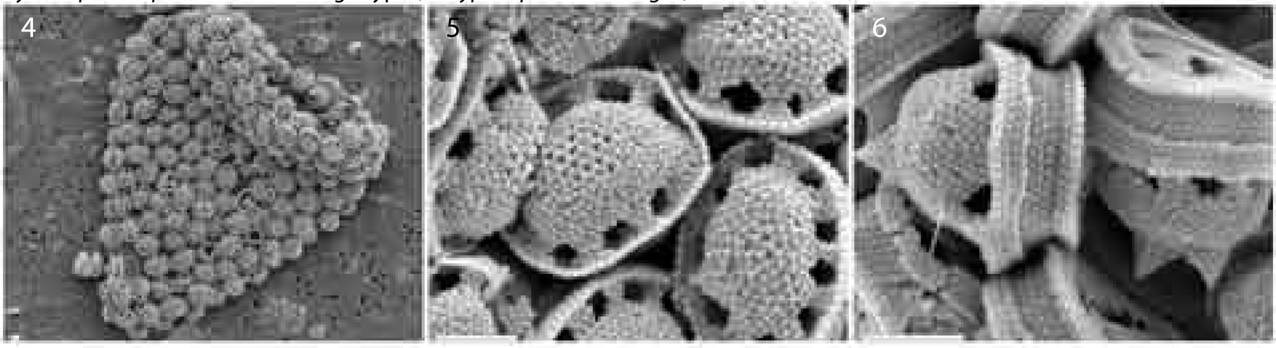
Like *C. divergens* but distal surface flatter and with numerous pores [some similarities to *C. multipora*, but pores less regular and walls flaring].

Calyptrosphaera galea Lecal-Schlauder 1951 *(not figured)*

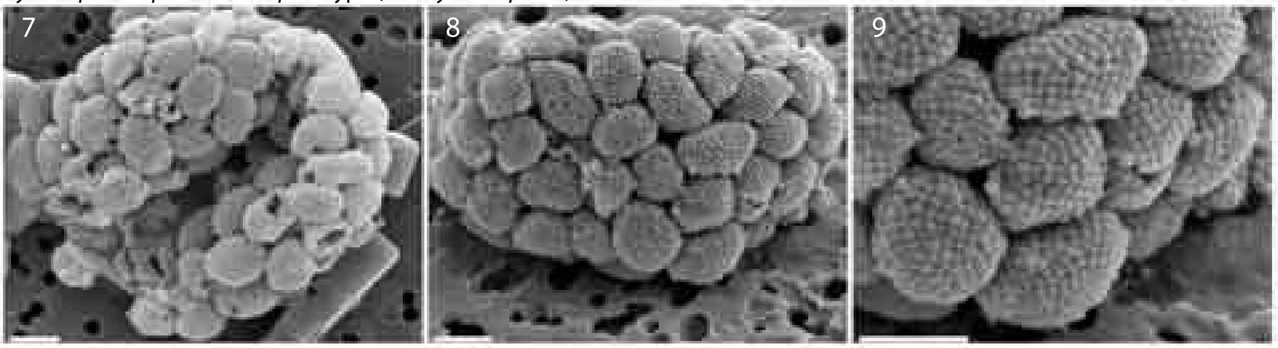
Like *C. divergens* but tube higher (ca. 7 crystallite layers vs. ca. 5), protrusion broader and rim/distal surface break less distinct. Hexagonal mesh fabric. Not common or widely recognised, but an unambiguous specimen was illustrated by Norris (1985, p. 624).



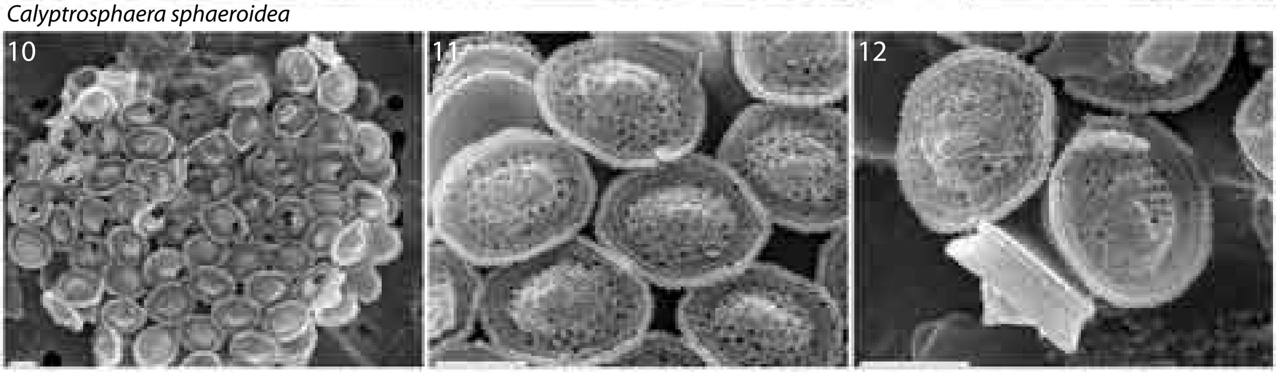
Syracosphaera pulchra HOL *oblonga* type ("*Calyptrosphaera oblonga*")



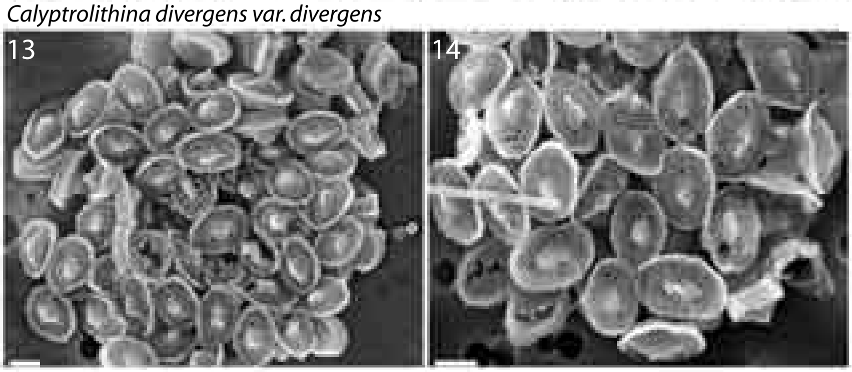
Syracosphaera pulchra HOL *pirus*type ("*Daktylethra pirus*")



Calyptrosphaera sphaeroidea



Calyptrolithina divergens var. divergens



Calyptrolithina divergens var. tuberosa

Plate 44 - Holococcoliths: Convex cover, *Calyptrosphaera* & *Calyptrolithina*

5.3.2 Convex, ornate forms

This is a mixed group of large distinctive holococcoliths with elevated tubes and more or less domal cover.

Calyptrosphaera heimdaliae Norris 1985
Liths pointed domes, hexagonal mesh fabric; large openings above tube, and often a circular apical opening. Liths about 2 μm high.

Calyptrosphaera radiata Sym & Kawachi 2000 *(not figured)*
Liths tubular with large openings near base and closed distal end. Up to 2μm long but height varies on coccosphere, about 0.8 μm wide. The species is only known from cultures and the coccoliths are not well-formed. The shape is somewhat similar to *Turrisphaera* (see below) but the cells have prominent chloroplasts and lack a haptonema, whilst the Papposphaeraceae cells have prominent haptonemata but lack chloroplasts (Thomsen et al. 1995). Molecular genetic data suggest affinity with the Coccolithaceae and with *Calyptrosphaera sphaeroidea*.

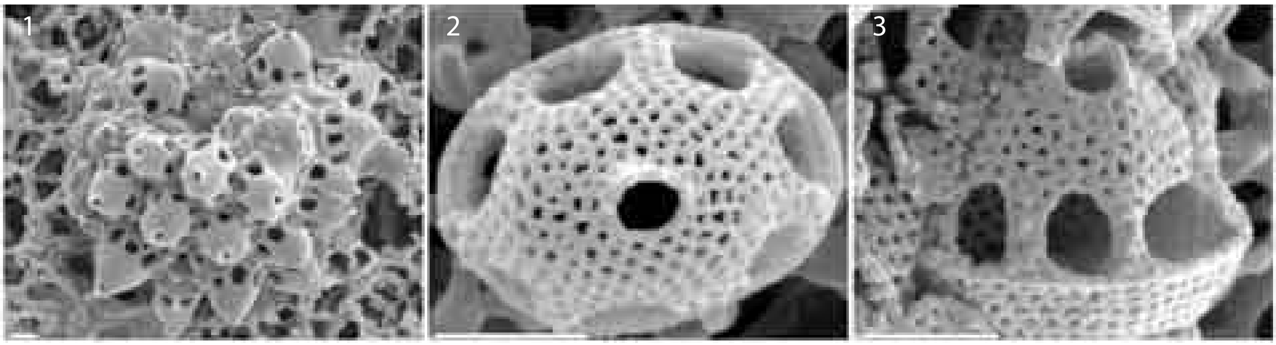
Flosculosphaera Jordan & Kleijne *in* Kleijne *et al*. 1991
Flaring tube-shaped coccoliths with distal cover - flosculoliths. Monomorphic. TYPE: *F. calceolariopsis*.

Flosculosphaera calceolariopsis Jordan & Kleijne *in* Kleijne et al. 1991
Liths 3-4 μm tall, with two proximal flanges. Reference: Kleijne (1991) p. 29, pl. XX.

Flosculosphaera sacculus Kleijne & Jordan *in* Kleijne et al. 1991
Liths ca. 3 μm tall, with one proximal flange. Reference: Kleijne (1991) p. 29, pl. XX.

Gliscolithus Norris 1985
Bulb-shaped coccoliths - gliscoliths. Monomorphic. TYPE: *G. amitakareniae*.

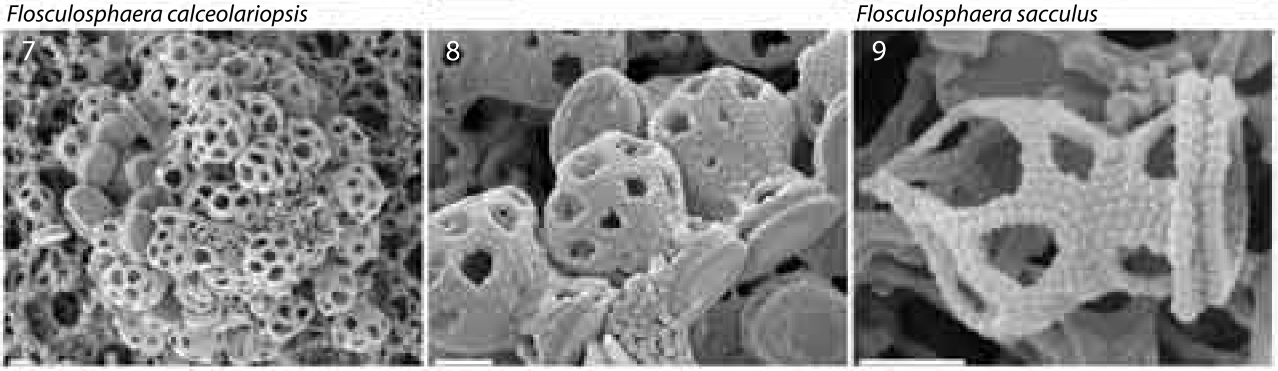
Gliscolithus amitakareniae Norris 1985 orthog. emend. Jordan & Green 1994
Liths 4 μm tall, with two proximal flanges and numerous large openings. Reference: Kleijne (1991) p. 29, pl. V.



Calyptrosphaera heimdaliae

Flosculosphaera calceolariopsis

Flosculosphaera sacculus



Gliscolithus amitakareniae

Plate 45 - Holococcoliths: Convex top, elevated

5.4 Open-topped tube

5.4.1 *Calicasphaera* - cup-shaped

Calicasphaera Kleijne 1991
Chalice-shaped coccoliths - calicaliths. Possible affinities to *Turrisphaera*. Monomorphic. TYPE: *C. diconstricta*.

Calicasphaera blokii Kleijne 1991
Liths oval, low, with blocky crystallites.
Spheres 6-7 μm, liths ca. 1 μm. Reference: Kleijne (1991) p. 24, pl. II.

