ATLAS OF NORTHWESTERN MEDITERRANEAN COCCOLITHOPHORES

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INTRODUCTION

These pages consider coccolithophores, a group without rigorous taxonomic meaning, as embracing all (golden-brown) microalgae which at least at some point in their life cycle, produce and bear coccoliths. The coccoliths are minute, delicate and very beautiful scales of calcium carbonate which make an important contribution to transport of the inorganic carbon produced in pelagic areas to the ocean floor and thus to the sedimentary archive. Since they are biologically-formed and sediment-forming, coccoliths are extremely valuable for stratigraphic and palaeoceanographic purposes; they have been extensively used as stratigraphic fossils in sediments of Jurassic to Quaternary age (Perch-Nielsen, 1985 a, b; Bown, 1998) and detailed chronostratigraphic and palaeoecological reconstructions have been successfully established (e.g. the studies of NW Mediterranean Pliocene sediments by Matias, 1990, and of W Mediterranean Pleistocene-Holocene sediments by Flores et al. 1997).

The coccolithophores play key roles in global biogeochemical cycles, particularly in the carbon-carbonate cycle (Honjo, 1976; Westbroek, 1991; Westbroek et al., 1994), but also in the sulphur cycle.
since they produce dimethylsulphoniopropionate (DMSP), the precursor of dimethyl sulphide (DMS) (Keller et al., 1989; Malin and Kirst, 1997) which may influence climate through stimulating cloud formation and influencing the Earth’s radiative balance (Charlson et al., 1987; Simó and Pedrós-Alió, 1999). Some coccolithophores are known to produce stable lipid compounds which can be used as a tool to evaluate paleoclimatic changes (Volkmen et al., 1980; Brassell et al., 1986). These properties, together with the fact that the ubiquitous species Emiliania huxleyi is a recognized bloom-forming alga (Holligan et al., 1993), confer on the coccolithophores an important role as active biogeochemical and climatic agents.

**First records**

The first recorded observation of elliptical, flattened discs, having one or several concentric rings on their surface, was made by C.G. Ehrenberg in 1836 while examining Cretaceous chalk from the island of Rugen in the Baltic Sea. Later, in 1858, T.H. Huxley, working with North Atlantic sediments, was the first to name these small structures ‘coccoliths’. Both authors, Ehrenberg and Huxley, considered these platelets as of inorganic origin. G. C. Wallich observed coccospheira in a sample from salp gut, collected on his return from India in 1857. From a study of English chalk in 1860, H. C. Sorby (1861) realized that the small discs were concave on one side and convex on the other and predicted, and later found, that coccoliths were united as small, hollow spheres in the chalk. Like Wallich, Sorby believed that these coccospheira had an organic origin. The first living coccolithophores, Coccosphaera pelagica and Coccosphaera carterii, were described by Wallich (1877) as free-floating cells. Numerous studies have subsequently been made, using both the light microscope (LM) and later using the techniques of transmission electron microscopy (TEM) and scanning electron microscopy (SEM) (see Siesser, 1994, for a detailed review of the early studies on coccolithophores).

**The living cell, reproduction and life cycles**

*The coccolithophore cell*

Coccolithophores are typically marine, planktonic, unicellular, biflagellate cells which are surrounded by coccoliths and also have an haptonema, but they can exist without one or several of these characters. Cell size is usually between 3 and 30 µm and cells may be spherical, subspherical, ovoid to oval or obpyriform in shape, but can take other forms, sometimes being elongated and even spindle-shaped (Heimdal, 1993; Young et al., 1997). Detailed cytological investigations have been undertaken, including studies of the formation of coccoliths and scales (Klaveness and Paasche, 1971; Inouye and Pienaar, 1984; Inouye and Pienaar, 1988; Fresnel, 1989; Fresnel and Billard, 1991) and detailed descriptions of complex organelles such as the haptonema (Inouye and Kawachi, 1994). Two structurally very different types of coccoliths, heterococcoliths and holococcoliths, formed by different types of biomineralisation, are recognizable. The heterococcoliths are formed by crystal-units of variable shape and size, and their biomineralisation, initiated by nucleation of a proto-coccolith ring, occurs intracellularly (Manton and Leedale, 1969; Inouye and Pienaar, 1988; Westbroek et al., 1989; Young, 1989; Fresnel, 1989; Fresnel and Billard, 1991; Pienaar, 1994). The holococcoliths are formed of numerous minute (<0.1 µm) crystallites; their calcification appears to occur extra-cellularly (Manton and Leedale, 1963; Klaveness, 1973; Rowson et al., 1986), but within the periplast (on the periplasmic side of the plasma membrane, de Vrind-de Jong et al., 1994). Rowson et al. (1986) showed that the periplast of a holococcolithophore is composed of a layer of columnar material, several layers of scales, crystalloliths and an external membrane layer called the envelope, which seems to be responsible for crystalolithogenesis.

*Reproduction strategies and heteromorphic phases*

Coccolithophores multiply vegetatively by binary fission (Heimdal, 1993, Fresnel, 1989) and mitosis in Pleurochrysis and Emiliania has been studied in detail (Stacey and Pienaar, 1980; Hori and Inouye, 1981; Hori and Green, 1985).

The studies of von Stosch (1967), Parke and Adams (1960), Klaveness and Paasche (1971) and Fresnel (1989) have shown that coccolithophores of very different types can be involved in highly complex life cycles (Billard, 1994). Parke and Adams (1960) demonstrated that monoclonal strains of the heterococcolithophore Coccolithus pelagicus (Wallich) Schiller can give rise to what previously was believed to be a distinct species; the holococcolithophore Crystallolithus hyalinus Gaarder et
Markali. In studies on shadowcasted material, Manton and Leedale (1963, 1969) found different patterns on the body scales of these two life stages, leading to speculation about the existence of a haplo-diploid life cycle, where the *Coccolithus pelagius* cells would be diploid, whereas those named *Crystallolithus hyalinus* would be haploid (Billard, 1994). In addition, Rowson et al. (1986) showed that two distinct holococcolith morphologies could be produced, the typical ‘*Crystallolithus hyalinus*’ type and a more fenestrate type which had previously been described as a separate species, *Crystallolithus braarudii* Gaarder 1962.

Life cycles involving coccolith and non-coccolith-bearing phases have been well documented, particularly in the coastal genera of the families Pleurochrysidaceae and Hymenomonadaceae. Studies on the species now known as *Pleurochrysis carterae* (Braarud and Fagerland) Christensen revealed an elaborate life cycle with a diploid heterococcolith bearing phase, including both motile and non motile stages, and an haploid benthic pseudofilamentous phase (*Apistonema* stage in the sense of von Stosch, 1967). This non-motile stage may form naked swarmer or motile gametes, which fuse to form a zygote which develops coccoliths. Both phases appear to have an unlimited capacity for vegetative reproduction (Rayns, 1962; Leadbeater, 1970). Gayral and Fresnel (1983) observed both meiotic division and syngamy in the life cycle of *Pleurochrysis pseudoroscoffensis*. Culture studies have demonstrated that the heterococcolithophore phase of these life-cycles is diploid and the benthic non-calculifying phase is haploid, and that each phase has a characteristic microfibrillar pattern on the organic body scales (Fresnel, 1989, 1994; Fresnel and Billard, 1991).

*Emiliania huxleyi* presents an interesting life cycle with coccolith-bearing cells (the C-cells) and non-coccolith-bearing stages (the naked N-cells and the scale-bearing swarmer S-cells), each cell type being capable of independent vegetative reproduction (Klaveness and Paasche, 1971). In addition, amoeboid cells can be found occasionally in cultures of C-, N- and S-cells and extremely large cells can be found in old cultures (Klaveness, 1972b). Flow cytometric analysis has shown that the C-cells have a DNA content twice that of the S-cells (Green et al., 1996). C- and N-cells are presumably diploid cells whilst the S-cells might represent the haploid stage (Paasche and Klaveness, 1970; Green et al., 1996).

**Combination coccospheres recorded from plankton samples**

Besides the well documented combination specimens of *Coccolithus pelagicus - Crystallolithus hyalinus*, as quoted above, other combinations have occasionally been observed in plankton samples. Some of these specimens have been clearly documented with SEM images, but others have been admirably recorded, despite considerable technical difficulties, with LM techniques.

Among natural specimens examined by LM, Kamptner (1941) described, and in some cases illustrated, several combination or ‘hybrid’ coccospheres (‘Individuen mit kombinierter Schale’). He gave a detailed account of various combinations of heterococcolithophore *Syracosphaera* species with holococcolithophores, particularly of two living cells exhibiting coccoliths of both *Syracosphaera tuberculata* Kamptner (now known as *Coronasphaera mediterranea* (Lohmann) Gaarder) and *Zygosphaera wettsteinii* Kamptner (now *Calyptrolithina wettsteinii* (Kamptner) Norris). He noted the similarity of his observation of *Calyprosphaera oblonga* combining with big coccoliths (possibly of *Syracosphaera*) with the drawings of Lohmann (1902), and among other findings, observed several combination specimens of *Anthosphaera robusta* with *Calyprosphaera quadridentata*. Moreover he described the association of two holococcolithophores: *Corisphaera gracilis* Kamptner with *Zygosphaera helenica* Kamptner.

Lecal-Schlauder (1961), also using LM, recorded four more combinations. One combination (not figured) is described as a specimen bearing coccoliths of both *Syracosphaera palchra* Lohmann and *Calyprosphaera pirus* Kamptner (now *Daktylithra pirus* (Kamptner) Norris). The other hybrid cells are figured and one appears to combine both *Helicosphaera carteri* coccoliths and holococcoliths tentatively identifiable as *Syracolithus confusus*; another is an obpyriform coccosphere of *Calyprosphaera oblonga* also bearing big heterococcoliths which are difficult to identify since they are seen in proximal view behind the thickness of the coccosphere; the last is recorded as a combination of *Acanthocha acanthos* Schiller with *Syracosphaera aperta* Schlauder.

Among natural specimens examined by SEM, Kleijne (1991) found a composite cell of the heterococcolithophore *Calcisiscus leptoporus* (Murray et Blackman) Loeblich Jr. and Tappan and the
holococcolithophore *Crystallolithus rigidus* Gaarder; this association has been repeatedly figured in recent publications (Cortés, 2000; Renaud and Klaas, 2001) and it has been observed in culture (I. Probert, pers. comm.). In addition, a spectacular combination coccosphere composed of a complete coccosphere of *Calcisiscus leptoporus* surrounded with coccoliths of *Syracolithus quadriperforatus* (Kamptner) Gaarder has been found in the Alboran Sea, W Mediterranean (Geisen et al. 2000).

Kleijne (1991) also recognized an association of *Syracosphaera* sp. type A with a holococcolithophore bearing both laminar ordinary coccoliths and zygololith-like circum-flagellar coccoliths.

Thomsen et al. (1991), examining natural Arctic samples with TEM techniques, recognized cells of the heterococcolithophore genera *Papposphaera* Tangen, *Pappomonas* Manton and Oates and *Wigwamma* Manton, Sutherland and Oates that included or combined elements typical of the holococcolithophore genera *Turrisphaera* Manton, Sutherland and Oates, *Trigonaspis* Thomsen and *Calcarius* Manton, Sutherland and Oates respectively.

The well established association of *Coccolithus pelagicus* with *Crystallolithus hyalinus* was found in Arctic surface waters and figured in a SEM micrograph by Samtleben and Schröder (1992); another specimen with *C. pelagicus* heterococcoliths covered by holococcoliths of *Crystallolithus hyalinus* is figured by Samtleben in Winter and Siesser (1994) and in Samtleben et al. (1995).

Alcober and Jordan (1997) presented for the first time an association, found in natural samples from the central North Atlantic, involving elements of the heterococcolithophore *Neosphaera coccolithomorpha* Lecal-Schlauder with the nannolith bearing species *Ceratolithus cristatus* Kamptner. This association was subsequently found on two further occasions by Young et al. (1998). Recently, Spengel and Young (2000) represented the combination of *Ceratolithus cristatus*, *Neosphaera coccolithomorpha* coccoliths and hoop-like coccoliths (i.e. all the known coccoliths of *Ceratolithus cristatus* being together).

During the present study several combination coccospheres showing known associations and several more with new associations were found from NW Mediterranean waters. These specimens, most of which are already published in Cros et al. (2000b), are figured in the present atlas.

## Classification and taxonomic status

Despite increasing awareness of the limitations involved, coccolith morphology still remains the most important character in the classification of the coccolithophores. Distinct coccolith types have been recognized and the species, genus and family concepts formed around them (Jordan et al., 1995). The coccolithophores are difficult to classify, as testified by the numerous changes that the taxonomy of this group has experienced in the higher (see a revision in Cros, 2001) and in the lower taxonomic ranks (see below). Nevertheless the families as accepted here behave as robust taxa (Jordan and Green, 1994) and they have been universally accepted as the main level of classification (Young and Bown, 1997a), to which relatively few changes have been introduced in recent years.

Braarud et al. (1955) classified the coccoliths into three groups: heterococcoliths, holococcoliths and pentaliths. The latter group is now included, in broader grouping nannoliths (Young and Bown, 1997a). The heterococcoliths, formed by crystal-units of complex shape, are well structured and well represented in the fossil record. Their structural inter-specific differences are generally large and are used to characterize species, genera and families. The holococcoliths, constructed of numerous minute calcite crystals, are easily disintegrated; their fossil record is not so good and their classification is difficult (Kleijne, 1991) with differentiation above the genus level generally not possible. Holococcolithophores (coccolithophores that present only holococcoliths, according to present knowledge) are grouped into a single family, the Calyptrosphaeraceae (Kleijne 1991, Jordan and Green, 1994; Young and Bown, 1997b) although it is increasingly apparent that this is an artificial grouping.

## Terminology

Since the taxonomy of calcareous nannoplankton is based on the morphological characters of the coccoliths, the adopted terminology of coccolith parts has always been important. The development of electron microscopy permitted much greater resolution of the structural details of coccoliths, leading to the necessity for a review of previous terminology. A co-operative effort to compile and standardize the new nomenclature was made by several authors (Braarud et al., 1955; Halldal and Markali, 1955; Hay et al., 1966) and other authors have included in
their papers glossaries or terminological explanations (Perch-Nielsen, 1985a,b; Heimdal, 1993; Kleijne, 1993). Three work sessions have even been held concerning this subject: a round table session at the 1970 Rome Plankton Conference (Farinacci, 1971), a terminology workshop held during the International Nannoplankton Association (INA) conference in Prague, 1991, and the subsequent terminology working group meeting held in London in 1992 (Young, 1992b). The last two workshops yielded syntheses of descriptive terminology (Jordan et al., 1995; Young et al., 1997) which are essentially followed in the present study.

Objectives of the present atlas

The main objective of the atlas is to illustrate the coccolithophore species present in NW Mediterranean waters using Scanning Electron Microscopy (SEM) micrographs. In the course of examining the samples collected, many species identification problems were encountered, prompting a taxonomic survey of the literature.

MATERIAL AND METHODS

Cruises and stations sampled

The samples were collected in the North-western Mediterranean during several cruises of the Institut de Ciències del Mar (CSIC) on board the R/V “Garcia del Cid” during the years 1995, 1996 and 1997. In 1995, cruise Meso-95 was undertaken from 30 May to 16 June, and cruise Fronts-95 from 17 to 23 June. In 1996 there were the cruises Meso-96, from 18 June to 3 July, and Fronts-96, from 16 to 21 September. Figure 1 and Figure 2 show the positions of the stations sampled in the 1995 and 1996 cruises respectively, and Table 1 and Table 2 detail the geographic positions of the 1995-96 stations as well as the date and time (in GMT) that they were visited. In addition a programme of three cruises held in different seasons of the year was conducted offshore of the Ebro Delta (Fig. 3): from 01 to 10 November 1996 (Fans 1); from 04 to 14 February 1997 (Fans 2), and from 13 to 15 July 1997 (Fans 3). Figure 3 illustrates the position of the stations sampled in the
Fig. 2. – Position of the sampled stations during the cruises Meso-96 and Fronts-96.

Fig. 3. – Position of the sampled stations during the cruises Fans-1, Fans-2 and Fans-3.
### Table 1. Spatial and temporal position of samples collected during the 1995 cruises (Fig. 1).

| Series     | Meso-95                             | Date       | Latitude     | Longitude     | Sampled depths (m) |
|------------|-------------------------------------|------------|--------------|---------------|--------------------|
| 005        | 007                                 | 01-06-95   | 41°01.5'N    | 2°32.2'E      | 0, 40              |
| 011        | 015                                 | 02-06-95   | 40°36.8'N    | 2°55.2'E      | 0, 40              |
| 021        | 023                                 | 02-06-95   | 40°12.6'N    | 3°06.8'E      | 0, 40              |
| 112        | 114                                 | 11-06-95   | 40°39.1'N    | 1°15.0'E      | 0, 40              |
| 115        | 117                                 | 12-06-95   | 39°35.4'N    | 1°38.2'E      | 0, 40              |
| 118        | 119                                 | 12-06-95   | 39°16.7'N    | 1°44.1'E      | 0, 40              |
| 132        | 136                                 | 13-06-95   | 39°33.7'N    | 0°54.5'E      | 0, 40              |
| 138        | 140                                 | 13-06-95   | 39°36.3'N    | 0°22.1'E      | 0, 40              |
|            | 142                                 | 14-06-95   | 39°39.4'N    | 0°36.5'E      | 0, 40              |
|            | 147                                 | 14-06-95   | 39°27.6'N    | 0°38.5'E      | 0, 40              |
|            | 152                                 | 15-06-95   | 38°59.6'N    | 0°16.5'E      | 0, 40              |
|            | 156                                 | 15-06-95   | 38°59.0'N    | 0°33.4'E      | 0, 40              |
|            | 162                                 | 15-06-95   | 38°49.8'N    | 0°37.3'E      | 0, 40              |

### Table 2. Spatial and temporal position of samples collected during the 1996 cruises (Fig. 2).

| Series     | Meso-96                             | Date       | Latitude     | Longitude     | Sampled depths (m) |
|------------|-------------------------------------|------------|--------------|---------------|--------------------|
| A1         | 19-06-96                            | 42°00.0'N  | 3°17.3'E     | 5, 10, 20, 30, 40, 50, 60, 65 |
| A3         | 19-06-96                            | 41°54.0'N  | 3°37.1'E     | 5, 10, 20, 30, 40, 50, 60, 70, 85 |
| A5         | 19-06-96                            | 41°48.0'N  | 3°56.9'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| D2         | 21-06-96                            | 41°38.9'N  | 3°15.0'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| D4         | 21-06-96                            | 41°26.6'N  | 3°26.5'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| D6         | 20-06-96                            | 41°14.3'N  | 3°38.0'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| D8         | 20-06-96                            | 41°02.0'N  | 3°49.5'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| E2         | 30-06-96                            | 41°33.0'N  | 3°03.0'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| E3-4       | 01-07-96                            | 41°23.0'N  | 3°10.2'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| E5         | 01-07-96                            | 40°55.1'N  | 3°36.6'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| E8         | 02-07-96                            | 41°22.1'N  | 2°17.8'E     | 5, 10, 20, 30, 40, 50, 60, 65 |
| F2         | 23-06-96                            | 41°32.8'N  | 3°15.0'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| F4         | 24-06-96                            | 41°13.7'N  | 2°59.7'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| G2         | 24-06-96                            | 41°20.9'N  | 2°33.7'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| G4         | 24-06-96                            | 41°08.4'N  | 2°45.2'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| G6         | 25-06-96                            | 40°56.3'N  | 2°56.7'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| I1         | 29-06-96                            | 41°17.0'N  | 2°17.8'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| I2         | 24-06-96                            | 41°13.9'N  | 2°20.7'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| I3         | 28-06-96                            | 41°07.7'N  | 2°26.3'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| I6         | 25-06-96                            | 40°49.3'N  | 2°43.7'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |
| I8         | 27-06-96                            | 40°37.0'N  | 2°55.2'E     | 5, 10, 20, 30, 40, 50, 60, 70, 80 |

**NW MEDITERRANEAN COCCOLITHOPHORES 13**
Fans cruises and Table 3 gives the geographic positions of stations as well as the date of the operations. During cruise Meso-95, only water from the surface and 40 m. depth was sampled; on the other cruises samples were taken from different depths, which are also specified for each station, in Tables 1, 2 and 3. Additional water samples were collected off-shore of Masnou (Medea-98 sampling, March 1998), off-shore and in the harbour of Barcelona (Picasso workshop, July 1998) and during the cruise Hivern-99 (20th February to 14th March 1999) aboard the R/V “García del Cid” (St. 20 at 40º 18’N, 3º 14’E; St. 25 at 40º 19’N, 2º 45’E; St. 30 at 41º 19’N, 2º 15’E; St. 64 at 40º 40’N, 2º 52’E; St. 69 at 41º 8’N, 2º 27’E; St.76 at 41 14’N, 3º 36’E).