Calicasphaera concava Kleijne 1991
Liths circular, almost as high as wide, opening continuously from narrow base.
Spheres 7-11 μm, liths ca. 1.5-2 μm. Reference: Kleijne (1991) p. 24, pl. I.

Calicasphaera diconstricta Kleijne 1991
Liths sub-circular; tall stem, with two constrictions.
Spheres 6-9 μm, liths 1-1.5 μm. Reference: Kleijne (1991) p. 22, pl. I.

5.4.2 *Papposphaera* holococcoliths *{Turrisphaera}*

{Genus *Turrisphaera* Manton, Sutherland & Oates 1976}
Tower-like holococcoliths with hexagonal crystallite groups. TYPE: *T. borealis*. The three described species are all thought to be HOL phases of *Papposphaera* spp. so the generic name *Turrisphaera* is redundant (Thomsen et al. 1991).

Papposphaera borealis HOL = {*T. borealis* Manton, Sutherland & Oates 1977}
Coccosphere elongate l.6-8 μm, varimorphic, liths higher at flagellar end, liths are not widened distally. (NB HET phase was previously called *P. sagittifera*).

Papposphaera arctica HOL = { *T. arctica* Manton, Sutherland & Oates 1976b}
Coccosphere spherical, ca. 7 μm, monomorphic. Coccoliths, ca. 1-1.5 μm long, apple-core shaped. (NB HET phase was previously called *P. sarion*).

Papposphaera polybotrys HOL Thomsen 1980 ={*T. polybotrys* Thomsen 1980}
Coccosphere, ca. 5 μm, spherical, dimorphic, liths larger at flagellar end. Liths goblet-shaped, sub-circular base, narrow stem flaring; BCs ca. 1 μm high, CFCs ca. 3 μm high, unilaterally enlarged and closed distally. (NB HET phase observed by Thomsen et al. 1991, but not well enough for description).

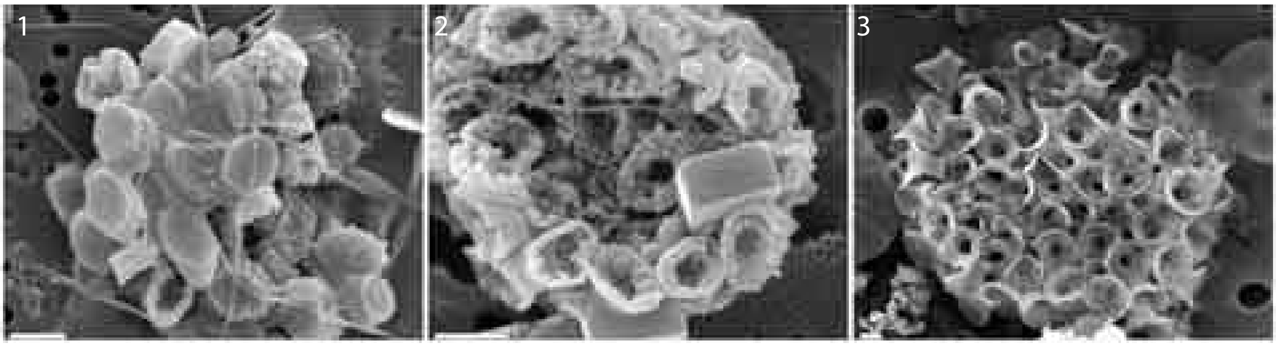
5.4.3 *Trigonaspis* - tower like

Trigonaspis Thomsen 1980
Holococcoliths formed of triangular crystallite groups (ca. 0.15 μm across), each composed of three (?hexagonal) sub-units. Dimorphic CFCs tower-like, BCs simple disks. TYPE: *T. diskoensis*.

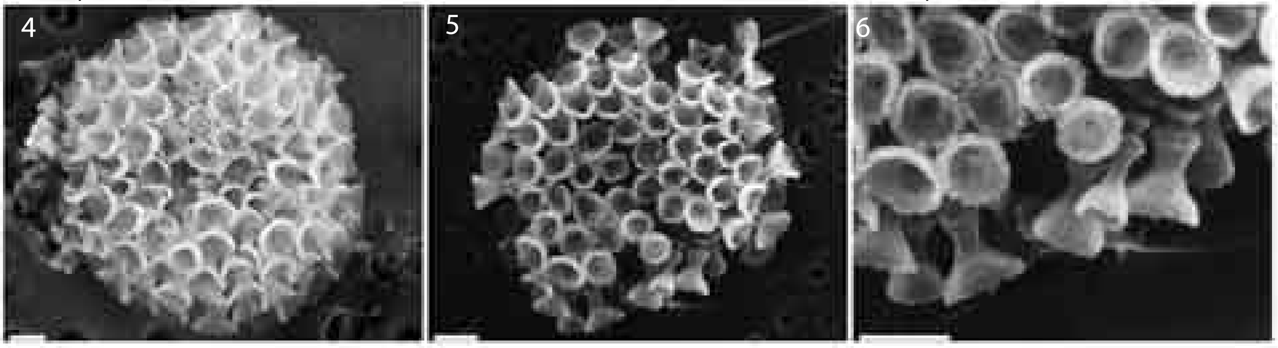
Trigonaspis diskoensis Thomsen 1980
Cell spherical 5-6 μm; CFCs tower-like 1.5-2.5 μm high, ca. 1 μm wide, centre of tube narrower; BCs flat plates, ca. 1-1.5 μm long, with monolayer of crystallites.
Life-cycle: Possibly the HOL phase of *Papposphaera flabellifera* var. *borealis,* a combination cell of *P. flabellifera* var. *borealis* with *Trigonaspis* coccoliths was illustrated by Thomsen et al. (1991) but identification as *T. diskoensis* was uncertain.

Trigonaspis melvillea Thomsen *in* Thomsen et al. 1988
Cell spherical 3-4 μm. CFCs with slender tube ending distally in a single distally directed triangular plate. BCs are only slightly raised above the baseplate.

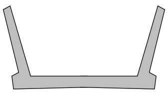
Trigonaspis minutissima Thomsen 1980
Similar to *T. diskoensis* but smaller, cell 2-3.5 μm; CFCs tower-like 1.0-1.5 μm high; BCs flat plates, < 1 μm long.



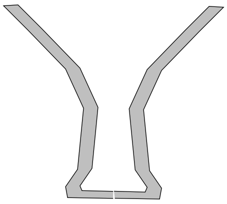
Calicasphaera blokii *Calicasphaera concava*



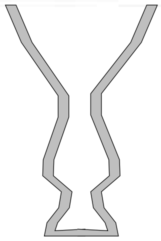
Calicasphaera diconstricta



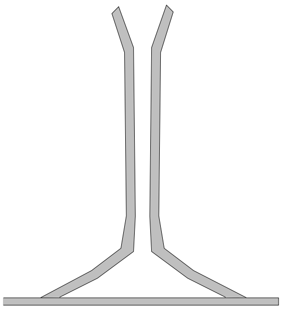
Calicasphaera blokii



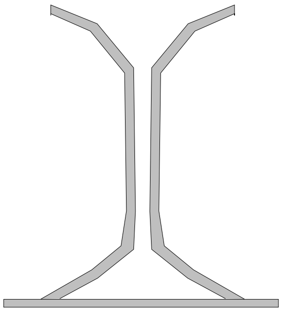
Calicasphaera concava



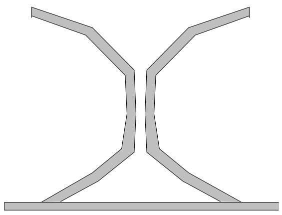
Calicasphaera diconstricta



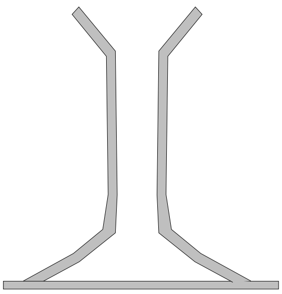
Papposphaera borealis HOL
{*Turrisphaera arctica*}



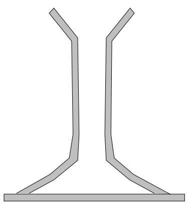
Papposphaera sarion HOL
{*Turrisphaera borealis*}



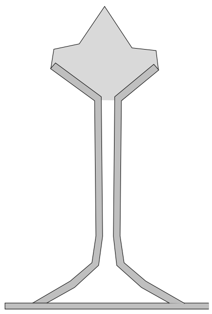
Papposphaera polybotrys HOL
{*Turrisphaera polybotrys*}



Trigonaspis diskoensis



Trigonaspis minutissima



Trigonaspis melvillea

Plate 46 - Holococcoliths: open, *Calicasphaera, Papposphaera, Trigonsaspis*

5.4.4 *Syracolithus* - internal septae

Syracolithus spp. with internal septae

Coccospheres monomorphic, coccoliths are open tubes with internal septae (walls), extending down to proximal surface. The tube wall shows hexagonal fabric and the crystallites have radial *c*-axes (birefringent in plan view in LM). The fabric of the septae is not obviously different but they are non-birefringent in plan view in LM and so the calcite crystallites must have vertical *c*-axes. This is a very different ultrastructure to the rest of the species of *Syracolithus* (see section 5.5.3) and the two sets of "*Syracolithus*" species are almost certainly not closely related, although they can look superficially similar in SEM. This is supported by life-cycle evidence showing that the two holococcolith types are formed respectively by the Calcidiscaceae and Helicosphaeraceae.

Calcidiscus leptoporus ssp. *quadriperforatus* HOL (Kamptner 1937) Geisen et al 2002. = {*Syracolithus quadriperforatus* (Kamptner 1937) Gaarder 1962 [*Syracosphaera*]}

Internal walls define 4-6 pores. Tube 10-15 crystallites high, castellated, higher where it meets internal walls. Tube double layered, base open.

Liths 2-2.5 μm long. Reference: Kleijne (1991) p. 37, pl. VII.

Life-cycle: The association of this holococcolith with the large *C. leptoporus* morphotype is based on a single specimen, but it is an exceptionally clear combination coccosphere (Geisen et al. 2002).

Syracolithus bicorium Kleijne 1991

Liths similar to *S. quadriperforatus* but walls double layered with open hexagonal mesh fabric. Reference: Kleijne (1991) p. 38, pl. VII.

Syracolithus schilleri (Kamptner 1927) Loeblich & Tappan 1963

Liths similar to *S. quadriperforatus* but larger (3-4 μm) and with more pores (8-20). LM observations show that the ultrastructure is similar to *S. quadriperforatus*. NB Similar holococcoliths occur sporadically in the fossil record through the Neogene, and are usually assigned to *Holodiscolithus macroporus* (see e.g. Young 1998, p.254).

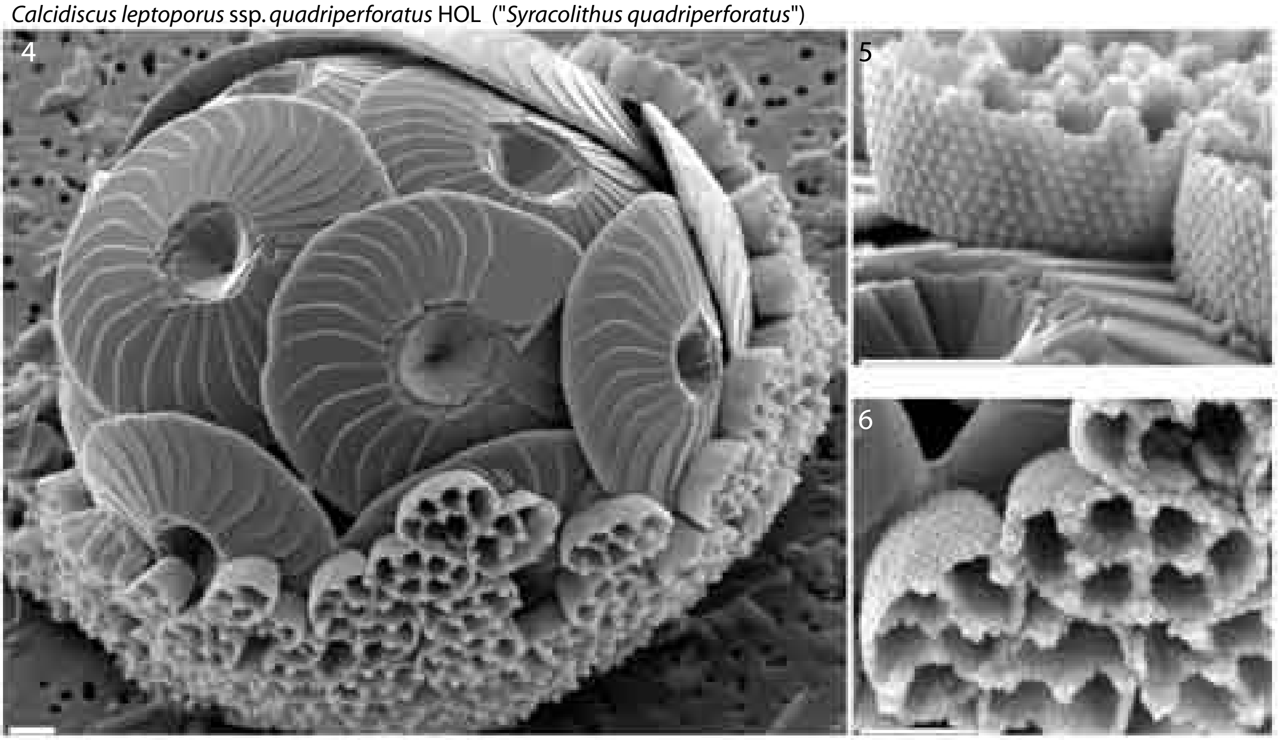
Syracolithus sp. type A of Kleijne (1991)

Coccoliths with area inside tube almost filled by concentric walls, distal surface ornamented by 10-15 pyramidal bosses. The affinities of this species are not sure, and it has not been observed by light microscopy. The structure looks similar to *Zygosphaera*, especially *Z. marsilii,* but it is monomorphic whilst *Zygosphaera* species all have well-differentiated CFCs, and there is no central ridge. So rather tentatively, it is left here. Reference: Kleijne (1991) p. 38, pl. VIII.

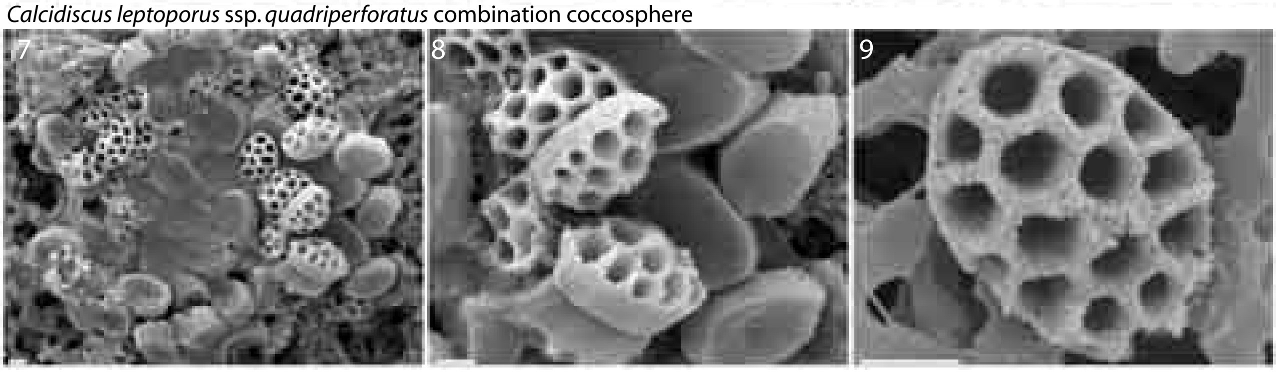
Syracolithus sp. type B of Kleijne (1991) *(not figured)*

Liths similar to *S. quadriperforatus* but more delicate and with open hexagonal mesh fabric. Reference: Kleijne (1991) p. 38, pl. VI.

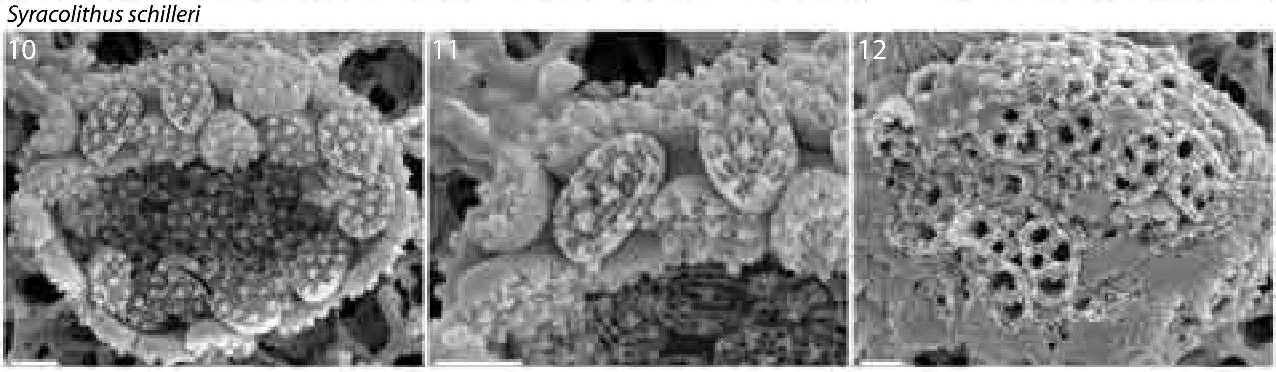
Calcidiscus leptoporus ssp. *quadriperforatus* HOL ("*Syracolithus quadriperforatus*")



Calcidiscus leptoporus ssp. *quadriperforatus* combination coccosphere



Syracolithus schilleri



Syracolithus sp. type A

Syracolithus bicorium

Plate 47 - Holococcoliths: open, septate, tubes, *Syracolithus*

5.5 BCs Bridged tube

5.5.1 *Poritectolithus* - stringy bridge

Poritectolithus Kleijne 1991

Distinctive set of similar spp. TYPE: *P. poritectum*.

BCs zygolith with bridge formed of sub-parallel strings of crystallites. CFCs helladoliths - bridge narrower and extended into leaf.

Poritectolithus species without openings

Poritectolithus poritectum (Heimdal *in* Heimdal & Gaarder 1980) Kleijne 1991 [*Helladosphaera*]

BCs tube about 4 crystallites high with basal flange. Bridge modified into mound extending along the length of coccoliths. CFCs tube raised at sides; well-developed leaf.

NB This is *not* the form described and illustrated by Kleijne 1991 as *P. poritectum*.

Poritectolithus tyronus Kleijne 1991

Like *P. poritectum* but less convex and CFC leaf terminated in narrow spinelet (distinction of these two species may prove unsound). Reference: Kleijne (1991) p.63, pl. XVII.

Poritectolithus sp. 1 of Cros & Fortuño 2002 *(not figured)*

Like *P. tyronus* but BCs tube very low, only 2 crystallites high and mound rather flat. CFCs with well-developed leaf.

Poritectolithus species with openings

Poritectolithus maximus Kleijne 1991

BCs tube about 4 crystallites high, with basal flange and row of pores above; convex strings of small crystallites form a high bridge; 2-2.5 μm long. CFCs tube raised at sides; well developed leaf.

Reference: Kleijne (1991) p. 62, pl. XVI.

Poritectolithus sp. 2 of Cros & Fortuño 2002 *(not figured)*

Similar to *P. maximus* but BCs smaller (1.5-2 μm long) and leaf pointed rather than flaring.

NB This *is* the form described and illustrated by Kleijne 1991 (p. 62, pl. XVI) as *P. poritectum*.

5.5.2 *Homozygosphaera* - monomorphic with zygoliths

Homozygosphaera Deflandre 1952

Coccoliths with tube spanned by bridge - zygoliths. Monomorphic. TYPE: *H. spinosa*

Homozygosphaera arethusae (Kamptner 1941) Kleijne 1991 [*Corisphaera*]

BCs bridge smooth continuation of tube, wide and broad arch, broadens toward top, as high as lith is long, ca. 1.5 μm long.

CFCs with slightly higher bridge. Reference: Kleijne (1991) p. 31, pl. V.

Life-cycle: two possible combination coccospheres with *Syracosphaera* sp. type D were observed by Cros et al. (2000). Since this association is unproven, we retain the traditional name here.

Homozygosphaera spinosa (Kamptner 1941) Deflandre 1952 [*Corisphaera*]

Like *H. arethusae* but bridge higher (taller than coccolith length) and narrower.

Liths 1.5-2.5 μm high. Reference: Kleijne (1991) p. 31, pl. VII.

Homozygosphaera triarcha Halldal & Markali 1955

Like *H. arethusae* but bridge has three struts (Y-shaped in plan view).

Liths ca. 2.5 μm long, 2-3 μm high. Reference: Kleijne (1991) p. 31, pl. V.

5.5.3 *Periphyllophora* - monomorphic with helladoliths

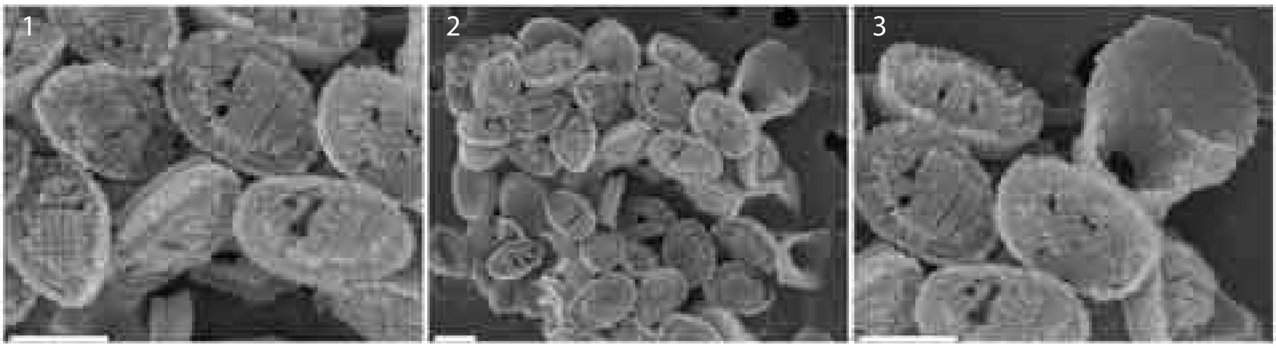
{*Periphyllophora* Kamptner 1937}

Monomorphic BCs and CFCs are helladoliths. TYPE: *P. mirabilis*.

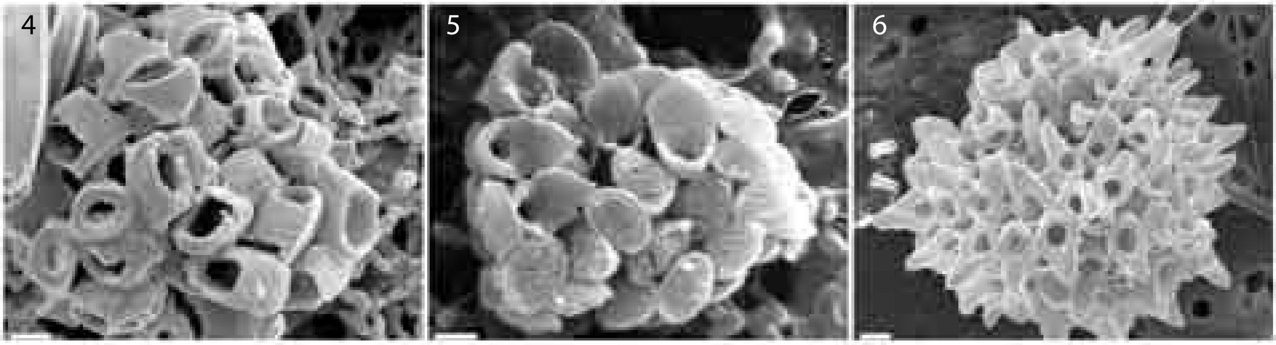
Syracosphaera anthos HOL = {*Periphyllophora mirabilis* (Schiller 1925) Kamptner 1937 [*Calyptrosphaera*]}

Tube about ten crystallites high, no flange, double walled; Leaf double layered, with very regular hexagonal array fabric, layers diverge as they reach tube and develop prominent opening. This is the only species with helladolith body coccoliths.