### Sampling techniques

The water samples were collected at selected depths using a rosette with Niskin bottles attached to a Conductivity, Temperature, Depth (CTD) probe, except during the Meso-95 cruise, when surface water was sampled with a bucket. In the 1995 cruises, all of the samples were fixed with neutralized formaldehyde except in four stations where parallel samples were filtered on board without fixation in order to compare the results. The best results were obtained without fixation of the material. Loss of holococcolithophore species and poor preservation of some heterococcolithophores were clearly observed in the fixed samples (Cros, 2001). Afterwards, knowing the risk to lose coccolithophores using fixation methodologies, all the samples were directly filtered on board without adding chemicals.

### Filtration methodology

About 200 ml of sea water were filtered, using a vacuum pump, onto polycarbonate Nucleopore filters of 0.8 μm pore size and 25 mm diameter (Kleijne, 1991, considers that polycarbonate membrane filters, with their smooth surface, have the best properties to allow observation of the smallest coccolithophores in the SEM). Another filter with pore size of 3 μm (usually Millipore cellulose acetate nitrate) was placed below the Nucleopore filter, in order to ensure an even distribution of filtered particles. Salt was removed by washing the filters with about 2 ml of bottled drinking water (pH 7.9 – 8.3). The filters were air dried and stored under partial vacuum in hermetically closed boxes until preparation for the Scanning Electron Microscope (SEM).

### Microphotographs and measurements

A part of the filter was placed on a SEM stub and coated with a film (about 150 Å thick) of gold or gold-palladium to avoid electric charges; the sputter coater used was a Polaron SC-500. The examination and microphotography of the specimens were conducted in a Hitachi S-570 Scanning Electron Microscope.
The coccosphere and coccolith measurements as well as the enumeration of the number of coccoliths were made on the available micrographs, which had been obtained for taxonomic purposes. The measurements, where possible, were taken from several specimens and the numbers recorded reflect the minimum and maximum as well as the most common values obtained (always in µm). Where measures are reported from other authors or from other areas, the reference is given next to the number.

CLASSIFICATION OF LIVING SPECIES

Basic nomenclature

Before introducing the adopted classification, the most common terms used when describing coccolithophores and in particular their coccoliths are reviewed. More detailed terminological information can be found in the literature quoted above (Terminology, Introduction).

Coccolithophores and coccospheres

In a motile coccolithophore cell (Fig. 4), the coccosphere composed of coccoliths has a flagellar opening in the apical pole through which emerge the two flagella and the haptonema. In some coccospheres the coccoliths around the flagellar opening are morphologically differentiated, in which case they are termed circum-flagellar coccoliths (in contrast to the body coccoliths which constitute the rest of the coccosphere). Some coccolithophores also possess differentiated coccoliths in the antapical pole, termed antapical coccoliths.

The coccospheres of some coccolithophores, members of the genus Syracosphaera for example, consist of two layers of coccoliths; the inner endotheca and an external layer, the exotheca, characterised by a very different kind of coccoliths. Such coccospheres are termed dithecate (Fig. 5), in contrast to monothecate coccospheres, which possess only one coccolith layer. When several layers of the same kind of coccoliths are present, as is often the case in Emiliania huxleyi for example, the coccosphere is described as being multilayered.

In the literature, an endotheca which has only one kind of coccoliths is qualified as monomorphic; if it has two different kinds of coccoliths it is termed dimorphic, and if it has three or more kinds, as polymorphic. When gradual morphological dif-
ferences between coccoliths at the apical and antapical poles are observed, the coccosphere is described as being varimorphic.

The shape of coccospheres has been used as a character for coccolithophore classification, particularly in early descriptions using light microscopy (LM) techniques. With the advent of electron microscopy (TEM and SEM) the morphology of the coccoliths has become the most important character in the classification of the coccolithophores, and indeed the shape of coccospheres has been demonstrated not to usually be a constant and conclusive character.

**Coccoliths**

The most common form of coccoliths (especially of those found in sediments and fossil deposits) are the heterococcoliths, formed of complex arrays of crystal units typically arranged in rings (cycles) (Fig. 6A). Heterococcoliths have two morphologically differentiated parts, the central-area and the rim (Figs. 7 and 8). The central area can be unfilled or possess different types of elements (e.g., radial laths, rods, etc) or even have highly elaborated structures or spines (Young 1992a). Can be recognized three principal morphologically different heterococcolith types: planoliths, muroliths and placoliths (Young 1992b, Young et al. 1997). These types essentially differ in having the rim at different angles relative to the central area: (a) in the same plane (planoliths); (b) with all or most of the rim perpendicular or sub-perpendicular to the central area (muroliths); and (c) with a small part of the rim perpendicular, and two well developed parts, the shields, parallel to the central area (placoliths) (Fig. 7). It should be noted that a murolith without flanges resembles a planolith with the rim bent upwards, and that a placolith can have the appearance of a murolith with two well developed flanges. Placoliths form the most robust coccospheres, their structure allowing tight interconnection and hence the formation of a compact case.

In addition to these heterococcolith types, many other taxo-descriptive terms for heterococcoliths are found in the literature (Tappan, 1980; Chrétiennot-Dinet, 1990; Heimdal, 1993; Siesser and Winter, 1994; Jordan et al., 1995; Young et al., 1997). The other main coccolith form, the holococcoliths (Fig. 6B), constructed of numerous minute euhedral crystallites, show a high degree of morphological diversity (Heimdal and Gaarder, 1980; Norris, 1985; Kleijne, 1991; Young et al., 1997).

In addition to heterococcoliths and holococcoliths, a third type of calcified structure are the nanoliths (Fig. 6C), which were originally defined, by exclusion, as calcareous nannofossils lacking the typical features of calcareous dinophytes, heterococcoliths or holococcoliths and so of uncertain affinity (Perch-Nielsen, 1985). Nowadays the same name, by extension, can be applied to a few living taxa where the calcareous structures are not definitely homologous (even architecturally) with heterococcoliths or holococcoliths e.g. *Braarudosphaera* (pentaliths), *Florisphaera* (plates), *Ceratolithus* (ceratoliths), *Polycrater* (usually bowl-shaped coccoliths) (Young, 1992b; Young and Bown, 1997a; Bown and Young, 1998).

![Fig. 6. – Types of coccoliths: (A) Heterococcoliths; one in distal view (left) and the other, partially obscured, in proximal view. (B) Holococcoliths, formed of numerous minute crystallites; one in distal view (upper centre) and one in latero-proximal view (lower right); (C) A ceratolith, considered to be an irregularly shaped nanolith.](image-url)
General taxonomic list and abridged descriptions of the observed species

The formal classification of coccolithophores is in a state of flux. The present classification scheme, one of several possible today, follows essentially Cavalier-Smith (1998), Edvaren et al. (2000) and Young and Bown (1997a, b) for the higher classification; Jordan and Kleijne (1994) and Jordan and Green (1994) for family and lower ranks and Kleijne (1991) and Kleijne (1992) for the families Calyptrosphaeraceae and Rhabdosphaeraceae respectively. The published PhD thesis of Kleijne (1993) and the publications of Perch-Nielsen (1985a, b), Chrétiennot-Dinet (1990) Heimdal (1993) and Bown (1998) have been of valuable help. The descriptions are focussed on contributing to knowledge of the limits and variability of each species. All measures, coccolith counts, shapes, etc. refer to the specimens actually observed in the Mediterranean through the present study. Since it is generally not possible to count all coccoliths on a given coccosphere, estimates of the coccolith numbers on the total coccosphere are given, based on counts of coccoliths on the visible parts of the coccosphere. The annotated dimensions, always in µm, of both coccospheres and coccoliths refer to the long axis if no other indication is given. A question mark next to a reference indicates that the mentioned species may be, or is, morphologically similar to the studied species.

The taxa referred to with the epithet “sp.” are not known to science or not recognized, at present, from the older light microscopy descriptions; these taxa, whenever possible, will be described as new species, or redescribed on the basis of SEM images, in further publications.
Kingdom CHROMIST A Cavalier-Smith 1981 emend. Cavalier-Smith 1998
Subkingdom CHROMOBIOTA Cavalier-Smith 1991
Infra kingdom HAPTOPHYTA Cavalier-Smith 1995
Division HAPTOPHYTA Hibberd 1972
ex Edvardsen et Eikrem 2000
Class PRYM NESIOPHYC EAE Hibberd 1976 emend. Cavalier-Smith, 1996.
Subclass PRYM NESIOPHYCIDAE Cavalier-Smith 1986
ex Edvardsen et Eikrem 2000
Extant species are motile, forming ellipsoidal coccospheres. The characteristic heterococcolith of this family is the helicolith with the outer rim modified into a helical flange, ending in a wing or spike.

Genus Helicosphaera Kamptner, 1954

Ellipsoidal coccospheres with coccoliths arranged spirally around the coccosphere in a characteristic manner. The heterococcoliths, called helicoliths, have a characteristic helical flange. Species and subspecies can be recognized based on presence/absence of a conjunct or disjunct bar (a bar formed from the rim or not, respectively), bar orientation and flange shape (Young and Bown, 1997b).

Within this genus, Jordan and Kleijne (1994) and Jordan and Green (1994) recognized two extant species (H. carteri and H. pavimentum) with three varieties in H. carteri.

Order ZYGODISCALES Young and Bown 1997

The heterococcoliths are muroliths, and modified derivatives, with an outer rim with anticlockwise imbrication and an inner rim with clockwise imbrication. Central area structures include transverse bars, diagonal crosses and perforate plates but no spines.

Family HELICOSPHERACEAE Black, 1971, emend. Jafar et Martini, 1975.

Cells normally bearing heterococcoliths in at least one stage of their life-cycle (Jordan and Green, 1994). A member of this family, Helicosphaera carteri, has been shown to form combination coccospheres with holococcoliths (Cros et al., 2000). Extant species are motile, forming ellipsoidal coccospheres with a prominent flagellar opening (Young and Bown, 1997b). The characteristic heterococcolith of this family is the helicolith with the outer rim modified into a helical flange, ending in a wing or spike.

Genus Helicosphaera Kamptner, 1954

Ellipsoidal coccospheres with coccoliths arranged spirally around the coccosphere in a characteristic manner. The heterococcoliths, called helicoliths, have a characteristic helical flange. Species and subspecies can be recognized based on presence/absence of a conjunct or disjunct bar (a bar formed from the rim or not, respectively), bar orientation and flange shape (Young and Bown, 1997b).

Within this genus, Jordan and Kleijne (1994) and Jordan and Green (1994) recognized two extant species (H. carteri and H. pavimentum) with three varieties in H. carteri.

Helicosphaera carteri (Wallich 1877) Kamptner, 1954 var. carteri (Figs. 9, 10 and 11)

The former Syracolithus catilliferus (Kamptner, 1937) Deflandre, 1952 and Syracolithus confusus Kleijne, 1991, are now considered as the holococcolith phases of Helicosphaera carteri (Cros et al., 2000). Two combination coccospheres of Helicosphaera carteri with Syracolithus catilliferus (Figs. 9D, 10A, B) and coccospheres bearing laminoliths of both S. catilliferus and S. confusus (Cros et al., 2000, and Figs. 11C, D) have been found.

Heterococcolith phase (Figs. 9A-C).

Coccolithus carteri (Wallich) Kamptner, in Kamptner 1941, pp. 93-94, 111-112, Pl. 12, fig. 134, Pl. 13, figs. 135-136. Helicosphaera carteri (Wallich) nov. comb. Kamptner 1954, pp. 21, 23 Figs. 17-19. Helicopontosphaera kamptneri Hay et Mohler, in Hay et al., 1967, p. 448, Pl. 10-11, fig. 5; Perch-Nielsen, 1985b, figs. 43, 45 (25, 27 and 28), 46 (4); pp. 485-492. Helicosphaera carteri (Wallich) Kamptner, in Gaarder 1970, pp. 114-117, Fig. 2e, f.; Borsetti and Cati 1972, p. 405, Pl. 52, figs 1-2; Nishida, 1979, pl. 9, fig. 4; Heimdal 1993, p. 215, Plate 5; Kleijne 1993, pp. 232-233, Pl. 1 fig. 7; Winter and Friedinger in Winter and Siesser 1994, p. 121 Fig. 23A, B.

The coccoliths, termed helicoliths, usually possess a conjunt transverse bar separating two aligned openings in the central area and a well developed wing in the distal flange.

Coccosphere consists of (16-) 18-22 (-30) helicoliths.

Dimensions. Coccosphere long axis (15-) 17-23 (-26) µm, short axis (12-) 13-15 (-17) µm; coccoliths length (8-) 8.8-9.7 (-11) µm.

Holococcolith phase (solid), formerly Syracolithus catilliferus (Kamptner, 1937) Deflandre, 1952 (Figs. 10C and D).

Syracosphaera (Syracolithus) catilliferus Kamptner, in Kamptner 1941, pp. 81-103, pl. 4, figs. 43-45. Syracolithus catilliferus Kamptner, Deflandre, 1952, p. 453, figs. 351c, d. Calyptronithaphora catillifer (Kamptner) Gaarder, Nishida, 1979, pl. 17, fig. 3ab. Calyptronithophora catillifer (Kamptner), Norris, 1985, p. 626, fig. 33. Syracolithus catilliferus (Kamptner) Deflandre, Kleijne, 1991, p. 34, pl. 6, fig. 1.2.

The coccoliths, termed laminoliths, are elliptical and solid consisting of 6-8 layers of microcrystals and have a laminated, sharply pointed, central protrusion.

Since coccospheres bearing this morphotype and the perforate morphotype have been observed (Cros et
al., 2000, and Figs. 11C, D) we infer that this variation is ecophenotypic rather than genotypic. It may prove ecologically significant to distinguish these morphotypes but we do not regard them as discrete taxa.

The coccospheres possess 60 to 100 coccoliths (5 specimens).

**Dimensions.** Coccosphere long axis 12-15.5 µm; coccolith length (1.8-2.7) 3.0 (-3.5) µm, protrusion height 0.8-1.0 µm.

Holococcolith phase (perforate), formerly *Syracolithus confusus* Kleijne, 1993 (Fig. 11B).

*Syracolithus confusus* Kleijne, 1991, p. 34, 37, pl. 6, figs. 3-5; *Syracolithus confusus* Kleijne, Winter and Siesser, 1994, p. 147, fig. 159.

The laminoliths have a pointed protrusion surrounded by 5-8 surface pits. (see above in Holococcolith phase (solid), formerly *Syracolithus catillusferus*.

Coccosphere consists of 44 to 124 coccoliths (5 specimens).

**Dimensions.** Coccosphere long axis (9-) 10-11.5 (-14) µm; coccolith length (2.1-) 2.6-2.8 (-3.1) µm.

**Helicosphaera carteri** var. *hyalina* (Gaarder)
Jordan *et* Young, 1990 (Fig. 12A)

*Helicosphaera hyalina* Gaarder 1970, pp. 113-119, figs. 1a-g, 2a-d, 3a.; Borsetti and Cati, 1972, p. 406, pl. 52, figs. 3-4; Nishida, 1979, pl. 9, fig. 1; Heimdal, 1993, p. 215, pl. 5.

**Helicosphaera carteri** var. *hyalina* (Gaarder) Jordan *et* Young, 1990, pp. 15-16.

*Helicosphaera carteri* (Wallich 1877) Kamptner, 1954, Kleijne 1993 p. 232-233, pl. 1, fig. 8.

The studied helicoliths of var. *hyalina* were smaller than those of var. *carteri* (ca. 6.5 µm compared to ca 9.2 µm), did not have pores, and showed a well differentiated central area filled with large sized needle-shaped elements. We suspect they may prove to be a discrete taxon although this is not yet certain.

Coccosphere consists of 12-22 helicoliths.

**Dimensions.** Coccosphere long axis (11-) 13-14 (-16) µm, short axis (10-) 11.5-12.5 (-13) µm; coccolith length (5.5-) 6.2-6.8 (-7.5) µm.

**Helicosphaera carteri** var. *wallichii* (Lohmann)
Theodoridis, 1984 (Fig. 12B)

*Helicosphaera wallichii* (Lohmann) Okada *et* McIntyre, 1977, p. 14, pl. 4, fig. 8; Delgado and Fortuño, 1991, p. 20, pl. 86, fig. d.

Specimen figured in p. 223, Fig. 421-422 in Chrétiennot-Dinet, 1990, to illustrate the genus *Helicosphaera*.

The helicoliths of this variety have two offset slit-like openings instead of the two central openings arranged in a horizontal line present in *H. carteri* var. *carteri*.

Transitional shapes between *H. carteri* v. *carteri* and *H. carteri* v. *wallichii* exist, even on the same coccosphere, as reported by Jordan and Young (1990) and Kleijne (1993) and illustrated by Nishida 1979, pl. 9 Fig. 4a, b, c. Even Okada and McIntyre (1977), who described *H. wallichii* new comb., remarked that the separation at species level was tentative due to the occasional specimens showing transitional forms between these two types.

**Dimensions.** (Only one specimen) coccosphere long axis 14.7 µm, short axis 13.4 µm; coccolith length ca. 9 µm.

**Helicosphaera pavimentum**
Okada *et* McIntyre, 1977 (Figs. 12C, D)

*Helicosphaera pavimentum* Okada *et* McIntyre 1977, p. 14, Pl. 4, figs. 6-7.

*Helicosphaera pavimentum* Okada *et* McIntyre 1977, Borsetti and Cati 1979, p. 159, Pl. 15, fig. 1-2; Nishida 1979, Pl. 9, fig. 2; Kleijne, 1993, p. 233, Pl. 1, fig. 9; in Winter and Siesser, 1994, p. 122 (micrograph from Winter and Friedinger).

Thin helicoliths with narrow spiral flange and one or two central perforations or one or two aligned slits present or absent. These helicoliths resemble particularly the helicoliths of *H. carteri* var. *hyalina* but are smaller and thinner and have a narrower flange. We infer that this is a discrete species.

Coccosphere consists of 17-30 helicoliths.

**Dimensions.** coccosphere long axis (9-) 12.5-13.5 (-15) µm, short axis (8-) 11.5-12.5 (-13) µm; coccolith length (3.5-) 4.4-5.2 (-6) µm.

Family **PONTOSPHAERACEAE** Lemmermann, 1908

Cells normally bearing heterococcoliths in at least one stage of their life-cycle (Jordan and Green, 1994). Extant species apparently non-motile, coccospheres sub-spherical and they may have highly-modified equatorial coccoliths (*Scyphosphaira*). The coccoliths have an outer rim with a very clear anticlockwise imbrication. The characteristic heterococcolith of this family is the discolith, also named cribrilith, which is a murolith without flanges.
possessing roundish pores in the central area; the possession or not of lopadoliths, large equatorial barrel-shaped coccoliths, separates the two extant genera, *Scyphosphaera* and *Pontosphaera*.

Close affinity of the Helicosphaeraceae and Pontosphaeraceae is not obvious from coccolith morphology but was inferred from palaeontological studies (Romein, 1979; Aubry, 1989) and has been confirmed by molecular genetics (Saez and Medlin, pers. comm.).

Genus *Scyphosphaera* Lohmann, 1902

Coccoliths with central area solid or with a variable number of pores (discoliths-cribriliths) and also possessing elevated equatorial coccoliths (lopadoliths). The lopadoliths have vertical ribs crossed by transverse lines resulting in a reticular appearance with nodules and depressions. The shape of the lopadoliths is the main criterion adopted to distinguish species (see revision, in Siesser, 1998).

*Scyphosphaera apsteinii* Lohmann, 1902

(Figs. 13A-C)

*Scyphosphaera apsteinii* Lohmann, 1902, p. 132, pl. 4, figs. 26-30; Boudreaux *et* Hay, 1969, pp. 274-275, pl. 4, figs 16-18; Borsetti and Cati, 1972, p. 399, pl. 41, Fig. 3, pl. 42, figs. 1-2; Delgado and Fortiulo, 1991, p. 20, pl. 85, fig. a, b.; Heimdal, 1993, pp. 223-224, pl. 6; Siesser, 1998, p. 358, pl. 1 fig. 5a-b and text-fig. 2, 3, 4, 5 , 12, 13, 16.

*Scyphosphaera apsteinii* Lohmann *et* Gaarder, 1970, fig. 4e; f. Mostajo, 1985, figs. 43-45; Winter and Siesser, 1994, p. 127 fig. 66 (micrograph from J. Alcober).

*Scyphosphaera apsteinii* Deflandre, Nishida, 1979, pl. 2 fig. 2a.

The lopadoliths of this species characteristically have a gently convex outline. The margin terminates simply at the distal opening or curves slightly inward. Nevertheless, Lohmann (1902), Gaarder (1970), Aubry (1989) and Siesser (1998) noticed the high degree of morphological variability of coccoliths of this dimorphic species, which could therefore be characterised as polymorphic (Siesser, 1998).

*Dimensions. Coccosphere long axis (28-) 30-40 (-45) μm, short axis (21-) 25-30 (-33) μm; discoliths length (7-) 8.5-9.1 (-10) μm, width (4-) 5.9-6.6 (-7.5) μm; discoliths with rim length (6-) 6.5-7 (-8) μm, width (4-) 4.5-5 (-6) μm; lopadoliths length (11-) 11.5-13 (-13.5) μm, width (11-) 12.5-14 (-15) μm.

*Scyphosphaera apsteinii* f. *dilatata* Gaarder, 1970.

(Fig. 13D)

*Scyphosphaera apsteinii* f. *dilatata* Gaarder, 1970, p. 119, figs. 4-6; Mostajo, 1985, fig. 46.

*Scyphosphaera cohenii* Boudreaux *et* Hay, Siesser, 1998, p. 359.

360, pl. 2 fig. 2a.

*Scyphosphaera apsteinii* f. *dilatata* differs from *S. apsteinii* f. *apsteinii* in having lopadoliths without distal decrease in width.

Gaarder (1970), when describing *S. apsteinii* f. *dilatata* pointed out that within some coccospheres of *S. apsteinii* one lopadolith was observed which shows the flaring outline characteristic of the described variety *S. apsteinii* f. *dilatata* (Gaarder, 1970, Fig. 4e), but she concluded that these forms may be earlier stages of *S. apsteinii* and may represent abnormal cells where the formation of lopadoliths has stopped at an intermediate developmental stage.

The coccosphere figured in 13C has a lopadolith inside it, but since the lopadolith is partially covered by cribriliths, it is not possible to definitively establish whether its width decreases distally. Further work might prove that *S. apsteinii* f. *dilatata* is merely an early developmental form of *S. apsteinii* f. *apsteinii*.

Siesser (1998) argues that the three supposedly different species, *Scyphosphaera cohenii*, *S. antilleana* and *S. apsteinii* f. *dilatata* can be considered conspecific. In the belief that in the near future it should be proven that *S. apsteinii* f. *dilatata* belongs to *S. apsteinii* f. *apsteinii*, it can be wise to maintain the *dilatata* form related to *S. apsteinii* species and not to transfer it to *S. cohenii*.

*Dimensions. Discoliths (six specimens) length (6.5-) 8-10.5 (-9) μm, width (5-) 6-8 (-7) μm; lopadolith (one specimen) length 6 μm, width 9.2 μm.

Order *STEPHANOLITHALES* Bown and Young 1997

The coccoliths are muroliths with the wall composed of non-imbricating elements, i.e. in side-view, the sutures are vertical or near-vertical (Bown and Young, 1997)

Family *CALCIOSOLENIACEAE* Kamptner, 1927

Extant species have elongate fusiform coccospheres, which may possess spine-bearing polar coccoliths. Coccoliths are rhomboidal muroliths (named scapholiths), which diminish in width towards the poles where they justify the name of scapholiths (in the poles, the coccoliths are like a “skaphos”, boat). The scapholiths are muroliths without flanges; the central area has laths with a perpendicular disposition to the major diagonal and no a differentiated central structure is present.
This family has very clear and unmistakable characteristics, but the systematics at generic and specific level are not easy (Black, 1968; Manton and Oates, 1985). It is clear that in the future much work is necessary to attempt to clarify how many and which species make up this family. In the present study the specimens were measured with great precision to perceive differences in the studied taxa.

It is interesting to remark that this family has representatives from the early Cretaceous to the Holocene, but without stratigraphic interest due to the sporadic nature of their occurrence. Perch-Nielsen (1985a, b) points out that Scapholithus fossilis and Anaplosolenia brasiliensis are two of the few species that survived the event(s) of the Cretaceous/Tertiary boundary.

Genus Anoplosolenia Deflandre, 1952

Large-sized coccosphere with long, gradually tapering ends, which do not bear spine-like coccoliths. One species only recognized: A. brasiliensis (Lohmann) Deflandre.

**Anoplosolenia brasiliensis** (Lohmann 1919)

Deflandre, 1952 (Figs. 14A-C)

*Calciosolenia* Gran, 1912

Large-sized coccosphere with tapering ends and bearing polar spine-like coccoliths. This genus differs from *Anoplosolenia* in being slightly smaller, in having more abruptly tapering ends and in possessing long polar spine-like coccoliths.

**Calciosolenia murrayi** Gran, 1912

(Figs. 15A-D)

In the present study all fusiform coccospheres with spine-bearing polar coccoliths and having the rhomboidal coccoliths with real laths or plate-like laths are reported as *C. murrayi*. The coccospheres are shorter and the scapholiths are larger than those of *Anoplosolenia brasiliensis*, and long spines are present on apical and antapical poles.

The coccospheres possess 110-160 scapholiths and 3-16 polar spines.

**Dimensions.** Coccosphere (2 specimens measured) long axis without spines 28.5-29.0 μm, short axis 5.3-7.7μm; length/width ratio ca. 4.5; spines 16-25 μm; coccoliths (6 measured) major diagonal 3.4 - 3.7 μm, minor diagonal 1.6-1.8 μm, long side ca. 2.3 μm, short side ca. 1.8 μm, ratio long/short diagonals ca. 2.1, ratio long/short sides ca. 1.3.
Order SYRACOSPHAERALES Hay 1977

This order, embracing Syracosphaeraceae and Rhabdosphaeraceae, groups taxa which basically bear muroliths, planoliths or both together. The coccospores can exhibit different kinds of coccoliths in only one theca, or in different thecas and even, several species of the genus Syracosphaeraceae, can have jointly dithecatism and polymorphic coccoliths in the endotheca. A distinctive radial lath cycle is a common feature of body coccoliths in Syracosphaeraceae and in most of the species of Rhabdosphaeraceae. Representatives of both families, Syracosphaeraceae and Rhabdosphaeraceae, present hetero-holococcolithophore combination coccospheres.

Family RHABDOSPHAERACEAE Haeckel, 1894

The coccoliths of this family are named rhabdoliths, a name first employed to designate coccoliths with a central styliform process, but since extended to include all coccoliths with the distinctive rim structure of the family (Kleijne, 1992). The body coccoliths have the rim formed of two rings of elements and a central area consisting of one to several rings (cycles) of different types of elements, which are disposed in the following order from the external to inner part: radial laths, lamellae elements, needle-shaped/elongated elements, tile shaped elements and cuneate elements. Central area often with a conical or sacculiform shape or having a robust spine.

Some representatives of this family, in the genera Acanthoica and possibly Rhabdosphaera, can form combination coccospheres with holococcoliths (Cros et al. 2000 and Figs. 18B-D and 114).

Genus Acanthoica Lohmann, 1903, emend. Kleijne, 1992

Monothecate coccospheres with polymorphic coccoliths. Four types of rhabdoliths: body coccoliths with a well developed ring of laths and three different types of pole rhabdoliths with a central spine.

Acanthoica acanthifera Lohmann, 1912 ex Lohmann, 1913 (Figs. 16 A, B)

Acanthoica acanthifera sp. nov. Lohmann, 1912 (nomen nudum). Validated by Lohmann, 1913, pp. 348, 349, figs. 13b, c. Acanthoica acanthifera Lohmann, ex Lohmann, Kleijne, 1992, p. 22, 23 pl. 1 Figs. 1-7; Winter and Siesser, 1994, p. 127, fig. 68 (phot. from Kleijne).

The body coccoliths have a conical to somewhat sacculiform protrusion, which is slightly distally flattened and slightly compressed along its long sides; radial laths are somewhat tilted and separated by very narrow openings. Body coccoliths of this species are more robust but smaller than in other Acanthoica species. The spines of pole rhabdoliths are more robust than those of other Acanthoica pole rhabdoliths.

In the course of the present study some specimens have been found with the characteristics of this species (Figs. 16 A, B) but other specimens have less tilted radial laths and a less sacculiform and flattened protrusion, suggesting that some transitional forms between this species and A. quattrospina may occur. More work is necessary to clarify this point.

Coccosphere consists of ca. 50 coccoliths.

Dimensions. Coccospheres 6-7 µm; longest spines ca. 6 µm; intermediate spines ca. 3 µm; shortest spines 1.2-2.2 µm.; body coccoliths length (1.5-) 1.8-1.9 (-2.2) µm.

Acanthoica quattrospina Lohmann, 1903 (Figs. 17 and 18)

Acanthoica aeonata Lohmann, 1903, p. 68, pl. 2, figs. 21-22
Acanthoica quattrospina Lohmann, 1903, p. 68, pl. 2, figs. 23-24; Kleijne, 1992, p. 26-27, pl. 3, figs 1-6; Pl. 4, figs. 1-3; Winter and Siesser, 1994, p. 128, fig. 72 (phot. from Nishida).

Acanthoica quattrospina presents combination coccospheres with an undescribed holococcolithophore, which can be related to the Sphaerocalyptera genus (Figs. 18B-D). Moreover, Figs. 114C, D show several coccoliths of Acanthoica aff. A. quattrospina with coccoliths figured here as Sphaerocalyptera sp. 2 (Fig. 105A).

Heterococcolith phase (Fig. 17).

Acanthoica quattrospina, the most common of all the Acanthoica species, differs from A. acanthifera in having the body rhabdoliths with a lower central protrusion, and not clearly tilted laths separated by wider openings. However, the observation of morphological variability in specimens of A. acanthifera (see A. acanthifera description) leads to think that more material has to be examined to ascertain if A. acanthifera is a real species or just a variety of the highly variable A. quattrospina.

It is well known that the position of the spines is highly variable in this species (Kleijne, 1992) and the specimen figured in Fig. 17B is perhaps typical, with one long and three short spines at one pole and two long spines with laterally flattened bases at the
other pole. The disposition figured in Fig. 17C with all the spines at one pole was originally described by Lohmann (1903) as *Acanthoica coronata* (more information is given in the revision of Kleijne, 1992).

The coccospheres possess between 45 and 105, including polar spines.

*Dimensions.* Coccospheres (6-) 7-8 (-12) µm; longer spines ca. 9 µm; intermediate spines ca. 7µm; shortest spines 1.5-3.0 µm.; body coccoliths (flat rhabdoliths) length (1.6-) 1.9-2.2 (-2.6) µm.

Holococcolith phase (Fig. 18A).

Body coccoliths are calyptroliths with a flat basal ring of well packed crystallites and a steeply tapered central protrusion tipped by one crystallite; usually these coccoliths present a few euhedral crystallites on the distal side forming the distal tip. Circum-flagellar calyptroliths are notably higher than body calyptroliths and are tipped by a thin and acute protrusion.

*Dimensions.* Body coccolith length ca. 1.4 µm.

Genus *Algirosphaera* Schlauder, 1945, emend. Norris, 1984

Monothecate coccosphere with dimorphic coccoliths with a large sacculiform protrusion. Kleijne (1992) gave a detailed revision of the taxonomic changes in this genus and clarified the taxonomic and historic relationships between the names *Algirosphaera* and *Anthosphaera*; nowadays, *Anthosphaera* is an accepted holococcolith bearing genus. Following Kleijne (1992), in the present study, *Algirosphaera robusta* embraces all the *Algirosphaera* “until more specimens from different areas have been examined in more detail”.

*Algirosphaera robusta* (Lohmann, 1902) Norris, 1984 (Figs. 19A-D)

*Algirosphaera robusta* (Lohmann, 1902) Norris, 1984, p. 38 - 40, figs. 14-16; Kleijne, 1992, p. 28-31, pl. 6, fig. 1-7; Giraudieu and Bailey, 1995, pl. 3, fig. 1.

Body rhabdoliths have a globular distal shape due to the large central area protrusion which usually obscures, in distal view, the rim and the radial laths; the proximal side of the hollow protrusion is covered by a layer of randomly arranged elements; three flattened and variably shaped circum-flagellar rhabdoliths are present which are higher than the body coccoliths and slightly undulated.

The morphology of the rhabdoliths of this species is highly variable, even on the same specimen. A detailed description of the rhabdoliths is given in Kleijne (1992).

*Dimensions.* Coccospheres (7-) 8.5-10.0 (-12) µm; body rhabdoliths length (1.2-) 1.8-2.2 (-2.8) µm, width (0.7) 0.9-1.1 (-1.3) µm; height (with central protrusion) 1.4-1.6 µm; circum-flagellar rhabdoliths length ca. 3 µm.

Genus *Anacanthoica* Deflandre, 1952

Monothecate coccosphere with only one type of coccoliths with a conical central protrusion.

*Anacanthoica acanthos* (Schiller, 1925) Deflandre, 1952 (Figs. 16C, D)

*Anacanthoica acanthos* Schiller, 1925, p. 34, pl. 3, figs. 32, 32a. *Anacanthoica acanthos* Schiller, Deflandre, 1952, p. 452, fig. 350d; Kleijne, 1992, p. 31-32, pl. 7, fig. 1; Winter and Siesser, 1994, p. 129, fig. 77 (from Kleijne).

The coccospheres have a wide rim, a ring of radial laths and a wide blunt ended protrusion.

The coccospheres possess around 78 coccoliths

*Dimensions.* coccosphere long axis (only one specimen) 8.5 µm; rhabdoliths length 2.1-2.6 µm, width 1.7 - 2.1 µm.

Genus *Cyrtosphaera* Kleijne, 1992

Monothecate coccosphere with variformic coccoliths. These rhabdoliths have a rim, radial laths and a conical or sacculiform protrusion formed by lamellar and needle-shaped elements arranged in a clockwise disposition and tipped by a papilla of cuneate elements; the protrusion increases in height towards one pole of the coccosphere.

*Cyrtosphaera aculeata* (Kamptner, 1941) Kleijne, 1992 (Figs. 20A, B)

*Cyrtosphaera aculeata* Kamptner, 1941, pp. 76, 133.pl. 1, figs 1, 3; Samtleben and Schröder, 1992, pl. 2, fig. 6. *Cyrtosphaera aculeata*, Kleijne, 1992, p. 33-34, pl. 1, fig. 1-3.

The coccoliths have the rim somewhat bent upwards and showing a well developed inner rim cycle (Kleijne, 1992), which is homologous to the external connecting ring in the genus *Syracosphaera*. The radial laths have a length/width ratio of around 3. The conical and relatively low protrusion has a well formed lamellar ring of dextrally arranged wide lamellae at its base, followed by some
narrow and somewhat irregularly arranged needle-shaped elements, and a blunt distal end which is tipped by a small papilla of cuneate elements.

The coccospheres possess from 40 to 60 rhabdoliths; each coccolith has from (28-) 38 to 41 (-45) laths.

**Dimensions.** Coccospheres 6-10 µm; coccolith length (2.1-) 2.5-2.8 (-3.1) µm, width (1.4-) 1.7-2.0 (-2.3) µm.

**Cyrtosphaera cucullata** (Lecal-Schlauder, 1951) Kleijne, 1992 (Figs. 21A, B)

*Cytosphaera aculeata* (Kleijne, 1992)

Coccoliths have a bowler hat shape due to the large central protrusion; the rim and the radial laths form a flat area surrounding the protrusion like the brim of a hat. The protrusion starts with a ring of very short laths at its base which are perpendicular and appear intercalated with the laths of the radial cycle, followed by elements of the lamellar cycle which become needle-shaped and are separated distally by small openings, and is tipped by a small papilla constructed of cuneate elements.

The dimensions of the three coccospheres as well as the long axis of the coccoliths measured in the present study are closer to those given by Lecal-Schlauder (1951) for Mediterranean specimens from the North Africa area than the larger North Atlantic specimens reported by Kleijne (1992). Too few specimens are available to determine if this is a systematic trend, but if so, differences of water temperature may be responsible.

Coccospheres possess from 45 to 70 rhabdoliths each of which has from 42 to 48 laths.

**Dimensions.** Coccospheres 8-11 µm; coccolith length (2.1-) 2.5-2.7 (-3.0) µm, width 1.9-2.2 µm, height 1.2-2.3 µm.

**Cyrtosphaera lecaliae** Kleijne, 1992 (Figs. 20C, D)

*Syracorhabdus lactaria* sp. nov. - (nomem nudum) Lecal, 1965b, p. 65, text-fig. D, pl. 1, fig. 2; Lecal, 1965a, pp. 256-257, pl. 6, figs. 18-21, pl. 7, figs. 22-23.

*Cyaithoclypeus aculeatus* Kampner, Borsetti et Cati, 1976, pp. 209-210, pl. 12, fig. 1.

*Cyrtosphaera lecaliae* Kleijne, 1992, p. 34-36, pl. 1 fig. 4.

This species resembles *C. aculeata* but has larger rhabdoliths, each with more laths; the laths are slender and have a higher height-width relationship than in *C. aculeata* (around 5 compared with around 3); the central protrusion in *C. lecaliae* is higher and more steeply sloped than in *C. aculeata*. See Kleijne (1992) for a detailed description.

Coccospheres consist of 30 to 55 rhabdoliths each with between 40 and 60 laths.

**Dimensions.** Coccospheres 8-12 µm; coccolith length (2.4-) 2.9-3.2 (-3.7) µm, width 1.9-2.2 µm.

**Genus Discosphaera** Haeckel, 1894

Monothecate coccosphere with only one type of coccoliths which have a characteristic trumpet-like central structure, and so have been termed salpingiform rhabdoliths.

**Discosphaera tubifera** (Murray et Blackman, 1898) Ostenfeld, 1900 (Figs. 21C, D)

**Genus Palusphaera** Lecal, 1965 emend. R.E. Norris, 1984

Monothecate coccosphere with only one type of coccolith which has a long styliform central structure on the distal surface and a central pore in the proximal side.

**Palusphaera vandelii** Lecal, 1965 emend. R.E. Norris, 1984 (Figs. 22A, B)

This species resembles *C. aculeata* but has larger rhabdoliths, each with more laths; the laths are slender and have a higher height-width relationship than in *C. aculeata* (around 5 compared with around 3); the central protrusion in *C. lecaliae* is higher and more steeply sloped than in *C. aculeata*. See Kleijne (1992) for a detailed description.

Coccospheres consist of 30 to 55 rhabdoliths each with between 40 and 60 laths.

**Dimensions.** Coccospheres 8-12 µm; coccolith length (2.4-) 2.9-3.2 (-3.7) µm, width 1.9-2.2 µm.
towards the distal tip. In proximal view the rhabdolith has a central pore which is surrounded by two or three small nodes.

*Dimensions.* Coccosphere diameter without processes 4-5 µm; coccosphere diameter including processes 10-14 µm; coccolith proximal disc width (1.2-) 1.5-1.9 (-2.1) µm; spine length 3.5-9 µm, spine thickness ca. 0.1 µm (maximum ca. 0.3 µm in the thicker proximal part).

**Palusphaera** sp. 1 (type robusta)
(Figs. 22C, D)

*Coccosphere of Palusphaera* affinity found in North Atlantic (Cruise APNAP 1) which is described, but not shown, by Kleijne, 1992, p. 38 in Remarks.

Rhabdolith figured in lateral view, but without description, at the bottom of pl. 6, fig. 7 in p. 261 of Kleijne, 1993.

Rhabdoliths have a thick styliform process, which is characteristically thickest at 1/2-1/3 height from the disc; the distal rim appears narrower than in *P. vandelii* and in proximal view has robust angular nodes around the central pore.