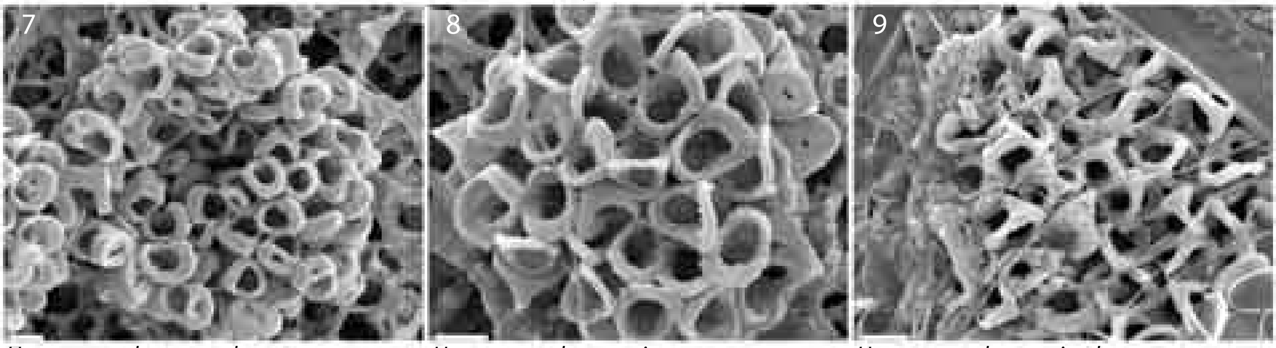
Liths ca. 2 μm long, ca. 3.5 μm high. Reference: Kleijne (1991) p. 33, pl. XIV. Life-cycle: two combination coccospheres observed by Cros et al. (2000), one of which is totally unambiguous.



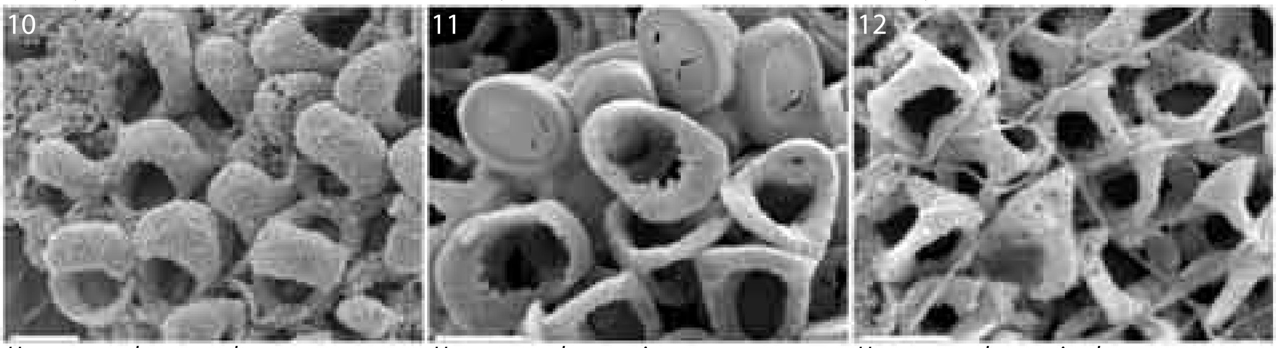
Poritectolithus poritectum *Poritectolithus poritectum* *Poritectolithus poritectum*



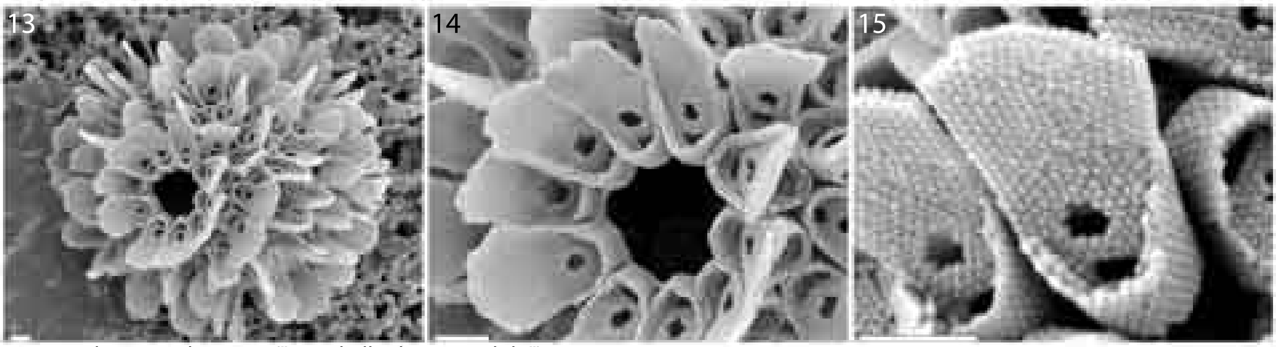
Poritectolithus maximus *Poritectolithus tyronus* *Homozygosphaera triarcha*



Homozygosphaera arethusae *Homozygosphaera spinosa* *Homozygosphaera triarcha*



Homozygosphaera arethusae *Homozygosphaera spinosa* *Homozygosphaera triarcha*



Syracosphaera anthos HOL ("*Periphyllophora mirabilis*")

Plate 48 - Holococcoliths: Bridged

5.5.5 *Corisphaera* - weakly dimorphic

Corisphaera Kamptner 1937
Both BCs and CFCs are zygoliths (i.e. have bridges but these are not extended into leaves). TYPE: *C. gracilis*.

Corisphaera gracilis Kamptner 1937
BCs tube simple, with 2-layered wall; distal surface open except low, narrow, slightly oblique, s-shaped, bridge. Liths ca. 1.5 μm long.
CFCs bridge extended into leaf. Reference: Kleijne (1991) p. 52, pl. XII.
NB Rather variable morphotypes are assigned to *C. gracilis* and it may prove to include several discrete species, see Cros & Fortuño (2002).

Corisphaera tyrrheniensis Kleijne 1991
Like *C. gracilis* but with open perforate wall structure, with three concentric cycles (possibly indicating affinities to *Zygosphaera*). Reference: Kleijne (1991) p. 53, pl. XII.

Corisphaera sp. type A - (in Kleijne (1991) p. 54 pl. XIII) -> see *Zygosphaera bannockii* (Plate 51)

Corisphaera sp. type B Kleijne (1991) p. 54, pl. XIII
Similar to *H. cornifera* but BCs more delicate and symmetrical, CFCs with less well developed leaf. (zygoliths rather than helladoliths).
NB Life-cycle: Cros et al. (2000) documented a possible association with *Syracosphaera delicata*, we use the traditional name here since the association is unproven.

Corisphaera strigilis -> see above (Plate 41).

5.5.6 *Helladosphaera* - strongly dimorphic

Helladosphaera Kamptner 1937
Dimorphic - BCs are zygoliths but CFCs are helladoliths (i.e. have bridges which are extended into leaves). TYPE: *H. cornifera*.

Helladosphaera cornifera (Schiller 1913) Kamptner 1937 [*Syracosphaera*]
BCs simple tube, ca 6 crystallites high, no basal flange or baseplate; bridge asymmetrical, thin and high ending in weak leaf. Liths ca. 1.5 μm long.
CFCs bridge extended into large pointed leaf, ca. 2.5 μm high.
Reference: Kleijne (1991) p. 57, pl. XIV.

Helladosphaera pienaarii Norris 1985
BCs tube with basal flange; H-shaped set of septae rise from distal surface, forming bridge parallel to long axis. Liths ca. 2 μm long.
CFCs bridge extended into large leaf ca. 1.5 μm high.
Coccosphere pear-shaped. Reference: Kleijne (1991) p. 59, pl. XV.

Helladosphaera vavilovii (Borsetti & Cati 1976) Young & Kleijne n. comb. [*Homozygosphaera*]
BCs like *H. arethusae* but bridge triangular in profile, terminated by ridge parallel to long axis of coccolith; open wall structure.
CFCs are well differentiated, helladoliths. Since the genus *Homozygosphaera* is defined as being monomorphic, we introduce this new combination.
AACs with higher bridge than BCs.

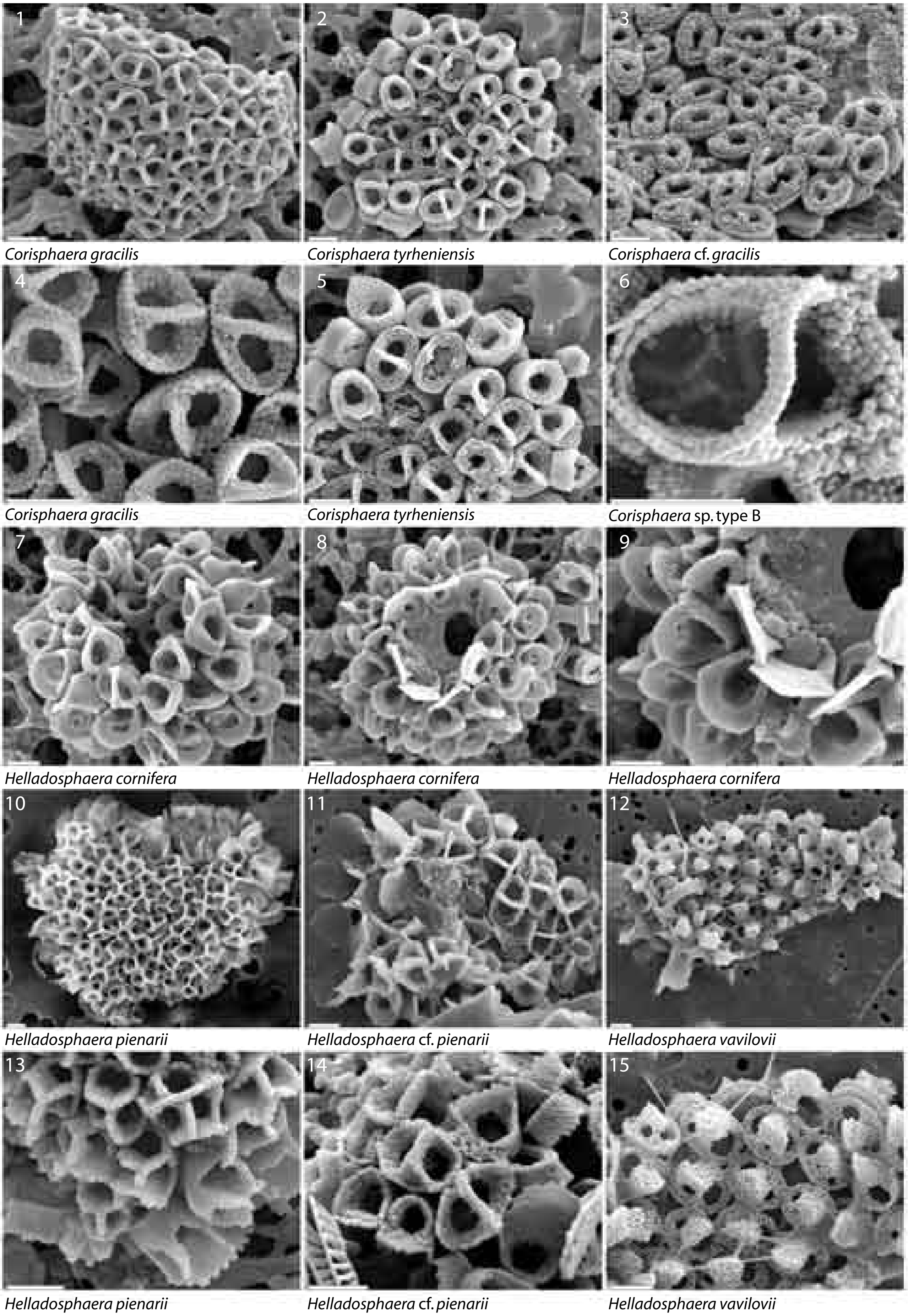


Plate 49 - Holococcoliths: Bridged

5.6 Flat-covered tube

5.6.1 *Coronosphaera* holococcoliths and associated species

Calyptrolithina Heimdal 1982
Dimorphic - BCs are calyptroliths, CFCs are zygoliths. TYPE: *C. divergens*.