The central process of coccoliths of *Palusphaera* sp. 1 differs from that of *P. vandelii* in being thicker, especially in the middle part, and in being constructed by strong, thick elements. Further study is required to ascertain if this *Palusphaera* is another species or merely a variety, as is the case in *Rhabdosphaera stylifera*, which can show rhabdoliths with a thick spine (variety *clavigera*) or a thin spine (variety *stylifera*).

**Dimensions.** Coccosphere diameter without processes 6-9 µm; coccosphere diameter including processes 17-23 µm; coccolith proximal disc width (1.3-) 1.7-1.9 (-2.1) µm; spine length (3.6-) 6-7 (-8.9) µm, spine thickness ca. 0.5 µm.

Genus *Rhabdosphaera* Haeckel, 1894

Dithecate coccosphere with two different types of coccoliths; planoliths with and without styliform central structure as endothecal and exothecal coccoliths respectively. The exothecal coccoliths, without spine, are distributed all around the coccosphere and partially cover the basal discs of the endothecal styliform rhabdoliths.

**Rhabdosphaera clavigera**
Murray et Blackman, 1898 (Figs. 23A, B)

Rhabdoliths of the endothea with a robust spine which is constructed of spirally arranged elongate elements and tipped by a papilla; this central structure has a highly variable shape and thickness. The short axis of exothecal (non spine-bearing) coccoliths is slightly shorter than that of endothecal coccoliths, and the former, in distal view, have a narrower rim.

The shape of the process varies between claviform (characteristic for specimens originally described as *R. clavigera*) and styliform (characteristic for specimens originally described as *R. stylifera*) (Fig. 23A). The latter shape, with small “wings” of laterally extending elements (Fig. 23B) instead of a straight end, was denominated *R. stylifera* var. *capitellifera* in Kamptner, 1937, p. 313, pl. 17, figs. 43-45. Nowadays, the process shape is considered characteristic of individual rhabdoliths (Kleijne, 1992) and not of entire rhabdospheres and hence it seems better to distinguish the coccospheres as “formae” rather than varieties *clavigera* and *stylifera*.

*R. clavigera* formae *stylifera* and particularly the formae *capitellifera* (with wings) are the most common in NW Mediterranean waters.

A coccosphere belonging to *Sphaerocalyptra quadridentata* half surrounded by part of a collapsed coccosphere of *R. clavigera* (Fig. 114A) was found in the Barcelona offshore station T1, from the workshop named “Picasso” (July, 1998). In the station T5 of the same Picasso workshop, a disintegrated coccosphere of *S. quadridentata* was found next to several exothecal coccoliths of *R. clavigera* that appears a random product (Fig. 114B). Nevertheless, Kamptner (1941) noticed that *S. quadridentata* is combining with *Algirosphaera robusta*. These data appear, at the moment, inconsistent and so it is wise to think that more data is necessary to clarify the life-cycle of these coccolithophores.

Coccosphere consists of (22-) 40-50 (-64) coccoliths (10 to 32 exothecal, 12 to 32 endothecal)

**Dimensions.** Coccosphere diameter without spines (6-) 8-9.2 (-10.5) µm; coccosphere diameter including spines (14-) 17-20 (-21) µm; endothecal coccolith base plate length (3.1-) 3.3-3.7 (-3.9) µm, width 2.5-2.8 µm, rim width 0.4-0.5µm; spine length (3.7-) 5.0-5.3 (-5.8) µm; exothecal coccolith length (3.7-) 5.0-5.3 (-5.8) µm; exothecal coccolith length
Rhabdosphaera xiphos (Deflandre et Fert, 1954)
Norris, 1984 (Figs. 23C, D)

Rhabdosphaera xiphos Deflandre et Fert, 1954, pp. 42, 43 pl. 8, figs. 1-3 (sediments)
Rhabdosphaera longistylis Schiller, Okada and McIntyre, 1977, p. 17, pl. 5, fig. 6.
Rhabdosphaera xiphos (Deflandre et Fert) comb. nov. Norris, 1984, pp. 33, 34, figs. 1d, e, 6-8; Kleijne, 1992, pp. 41-42, pl. 8, figs. 2, 5.

Endothecal rhabdoliths have a circular base; a long and thin process with a short and blunt ended collar at the base is present on the distal surface; the proximal side has a central pore. Exothecal coccoliths have no spine; they are somewhat elliptical (the base being larger than that of endothecal coccoliths) and possess a characteristic distal star-like central structure.

Coccosphere possesses 25-80 coccoliths (15 to 35 endothecal, 10 to 50 exothecal).

Dimensions. Coccosphere diameter without spines 4-6 µm; coccosphere diameter including spines 15-20 µm; endothecal coccolith diameter 1.1-1.3 µm, spine length 5-7 µm; exothecal coccolith length (1.4-) 1.7-1.8 (-1.9) µm, width 1.1-1.4 µm.

Family SYRACOSPHAERACEAE (Lohmann, 1902)
Lemmermann, 1903

This family groups genera which bear muroliths with a radial lath cycle, the caneloiths, but they can possess planoliths and/or modified derivatives on the same coccosphere. Most genera have a very high architectonic complexity (e.g. they can show either dimorphism, polymorphism or variformism associated sometimes with dithecatism or even possess large modified coccoliths as real appendages).

Some of the representatives of this family in the genera Syracosphaera and Coronosphaera, show combination coccospheres with holococcoliths (Cros et al. 2000).

The family Syracosphaeraceae is the most diverse within the extant coccolithophores (Jordan and Kleijne, 1994) but has few fossil representatives (Perch-Nielsen, 1985) due to the small sized coccoliths with low preservation potential (Young, 1998).

Genera with appendages

Genus Calciopappus Gaarder et Ramsfjell 1954 emend. Manton et Oates, 1983

Coccospheres with at least three kinds of coccoliths: the body caneloiths without flanges, an apical ring of whorl coccoliths and, attached distally to the whorl coccoliths, another ring of very modified spine-like coccoliths. These characteristic spines have a split base with a horseshoe-like end.

This genus contains two recognized species, C. caudatus and C. rigidus, which are differentiated in electron microscopy studies by their coccoliths. C. caudatus has oblong caneloiths with central laths running somewhat obliquely to the sides, whilst C. rigidus has narrowly elliptical caneloiths with a developed wall. C. caudatus is a species typical of subpolar waters (Okada and Honjo, 1973; Okada and McIntyre, 1979) found particularly in shallow waters (Samtleben and Schröder, 1992; Samtleben et al., 1995) whilst C. rigidus is a species described from the subtropical North Atlantic (Heimdal and Gaarder, 1981), possibly related to subtropical to tropical waters and particularly to nutrient-enriched environments (Kleijne, 1993).

Calciopappus rigidus Heimdal, 1981, in Heimdal and Gaarder, 1981 (Figs. 24A, B)

C. rigidus Heimdal, in Heimdal and Gaarder, 1981, pp. 42, 44, Plate 2, Figs. 5-8; Kleijne 1993, p. 234-235, pl. 2, fig. 12.
Calciopappus, Gaarder et Ramsfjell 1954, Manton and Oates 1983, pp. 452-455, pl. 7-8.

Coccosphere stiff, slender, cone-shaped; this species is described as having tetramorphic coccoliths (Heimdal and Gaarder, 1981, Kleijne, 1993) but in the studied specimens the central apical caneloith with spine described in the diagnosis of the species was not observed, and only three different kinds of coccoliths have been seen. The body caneloiths are narrowly elliptical and are arranged in co-axial rings with the long axis parallel to the long axis of coccosphere and having most of the laths arranged at approximately right angles to the side of the caneloith; they have a high wall. Surrounding the flagellar opening the coccosphere has a whorl of subcircular, overlapping planoliths with the central opening partially filled by flat bands, and each with finger-like projections towards the centre of the whorl. A ring of spine-like appendages surround the whorl planoliths.

Coccospheres consist of 60-85 body caneloiths, 7-12 subcircular planoliths; 4-9 spine-like appendages.

Dimensions. Coccosphere (7 specimens measured) long axis (8-) 9-11 (-15) µm, short axis (4-) 6-7 (-8) µm; body caneloiths length (1-) 1.3-1.6 (-2)
µm, width (0.5-) 0.75-0.9 (-1.1) µm; whorl plano-
liths length (0.95-) 1.5-1.7 (-1.75) µm; width ca. 1.2
µm; spine length (13-) 15-18 (-21) µm.

*Calciopappus* sp. 1 (very small)
(Figs. 24C, D)

Small and weekly calcified *Calciopappus*. Small
coccosphere with delicate caneoliths which have only
the rim well calcified; the whorl planoliths have two
finger like spines, one directed towards the coccus-
phere and the other, approximately at 90º forming a
tangential anticlockwise pattern on the coccosphere
in distal view; the appendages are short and thin.

Coccospheres consist of 60-70 body caneoliths,
around 10 subcircular planoliths; around 10-12
spine-like appendages.

**Dimensions.** Coccosphere (2 specimens) long
axis 5-6.5 µm, short axis ca. 3.4 µm; body caneoliths
length (0.7-) 0.8-0.9 (-1.2) µm; spine length (3-) 6.5-
7.5 (-8) µm.

**Genus Michaelsarsia** Gran
emend. Manton *et al.*, 1984

Coccospheres with four kinds of coccoliths: flan-
geless body caneoliths, rhomboid circum-flagellar
muroliths with spine, an apical ring of whorl coc-
coliths (ring-shaped planoliths) attached to which is
another ring of appendages which consist of three
highly modified, elongated coccoliths (link coccol-
iths).

*M. elegans* Gran 1912,
emend. Manton *et al*. 1984 (Figs. 25A-D)

*Michaelsarsia elegans* Gran, 1912, p. 332; Heimdal and Gaarder,
1981, pp. 56, 58, pl. 7; Manton *et al*., 1984, pp. 187-191, 198, pl. 1-4.

Coccosphere with 50 to 80 body caneoliths,
around 4 to 6 apical caneoliths with spine, 8 to 18
whorl coccoliths and 8 to 18 appendages each of
which is composed of three link coccoliths. The coc-
cosphere has a robust appearance with the body
caneoliths having a wide and raised central struc-
ture; small rhomboidal circum-flagellar coccoliths
having a solid process (spine); the ring-shaped
planoliths and the link coccoliths have wide central
openings.

*M. elegans* differs from *M. adriaticus* (formerly
*Halopappus adriaticus*) in having stronger body
caneoliths with a wider and thicker central structure,
circum-flagellar caneoliths having a solid instead of
centrally opened process, ring-shaped coccoliths
with wider central opening and wider link coccoliths
with a broad central opening.

**Dimensions.** Coccosphere long axis (10-) 13-15
(-16) µm, short axis (8-) 9-11 (-13) µm; body cane-
olith length (1.8-) 2.2-2.5 (-2.7) µm, width (1.1-) 1.2-1.5
(-1.7) µm; small apical caneoliths with
occluded tube ca. 1.5 µm; ring-shaped coccoliths
length ca. 3.5 µm; appendage (composed of three
link coccoliths) length ca. 22 µm

**Genus Ophiaster** Gran 1912
emend. Manton *et Oates*, 1983

Coccospheres with flangeless body caneoliths,
circum-flagellar caneoliths having a long spine and
one antapical appendage with flexible arms formed
of elongated transformed coccoliths called oste-
oliths; the most proximal osteoliths are larger than
the others and have loop-like proximal ends which
can overlap ("like the lamellae of an optical
diaphragm" Gaarder, 1967).

**Ophiaster formosus** Gran 1912, sensu Gaarder
1967, emend. Manton *et Oates*, 1983,
var. *formosus* (Figs. 26A, B)

*Ophiaster formosus* Gran, Gaarder 1967, p. 185, text-fig. 1A, pl. 1,
fig. C, pl. 5, figs. B, E; Winter *et al*., 1979, p. 206, pl. 3, fig. 6; Man-
ton and Oates, 1983, p.p. 449-450, 460; Kleijne, 1993, p. 236, pl. 3,
fig. 7.

Coccosphere with 50 to 80 body caneoliths,
around 4 apical caneoliths with spines and usually 6
to 10 antapical appendages. These appendages
resemble band-like articulate arms and are each
composed of around 8 osteoliths, which are relatively
short and broad with more or less parallel sides
and a length/width ratio of approximately 3 (in the
studied specimens (2.1-) 2.4-3 (-3.7)).

**Dimensions.** Coccosphere (without appendages)
4.5-7.5 µm; body caneolith length (0.7-) 1.1-1.3 (-
1.45) µm, width 0.7-0.8 µm; apical caneolith spine
length ca. 1.3 µm; osteolith length (1.9-) 2.6-2.8
(3.2-) µm, width (0.7-) 0.9-1.1 (-1.2) µm.

**Ophiaster hydroideus** (Lohmann) Lohmann
emend. Manton *et Oates*, 1983 (Figs. 26C, D)

*Ophiaster hydroideus* (Lohmann) Lohmann,
Gaarder, 1967, pp. 184-185, text-fig. 1C, pl. 1, fig. A, B, pl. 2, fig. A, pl. 3, fig. A;
Manton and Oates 1983, pp. 441-443, 460, T. 1-2; Kleijne, 1993, p.
236, pl. 3, fig. 8.

Coccosphere with 50 to 85 body caneoliths,
around 4 apical caneoliths with spines and around 7
antapical appendages which resemble cord-like articulate arms; these appendages consist of relatively long, centrally constrictal osteoliths (around 5 osteoliths per appendage); the length/width ratio of the osteoliths is between 5 and 7.

O. hydroideus mainly differs from O. formosus in having narrower osteoliths which are constricted centrally having a higher length/width ratio (around 6 compared to around 3).

**Dimensions.** Coccosphere diameter (without appendages) ca. 6 µm; body caneoliths length (0.6-) 1.1-1.3 (-1.4) µm, width 0.7-0.9 µm; apical caneolith spines 1.1-1.4 µm; osteolith length (2.1-) 2.6-2.8 (-3.1) µm, width 0.4-0.5 µm.

**Genera without appendages**

**Genus Coronosphaera** Gaarder in Gaarder et Heimdal, 1977

The coccosphere is monothecate and possesses dimorphic muroliths. These muroliths are caneoliths with a thick and strongly imbricate (anticlockwise) wall and have neither distal nor mid-wall flanges. The circum-flagellar caneoliths possess a robust spine.

Young and Bown (1997b) place this genus in the Syracosphaeraceae, but they point out that the imbricate rim is anomalous in this family.

**Coronosphaera binodata** (Kamptner, 1927)

Gaarder, in Gaarder et Heimdal, 1977 (Figs. 27A-C)

*Syracosphaera binodata* Kamptner, in Borsetti et Cati 1972, p. 400, pl. 44, fig. 2.

**Coronosphaera binodata** (Kamptner) Gaarder, in: Gaarder and Heimdal, 1977, p. 62, pl. 5, figs. 27-32; Nishida, 1979, pl. 6, fig. 2; Kleijne 1993, p. 235, pl. 3, fig. 1.

The most characteristic feature of this species is the pair of pointed knobs in the central structure of the body caneoliths.

The coccosphere has 40 to 75 body caneoliths and around 6 circum-flagellar caneoliths with spines.

**Dimensions.** Coccosphere (only one complete coccosphere studied) major axis 15.6 µm, short axis 14.6 µm; body caneoliths length (3.5-) 3.9-4.1 (-4.5) µm, width (2.5-) 2.75-2.85 (-3.0) µm; apical caneolith spine length 1.6 µm.

**Coronosphaera mediterranea** (Lohmann) Gaarder in Gaarder et Heimdal, 1977

(Figs. 27D and 28)

*Syracosphaera mediterranea* Lohmann, 1902, p. 133, 134, pl. 4.

**Coronosphaera mediterranea** (Lohmann) Gaarder in Gaarder and Heimdal, 1977, pp. 60, 62. Pl. 4; Nishida, 1979, pl. 6, Fig. 1a-b. Similar shaped coccosphere and coccoliths to *C. binodata* but both coccosphere and coccoliths slightly smaller than the latter species and having a central structure composed of two flattened parts instead of the two pointed knobs present in *C. binodata*.

The coccosphere has 30 to 65 body caneoliths and around 2 to 6 circum-flagellar caneoliths with spine.

**Dimensions.** Coccosphere (3 complete coccospheres studied) major axis 13-15.5 µm, short axis 13-14.5 µm; body caneoliths length (3-) 3.3-3.7 (-4) µm, width (2.3-) 2.4-2.6 (-2.7) µm; apical caneolith spine (1.2-) 1.3-1.7 (-2.1) µm.

Holoococcolith phase, formerly *Calyptrolithina wettsteinii* (Kamptner, 1937) Norris, 1985 (Figs. 28C, D).

*Zygosphaera wettsteinii*, Kamptner (1937), pp. 306, 307, pl. 10, figs. 103-106.

*Zygosphaera wettsteinii* (Kamptner), Halldal et Markali (1955), p. 9, pl. 5.

*Zygosphaera wettsteinii* (Kamptner). Kleijne, 1991, p. 46, 48, pl. 11, fig. 1-3.

The calyptroliths have a prominent distal rim and 2-7 pores in the distal surface; on the distal surface only the blunt central protrusion extends above the rim (when seen in lateral view). Zygolith structure is similar to that of the calyptrolith, but with a high bridge which has a pointed protrusion. Certain circum-flagellar coccoliths are in fact transitional forms between zygoliths and calyptroliths.

Coccospheres possess around 6 to 12 circum-flagellar zygoliths; 60 to 116 body coccoliths.

**Dimensions.** Coccosphere major axis (9.5-) 12-14 (-14.5) µm; zygolith length ca. 2.2 µm; body coccolith length (1.9-) 2.1-2.3 (-2.6) µm.
Genus *Gaarderia* Kleijne, 1993

The coccosphere is dithecate. Both endothecal and exothecal coccoliths are caneoliths with an anti-clockwise rim; exothecal coccoliths are larger than endothecal coccoliths.

This genus was erected to contain only one species (*G. corolla*), which was first placed inside the genus *Syracosphaera* and subsequently in *Umbellosphaera*.

**Gaarderia corolla** (Lecal 1965) Kleijne 1993 (Figs. 29A-D)

*Syracolithus corolla* Lecal, 1965a, pp. 252-253, pl. 1, fig. 1-4; Okada and McIntyre, 1977, p. 20, p. 20, pl. 8, figs 1-2. *Umbellosphaera corolla* (Lecal) Gaarder, in: Heimdal and Gaarder 1981, pp. 62, 64, pl. 11, figs. 52-57. *Gaarderia corolla* (Lecal) Kleijne, 1993, pp. 200-201, Plate 6, figs. 3-6.

Endothecal caneoliths have a beaded mid-wall flange but have no clear distal flange, which rather an apparent continuation of the highly variably developed wall. The exotheca is composed of large and very modified caneoliths which are preferentially placed around the apical area. These exothecal caneoliths have a petaloid-shaped distal flange with a strong sinistral direction of the elements; in proximal view they show no bilateral symmetry.

This species was erected as *Syracolithus corolla*, with *Syracolithus* being a subgenus of *Syracosphaera* by Lecal (1965a). Later, Gaarder, in Heimdal and Gaarder (1981), in view of the high degree of size variation in the coccoliths and especially with regard to the development of the wall, included this species in the genus *Umbellosphaera* Paasche. Kleijne (1993) introduced a new genus, *Gaarderia*, to include this controversial species possessing umbelloliths and caneoliths. However, the exothecal and endothecal coccoliths are very similar, and more closely resemble caneoliths than umbelloliths; moreover, in the present study, it is clearly demonstrated that members of the genus *Syracosphaera* can bear caneoliths as exothecal coccoliths. In view of this evidence, *Gaarderia corolla* could be placed back in the genus *Syracosphaera*. Nevertheless it may be convenient to maintain, at present, the genus *Gaarderia* to contain this species with unusual exothecal and endothecal coccoliths. Coccosphere with (25-) 35-45 (-60) body caneoliths and 6 to 18 exothecal coccoliths.

**Dimensions.** Coccosphere length (9-) 10-11 (-15) µm; body coccolith length (2-) 2.2-2.6 (-3.1) µm, width (1.1-) 1.3-1.8 (-2.3) µm; exothecal coccolith length (4-) 4.5-5.1 (-5.5) µm, width (2.8-) 3.0-3.5 (-4.1) µm.

Genus *Syracosphaera* Lohmann, 1902

Coccospheres usually dithecate. Endothecal coccoliths are caneoliths with one, two or three flanges; dimorphism is frequent, with apical spine-bearing coccoliths, and sometimes also differentiated antapical coccoliths or even varimorphic body coccoliths. Exothecal coccoliths usually differ from endothecal coccoliths and can be planoliths or muroliths, but, as proven in the present study, may sometimes be caneoliths with a very similar structure to endothecal coccoliths; the exothecal coccoliths can cover totally or partially the coccosphere or, in some species, may only be present around the apical area (as deviating coccoliths). Representatives of this genus present hetero-holococcolithophore combination coccospheres (Cros et al. 2000b).

This complex genus contributes significantly to the high diversity of the extant coccolithophores; it contains numerous species, several of which (mainly small sized species) do not yet have an official name or diagnosis.

Morphologically, a caneolith, which is a type of murolith, is constituted by the rim and the central area. The rim consists of the wall and flanges (proximal, mid-wall and distal) (Fig. 7). The central area contains laths, a connecting external ring and a connecting central structure (Fig. 8).

The connecting external ring morphologically belongs to the central area, but structurally the elements are a continuation of the rim elements and it is homologous to the “internal rim” described by Kleijne (1992) in the family Rhabdosphaeraceae. This group was divided into three genera (*Syracosphaera “sensu stricto”, Caneosphaera* and *Coronosphaera*) by Gaarder and Heimdal (1977). The purpose was to group the species as follows: 1) double-layered case, *Syracosphaera “sensu stricto”*, 2) single layer (but may possess deviating coccoliths) with complete caneoliths *Caneosphaera*, and 3) one layer of caneoliths with extremely narrow proximal rim and a rather complex wall, *Coronosphaera*. Other authors defined the genus *Syracosphaera* more widely in the morphological sense (Okada and McIntyre, 1977) and considered the proposed classification of Gaarder and Heimdal unpractical for stratigraphic purposes and also when working with actual specimens, since the exothecal coc-
coliths are not always present in the dithecate species and isolated caneoliths are often difficult to identify (Janin, 1987).

At present, the genus Syracospaera can be considered as a group of species of widely variable morphology, but related by the possession of caneoliths (having one, two or three flanges), with the endothe-ca having monomorphic, dimorphic or varimorphic coccoliths, with or without exothecal coccoliths, but always lacking the kind of highly specialised polar coccoliths that are found in Michaelsarsia and other syracosphaerid genera (Jordan and Young, 1990). In recent taxonomical work (Jordan, 1991; Kleijne 1993, Jordan and Kleijne 1994, Jordan and Green, 1994, Young and Bown, 1997b) the genera Caneosphaera and Deutschlandia are eliminated and their species placed back in Syracospaera. In a near future the genus Gaarderia may also be placed back into Syracospaera (see explanations in Gaarderia text).

From the study of the variability of the exothecal coccoliths in the Syracospaera genus (Cros, 2000) groups of species which share common characters have been distinguished; these groupings are useful for classification purposes and may even help to understand phylogenetic and ecological relationships. Here, following Cros, 2000, we classify the Syracospaera species according to their exothecal coccoliths type.

**Syracosphaera species having undulating exothecal coccoliths, which appear as modified planoliths.**

All these Syracospaera species have endothe-cal caneoliths with proximal and distal flanges.

*Species with complex undulating exothecal coccoliths*

Exothecal coccoliths only around the flagellar area. The endothe-ca presents differentiated apical caneoliths with four-ended spines and, usually, one or two caneoliths with a spine in antapical position.

**Syracosphaera marginaporata** Knappertsbusch, 1993 (Figs. 30A-D)

Syracosphaera marginaporata Knappertsbusch, 1993, p. 72-74, pl. 2 figs. 1-4; Samtleben et al., 1995, plate 2 fig. 3; Cros, 2000, p. 49, Plate 5, fig. 3.

Unidentified heterococcolithophorid “E”, Heimdal et Gaarder, 1981, p. 67, pl. 13, fig. 64. Syracospaera sp. A, Samtleben et Schröder, 1990, pl.1, fig. 3. Syracospaera sp. type H, Kleijne, 1993, p. 258-259, pl. 5, fig. 6.

Coccosphere dithecate, with dimorphic endothe-cal caneoliths. The body caneoliths are highly variable in size and appear smooth due to the central area laths which seem to be fused together except along the margin, where a row of characteristic pore-like gaps occurs between the elements, next to the smooth distal flange; the number of pores is very variable (14 to 24). Circum-flagellar caneoliths are considerably smaller than ordinary caneoliths, have clear radial laths in the central area and bear a long rod-shaped process (about 1 µm length) tipped by four endings; usually they lack the distal flange, possibly because it is easily broken. The exothecal coccoliths, observed only around the apical pole, are irregularly-shaped with petaloid protrusions; they are defined in the present study as complex undulating coccoliths.

The smooth appearance of the caneoliths and the row of gaps between the central area and the distal flange is characteristic of this species. We agree with Kleijne (1993) about the resemblance of this species to Syracospaera ossa. Both species have a smooth distal flange, a high degree of size variability in body caneoliths, small circumflagellar caneoliths with a four pointed spine and similar shaped exothecal coccoliths. *S. marginaporata* differs, however, from *S. ossa* in having body caneoliths with a flat central area and no central structure, in not possessing circum-flagellar caneoliths with flattened spines and in having smaller coccoliths and coccospheres than *S. ossa*.

One coccosphere with heterococcoliths of *S. marginaporata* and unidentified holococcoliths, possibly belonging to Anthosphaera sp. type B, has been found in the studied samples (Figs. 112C, D). The coccospheres (13 specimens) have (16-) 28-36 (-42) body caneoliths; 2 to 6 circum-flagellar caneoliths with spines; when present (2-) 5-6 (-8) exothecal coccoliths.

**Dimensions.** Coccosphere long axis 3-6 µm; body caneolith length (1.0-) 1.4-1.7 (-1.9) µm; circum-flagellar caneolith spine length ca. 1µm; exothecal complex undulating coccolith diameter 1.3-1.9 µm.

**Syracosphaera molischii** Schiller, 1925 (Figs. 31A-D)

Syracosphaera molischii Schiller, Halldal et Markali, 1954b, p.
Coccosphere dithecate with dimorphic endothe-
cocal coccoliths. Body caneoliths have a wide curved
and ridged distal flange, sometimes with protrusions
towards the central area; central structure, when pre-
sent, an elongated or variably shaped mound; these
caneoliths are highly variable in size and morpholo-
ey, even on one coccosphere. Circum-flagellar cane-
oliths are smaller than the body caneoliths and have
a process tipped by four nodes. Exothecal coccoliths
are complex undulating coccoliths called deviating
coccoliths due to their characteristic position only
around the flagellar opening (Heimdal and Gaarder,
1981); the distal side is highly ornamented while the
proximal side is smooth with an oval central area
which is bordered by a depression and has two small
knobs near the centre and small parenthesis-like slits
at the ends. On several specimens a coccolith with a
small process was also observed at the antapical
pole. The smooth surfaced complex undulating
exothecal caneoliths. Body caneolith length (1.3-) 1.7-1.9 (-2.2) µm;
circum-flagellar caneolith spine length 1.8-2.3 µm;
caneoliths have a broad process characteristically
extended in the direction of the major axis (Figs.
32A, C, D; and Lecal, 1965a, pl. 2 fig. 8). A cane-
olithe with a short spine is usually present at the
antapical pole. The exothecal coccoliths are smooth,
complex and undulating and in the central part have
two parenthesis-like openings bordering the ends of
the ellipse; in proximal view one or two small nodes
are present in the central part.

S. ossa is a species closely related morphologi-
cally to S. molischii, but differs in having a smooth
distal flange on the body caneoliths and smooth dis-
tal side to the exothecal coccoliths rather than being
corrugated; moreover the circumflagellar caneoliths
of S. ossa are characteristically broader and more
laterally flattened than in S. molischii.

The coccosphere consists of between 26 and 62
body caneoliths (23 specimens); (1-) 2-4 (-8) spine-
bearing circum-flagellar caneoliths and from 6 to 9
exothecal caneoliths.

**Dimensions.** Coccosphere diameter (5-) 6-7 (-10)
µm; body caneolith length (1.4-) 1.9-2.1 (-2.6) µm;
circum-flagellar caneolith spine length (1.3-) 1.4-1.6
(-1.8) µm; exothecal coccolith length 2.0-2.4 µm.

**Syracosphaera** sp. (slender)
(Figs. 33A, B)

Syracosphaera sp. II cf. *S. epigrosa* Kleijne 1993, p. 237, pl. 4, fig.
3; Cros, 2000, p. 49, Plate 5, fig. 4.

Coccosphere with four kinds of coccoliths: body
caneoliths, circum-flagellar caneoliths with spines,
antapical caneolith with long spine and exothecal
complex undulating coccoliths around the apical
pole. The body caneoliths are irregularly sized, have
no mid-wall flange and a smooth distal flange; the
central area has a variable number of laths (14 to 28)
and no central structure. The circum-flagellar cane-
oliths have a long and thin, four-tipped central spine.
At the antapical pole, a characteristic caneolith with
a very long spine with a long and slender tip is pre-
sent. The smooth surfaced complex undulating
exothecal coccoliths resemble the exothecal coccol-
iths of *S. ossa*, *S. molischii* and *S. marginaporata*.

In the studied coccospheres 25, 28 and 56 body
caneoliths were estimated; around 5-6 circum-fla-
gellar caneoliths with spine; 1 antapical caneolith
with long spine; and from 4 to 10 exothecal cane-
oliths.

**Dimensions.** Coccosphere long axis 6-10 µm;
body caneolith length (1.3-) 1.7-1.9 (-2.2) µm; cir-
cum-flagellar caneolith spine length 1.8-2.3 µm;
antapical caneolith spine length 2-3 µm; exothecal caneolith length (2.3-) 2.5-2.7 (-3.1) µm.

**Species with simple undulating exothecal coccoliths**

The exothecal coccoliths are, usually, in one area of the coccosphere. The endotheca presents body caneoliths with proximal and distal flanges and has no differentiated caneoliths with spine.

**Syracosphaera** sp. (laths with rod protrusions).

**(Figs. 33C, D)**

*Syracosphaera epigrosa* auct. non Okada et McIntyre, Heimdal and Gaarder 1981, p. 60, pl. 8 figs. 38-39; Winter and Siesser 1994, p. 136 fig. 109 (phot. J. Alcober).

*Syracosphaera* sp. I cf. *epigrosa* Kleijne 1993, p. 237, pl. 4 fig. 1; Cros, 2000, p. 49, pl. 5, figs. 5 and 6.

Dithecate coccosphere (Cros, 2000) with monomorphic endothecal coccoliths. The body caneoliths have a narrow distal flange and the central area has characteristic perpendicular nodules/rods of variable size on the laths. The nodules of some specimens are positioned irregularly, but in others the nodules/rods are arranged very regularly; the coccoliths with a more regular rod distribution are typically smaller and more irregular in shape than the specimens in which the nodules are irregularly arranged. It could be useful to express such differences in the nomenclature. The exothecal coccoliths are simple undulating coccoliths with the ends bent upwards, giving a distally concave aspect.

Coccoliths of this species have nodules/rods in the central area like *Syracosphaera epigrosa* Okada et McIntyre 1977, but the distal flange is narrower and flaring (rather than wide, smooth and very flat), and no dimorphism of endothecal caneoliths is shown.

Kleijne (1993) relates this species to *Syracosphaera epigrosa* Okada et McIntyre 1977 and to *Syracosphaera* sp. II cf. *epigrosa* Kleijne, 1993. She reports that the morphology of the caneoliths of *Syracosphaera* sp. I cf. *epigrosa* is intermediate between that of *S. epigrosa*, with their wider distal flange and highly variable pattern of nodules, and that of *Syracosphaera* sp. II cf. *epigrosa*, with a narrow distal flange and no nodules. The presence or absence of dimorphic endothecal coccoliths between *S. epigrosa* and *Syracosphaera* sp. I cf. *epigrosa* and the very different aspect of the central processes in the circum-flagellar caneoliths between

*S. epigrosa* and *Syracosphaera* sp. II cf. *epigrosa* suggests that these three taxa are essentially different. So, the three taxa should be considered different species.

The coccosphere consists of (38-) 42-56 (-70) body caneoliths (15 specimens) and from 1 to 4 exothecal simple undulating coccoliths (very loosely attached to the coccosphere and so easily lost).

**Dimensions.** Coccosphere long axis (5.5-) 7-8.2 (-9) µm; body caneolith length (1.4-) 1.7-1.9 (-2.5) µm; exothecal coccoliths length (1.7-) 1.9-2.1 (-2.4) µm.

*Syracosphaera* species having disc-like exothecal coccoliths, which are planololiths. All these species have caneoliths without either distal or mid-wall flanges.

**Species with disc exothecal coccoliths**

Exothecal coccoliths can be placed around the endotheca with characteristic imbricate mode. Endotheca presents differentiated apical caneoliths with robust spines.

**Syracosphaera anthos** (Lohmann 1912) Janin, 1987 (Figs. 34 and 35)

*Periphyllophora mirabilis* (Schiller) Kamptner, 1937, is now considered as the holococcolith phase of *Syracosphaera anthos* (Cros et al. 2000b). Two combination coccospheres showing coccoliths of both, *S. anthos* and *P. mirabilis* were found in the studied samples (Figs. 35A, C, D).

Heterococcolithophore phase (Fig. 34).

**Deutschlandia anthos** Lohmann, Reid, 1980, p. 156, pl. 2 figs. 5-6; Heimdal and Gaarder, 1981, pp. 48-50, pl. 5 figs. 23-26.

*Syracosphaera variabilis* (Hallldal et Markali) Okada et McIntyre, 1977, p. 27, pl. 9 figs. 7-8; Nishida, 1979, pl. 8, figs. 1a-b.

*Syracosphaera anthos* (Lohmann) Janin, 1987, p. 112-113; Kleijne, 1993, p. 236, pl. 6 fig. 10; Giraudeteau and Bailey, 1995, Plate 3, figs. 11-12; Cros 2000, Plate 1, figs. 3 and 4.

Coccosphere dithecate with dimorphic endothecal coccoliths. Coccosphere consists of 40 to 60 body caneoliths, 4 to 6 circum-flagellar caneoliths with spine and 15 to 60 exothecal coccoliths. The body caneoliths have neither distal nor mid-wall flanges; in the central area the laths are curved near the wall forming a sort of roof gutter, and raised up towards the centre with a thickening where the slope changes (this sort of lath construction gives the appearance of an horizontal platform in the central part); the central structure is flat, irregular in shape.
Species with oval exothecal coccoliths

The endothea presents differentiated circum-flagellar caneoliths with small spines.

Syracosphaera nana (Kamptner, 1941) Okada et McIntyre, 1977 (Figs. 36 and 37)

Pontosphaera nana (Kamptner, 1941, p. 79, pl. 3, figs. 31-33; Syracosphaera sp. 1; Borsetti et Catu, 1972, p. 402, pl. 47, fig. 4).

Unidentified heterococcolithophorid "C", Heimdal et Gaarder 1981, p. 67, pl. 12, fig. 62.

Syracosphaera sp. type A, Kleijne, 1991, p. 21, pl. 20, figs. 5-6; Kleijne, 1993, p. 241, pl. 6, fig. 1.

Syracosphaera nana (Kamptner) Okada et McIntyre, in Cros, 2000, p. 46, plate 2, figs. 6 and 8; Cros et al. 2000, p. 13, pl. 5.

Coccosphere dithecate with dimorphic endotheal caneoliths. Hetero-holococcolithophore combination coccospheres involving this species have been observed and hence S. nana is considered to have an holococcolithophore life-cycle phase (Kleijne, 1991, Cros et al., 2000).

Heterococcolithophore phase (Fig. 36).

The heterococcolith coccosphere has body caneoliths with a short and thick wall with neither a distal nor a mid-wall flange; the laths of the central area raise up in the centre forming a structure which resembles a sloping tiled roof; these body caneoliths do not have complete bilateral symmetry since the central ridge formed by the union of the laths is slightly warped and shows some polarity at the two ends. The circum-flagellar caneoliths have a small central nodular spine. The exothecal oval coccoliths have a broad rim composed of similar elements, a ring of very short elements that connect the rim with the central part, the latter being covered by 12 to 14 plates which are triangular at the extremes of the coccolith ellipse and otherwise quadrate (Fig. 36B and Kleijne, 1991, pl. 20 fig. 6); this solid central part is slightly convex in distal view.

The ovoid shape of the coccosphere is characteristic (Fig. 36A), as illustrated by Kamptner (1941) plate 3 fig. 31-32, and detailed in Kamptner’s description (p. 79) “Die Schale ist kurz eiförmig”. The vaulted morphology of the caneoliths with the appearance of a sloping tiled roof, described as ‘hunchbacked caneoliths’ (“In der Mitte des Bodens tragen sie eine längliche buckelartige Erhebung”) by Kamptner (1941) is also typical. The oval, slightly vaulted coccoliths not described by Kamptner, but noticed by Kleijne (1993), are also characteristic in this Syracosphaera species.
The coccospheres figured as *S. nana* by Halldal and Markali (1955), by Okada and McIntyre (1977), by Nishida (1979) and in Winter and Siesser (1994) appear to be different (and not all the same) species. The heterococcolith coccosphere consists of (44-) 50-64 (-98) body coccoliths (11 specimens); in some coccospheres 2 to 4 caneoliths with a short spine were observed; some coccospheres have several exothecal coccoliths (1 to 17).

*Dimensions.* Heterococcolith coccosphere long axis 5.7 µm; body caneolith length (0.9-) 1.4-1.6 (-1.9) µm; circum-flagellar caneolith spine height 0.1-0.2 µm; exothecal coccolith length (1.8-2.2) µm.

Holococcolithophore phase (Figs. 37C, D)

Coccospheres of the holococcolithophore phase possess dimorphic coccoliths; body laminoliths and zygo-lite-like circum-flagellar holococcoliths. The holococcolith coccosphere consists of 94 to 112 body holococcoliths; sometimes with circum-flagellar holococcoliths (from 10 to 12).

*Dimensions.* Holococcolith coccosphere diameter 5.5-7.5 µm; body holococcoliths length (0.9-) 1.1-1.3 (-1.5) µm.

*Syracosphaera* sp. (aff. *S. nana*, laths with sinistral obliquity) (Figs. 38A, B)

The body caneoliths are very small with a very low wall and narrow proximal flange; the flat central area has no central structure and the laths are wider towards the coccolith wall, the inner end typically not being arranged radially. Circumflagellar caneoliths have laths oriented anticlockwise and a blunt low spine as a central structure. Anticlockwise precession of laths is very characteristic of both, body and circumflagellar caneoliths. Exothecal coccoliths are small, oval, disc-like coccoliths.

The body caneoliths of this species resemble the caneoliths of *Syracosphaera* sp. type B Kleijne (1993) p. 241 pl. 6 figs. 2-3, but the exothecal coccoliths do not have an indented periphery as the coccoliths figured in pl. 6 fig. 3 of Kleijne, 1993; moreover the coccosphere as well as the caneoliths of the *S.* sp. type B appear larger than *S.* sp. (aff. *S. nana*). The three coccospheres studied consist of 32, 40 and 40 body caneoliths; 1 to 5 circum-flagellar caneoliths with spine; some exothecal coccoliths on only one collapsed coccosphere.

*Dimensions.* Cocospheres diameter (all specimens collapsed) ca. 5 µm; body caneolith length (1.1-) 1.4-1.5 (-1.7) µm; circum-flagellar caneolith spine length ca. 0.3 µm; exothecal coccoliths length 1.6-1.9 µm.

Species with stratified exothecal coccoliths

Exothecal coccoliths are very thick. The endothea presents differentiated circum-flagellar caneoliths with spines.

*Syracosphaera* sp. (with stratified coccoliths) (Figs. 38C, D)

*Syracosphaera nana* auct. non (Kamptner) in Okada and McIntyre, 1977, pl. 8 fig. 9.

The coccosphere is dithecate with dimorphic endotheal caneoliths. The body caneoliths have neither distal nor mid-wall flanges and posses a very thick and short double layered wall; central area with around 25 (from 23 to 28) laths which fuse in a broad central part and slightly climb into the inner wall. The circumflagellar caneoliths have a high, thick single layered wall and possess a short and thick rod-shaped central structure with rounded end. The irregular, subcircular exothecal coccoliths are solid, compact, with well developed and stratified layers on the distal side (somewhat resembling a fish otolith).