Calyptrolithina multipora (Gaarder *in* Heimdal & Gaarder 1980) Norris 1985 [*Syracolithus*]
BCs tube simple; distal surface flat, slightly recessed below top of tube, with central boss surrounded by numerous hexagonal/star-shaped pores. Liths ca. 2.5 μm long.
CFCs zygoliths, open tube spanned by robust bridge, with low pointed leaf.
Reference: Kleijne (1991) p. 46, pl. X.
Life-cycle: One combination coccosphere of a rather atypical *C. multipora* with *Coronosphaera* sp. is illustrated in Plate 23.

Coronosphaera mediterranea HOL *wettsteinii-type* {*Calyptrolithina wettsteinii* (Kamptner 1937) Norris 1985 [*Zygosphaera*]}
Similar to *C. multipora* but only 4-6, irregular, pores on distal surface. Reference: Kleijne (1991) p. 46, pl. XI.
Life-cycle: Combination coccospheres illustrated by Kamptner (1941) and Cros et al. (2000), discussed by Geisen et al. (2002).

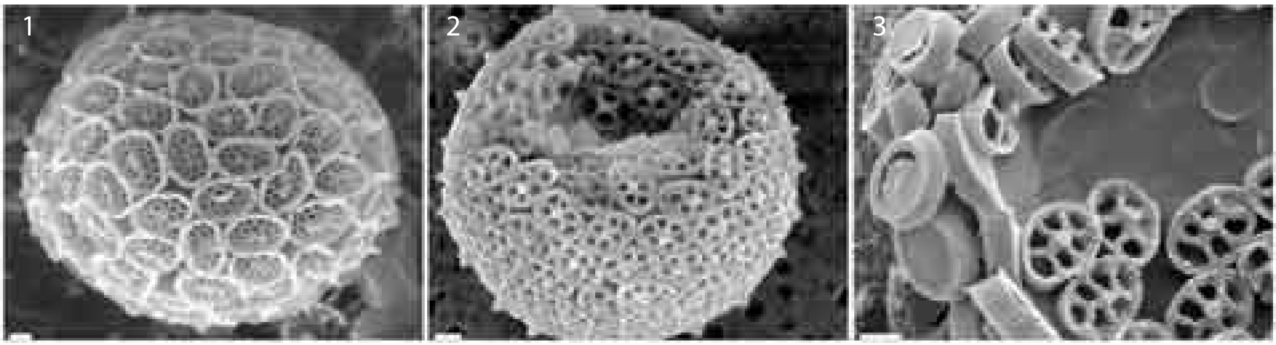
Homozygosphaera vercellii Borsetti & Cati 1979
Monomorphic, liths similar to BCs of *C. wettsteinii*, but pores more angular, separated by network of straight bars two crystallites wide, also boss smaller, often not central, some liths have two bosses. Weak basal flange. Rarely reported. (NB Specimen in Winter & Siesser 1994, fig. 155 = *C. wettsteinii*).

Calyptrolithophora Heimdal *in* Heimdal & Gaarder 1980
Dimorphic - both BCs and CFCs are calyptroliths, but in the CFCs, the distal surface is vaulted into a central ridge parallel to the short axis. TYPE: *C. papillifera*.

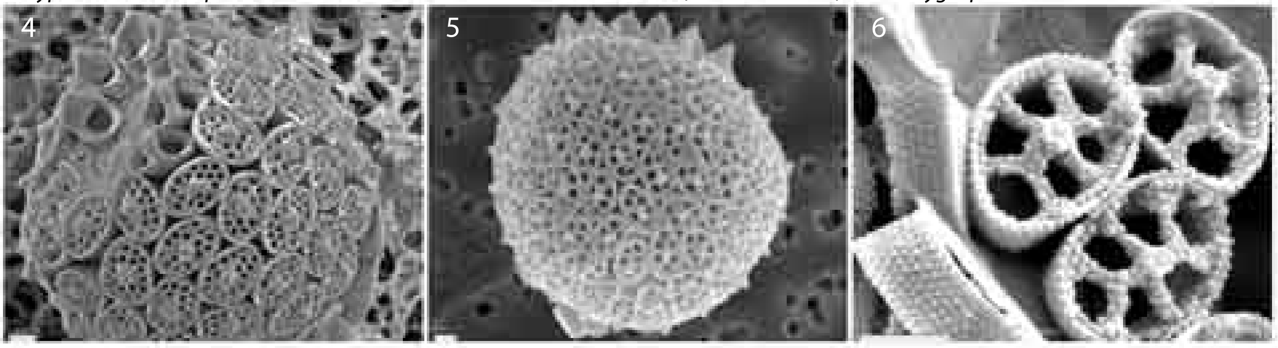
Coronosphaera mediterranea HOL *gracillima*-type {*Calyptrolithophora gracillima* (Kamptner 1941) Heimdal *in* Heimdal & Gaarder 1980}
BCs tube flaring, no flange, hexagonal mesh fabric; distal cover flat, hexagonal mesh fabric without larger pores; discontinuous rim formed from two rows of crystallites; boss, prominent, slightly off-centre, with irregular fabric.
SYNONYM: *Calyptrolithophora hasleana* (Gaarder 1962) Heimdal *in* Heimdal & Gaarder 1980 [*Corisphaera*]. Similar to *C. gracillima* but, central protrusion extended into bar and with rim around distal surface better developed (Kleijne 1991). Intergrades between the *hasleana* and *gracillima* morphotypes occur and the distinction is probably artificial.
Reference: Kleijne (1991) p. 48, pl. XI.
Life-cycle: A single, good, combination coccosphere has been observed by Cortes & Bollmann (2002), also discussed in Geisen et al. (2002).

Calyptrolithophora papillifera (Halldal 1953) Heimdal, *in* Heimdal & Gaarder 1980 ?= *S. histrica* HOL
BCs tube about 9 crystallites high, no flange; distal surface flat; hexagonal mesh fabric to tube and distal cover. Liths ca. 2 μm long.
CFCs vaulted with flat hexagonal mesh plates sloping towards centre from each end. Between these plates an irregular area of parallel strings of crystallites occurs.
Reference: Kleijne (1991) p. 48, pl. XII.
Life-cycle: Based on holococcolith morphology we might predict an association with a *Coronosphaera* species, however, a possible combination coccosphere with *Syracosphaera histrica* was shown by Cros et al. (2000).

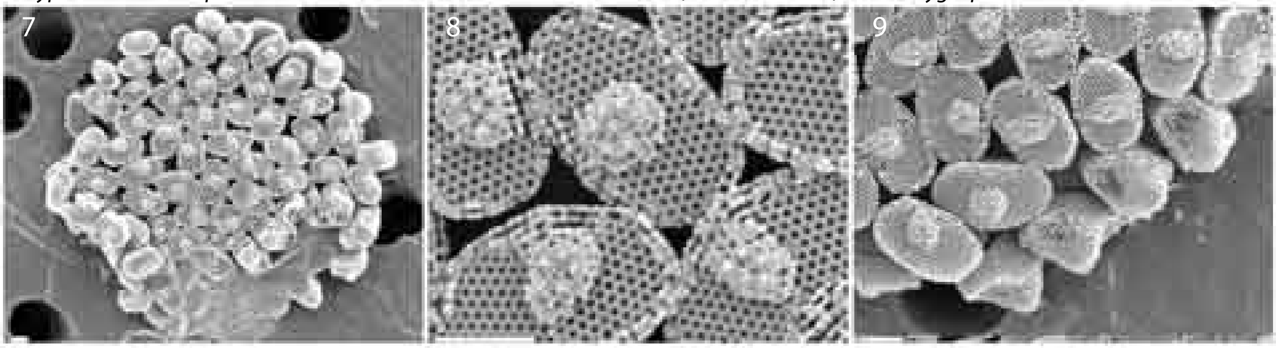
Coronosphaera mediterranea HOL *hellenica* type = {*Zygosphaera hellenica* Kamptner 1937}
BCs with central node; tube wall shows hexagonal crystallite fabric with row of perforations above base and a variable number of extra perforations. Variation: on the distal surface the concentric ring structure may be clear or obscure; some specimens have two pores. Liths ca. 2 μm long.
CFCs with node elevated into spine-like structure with three buttresses.
Reference: Kleijne (1991) p. 69, pl. XVIII.
Life-cycle: "*Z. hellenica*" coccoliths have been observed in culture to be formed by the alternate phase of a *Coronosphaera mediterranea* strain (Geisen et al. 2002; Houdan et al. in press).



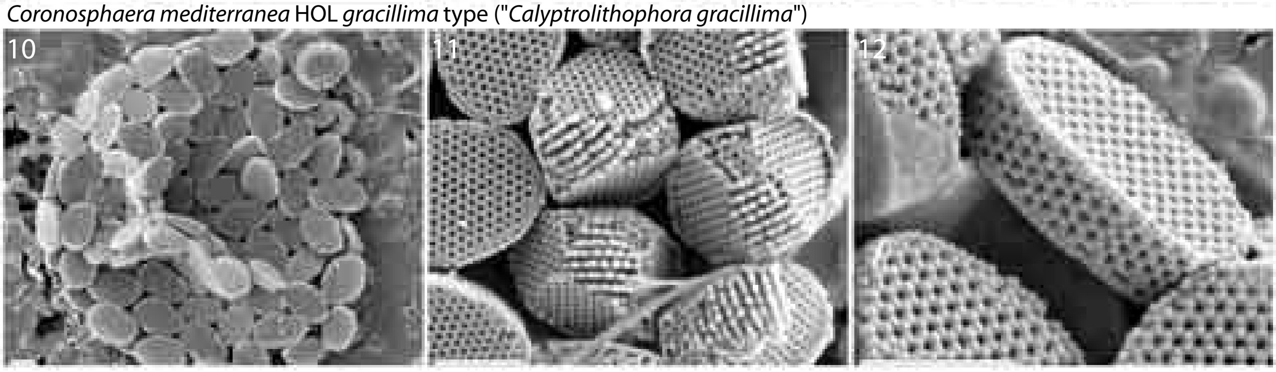
Calyptrolithina multipora | *Co. medit.* HOL *wettsteinii* ("*C'lithina wett.*") | *Homozygosphaera vercellii*



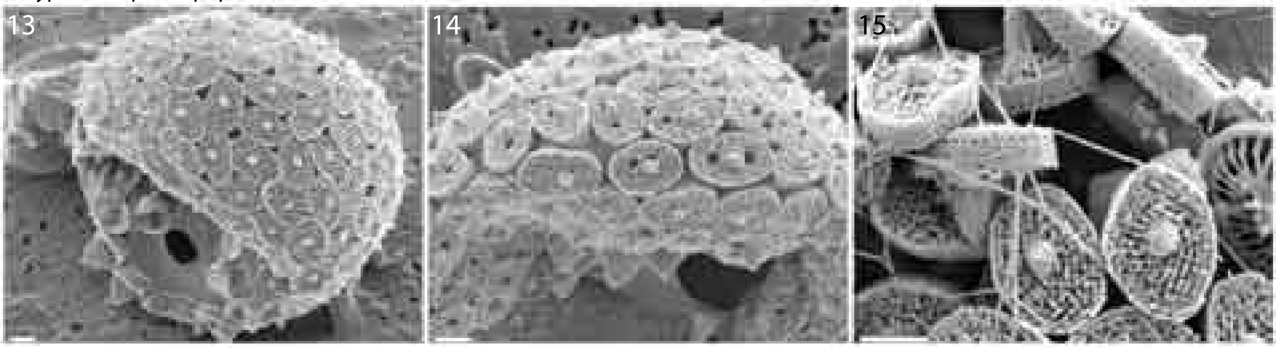
Calyptrolithina multipora | *Co. medit* HOL *wettsteinii* ("*C'lithina wett.*") | *Homozygosphaera vercellii*



Coronosphaera mediterranea HOL *gracillima* type ("*Calyptrolithophora gracillima*")



Calyptrolithophora papillifera



Coronosphaera mediterranea HOL *hellenica type* ("*Zygosphaera hellenica*")

Plate 50 - Holococcoliths: Flat-topped aff. *Coronosphaera*

5.6.2 *Zygosphaera* - concentric wall ultrastructure

Zygosphaera Kamptner 1936

Liths are semi-solid disks formed of concentric rings of crystallites (clearest in proximal view). Dimorphic. TYPE: *Z. hellenica* (see previous page).

BCs flat topped with node or ridge on distal surface, rather than a true bridge.

CFCs similar with transverse bridge or leaf.