The caneoliths of this *Syracosphaera* sp. have double layered body caneoliths resembling the caneoliths of *S. bannockii* but having a rather broad central part instead a more or less elongated low mound; however the exothecal coccoliths have a completely different morphology showing a characteristic stratified aspect in this *Syracosphaera* sp.

The specimens figured by Okada and McIntyre (1977) pp. 24-25, pl. 8 figs. 7-8 as *Syracosphaera nana* (Kamptner), by Heimdal and Gaarder (1981) p. 60, pl. 8, figs. 42a-b as *S.* cf. *nana* (Kamptner) Okada and McIntyre and *Syracosphaera* sp. type J Kleijne, 1993, p. 244, pl. 5 fig. 3 all resemble this *Syracosphaera* sp. but in the descriptions from these authors there is not mention of the double layered wall and the images do not show this structure; in addition the coccoliths of these quoted specimens are elliptical and not subcircular as in the specimen figured by Okada and McIntyre (1977) pl. 8 fig. 9 and the present *Syracosphaera* sp. Two different, but very close taxa may exist; the present *S.* sp. and *S.* sp. type J of Kleijne (1993).
Coccospheres consists of 40 to 44 body caneoliths; only a single spine-bearing circum-flagellar caneolith was observed; 3 and 34 exothecal coccoliths.

**Dimensions.** Coccosphere long axis 6.5-7.5 µm; body caneoliths length (1.5-) 1.6-1.8 (-2) µm; circum-flagellar caneolith spine length ca. 0.5 µm; exothecal coccoliths diameter 2.5-2.9 µm.

Species with asymmetrical exothecal coccoliths

The asymmetrical exothecal coccoliths appear usually grouped forming a ribbon of coccoliths, which can surround the endotheca. The endotheca has differentiated circum-flagellar caneoliths with spines.

*Syracosphaera bannockii* (Borsetti et Cati 1976)

*Cros et al.* 2000 (Figs. 39, 40 and 41)

*Corisphaera* sp. type A of Kleijne, 1991, and *Zygosphaera bannockii* (Borsetti and Cati, 1976) Heimdal, 1980, are considered as the holococcolith phases of *Syracosphaera bannockii* (Cros *et al.*, 2000b).

A combination coccosphere showing coccoliths of both, *Syracosphaera bannockii* and the formerly *Corisphaera* sp. type A is figured in Figs. 40A, B. Several coccospheres bearing laminoliths of *Z. bannockii* with coccoliths of *Corisphaera* type A Kleijne, 1991 have now been found (Figs. 40C, D; Heimdal and Gaarder, 1980, pl. 2, fig. 18 a,b; Winter *et al.*, 1979, pl. 5, fig. 7; *Cros et al.*, 2000b).

Heterococcolith phase (Fig. 39)

*Syracosphaera nana* Kampfner in Nishida, 1979, Plate 7, Fig. 4
*Syracosphaera orbiculus* in Samtleben *et al.*, 1995, Plate II, fig. 4.
*Syracosphaera bannockii* (Borsetti et Cati 1976) *Cros et al.* 2000 in *Cros*, 2000, Plate 3, figs. 3 and 4.

Coccosphere usually ovoid; dithecate with dimorphic endothecal caneoliths. Body caneoliths with low and thick wall and neither mid-wall nor distal flange; central structure from nearly flat to a slightly elongated mound, radial laths resting directly on the wall without external connecting ring. Circumflagellar coccoliths with a pointed spine which usually appears slightly bent. Exothecal coccoliths are asymmetrical disc-like coccoliths, broadly elliptical with a pointed extended rim.

This *Syracosphaera* strongly resembles *Syracosphaera* sp. type K Kleijne, 1993, p. 244, pl. 6 fig. 11, it differs mainly in having exothecal coccoliths without thickened or stratified parts as shown in the coccoliths of *Syracosphaera* sp. type K.

The coccosphere consists of (32-) 46-50 (-60) body caneoliths (15 specimens); 2 to 6 spine-bearing circum-flagellar caneoliths; from 4 to more than 30 exothecal coccoliths.

**Dimensions.** Coccosphere long axis 5.0-6.5 µm; body caneoliths length (1.3-) 1.5-1.7 (-2.0) µm; circum-flagellar caneolith spine length ca. 0.5 µm; exothecal coccoliths length (2.0-) 2.4-2.8 (-2.9) µm.

Holococcolithophore phase (perforate) (Figs. 41A, B)

*Helladosphaera cornifera* (Schiller) Kampfner, Hallegraeff (1984), p. 242, fig. 50.
*Corisphaera* sp. type A Kleijne, 1991, p. 54, pl. 13, figs. 1-2.

Body zygoform are cup-shaped with a central opening and a very low and short, curved, transverse bridge; the tube wall ends distally with a row of regularly arranged angular microcrystals. Circum-flagellar coccoliths have characteristic double-layered walls and bear a broad bridge with a pointed protrusion.

Coccospheres possess from 70 to 88 coccoliths.

**Dimensions.** Coccosphere long axis 5-7 µm; coccolith length (1.0-) 1.3-1.4 (-1.5) µm.

Holococcolithophore phase (solid) (Figs. 41C, D)

*Zygosphaera bannockii* (Borsetti and Cati, 1976) Heimdal, 1980.
*Sphaerocalyptra bannockii*, *Borsetti and Cati*, 1976, p. 212, pl. 13, figs. 4-6; Winter *et al.*, 1979, p. 212, pl. 5, fig. 7 (figure captions 7 and 8 have been changed).
*Laminolithus bannockii* (Borsetti and Cati) Heimdal, in Heimdal and Gaarder, 1980, pp. 8, 10, pl. 2, fig. 18a,b.
*Zygosphaera bannockii* (Borsetti and Cati) Heimdal, Heimdal, 1982, p. 53; Kleijne, 1991, p. 67, 69, pl. 18, fig. 1.

Body laminoliths have a transverse pointed ridge. Circum-flagellar zygoform coccoliths have a double-layered wall.

Coccospheres possess from 48 to 76 coccoliths (3 specimens).

**Dimensions.** Coccospheres long axis 4.5-6.5 µm; coccolith length (1.1-) 1.15-1.25 (-1.4) µm.

N.B. These two coccolith morphotypes (solid and perforated) are sufficiently distinctive to be worth separating, since they may be ecologically distinct. However their co-occurrence on single coccosphere makes it unlikely they are genotypes.

*Syracosphaera delicata* *Cros et al.* 2000.

(Figs. 42A-D)

*Syracosphaera delicata* *Cros et al.*, 2000, p. 29-32, pl. X; *Cros*, 2000, Plate 3, figs. 1-2.

Coccosphere dithecate with dimorphic endotheca-
cal caneoliths. The body caneoliths have a delicate, lightly calcified appearance, and are often bent or deformed; they have a narrow proximal flange and neither distal nor mid-wall flanges; the wall is low and smooth and its elements are easily distinguished; the central area has 19 to 26 laths which join forming a flat and smooth central part. The circum-flagellar caneoliths have a very short and thin central protrusion. The exothecal coccoliths are asymmetrical disc-like planoliths; they are formed of three rings of elements: a variably wide rim of juxtaposed elements, of which one is larger and laterally protruding giving the coccolith its pointed extension; a radial ring of around 20 short laths, separated by wide slits, and a central part of around 12 elements showing clockwise imbrication/obliquity in distal view; the central part and radial cycle are subcircular and flat but the rim is more elliptical to rhomboid in outline and bears a thin, almost straight, characteristic distal ridge. These exothecal coccoliths are often positioned in an imbricate arrangement, forming a ribbon.

A disintegrated specimen, which is not a conclusive combination coccosphere, with heterococcoliths of this *Syracosphaera* and holococcoliths of *Corisphaera* sp. type B of Kleijne (1991) was found through this study (Fig. 113C).

The coccosphere resembles the images and description of *Pontosphaera nana* by Halldal and Markali (1955), particularly with respect to the endothecal caneoliths; both have no distal flange, a wide and flat central area and a fragile appearance, but *Syracosphaera delicata* has caneoliths with lower walls and narrower and shorter slits between laths; the exothecal coccoliths also closely resemble each other, but Halldal and Markali’s exothecal caneoliths are more elongated and have shorter and more numerous laths in the radial ring (22-23 compared to 20 in *S. delicata*). *Syracosphaera delicata* also resembles *S. orbiculus* Okada and McIntyre (1977), both in terms of the morphology of the exothecal coccoliths and the large flat central structure of the caneoliths; it differs from this species, however, in having smaller caneoliths with a more fragile appearance, in having circum-flagellar coccoliths with a very small spine (around 0.3 µm compared to 1 µm described by Okada and McIntyre, 1977) and smaller exothecal coccoliths with a narrower rim.

Coccospheres possess 32, 34, 36, 40(2), 42, 48, 50 and 54 body caneoliths; 2 to 4 spine-bearing circum-flagellar caneoliths; from 10 to 23 exothecal coccoliths (very loosely attached to the coccosphere and hence easily lost).

It is remarkable that the coccosphere of this species is small, and appears delicate. The caneoliths have a characteristic smooth and fragile aspect and the circum-flagellar caneolith possesses a very thin, short and sharp spine. The exothecal coccoliths have a characteristic longitudinal ridge on a quarter of the rim.

**Dimensions.** Coccosphere long axis (6-) 6.5-7.5 (-10) µm; body caneolith length (1.2-) 1.8-2.0 (-2.3) µm; circum-flagellar caneolith spine length ca. 0.3 µm; exothecal coccolith length (2.3-) 2.5-2.6 (-2.7) µm.

*Syrosphaera* sp. aff. to *S. orbiculus* (ovoid) (Fig. 43A)

Coccosphere subspherical to ovoid; dithecate with dimorphic endothecal caneoliths. Body caneoliths with a thick and smooth wall and neither distal nor mid-wall flanges; central area with no connecting external ring, 25 to 26 short and irregularly widened laths, and a broad, flat and smooth internal connecting structure. Circum-flagellar caneoliths with a medium sized spine. The exothecal coccoliths are asymmetrical disc-like planoliths with a wide rim, very short radial laths and the central area filled with elements showing clockwise obliquity in distal view.

The caneoliths of this species are reminiscent of *S. orbiculus* caneoliths, but differ from them in not having a connecting external ring which is very clear in the caneoliths figured in Okada and McIntyre (1977) pl. 9 fig. 6, and in possessing smaller and more elliptical exothecal coccoliths.

The three studied coccospheres have around 64, 64 and 70 body caneoliths; 4 circum-flagellar caneoliths with spine and only two exothecal caneoliths.

**Dimensions.** Coccosphere long axis 8-9 µm; body caneolith length (1.8-) 1.9-2.1 (-2.3) µm; circum-flagellar caneolith spine length ca. 0.8 µm; exothecal coccolith length ca. 2.7 µm.

*Syrosphaera* sp. aff. to *S. orbiculus* (spherical) (Fig. 43B)

? *Syrosphaera variabilis* Verbeek, 1989, fig. 23.
? *Syrosphaera nodosa*, Findlay, 1998, pl. 3 fig. 1.

Coccosphere spherical; dithecate with dimorphic endothecal coccoliths. Body caneoliths with a thin and smooth wall and neither distal, nor mid-wall, flanges; central area with a well developed connect-
ing external ring, a flat, elongated internal connecting structure and 18 to 26 laths (characteristically at each end of the caneolith, a short lath which does not extend to the central structure but joins with the neighbouring lath is observed). Circum-flagellar caneoliths have a long and somewhat bent spine. The exothecal asymmetrical disc-like coccoliths have two longitudinal segments of the rim sides conspicuously bent.

The body caneoliths and the circum-flagellar spine-bearing caneoliths of these specimens strongly resemble those of *S. orbiculus* Okada and McIntyre, but the shape of the exothecal coccoliths differs between the two species.

This taxon was also found in North Atlantic waters (M. Cachão and A. Oliveira, personal communication, 1999).

The four studied coccospheres consist of 26, 42, 42 and 60 body caneoliths; 4 circum-flagellar caneoliths with spine and many detached exothecal caneoliths.

**Dimensions.** Coccosphere long axis 6-9 µm; body caneolith length (1.4-) 2.0-2.2 (-2.4) µm; circum-flagellar caneolith spine length ca. 1µm; exothecal caneolith length 2.5-3.0 µm.

**Species with thin (sub-)circular exothecal coccoliths**

The endotheca has no differentiated circum-flagellar caneoliths.

*Syracosphaera lamina* Lecal-Schlauder, 1951

(Fig. 44)

*Syracosphaera lamina* Lecal-Schlauder, 1951, pp. 286-287, figs. 23-24; Borsetti and Cati 1976, p. 215, plate 14 figs. 15-17; Okada and McIntyre, 1977, pp. 22-23, Plate 7 figs 7-8; Janin, 1987, p.114-116 pl.24 fig. 7 ; Cros, 2000, p. 46, Plate 2, fig. 1.

**Discolithus ribosus** Kampner, 1967, pp. 136-137, plate 5 figs. 30-31.

*Cyracosphaera ribosa* (Kampner) Borsetti et Cati 1972, p. 402, plate 46 fig. 1a-b.

Coccospheres very variable in shape; may possess exothecal coccoliths but no differentiated circum-flagellar endoetheal coccoliths. Endothecal caneoliths have a high wall with an undulated top, and a narrow proximal flange; the central area has 30 to 36 laths which become narrower towards the centre of the coccolith and a very characteristic elongate keel-like central structure which connects the laths on the distal face; the proximal side of the caneoliths has two conspicuous straight and low central longitudinal ridges, overlapping along one third of their length (Fig. 44D) and connecting the laths; the laths from the ends of the caneolith join one another, forming ear-like structures. Exothecal coccoliths are thin, subcircular, disc-like coccoliths with serrated edges; they are composed of three parts: a wide rim of wide elements, a radial cycle of narrow elements and a solid central part which appears to consist of two plates.

This species closely resembles *Syracosphaera tumularis*; it differs from the latter in having caneoliths with narrowly elliptical shape instead of a normally elliptical outline, in possessing centrally narrowing laths instead of straight laths and in having a high keel-like central structure which is not present in *S. tumularis*.

The coccospheres consist of 80 to 120 caneoliths, sometimes with a few exothecal coccoliths.

**Dimensions.** Coccosphere length 20-40 µm; body caneolith length (3.1-) 3.4-3.8 (-4.0) µm; exothecal coccolith diameter ca. 3.5 µm.

*Syracosphaera tumularis* Sánchez-Suárez, 1990

(Fig. 45)

*Syracosphaera tumularis* Sánchez-Suárez, 1990, p. 157-158, Fig. 4A-F.

*Syracosphaera* sp. (Kampner) Borsetti et Cati 1972, p. 402, plate 47 fig. 3.

*Pontosphaera* cf. *variabilis* Halldal et Markali in Reid, 1980, p. 156, plate 3 figs. 1-3.

*Syracosphaera* sp. Unidentified coccolithophorid A in Heimdal and Gaarder 1981, pp. 64-67, plate 10 fig. 51 a and b.

*Syracosphaera* sp. Hallegraef 1984, p. 239, fig.44.

*Syracosphaera lamina* auct. non Lecal-Schlauder in Nishida 1979, pl. 8, fig. 3; in Winter and Siesser 1994, p. 137, fig. 114 (phot. S. Nishida).

*Syracosphaera* sp. type C Kleijne 1993, p. 242, plate 5 figs.11-12.

*Syracosphaera* sp. 2, Giraudeau and Bailey, 1995, Plate 5, fig. 7.

*Syracosphaera tumularis* Sánchez-Suárez, in Cros, 2000, p. 46, Plate 2, fig. 2.

Coccosphere dithecate (Cros, 2000) with monomorphic endothecal caneoliths. The caneoliths have a high and thin wall and a central area with 33 to 37 straight laths that connect the wall with the central structure, which is an elongated mound constructed by irregular transverse elements (some of these elements are a narrow continuation of the laths). The exothecal coccoliths are broad, thin, subcircular and lamina-like with a central structure consisting of two plates resembling that of *S. nodosa*. The caneoliths of this species differ from those of *S. lamina* in having a relatively low, more or less complex central structure, instead of possessing an elongated conspicuous keel-like central structure, in having a lower length/width ratio, and a thinner wall; in addition the exothecal coccoliths are more rounded and have more complex polygonal central plates.

This species was described by Sánchez-Suárez (1990) as having dimorphic endothecal coccoliths
and with dithecatism not observed, but in the comments he points out that the differentiated circum-flagellar caneoliths have only been observed under light microscopy; Kleijne (1993) did not observe either dithecism or dimorphic coccoliths. From the observations in the present study, it can be concluded that this species is dithecate, with only one kind of endothecal coccolith.

The coccosphe res studied consisted of 36, 48, 50 and 58 body caneoliths and indeterminate numbers of exothecal caneoliths (more than 10-15 in several studied coccosphe res; they are very loosely attached to the coccosphere and in consequence they are easily lost).

**Dimensions.** Coccosphe re long axis 10-20 µm; body caneolith length (3.3-) 3.5-3.8 (-4.2) µm; exothecal coccolith diameter (3.8-) 4.0-4.4 (-4.6) µm.

*Syracosphaera* sp. type L of Kleijne 1993.

Figs. 43C, D.

Syracosphaera sp. type L, Kleijne 1993, p. 245 pl. 5 fig. 1-2; Cros, 2000, p. 46, Plate 2, figs. 5 and 7.

Dithecate coccosphe re with monomorphic endothecal caneoliths; these coccosphe res are usually spherical. The body caneoliths have a smooth wall with neither mid-wall nor distal flanges; the central area shows a well developed external connecting ring, 24 to 30 laths of irregular width and a low broad irregularly formed central structure. The thin, sub-circular exothecal coccoliths are characteristically smaller than the endothecal caneoliths.

The caneoliths of *Syracosphaera* sp. type L of Kleijne differ from the caneoliths of *S. nodosa* in having straight rather than irregular-undulating walls and in having irregular compared with regular laths, moreover the central mound is lower and more irregularly shaped; the exothecal coccoliths of both species are easily differentiated, since *Syracosphaera* sp. type L has no distinguishable radial laths.

In the studied coccosphe res 36, 40, 42(2), 46, 66 and 68 body caneoliths were estimated to be present and from 42 to 68 exothecal coccoliths (very loosely attached to the coccosphe re and hence easily lost).

**Dimensions.** Coccosphe re long axis 6-9 µm; body caneolith length (2.0-) 2.1-2.2 (-2.4) µm; exothecal coccolith diameter (1.7-) 1.8-1.9 (-2) µm.

*Species with wheel-like exothecal coccoliths*

Exothecal coccoliths are planoliths with a ring of conspicuous radial laths. The endotheca has differentiated circum-flagellar caneoliths with robust spines.

*Syracosphaera nodosa* Kamptner, 1941

(Fig. 46)

*Syracosphaera nodosa* Kamptner, 1941, pp. 84-85, 104, pl. 7 figs. 73-76; Nishida, 1979, plate 7, fig. 3; Winter and Siesser 1994, p.138 fig. 117 A-B (phot. Nishida and Jordan); Cros, 2000, p. 46, Plate 2, fig. 3.

Coccosphe re dithecate with dimorphic endothecal caneoliths. Body caneoliths, without either distal or mid-wall flanges, have characteristic vertical ribs on the outer surface of the wall; the central area is formed by a solid external connecting ring and the laths which meet in a connecting elongated central structure. The circum-flagellar caneoliths possess a strong spine. Exothecal coccoliths are characteristic wheel-like coccoliths composed of three different parts: an angular central part formed of two rectangular plates which are easily distinguished in distal view, a broad rim composed of similar elements and a radial cycle of laths (from 19 to 23) which overlap on the distal face of the rim.

A group of coccoliths which appeared to be a mixed collapsed coccosphe re of *S. nodosa* with *Hel ladosphaera cornifera* was found (Fig. 113D).

The coccosphe res consist of 24 to 44 body caneoliths (8 specimens); 4 to 6 circum-flagellar spine-bearing caneoliths; the number of exothecal wheel-like coccoliths ranges from (24-) 38-42 (-54).

**Dimensions.** Coccosphe re long axis (6.0-) 6.5-7.5 (-9.5) µm; body caneolith length (1.7-) 2.3-2.5 (-2.6) µm; circum-flagellar caneolith spine height 1.3 µm; exothecal coccolith diameter 2.5 µm.