Zygosphaera amoena Kamptner 1937

BCs with longitudinal ridge or mound, 1-1.5 μm long. Reference: Kleijne (1991) p. 67, pl. XVII.

Zygosphaera marsilii (Borsetti & Cati 1976) Heimdal 1982 [*Sphaerocalyptra*]

Like *Z. hellenica* but with three or four well-separated concentric rings of crystallites and low transverse ridge. Reference: Kleijne (1991) p. 69, pl. XVIII.

NB *Syracolithus* sp. type A of Kleijne (1991) is rather similar to *Z. marsilii* but monomorphic and with small pyramidal bosses rather than a central ridge (see above 5.2.4).

Syracosphaera bannockii HOL = {*Zygosphaera bannockii* (Borsetti & Cati 1976) Heimdal 1982 [*Sphaerocalyptra*]}

BCs with transverse ridge one crystallite wide, 1-1.5 μm long.

CFCs with central opening and well-developed triangular leaf. Reference: Kleijne (1991) p. 67, pl. XVIII.

Variant: *Corisphaera* sp. type A (Kleijne 1991) - similar but with central opening spanned by transverse ridge. Coccospheres with both this form and typical *Z. bannockii* occur (Cros et al. 2000, our obs.).

5.6.3 *Poricalyptra* - flush top and tube openings

Poricalyptra Kleijne 1991

Distinctive set of similar dimorphic species. TYPE: *P. aurisinae*

BCs flat topped with large openings in tube and variable openings in distal surface; tiered wall fabric; low transverse ridge. Liths 2-2.5 μm long.

CFCs helladoliths - ridge of BCs is extended into leaf, no openings in tube.

Poricalyptra aurisinae (Kamptner 1941) Kleijne 1991 [*Helladosphaera*]

4 elongate pores in distal surface, tube openings large, quadrate.

Poricalyptra gaarderiae (Borsetti & Cati 1976) Kleijne 1991 [*Helladosphaera*]

2 irregular pores in distal surface.

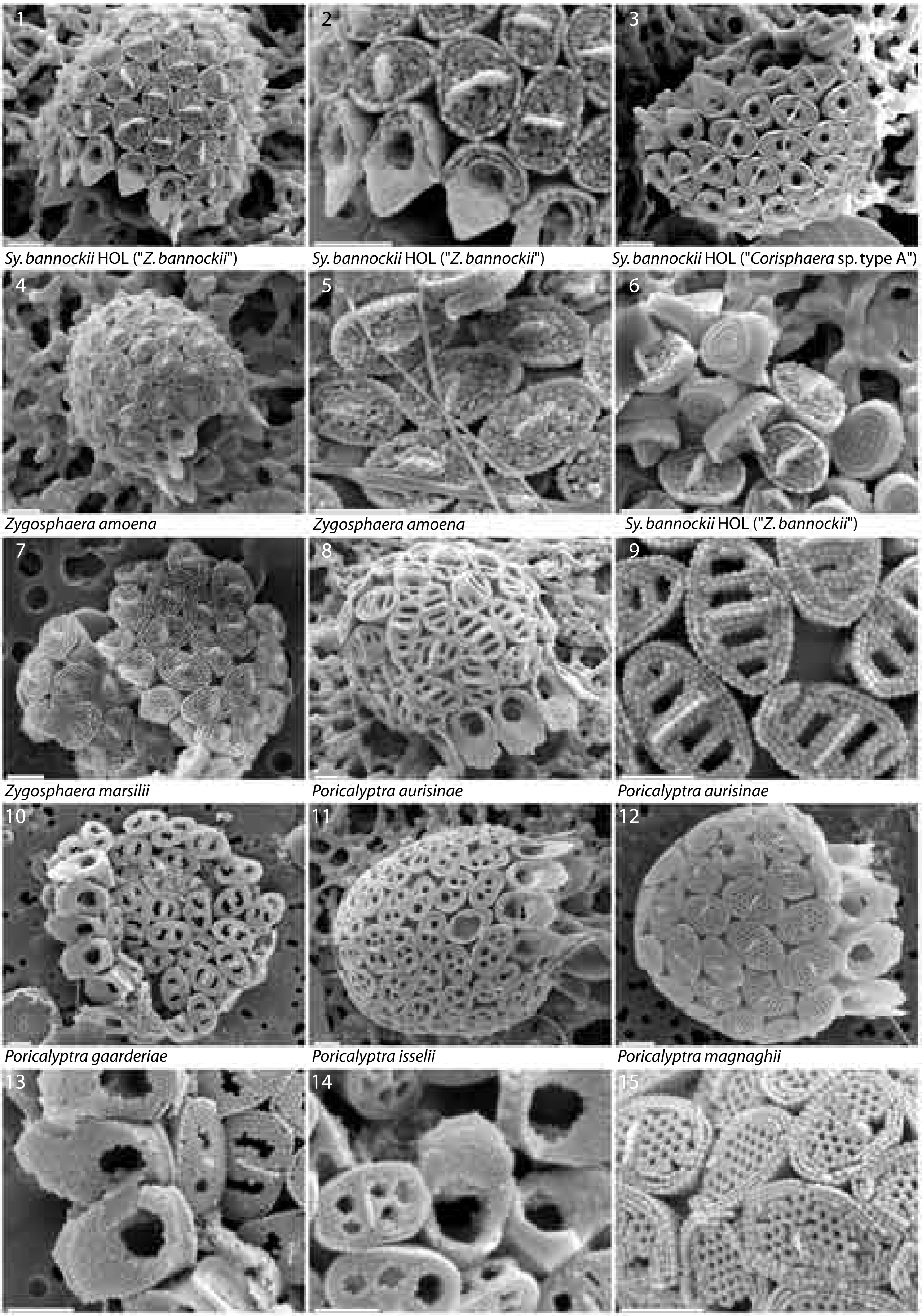
Poricalyptra isselii (Borsetti & Cati 1976) Kleijne 1991 [*Helladosphaera*]

4-7 irregular pores in distal surface, tube openings irregular, well separated. Reference: Kleijne (1991) p. 62, pl. XIV.

Poricalyptra magnaghii (Borsetti & Cati 1976) Kleijne 1991 [*Helladosphaera*]

Distal surface has hexagonal mesh fabric, but no large openings. SYNONYM: *H. fastigata*.

Reference: Kleijne (1991) p. 61, pl. XV.



1. *Sy. bannockii* HOL ("*Z. bannockii*")
2. *Sy. bannockii* HOL ("*Z. bannockii*")
3. *Sy. bannockii* HOL ("*Corisphaera* sp. type A")
4. *Zygosphaera amoena*
5. *Zygosphaera amoena*
6. *Sy. bannockii* HOL ("*Z. bannockii*")
7. *Zygosphaera marsilii*
8. *Poricalyptra aurisinae*
9. *Poricalyptra aurisinae*
10. *Poricalyptra gaarderiae*
11. *Poricalyptra isselii*
12. *Poricalyptra magnaghii*
13. *Poricalyptra gaarderiae*
14. *Poricalyptra isselii*
15. *Poricalyptra magnaghii*

Plate 51 - Holococcoliths: Flat-topped, *Zygolithus* & *Poricalyptra*

5.6.4 *Calyptrosphaera* species with flat top

Calyptrosphaera dentata Kleijne 1991

Monomorphic, tube wall flaring with basal flange, tiered fabric, double thickness. Tooth-like boss developed from tube near one end of lith. Distal cover flat, recessed below tube top, coarse hexagonal mesh fabric.
Liths 2.5-3 μm. Reference: Kleijne (1991) p. 26, pl. III.

Calyptrosphaera cialdii Borsetti & Cati 1976

Liths with broad flat rim and central depression, hexagonal mesh fabric. Not widely recognised.

5.6.5 *Syracolithus* - rhomboid array ultrastructure

Syracolithus Deflandre 1952

Monomorphic. Liths formed of superposed layers of aligned rhombohedral crystallites (in LM these behave optically as a single crystal with oblique c-axis orientation). TYPE: *Syracolithus dalmaticus*.
NB *S. quadriperforatus* and *S. schilleri* have very different structures (Plate 47) and are discussed in section 5.4.4.

Helicosphaera carteri HOL = {*Syracolithus catilliferus* (Kamptner 1937) Deflandre 1952 [*Syracosphaera*]}

Liths with flat top showing layered fabric with crystallites in rhombohedral array; pyramidal boss, or low spine near centre; rim one crystallite wide showing hexagonal arrangement, 5-6 crystallites high; central opening on proximal side small or absent; 2-3 μm long.

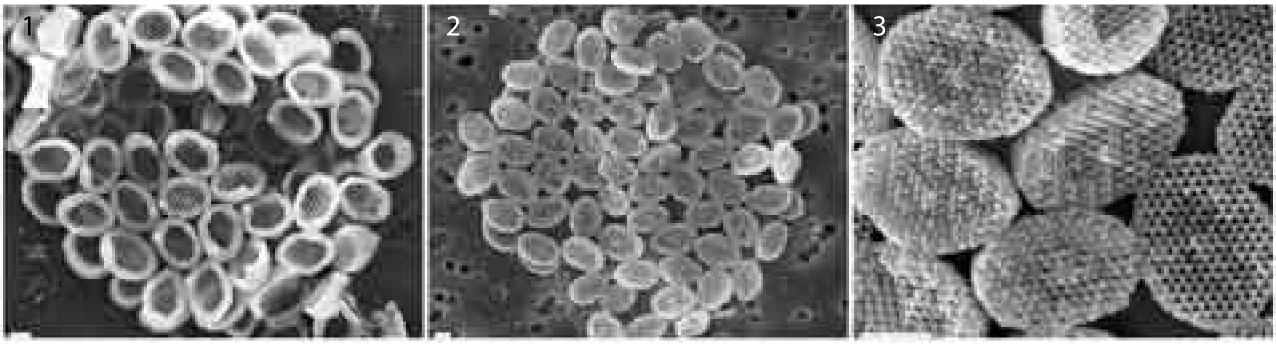
Variation: Forms with 7-10 circular depressions around the central boss occur and were previously distinguished as *S. confusus* Kleijne 1991. However, coccospheres with both variants occur (Cros et al. 2000, Geisen et al. 2002) and so it seems clear that the distinction is not genotypic. The variants can be termed *H. carteri* HOL solid and *H. carteri* HOL perforate.
Reference: Kleijne (1991) p. 34, pl. VI.

Syracolithus dalmaticus (Kamptner 1927) Loeblich & Tappan 1966 [*Syracosphaera*]

Liths with broad central mound with pores, 2-3 μm long. Outer part of disk similar to *S. catilliferus*, inner part appears to be open, but spanned by the central mound with 4-6 irregular ridges radiating from this to define pores. Distinct central opening on proximal side, and it is likely that beneath the central mound a cavity extends to the proximal surface.
SYNONYM: *Homozygosphaera halldallii* Gaarder 1980 *in* Heimdal & Gaarder (1980).
Reference: Kleijne (1991) p. 37, pl. VII.

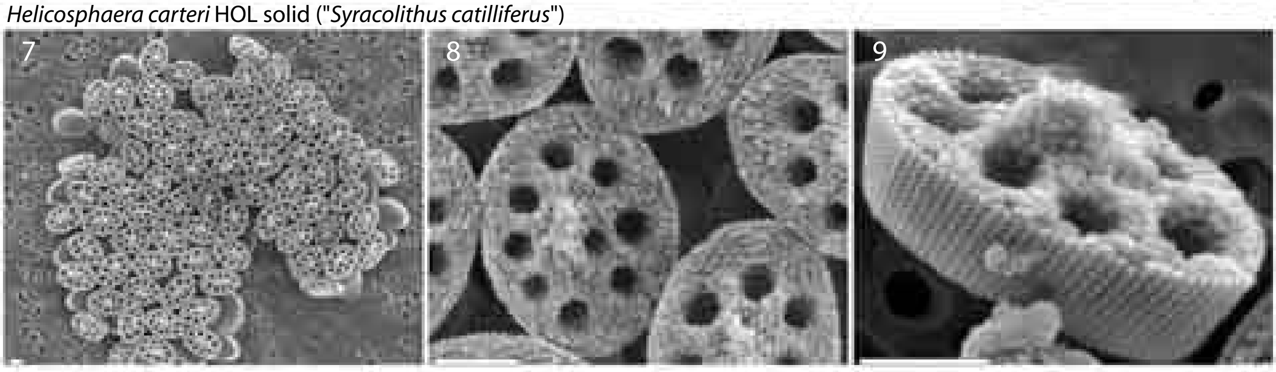
Syracolithus ponticuliferus (Kamptner 1941) Kleijne & Jordan 1990

Liths with two depressions, extending to proximal surface and separated by a bridge surmounted by a boss.
Liths 2.5-3 μm long.