*Syracosphaera* sp. aff. *S. nodosa* Plate 22, figs. 5-7

*Syracosphaera* cf. *nodosa*, Heimdal and Gaarder 1981, pl. 9, fig. 45. *Syracosphaera nodosa* Kamptner in Sánchez-Suárez, 1992, p. 117, fig. 3D-E. *Syracosphaera* sp. aff. *S. nodosa* in Cros, 2000, p. 46, Plate 2, fig. 4.

Dithecate coccosphe re with dimorphic endothecal caneoliths. Body caneoliths with a distally flared wall which is wavy ended and has vertical ribs on the outer surface; they possess a well developed proximal flange, but neither distal nor mid-wall flanges; the central area has 24 to 30 slender radial laths and an elongated mound as a central connecting structure. The circum-flagellar caneoliths possess a slender process. Exothecal wheel-like coccoliths resemble those of *S. nodosa*.  

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38 L. CROS and J.-M. FORTUÑO
Syracosphaera sp. aff. S. nodosa strongly resembles S. nodosa. Caneoliths of Syracosphaera sp. resemble caneoliths of S. nodosa in having a distally widening wall with characteristic vertical ribs on the outer surface and in having an elongated central mound, but differ in having a higher wall (0.6 µm high compared to 0.3 µm in S. nodosa), in connecting the lamellar elements of the central area directly to the wall instead of ending at the external connecting ring and in having more numerous and thinner laths. The spine of the circum-flagellar caneoliths is thinner and shorter than in S. nodosa. Exothecal wheel-like coccoliths have the same structure as those of S. nodosa, but are bigger, with a wider rim and central area and in having more numerous radial laths (24-29 compared to 19-23 in S. nodosa); moreover the rim of these exothecal coccoliths characteristically has narrow slits between the elements, which are not seen in S. nodosa. In the one specimen where it was possible to count, 28 body caneoliths and only 5 spine-bearing circum-flagellar caneoliths were present; more than 50 exothecal coccoliths can be present.

Dimensions. Coccosphere major axis 8-11 µm; body caneolith length (2.4-) 2.7-2.9 (-3.2) µm, rim height ca. 0.6 µm; circum-flagellar caneolith spine height ca. 1µm; exothecal coccolith diameter (3.0-) 3.2-3.3 (-3.5) µm.

Syracosphaera species having transitional exothecal coccoliths

Species with walled wheel-like exothecal coccoliths

The exothecal coccoliths appear as transitional forms between the wheel-like planoliths and the inverted muroliths. The endotheca has body caneoliths with proximal, mid-wall and distal flanges, and has no differentiated apical caneoliths.

Syracosphaera rotula Okada et McIntyre, 1977 (Fig. 48)

Coccosphere dithecate; no differentiated circum-flagellar endothecal coccoliths observed. Endothecal caneoliths with proximal and distal flanges, a very thin wall and no central structure. Exothecal coccoliths circular with a rim with its end bent through the proximal side, an intermediate ring of around 25 sinistrally radiating long, flaring laths, and a central part composed of two plates. Two specimens recorded from winter samples (Hivern-99 cruise)

The exothecal coccoliths of Syracosphaera rotula resemble those of S. nodosa, differing mainly in having longer laths, which are not in the same plane as the central structure, and in having a narrower and bent rim. The endothecal coccoliths are, however, very different.

The sole collapsed coccosphere consists of around 44 caneoliths and 10 exothecal coccoliths.

Dimensions. Coccosphere diameter (collapsed specimens) ca. 5-6 µm; body caneolith length 1.2 -2.3 µm; exothecal caneolith diameter ca. 2.5 µm.

Syracosphaera species with vaulted exothecal coccoliths

Exothecal coccoliths appear as inverted muroliths. The endotheca has body caneoliths with proximal, mid-wall and distal flanges, and presents differentiated apical caneoliths with bifurcated spines.

Syracosphaera histrica Kamptner, 1941 (Fig. 49)

Syracosphaera histrica Kamptner 1941 pp. 84, 104, Plate 6 Figs 65-68; Borsetti and Cati, 1972, p. 400, Plate 44 Figs 3a-b; Gaarder and Heimdal, 1977, p. 55-56, Plate 2; Nishida, 1979, Pl. 7. Fig. 1; Reid, 1980, p. 160, 162, Plate 5, Figs 7-8; Delgado and Fortuño, 1991, pl. 81 figs. b-c; Kleijne, 1993, p. 238, Plate 4 Fig. 7; Winter and Siesser, 1994, p. 136 fig. 113 (phot. M. Knappertsbusch); Cros, 2000, p. 45, Plate 1, fig. 2.

Coccosphere dithecate with dimorphic endothecal caneoliths. The body caneoliths have a rim with a low wall, narrow distal and proximal flanges and a beaded mid-wall flange; central area with a slightly convex floor consisting of about 30 laths directed and fused towards the centre where they form a short irregularly tipped spine. The circum-flagellar caneoliths have a long central spine with bifurcate endings. The exothecal coccoliths are very conspicuous vaulted coccoliths, with a narrow rim and an irregularly featured, slightly elevated central area which resembles a branching root system.

A collapsed coccosphere of Calyptrolithophora papillifera, surrounded by several coccoliths of S. histrica (Fig. 112B), was found, but it was not considered a conclusive combination coccosphere (Cros et al., 2000b)

Coccospheres consist of (35-) 40-50 (-80) body caneoliths; ca. 5 spine-bearing circum-flagellar
caneolits; (4-) 24-44 (-68) exothecal vaulted coccoliths.

**Dimensions.** Coccosphere diameter (9-) 10-12 (-14) µm; body caneolith length (1.9-) 2.3-2.7 (-3.3) µm; circum-flagellar caneolith spine length ca. 1.4 µm; exothecal caneolith length (2.1-) 3.0-3.2 (-3.6) µm.

*Syracosphaera pulchra* Lohmann, 1902 (Figs. 50 and 51)

Combination coccospheres of *Syracosphaera pulchra* with *Calyptrisphaera oblonga* Lohmann have been found and now it is recognized that *C. oblonga* is the holococcolithophore phase of *S. pulchra* (Cros et al. 2000b; and also Lohmann, 1902; Kamptner, 1941; and Lecal-Schlauder, 1961); Figs. 51A, B show the combination coccospheres found in the studied samples.

Geisen et al. (2000) presented a combination coccosphere with heterococcoliths of *S. pulchra* and holococcoliths of *Daktylethra pirus* (Kamptner) Norris, and they suggested a cryptic speciation, not clearly recognizable from the heterococcolithophore morphology, as a possible explanation for these very different associated holococcoliths.

**Heterococcolithophore phase (Fig. 50)**

*Syracosphaera pulchra* Lohmann, 1902, p.134, pl. 4, figs. 33, 36, 36a-b, 37; Kamptner, 1941, pp. 85-86, 105-106, pl. 7 figs. 77-78, pl. 8, figs. 79-84; Lecal-Schlauder, 1951, p. 286, fig. 22 pl. 9 figs. 1-5, 8-9; Loeblich and Tappan, 1963, p. 193; Okada and McIntyre, 1977, p. 27, pl. 10 figs. 11-12; Gaarder and Heimdal, 1980, p. 35 pl. 1 figs. 1-8; Borsetti and Cati, 1972, p. 402, pl. 46 figs. 2 a-b; Nishi-da, 1979, pl. 6 fig. 3; Hallegraeff, 1984, p. 239, fig. 46 a-b; Inouye and Pienaar, 1988, pp. 207-216 figs. 1-15; Delgado and Fortuño, 1991, p.21, pl. 79 fig. d, pl. 80 figs. a, b, c, d, pl. 81 fig. a; Heimdal, 1993, pp. 227-228, pl. 7 figs. a-b; Kleijne, 1993, p. 241, pl. 5 fig. 10; Winter and Siessser, 1994, p. 139, fig. 122 (phot. J. Alcobe). *Syracorhabdus pulchra* (Lohmann) Lecal, 1965a, pp. 257-258, pl. 4 figs. 11-13; Lecal, 1967, pp. 315-316, text-fig. 11, fig. 15.

Coccosphere dithecate with dimorphic endothe-cal caneoliths. The rim of body caneolits has a cor-rugated wall and three flanges, the distal one also being corrugated; the central area is filled by numerous narrow and short laths which fuse where they join, forming a flat surface with two circles of thinner laths alternating with solid parts. Circum-flagellar caneoliths have a thick spine forked at the end. The vaulted exothecal caneoliths have a central depression in the shape of an inverted cone, which is sometimes flattened laterally.

*S. pulchra* is the best known of the *Syra-cosphaera* species, possibly due to its relatively large size. The classical description was given by Lohmann, 1902, and the species was selected as type of the genus by Loeblich and Tappan (1963). Kamptner (1941, pl. 8, figs. 82-84) depicted *S. pulchra* cells with a double layer of caneoliths, a feature which he was the first to record (1939, p. 120). Gaarder and Heimdal (1977) showed that the proximal caneoliths are formed on a radially striped organic base-plate scale. A detailed study was provided by Inouye and Pienaar (1988) based on the examination under light and electron microscopes of cultured specimens.

Sediments as well as two samples of Mediterra-nean water contained some flower-shaped caneoliths with an extended wing or petal-like rim which seem related to *S. pulchra*, possibly representing malformed specimens of caneoliths of this species (Fig. 50B); such kind of *S. pulchra* caneoliths were previously observed by J.R Young in culture samples (personal communication).

The coccosphere consists of (12-) 26-36 (-56) body caneoliths (17 specimens); 2 to 6 (usually around 4) spine-bearing circum-flagellar caneoliths; and (1-) 10-20 (-38) exothecal caneoliths.

**Dimensions.** Coccosphere long axis (15-) 17-20 (-25) µm; body caneolith length (5.1-) 5.2-5.6 (-6.1) µm; circum-flagellar caneolith spine length 2.5-3.5 µm; exothecal caneolith length (4.7-) 5.2-5.8 (-6.7) µm.

**Holococcolithophore phase, formerly *Calyptrisphaera oblonga* Lohmann, 1902.** (Figs. 51C, D)

*Calyptrisphaera oblonga* Lohmann, 1902, p. 135, pl. 5, figs. 43-46; Halldal and Markali, 1955, p. 8, pl. 1; Heimdal and Gaarder, 1980, p. 3, pl. 1, figs. 4, 5; Reid, 1980, p. 164, pl. 6, figs. 9-10, pl. 7 fig. 1; Kleijne, 1991, p. 21, pl. 3, figs. 3-4.

The calyptroliths consist of a proximal rim, which is one crystallite thick, and a high cap-shaped structure with rather straight sides and slightly convex distal part. The coccoliths around the flagellar area are higher than the others and usually possess a small papilla.

Coccospheres possess from 60 to 178 caneoliths (6 specimens).

**Dimensions.** Coccosphere major axis 10-20 µm; caneolith length (1.8-) 2.2-2.5 (-2.8) µm.

**Syracosphaera species having caneoliths (muroliths) as exothecal caneoliths**

*Species having elliptical caneoliths with flanges as exothecal caneoliths*

The endotheca has body caneoliths with proximal, mid-wall and distal flanges, and presents spine-
bearing circum-flagellar caneoliths with robust spines.

**Syracosphaera** cf. *dilatata* Jordan, Kleijne et Heimdal, 1993 (Fig. 52)

*Caneosphaera halldalii* f. *dilatata* Heimdal, in Heimdal and Gaarder, 1981, p. 44, pl. 2, fig. 9a-b.

**Syracosphaera halldalii** f. *dilatata* (Heimdal, in Heimdal and Gaarder, 1981) Jordan et Young, 1990; Kleijne 1993 p. 238, pl. 4 fig. 10.

**Syracosphaera dilatata** Jordan, Kleijne et Heimdal, 1993, pp. 18, 20; Jordan and Green, 1994, pp. 156, 160, 161.

**Syracosphaera** cf. *S. dilatata* Jordan Kleijne et Heimdal, 1993; in Cros, 2000, Plate 6, figs. 1 and 2. Coccosphere considered dithecate (Cros, 2000) with dimorphic endothecal caneoliths. The coccosphere has from 35 to 65 body caneoliths, around 5 circumflagellar spine-bearing caneoliths and from 12 to 30 (or may be more) exothecal caneoliths. The body caneoliths have a relatively narrow distal flange that expands obliquely outwards and has a corrugated surface with a radially ribbed appearance, with regular undulate endings along the rim; the outer part of the wall has a row of beads, not previously recorded, which can form a sort of mid-wall flange; the central area is constituted of 19 to 26 laths and has an elongate mound as a connecting central structure. The circum-flagellar caneoliths have a beaded row, mentioned before by other authors (Heimdal and Gaarder, 1981; Hallegraef, 1984), and a robust process that ends in four small peaks. The exothecal coccoliths are caneoliths very similar to the body coccoliths, but larger, with higher fragile walls that have an almost imperceptible external row of beads positioned where the flared distal flange starts; the distal flange is radially ribbed and appears fragile; the central area consists of 20-30 radially placed laths fused along a central line. These exothecal caneoliths resemble the coccoliths reported by Heimdal and Gaarder (1981) pl. 2 fig. 9 as *Caneosphaera halldalii* f. *dilatata*.

The exothecal caneoliths differ from the endothecal coccoliths in being larger but thinner, in having higher, more fragile walls with almost imperceptible beaded mid-wall flanges (compared with shorter and thicker walls with clear beaded mid-wall flanges) and in having a smaller central structure. The fragility of these exothecal caneoliths sometimes results in the wall and distal flange splitting off.

The *Syracosphaera* described here differs from the last reported *Caneosphaera halldalii* f. *dilatata* Heimdal by having stronger and slightly smaller body coccoliths with more marked nodules on their outside wall. The circumflagellar caneoliths have the same dimensions and show similar nodules on the external side of the wall as the specimens recorded by Heimdal and Gaarder (1981) and Hallegraef (1984). The similarity between the exothecal caneoliths of this *Syracosphaera* and the caneoliths illustrated in Heimdal and Gaarder (1981) pl. 2 fig. 9 as *Caneosphaera halldalii* f. *dilatata*, suggests that the coccoliths shown in Heimdal and Gaarder (1981) might be exothecal coccoliths of this species or that the present studied specimens might be a different variety of the *S. dilatata* described and figured by Heimdal and Gaarder (1981).

Heimdal and Gaarder (1981) described this species as a variety of *Caneosphaera halldalii* f. *halldalii* Heimdal; Jordan and Young (1990) proposed that this species of *Caneosphaera* be transferred back to *Syracosphaera* as the reliability of the *Caneosphaera* generic description became doubtful (*C. molischii* possesses exothecal or deviating coccoliths and *C. halldalii* f. *dilatata* possesses circumflagellar coccoliths with bead-like knobs i.e. a kind of mid-wall flange). Finally, Jordan et al. (1993) elevated *S. dilatata* to species level, finding it significantly different from the type *S. halldalii* f. *halldalii* and in Jordan and Green (1994) this species is definitively validated as *S. dilatata* by reference to the published description and holotype negatives of Heimdal and Gaarder (1981). The recognition of dithecatism by Cros (2000) in this species strongly supports its separation from *S. halldalii*.

**Dimensions.** Coccosphere long axis (9-) (10-12) (-14) µm; body caneoliths length (2-) 2.3-2.5 (-2.7) µm, width 1.3-1.8 µm; circum-flagellar caneoliths diameter 1.5-2µm, spine length 1.5-2 µm; exothecal caneoliths length (2.3-) 2.7-2.9 (-3.1) µm, width 1.7-1.8 µm.

**Syracosphaera** sp. type D of Kleijne 1993. Fig. 53.

*Syracosphaera* sp. type D, Kleijne 1993, p.242, pl.6, figs.7-8; Riaux-Gobin et al., 1995, pl. 3 fig. 8.

*Caneosphaera exigua* auct. non Okada et McIntyre, Heimdal and Gaarder 1981, p. 60. pl. 8 figs. 40-41; Sánchez-Suárez 1992, p. 115-117, Figs. A-C.

Coccosphere dithecate (Cros, 2000) with dimorphic endothecal caneoliths. The body caneoliths have a proximal, a mid-wall, and a distal flange; the distal flange expands obliquely outwards, and has two concentric kinds of ribs, the inner wider than the outer (a feature that gives the impression that the distal flange bears two rows of nodules with the
inner ones thicker and less numerous); the central area has 20 to 30 laths and an elongate convex central structure made of sub-vertical elements. The circum-flagellar caneoliths, with beaded mid-wall flanges, have a robust square-shaped process tipped by four small rounded nodes. Exothecal coccoliths are caneoliths very similar to the ordinary ones; they are larger but seem more fragile than the body caneoliths, have higher walls, lack a well developed external mid-wall flange but have a wider distal flange without the thick inner row of nodules that is noticeable in body caneoliths.

This species closely resembles *S. cf. dilatata* (see above) in general shape, in the morphology of circum-flagellar caneoliths and in the structure of exothecal caneoliths. The body caneoliths have a fold-like rather than a beaded mid-wall flange, however, as well as the presence of nodules on the inner part of the distal flange; moreover the exothecal caneoliths have a wider distal flange than in *S. cf. dilatata*.

Figs. 113A, B represent two associations of *Syrracosphaera* sp. type D coccoliths with *Homozygosphaera arethusa* holococcoliths; but these associations could be a random product, as discussed in Cros et al. (2000).

Coccospheres consist of 34(2), 36, 44(3) 54, 56 and 58 body coccoliths; 4 to 6 spine-bearing circum-flagellar caneoliths; 1 to 37 exothecal caneoliths (which are very loosely attached to the coccosphere and hence are easily lost).

**Dimensions.** Coccosphere long axis (8-) 9-11 (-13) µm; body caneolith length (2.1-) 2.3-2.6 (-3.1) µm; circum-flagellar caneolith spine length 1.5-1.9 µm; exothecal caneolith length (3.1-) 3.4-3.6 (-3.8) µm.

**Species having elliptical caneoliths, with nodes, as exothecal coccoliths**

The endotheca has body caneoliths with neither distal nor mid-wall flanges, and presents spine-bearing caneoliths with bi-ended long spines around the flagellar area.

*Syrracosphaera noroitica* Knappertsbusch, 1993, orthog. emend. Jordan et Green, 1994 (Fig. 54)

*Syracosphaera* sp. type E of Kleijne (1993) (Fig. 55)

Coccosphere dithecate; endotheca presents polymorphic caneoliths. The body caneoliths have neither distal nor mid-wall flanges; show smooth and thick walls and the laths extend up the internal sides of the wall. These caneoliths show a gradually polar varimorphism; the most apical body caneoliths have higher and thicker walls and central processes, characters which diminish toward the antapical pole where caneoliths have low and thin walls and no central process; the smallest caneoliths, at the antapical pole, have lath extensions protruding as thorns above the rim of the wall (Fig. 54B). These body caneoliths thus appear in three basic morphologies: a) near the apical pole they are robust with a thick and blunt central spine and show varimorphism; b) near the antapical pole they lack the central spine; c) at the antapical pole there are some small caneoliths with two lateral spines which are prolongations of the central laths. The circum-flagellar caneoliths possess a long central spine, forked at the end. The exothecal coccoliths are true elliptical caneoliths (Cros, 2000) with slender laths in the central area that extend marginally and seem to protrude out the wall forming nodes; these nodes form a beaded proximal flange, similar to *S. prolongata* exothecal coccoliths. The exothecal caneoliths have a thinner central protrusion and thinner walls than the similar-sized endothecal ones and have a cobweb pattern in the central area of the proximal side. The central spines of the body and exothecal caneoliths are constructed by characteristic vertical elements.

The number of caneoliths in the coccosphere is between 46 and 68 body caneoliths (4 specimens); around 6 circum-flagellar caneoliths; and from 17 to 30 exothecal caneoliths.

**Dimensions.** Coccospheres long axis (8-) 9-11 (-13) µm; varimorphic body caneolith length (1.3-) 1.8-2.2 (-2.5) µm, with 20-29 laths; circum-flagellar caneolith spine length ca. 2 µm; exothecal caneolith length 2.0-2.5 µm, with 27-29 laths.