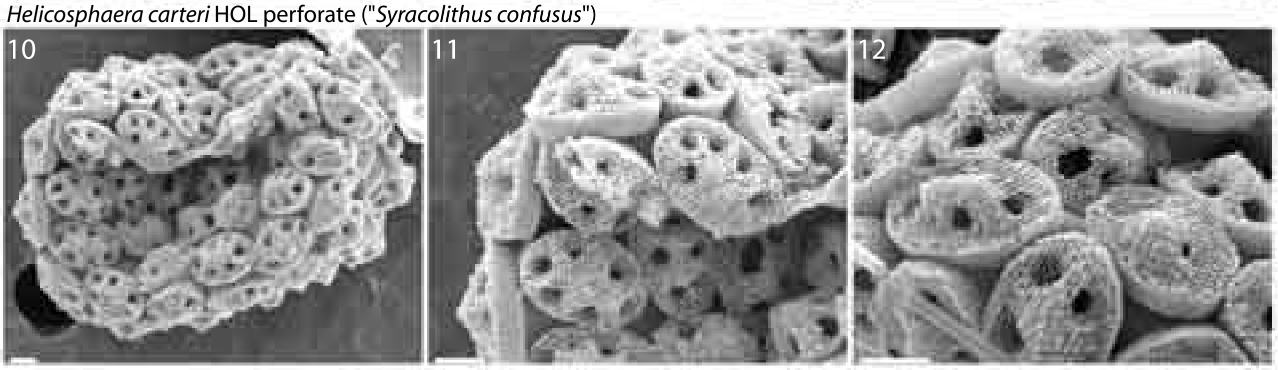


Calyptrosphaera dentata *Calyptrosphaera cialdii* *Calyptrosphaera cialdii*

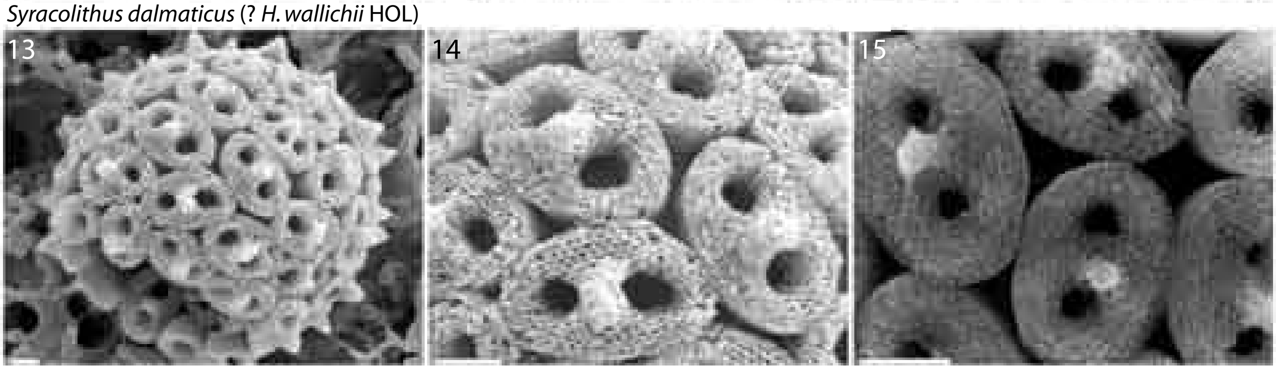
Helicosphaera carteri HOL solid ("*Syracolithus catilliferus*")



Helicosphaera carteri HOL perforate ("*Syracolithus confusus*")



Syracolithus dalmaticus (? *H. wallichii* HOL)



Syracolithus ponticuliferus

Plate 52 - Holococcoliths: Flat-topped

Systematic taxonomy

New families

Family **ALISPHAERACEAE** Fam. Nov. Young Kleijne & Cros

Diagnosis: *Cellulae coccolithiferae, status dominans cycli vitae erraticus, ferunt heterococcolithos dispositos secus series meridionales. Coccolithi irregulares cum margine directo versus polum flagellorum extenso in fimbriam vel extensionem. Coccolithus integer factus est ab monadibus labri; locus annuli proto-coccolithi intra tubum. V-elementi facunt tubum superum et fimbriam distalem; R-elementi facunt tubum bistratum inferum et constructiones proximales, aliquando cum extensione distali.*

Status alternatus cycli vitae erraticus, ferens nannolithos quadriangulatos aragoniticos. Nannolithi cum parte supero conico et base cruciforme.

Translation: Coccolithophores, dominant stage of life cycle typically: motile, bearing heterococcoliths arranged in meridional rows. Coccoliths asymmetrical with edge directed toward flagellar opening extended into a flange or protrusion. Entire coccolith formed of rim units; proto-coccolith ring locus within tube; V-units form upper tube and distal flange; R-units form two-layered lower tube and proximal structures, sometimes with distal extension.

Alternate life-cycle phase typically: motile, bearing quadrate, aragonitic, nannoliths. Nannoliths with conical upper part and cruciform base.

Type genus: *Alisphaera* Heimdal 1973.

Family **UMBELLOSPHAERACEAE** Fam. Nov. Young & Kleijne

Diagnosis: *Coccosphaera dimorpha; coccolithi consistunt ex parte distali infundibiliformi in fundo plano. Infundibli elementa continua sunt cum elementis plani basalis area centralis; interdum annulus circumdat aream basalem, consistens ex separato elementorum cyclo. Coccolithi variabiles quoad mensuram.*

Translation: Coccosphere dimorphic; coccoliths consist of a funnel-shaped distal part on a flat base. The funnel elements are continuous with the basal plate elements of the central area; a flange may be present around the basal plate, formed by a separate cycle of elements. Coccoliths are variable in size.

Type genus: *Umbellosphaera* Paasche, in Markali and Paasche 1955.

New genus and species

Placorhombus gen. nov. Young & Geisen

Generic diagnosis: *Coccosphaera rhomborum coccolithorum fecerunt cum labro ferti angusta proxime atque distali scuti cuius media a 4 laminis tecta est.*

Translation: Coccosphere formed of rhombic coccoliths with rim bearing narrow proximal and distal shields, central area covered by 4 plates.

Type species: *P. ziveriae*

***Derivatio nominis*:** from greek *placo-* flat plate or table and *rhombos* rhomb, reflecting the fact that the coccoliths are unique in having placolith rim morphology and rhombic shape.

Placorhombus ziveriae sp. nov. Young & Geisen

Specific diagnosis: *Coccosphaera producta 35-55 μm longa atque circa quattuor μm latitudine 100-200 coccolithos ferunt. Coccolithi 1.8-2.0μm longi cum eminente striae in distali superfice mediarum regionum laminarum, striae sub-paralleli ad brevum axem coccolithi.*

Species of *Placorhombus* with elongate coccospheres 35-55 μm long and ca. 4 μm wide, comprising 100-200 coccoliths. Coccoliths 1.8-2.2 μm long, with prominent striations on the distal surface of the central area plates, striations aligned sub-parallel to short axis of coccolith.

***Derivatio nominis*:** after Patrizia Ziveri, nannoplankton researcher and colleague.

Type specimen: coccosphere illustrated in plate 53, figs 1-3; plate 32, figs 11-12 (digital image file reference MG127-01 to 08).

Type material: NHM SEM stub 280/0, filter sample, MATER II cruise stn 69, collected during MATER II Cruise, 5 Oct. 1999, from Alboran Sea (W. Mediterranean), 37° 25.98' N, 00° 25.30' W, 42.5m water depth (deep chlorophyll maximum).

Type repository: Palaeontology Dept., The Natural History Museum, London.

Description: Coccospheres are cylindrical with parallel sides for most of their length. Eight specimens have been measured, with lengths of 35-55 μm and widths of 3.5-4.1 μm (measured on three specimens with uncollapsed sections of coccosphere). The number of coccoliths per specimen was estimated as double the number of visible coccoliths in distal view. For the eight specimens measured a range from 128 to 216 coccoliths was recorded, with a close correlation with coccosphere length (no of coccoliths = length x 3.77; r^2=0.93). On most coccospheres one end was tapered whilst the other was bluntly terminated, this is likely to be the flagellar pole but no specialised coccoliths were observed in this position and no direct evidence of flagella seen. At the tapered (?antapical) end usually a few (ca. 1-3) narrow coccoliths were present.

The coccoliths are diamond shaped, with all four sides of similar length. Coccolith length is 1.9-2.4 μm (40 specimens measured) with length to width ratios of 1.3 to 1.4, except for the narrow antapical coccoliths (ratio ca. 1.8). The rim is ca. 0.2 μm wide by 0.1 μm high, and is placolith-like with narrow but distinct proximal and distal shields, the distal

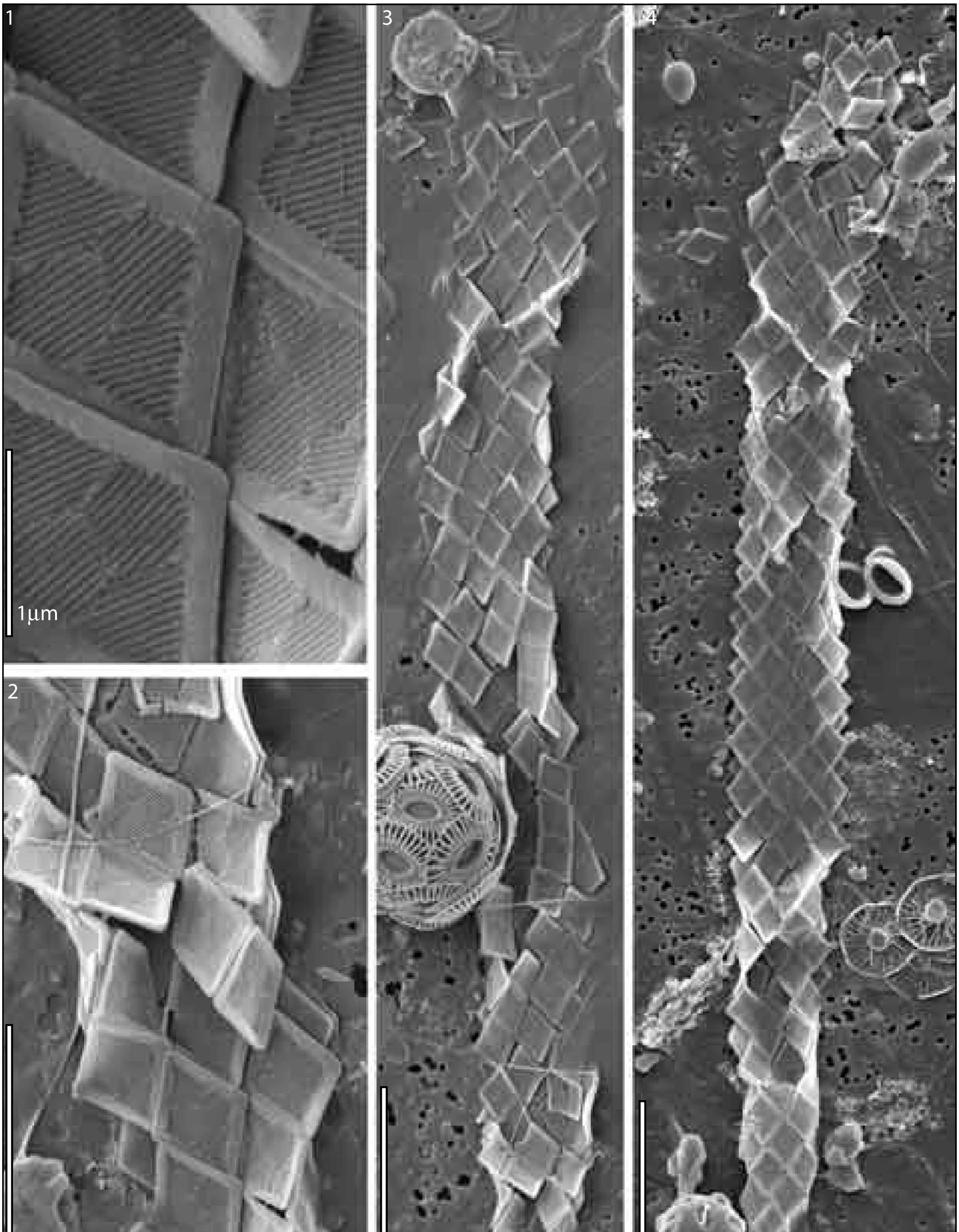


Plate 53 - *Placorhombus ziveriae* n. sp.

shield being slightly wider. Elements are not clearly visible on many specimens, when visible they show straight sutures with about ten elements per side (i.e. 40 elements per coccolith). On many specimens, a narrow groove runs around outer margin of distal shield. The central area is formed of four plates with sutures running form the centre of the coccolith sides; the end plates are rhombic, those at the sides pentagonal, meeting along a central suture. All four plates show ornament of striations sub-parallel to short axis of the coccolith, spaced at 0.05 to 0.06 μm. In proximal view the central area plates are smooth and slightly convex. On three specimens, base-plate scales were visible, with close-spaced oblique-radial fibrils in the outer 0.15 μm of the central area.

Remarks: The rhombic shape of the coccoliths and their regular arrangement on an elongate coccosphere are obviously reminiscent of *Calciosolenia*. However, both the rim morphology (placolith-like with two shields vs. murolith) and the central area structure (four plates vs. radial laths) are very different. Hence, the superficial similarity in gross morphology seems more likely to be a result of homeomorphy than homology. A more likely affinity is with *Tetralithoides quadrilaminata*, which also shows a narrow placolith rim and a central area formed of four plates. However, the coccoliths of *T. quadrilaminata* are much larger (4-8 μm long) and elliptical and the coccospheres are spherical, so this affinity is speculative.

All our specimens were found on stubs from a single sample, taken from the deep chlorophyll maximum. The sample contains an abundant and diverse coccolith assemblage including *Algirosphaera robusta*, *Alisphaera* spp., *Calciopappus* spp., *Calciosolenia murrayi*, *Emiliania huxleyi*, *Florisphaera profunda*, *Gephyrocapsa* spp., *Helicosphaera pavimentum*, *Homozygosphaera vercellii*, *Michaelsarsia elegans*, *Ophiaster hydroideus*, *Papposphaera* spp., *Poricalyptra gaarderiae*, *Reticulofenestra parvula*, *Rhabdosphaera clavigera*, *Syracosphaera pulchra* HOL and HET, *Syracosphaera* spp., and *Tetralithoides quadrilaminata*.

Placorhombus sp. cf. *ziveriae*

One specimen of *Placorhombus* was found in a sample from the Gulf of Mexico (sample collected by Vita Pariente, imaged by Claire Findlay). This specimen is similar to the type material in general coccolith form but differs in detail; the coccoliths are slightly smaller (1.6-1.9 μm vs. 1.9-2.4 μm), the striae are closer spaced (0.03 μm vs. 0.05 μm), and the striae on the end plates are aligned sub-parallel to the long axis of the coccolith. More specimens are required for a full description but it seems likely that this specimen represents a second species rather than intraspecific variation.

New combinations

The following new combinations are proposed in order to regularise various aspects of terminology. Explanations are given in the main text.

Algirosphaera cucullata (Lecal-Schlauder 1951) Young, Probert & Kleijne comb. nov.
Basionym: *Acanthoica cucullata* Lecal-Schlauder 1951 p. 269, 270; Text-fig. 6

*Reticulofenestra maceria (*Okada & McIntyre 1977) Young comb. nov
Basionym: *Umbilicosphaera maceria* Okada & McIntyre 1977 p. 12, 13. Pl. 1, Fig. 8

Umbilicosphaera anulus (Lecal 1967) Young & Geisen comb. *nov.*
Basionym: *Cyclolithus anulus* Lecal 1967; p. 321; Schéma 15, Fig. 22
NB Since *anulus* is a noun it does not change case, and the correct orthography is *U. anulus* not *U. anula*.

Calciosolenia brasiliensis (Lohmann 1919) Young comb. nov
Basionym: *Cylindrotheca brasiliensis* Lohmann 1919; p. 187; text-fig. 56

Helladosphaera vavilovii (Borsetti & Cati 1976) Young & Kleijne comb. nov.
Basionym: *Homozygosphaera vavilovii* Borsetti & Cati 1976 p.222, plate V, fig. 11-13.

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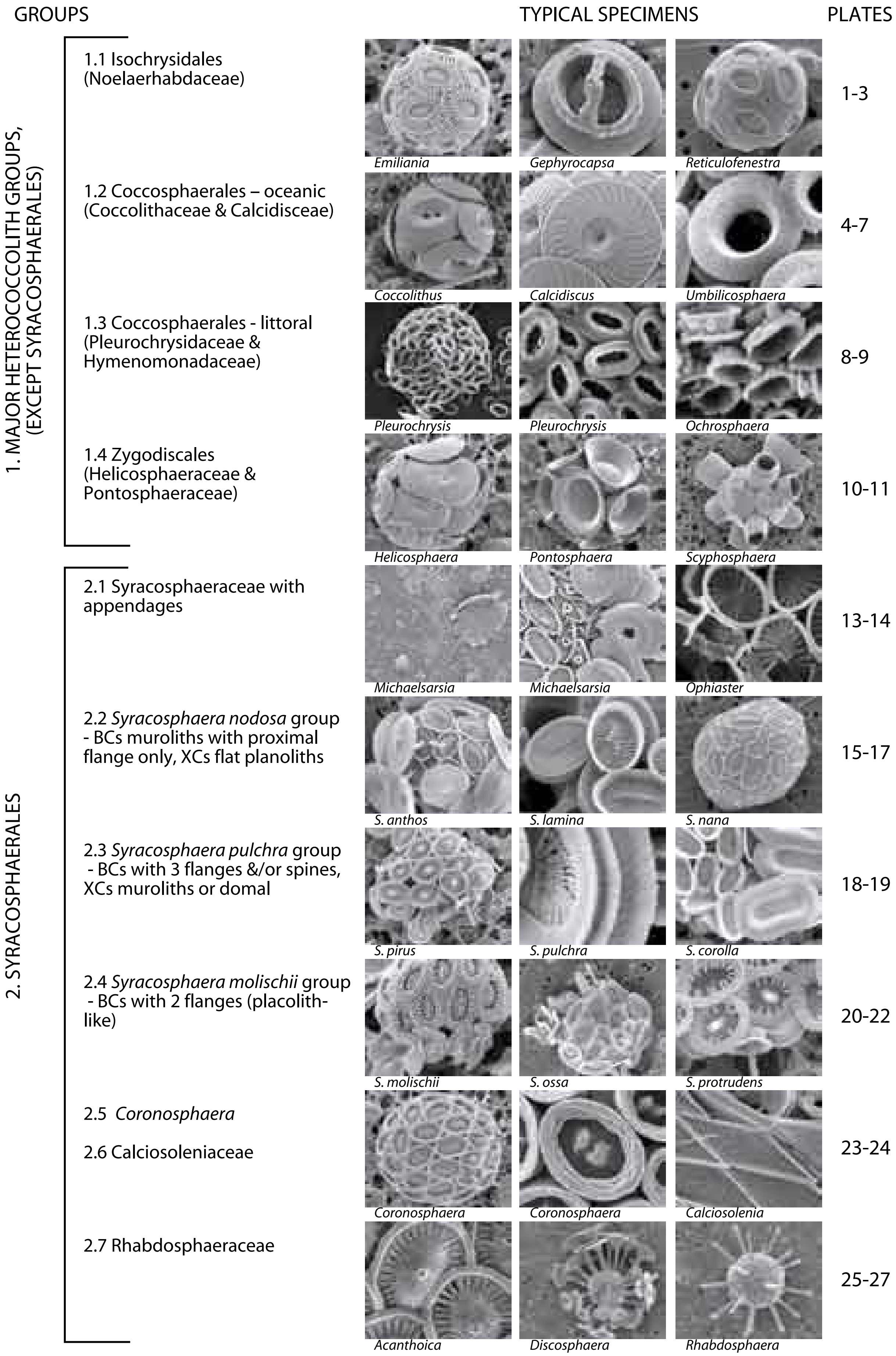

Figure 4a - Classification overview - major heterococcolith groups

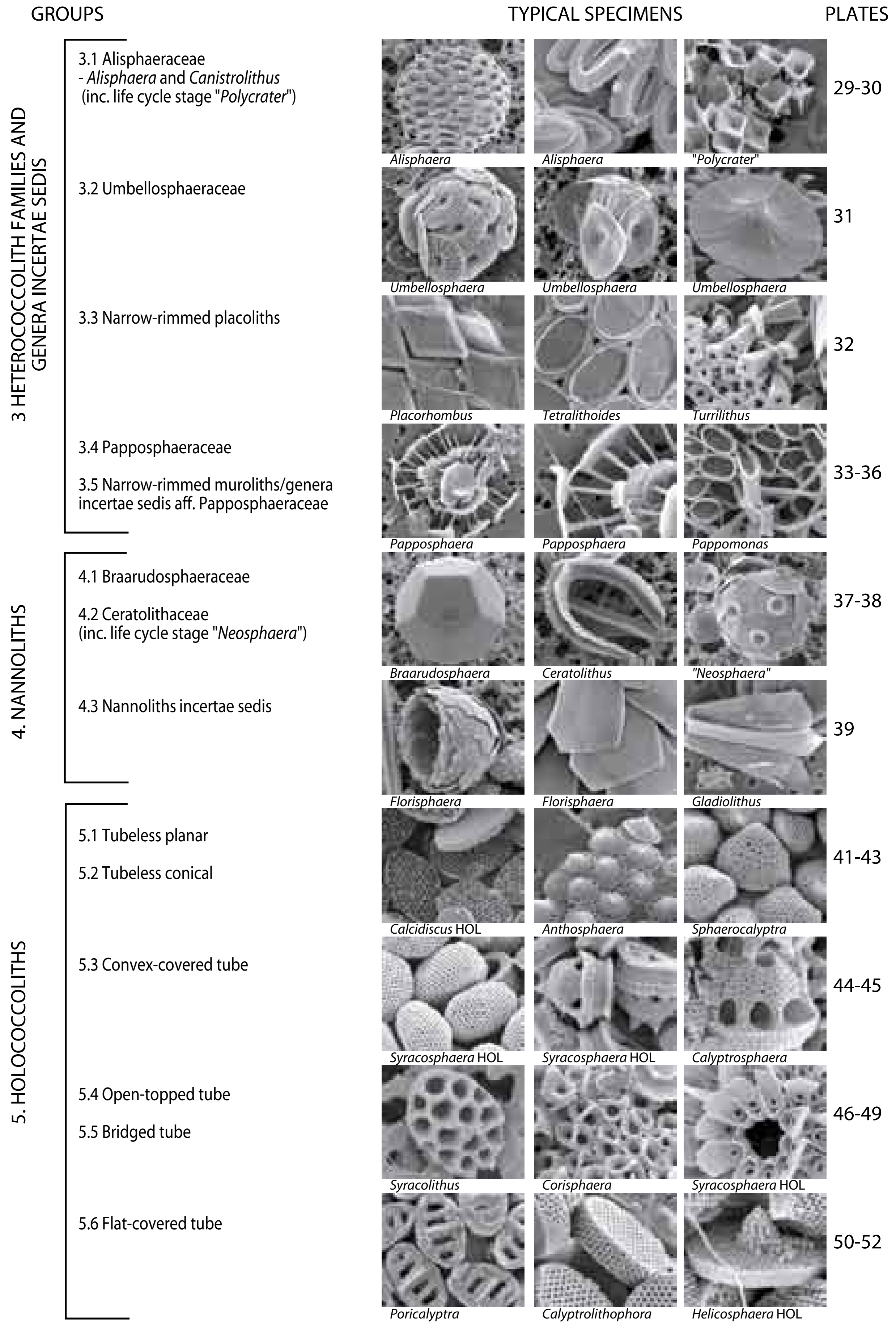

Figure 4b - Classification overview - incertae sedis, nannoliths and holococcoliths