*Syrracosphaera* sp. type G of Kleijne 1993 (Fig. 55)

*Coccosphere* dithecate (Cros 2000); the endotheca has differentiated circum-flagellar caneoliths and varimorphic body caneoliths. Body coccoliths have a low wall with a characteristically incised upper margin and neither distal nor mid-wall flanges; the central area possesses 16 to 27 radial laths and a nodular, blunt central structure consisting of vertical elements; the central structure diminishes from the apical to antapical zone, being absent in the most
antapical caneoliths. Circum-flagellar caneoliths have a long spine, forked at the tip. The exothecal coccoliths are caneoliths with a higher wall than the body caneoliths, the distal end of which is serrated, and have laths (25 to 28 radial laths) which protrude out of the wall forming small knobs around the coccolith, like a proximal flange.

*Syracosphaera* sp. type G is closely related to *S. noroitica* in both endothecal and exothecal coccolith structure, but differs from the latter in having smaller coccoliths with a thinner wall, fewer laths and a thicker nodular central protrusion. It closely resembles *S. florida* Sánchez-Suárez, 1990 and the Unidentified heterococcolithophorid “F”, Heimdal and Gaarder 1981, p. 67, pl. 13, fig. 65, but the central spines of *S. florida* are thinner and those of “F” are thicker and extended along the long axis; moreover the wall of *Syracosphaera* sp. type G is very low and distally is characterized different from that of the other related species.

The studied coccospheres were collapsed, consisting of more than 35 to around 60 body caneoliths; around 6 spine-bearing circum-flagellar caneoliths; and more than 4 exothecal caneoliths.

**Dimensions.** Body caneolith length (1.1-) 1.6-1.8 (-2.1) µm; circum-flagellar caneolith spine length 1.2-1.4 µm; exothecal caneolith length ca. 1.8 µm.

*Species having sub-circular caneoliths, with nodes, as exothecal caneoliths*

The endotheca has body caneoliths with proximal, mid-wall, and distal flanges, and presents differentiated apical caneoliths with bifurcated spines.

**Syracosphaera prolongata** Gran ex Lohmann sensu Throndsen, 1972 (Fig. 56)

*Syracosphaera prolongata* Gran ex Lohmann, 1913, in Throndsen, 1913, in Throndsen, 1972, pp. 57-59, figs. 22-28; Okada and McIntyre 1977, p. 26, pl. 7 figs. 2-3; Kleijne 1993, p. 240-241, pl. 5 fig. 8; *Syracosphaera pirus* auct. non Halidal et Markali, in Gaarder and Heimdal 1977, pp. 56-58, pl. 3; in Winter and Siesser 1994 p. 139 fig. 120 (phot. from Winter).

The coccosphere is dithecate with dimorphic endothecal caneoliths; it can be elongated (Throndsen, 1972, figs. 22-25) or can be from spherical to obpyriform (Fig. 56A). The body caneoliths have a low wall with three smooth flanges and a small rounded central node. The circum-flagellar caneoliths have a long spine, forked at the end. The exothecal caneoliths are sub-circular caneoliths; wider gaps are present between the laths than on the body caneoliths and near the centre the laths seem to join to form a hollow cone, whereas around the internal margin of the rim the laths protrude out of the wall forming a beaded proximal flange; the low wall has a very narrow distal flange. Both endothecal and exothecal caneoliths often show a characteristic thread-like pattern across the laths around the coccolith (Figs. 56B, D).

This species is structurally similar to *S. pirus*. According to Kleijne (1993) *S. prolongata* differs from *S. pirus* in having caneoliths with a smaller nodular protrusion and a larger number of radial laths in the central area, while also its exothecal caneoliths have a larger number of radial laths in the central area.

The studied coccospheres consist of (42-) 50-66 (-94) body caneoliths (7 specimens); 3 to 8 circum-flagellar caneoliths with spine; and from 14 to 24 exothecal caneoliths (the exothecal caneoliths are very loosely attached to the coccosphere and so are easily lost).

**Dimensions.** Coccosphere long axis ca. 10 µm (but in the literature it is described as reaching 70 µm: Throndsen, 1972, Okada and McIntyre 1977); body caneolith length (1.7-) 2.0-2.4 (-2.6) µm, with 25 to 32 laths; circum-flagellar caneolith spine length ca. 1.5 µm; exothecal caneolith diameter ca. 2.4 µm, with 28 to 36 laths.

*Syracosphaera prolongata* Gran ex Lohmann, 1913 sensu Heimdal and Gaarder, 1981 (Figs. 57A, B)

*Syracosphaera prolongata* Gran ex Lohmann, Heimdal and Gaarder, 1981, p. 60-62, pl. 10 figs. 48-50; in Winter and Siesser, 1994, p. 139 fig. 121 (Phot. from Knappertsbusch); Giraud and Bailey, 1995, Plate 5, figs. 2-3.

The coccosphere is dithecate with dimorphic endothecal caneoliths; it can be elongated, slender cone-shaped or more or less pear-shaped. Body caneoliths have a thin wall with three smooth flanges; the central area has from 30 to 36 slightly vertically curved laths, resembling that of *S. anthos* caneoliths; the laths connect in the centre to form a low and twisted mound-like central structure. The circum-flagellar caneoliths have a long spine forked at the end. The exothecal caneoliths are circular caneoliths with 32-42 separate laths which join near the centre to form a hollow twisted mound; these laths protrude out of the wall as small nodes forming a beaded proximal flange; the low wall appears to have a very narrow distal flange; in the central area, some of these coccoliths have the remains of a
thread-like structure crossing the laths around the coccolith. The exothecal caneoliths are bigger, but appear more fragile than the endothecal coccoliths.

The most characteristic feature of this species is the twisted central mound, present in body coccoliths as well as exothecal coccoliths; it differs from *S. prolongata sensu* Throndsen mainly in having larger caneoliths with this characteristic twisted mound central structure as opposed to a small rounded nodule.

The coccosphere consists of (66-) 102-110 (-120) body caneoliths (10 specimens); 2 to 8 spine-bearing circum-flagellar caneoliths (the most frequent number is probably 8, but it is often difficult to see all of them); and from 2 to 27 exothecal caneoliths (very loosely attached to the coccosphere and hence easily lost).

**Dimensions.** Coccosphere long axis (13-) 20-35 (-43) µm; body caneolith length (1.9-) 2.4-2.7 (-3.3) µm; circum-flagellar caneolith spine length ca. 2µm; exothecal caneolith diameter (2.3-) 2.7-3.0 (-3.8) µm.

**Syracosphaera species without described exothecal coccoliths**

*Syracosphaera ampliora* Okada et McIntyre, 1977

Figs. 57C, D.

*Syracosphaera ampliora* aff. *ossa* Lecal Borsetti et Catì, 1972, p. 401, pl. 45, fig. 1a-b; Gaarder and Heimdal, 1977, pl. 8, fig. 51.

*Syracosphaera ampliora* Okada et McIntyre, 1977, p. 19-20, pl. 7, fig. 9-10.

Neither dithecatism nor differentiated circum-flagellar coccoliths recognized. The caneoliths have a wide distal flange and a central area that consists of a large central structure and 18 to 30 centrally widened laths.

The special characteristic of this species is the medial expansion of the laths. It differs from *S. ossa* in not having spine-bearing caneoliths around the flagellar area, in possessing more regularly shaped caneoliths and in not having a smooth distal flange as in *S. ossa*.

Coccosphere with around 40 caneoliths (38 to 40 in three specimens studied).

**Dimensions.** Coccosphere long axis 6.5-8.5 µm; caneolith length (1.8-) 2.4-2.7 (-3) µm, width (1.5-) 1.8-2.0 (-2.2) µm.

*Syracosphaera halldalii* Gaarder ex Jordan et Green, 1994 (Fig. 58)

*Caneosphaera protudens* Okada et McIntyre, 1977, p. 23, 26, plate 10, figs. 1-2.

*Caneosphaera halldalii* Gaarder f. *halldalii* in Kleijne 1993 p. 237-238, plate 4 figs. 4-6; Winter and Siessers, 1994, p. 136 fig. 111 (phot. A. Winter/P. Friedinger)

*Caneosphaera halldalii* (Gaarder) Gaarder in Gaarder and Heimdal 1977, p. 64, 66, plate 6 figs. 36-39.

*Caneosphaera protudens* Okada et McIntyre, 1977, pp. 26-27, plate 10 fig. 3.

*Caneosphaera halldalii* Gaarder ex Jordan et Green, 1994, p. 160.

Coccosphere monothecate with dimorphic coccoliths. Body caneoliths have a high and almost vertical wall with two flanges, the distal flange usually being wide and smooth; the central area has a longitudinal and very narrow central structure sometimes forming a low ridge. Circum-flagellar caneoliths very few in number, with a central spine, square in section.

Three different morphologies can be distinguished in *S. halldalii*: a) the “ordinary form” (Plate 4 Fig. 4 in Kleijne, 1993) the coccoliths of which have a flat distal flange without protrusions, b) the “tooth-like form” (Figs. 58A, B) with a very wide and smooth distal flange that has tooth-like protrusions, and c) the “finger-like form” (Figs. 58C, D) with a relatively narrow distal shield, the surface of which is slightly ribbed by the edges of elements; this latter form is the former *Syracosphaera protudens* described by Okada and McIntyre (1977). In our opinion the “ordinary form” and the “tooth-like form” may be the same species (see in Fig. 58A a “tooth-like form” specimen having some coccoliths resembling those of the “ordinary form” figured in Gaarder and Heimdal, 1977, fig. 36), whereas the “finger-like form” (former *S. protudens*) is a different variety or even a different species, as Okada and McIntyre (1977) described. Further observations are required to clarify this taxonomic problem.

The classical description of a complete caneolith, given by Halldal and Markali (1954b), was based on thorough studies under the transmission electron microscope of a specimen identified as *Syracosphaera mediterranea* Lohmann. This name was, however, already employed for another species (see *Coronosphaera mediterranea*). As a consequence, Gaarder and Hasle (1971) proposed the new name of *S. halldalii* Gaarder for Halldal and Markali’s specimen. Further studies on this species were carried out by Gaarder and Heimdal (1977) leading to a re-identification of Halldal and Markali’s coccoliths with the new generic name of *Caneosphaera*. Jordan and Green (1994) validated the name of *Syracosphaera halldalii* with a Latin
diagnosis and redescribed the species on the basis of the observations made by Halldal and Markali (1954b) and Gaarder and Heimdal (1977) which included the $S$. protudens described by Okada and McIntyre (1977).

**Dimensions.** “Tooth-like form” coccosphere 45 to 75 body caneoliths, around 6 apical spine-bearing caneoliths, coccosphere diameter 9-12 µm, body caneolith length (2-) 2.5-3.0 (3.2) µm.; “finger-like form” coccosphere 50 to 120 body caneoliths, coccosphere diameter 9-12 µm, body caneolith length (1.6-) 2-2.5 (-3) µm.

**Order Prinsiales Young et Bown, 1997**

Monomorphic coccospheres with placoliths that usually have grill-like structures in the central area and straight and non-imbricate shield elements. Among the representatives of this order, *Emiliania huxleyi* and *Gephyrocapsa oceanica* are known to alternate with non coccolith-bearing phases.

**Family Noëlaerhabdaceae Jerkovic, 1970 emend. Young et Bown, 1997b**

Placoliths of the *Reticulofenestra*-type (Young, 1989): proximal and distal shields, two tube element cycles with opposite senses of imbrication and usually a central area structure. The members of this family differ from other coccolith bearing species in that they lack haptonema and produce unusual long-chain lipids similar to those found in species of *Isochrysis* and *Chrysothila* (Marlowe et al., 1984; Jordan and Green, 1994), and in recent phylogenetic studies (Kawachi and Inouye, 1999; Fujiwara et al. 2001; Saez et al., in prep.) they appear to be related to *Isochrysis galbana* Parke emend. Green et Pienaar. Even authors who follow the classification of Parke and Green, in Parke and Dixon (1976) for the bulk of coccolithophores took this family out of the order Coccospherales, to place it in the order Isochrysidales (e.g. Kleijne, 1993; Jordan and Green, 1994).

**Genus Emiliania** Hay and Mohler in Hay et al., 1967

The placoliths have slits between all of the elements of the distal shield; these elements are T-shaped with interlocking ends at the margin.

**Emiliania huxleyi** (Lohmann, 1902) Hay and Mohler in Hay et al., 1967.

*Fig. 59.*

*Pontosphaera huxleyi* Lohmann, 1902, pp. 129-130, pl. 4, Figs 1-9, Pl. 6 fig. 69.

*Coccolithus huxleyi* (Lohmann) Kamptner (Kamptner, 1943, p. 43); McIntyre and Bé, 1967 pp. 568-569, pl. 5, Fig. D, Pl. 6.

*Emiliania huxleyi* (Lohmann, 1902) Hay and Mohler, in Hay et al., 1967, p. 447, pl. 10 - 11, figs. 1-2; Kleijne, 1993, p. 229, pl. 1, figs 10-11.

*Emiliania huxleyi* (Lohmann, 1902) Hay and Mohler type A, Young and Westbroek 1991, p. 21, pl. 1, figs. 1-12, pl. 2, figs. 1-3, 7-8, pl. 3, figs. 6-8.

*Emiliania huxleyi* (Lohmann, 1902) Hay and Mohler type B, Young and Westbroek 1991, p. 22, pl. 2, figs. 4-6, 9-10.

*Emiliania huxleyi* (Lohmann, 1902) Hay and Mohler type C, Young and Westbroek 1991, p. 22, pl. 3, figs. 1-5.

This species is the most ubiquitous and the most abundant of the coccolithophores.

Observations in cultures (Klaveness, 1972; Green et al., 1996) have elucidated a complex *E. huxleyi* life-cycle with a dominant phase that produces non-motile heterococcolith bearing cells (C - cells), which sometimes give rise to non-motile naked cells (N-cells), and an alternate phase that produces motile non-calcifying cells with organic body scales (S - cells).

This species can be covered by several layers of placoliths which may show a high diversity in structure. This diversity has lead to recognition of distinct morphotypes, referred to as Types A, B, and C (Young and Westbroek, 1991) and *E. huxleyi* var. *corona* Okada and McIntyre (1977). Indeed, types A, B, and C have been considered as distinct taxonomic varieties, being called respectively *E. huxleyi* (Lohmann) Hay et Mohler var. *huxleyi*, *E. huxleyi* var. *pujosae* (Verbeek) Young et Westbroek ex Medlin et Green, and *E. huxleyi* var. *kleijniae* Young et Westbroek ex Medlin et Green (Medlin et al., 1996). Not all authors accept and follow this nomenclature.

The most abundant morphotype in the samples in this study was clearly Type A (Figs. 59A, B). Type C coccospheres (Fig. 59C) were found less frequently, but type B was not definitively identified and *E. huxleyi* var. *corona* was not found. However, in the studied samples other types of *Emiliania huxleyi* coccospheres, not previously described as existing morphotypes, were abundant and easily recognizable. These included a type with a non-calciﬁed central area, with or even without an organic plate, a morphology related to type C, and an overcalciﬁed type with the inner tube elements growing into the central area (Fig. 59D), which was frequently observed in waters deeper than 40 m. At present, it
would be cautious not to separate these different *E. huxleyi* into morphotypes or varieties, and to delay any proposal of classification until a more complete study of this species in this area has been conducted.

Coccospheres consist of (9-) 14-20 (-50) coccoliths.

**Dimensions.** Coccosphere diameter (4.4-) 5-6 (9.5) μm; coccolith length (2.7-) 3.2-3.6 (-4.2) μm.

**Genus Gephyrocapsa** Kamptner, 1943

The placoliths have a reticulate grid covering the proximal side of the central area and a characteristic bridge formed of two diametrically opposite extensions of inner tube elements.

*Gephyrocapsa* is a complex genus with considerable interspecific variability. Some authors (Samtleben, 1980) use size and bridge angle to distinguish between species or to relate the characteristics with environmental conditions (Bollmann, 1997). Thus, the taxonomy at the species level is still in a state of flux. Well established species such as *G. huxleyi* McIntyre or *G. ornata* Heimdal may represent different morphotypes of the species *G. ericsonii* McIntyre and Bé (Kleijne, 1993). In the present study, *G. huxleyi* is considered as a synonym of *G. ericsonii* because transitional forms have been found between them, but *G. ornata*, due to its singular characteristics, is presented provisionally as a different species, until more work is carried out on this subject.

**Gephyrocapsa ericsonii** McIntyre et Bé, 1967 (Fig. 60)

*Gephyrocapsa ericsonii* McIntyre and Bé 1967, p. 571, pl. 10, pl. 12, fig. b; Borsetti et Cati, 1979, p. 158, pl. 14, fig. 1-2.

*Gephyrocapsa protohuxleyi* McIntyre, Winter et al. 1978, pp. 295-297, pl. 1.

*Gephyrocapsa aff. protohuxleyi* McIntyre, Borsetti et Cati, 1979, p. 158, pl. 14, fig. 4.

*Gephyrocapsa ericsonii* McIntyre and Bé / *G. ornata* Heimdal 1973, Kleijne, 1993, p. 230, pl. 2, figs. 1-2.

The placoliths are small (< 2.3 μm length) and have the bar at a low angle (around 15º) with the length (Samtleben, 1980).

*Gephyrocapsa ericsonii* is the second most abundant coccolithophore in NW Mediterranean waters after *Emiliania huxleyi*.

Considerable morphological variability was found in *G. ericsonii* and the specimens can be classified into three groups with more or less clear limits: *ericsonii* (without slits between distal shield elements, Fig. 60A), *protohuxleyi* (with slits between distal shield elements, Fig. 60B), and *protohuxleyi-\*  with thorn\*` (with well developed slits and also a slender thorn that grows from the placolith inner tube, Fig. 60D). These groups may be different species or morphological variants along a continuous gradient; the presence of intergrades between *protohuxleyi* and *protohuxleyi-\*  with thorn\*` (Fig. 60 C) may prove ecophenotypic rather than genotypic variation.

The type *protohuxleyi-\*  with thorn\*` was figured by Borsetti and Cati (1979) p. 158, pl. 14, fig. 4, and by Kleijne (1993) p. 230, pl. 2, fig. 2 (notice that these specimens were also from the Mediterranean Sea). Kleijne (1993) related this kind of *G. ericsonii* to *G. ornata* and Samtleben (1980) presented *G. ornata* as a species closely related with *G. ericsonii*, particularly with the *protohuxleyi* type.

Coccospheres possess between 12 and 18 (-26).

**Dimensions.** Type *ericsonii* coccosphere diameter 3.0-3.7 μm, coccolith length (1.4-) 1.6-1.7 (-1.9) μm; type *protohuxleyi* coccosphere diameter (3.0-) 3.7-4.2 (-4.7) μm, coccolith length (1.4-) 1.7-1.9 (-2.3) μm; type *protohuxleyi-with thorn* coccosphere diameter (3.2-) 3.5-4.0 (-5.0) μm, coccolith length (1.4-) 1.7-2.0 (-2.3) μm, spine 0.5 - 1 μm.

**Gephyrocapsa muellerae** Bréhéret, 1978 (Fig. 61A)

*Gephyrocapsa muellerae* Bréhéret, 1978, p. 448, pl. 2, figs. 3-4; Samtleben 1980, p. 106, pl. 14, figs. 6-8, pl. 15, figs. 1-4; Kleijne, 1993, p. 230, pl. 2 fig. 4.

The placoliths are larger than those of *G. ericsonii* and have the bar forming a higher angle with the long axis than in *G. ericsonii* (Samtleben, 1980). Coccospheres possess between 14 and 24 coccoliths (5 coccospheres).

**Dimensions.** Coccosphere diameter (5.3-) 7-8 (8.8) μm; coccolith length (3.1-) 3.5-3.7 (-3.9) μm.

**Gephyrocapsa oceanica** Kamptner, 1943 (Fig. 61B)

*Gephyrocapsa oceanica* Kamptner, in Okada and McIntyre 1977, pp. 10-11, pl. 3, figs. 3-9; Nishida, 1979, pl. 2, fig. 1; Kleijne, 1993, p. 230, pl. 2, fig. 5.

The placoliths are large and have the bar almost perpendicular to the long axis. Coccospheres consist of 9 to 14 coccoliths (5 coccospheres).

**Dimensions.** Coccosphere diameter (5.8-) 6-7 (-10) μm; coccolith length (3.4-) 4.2-5.0 (6.0) μm.
**Gephyrocapsa ornata** Heimdal 1973
(Fig. 61C)

*Gephyrocapsa ornata* Heimdal, 1973, pp. 71, 72 and 74, Figs. 1-5; Nishida, 1979, pl. 2, figs. 2 a, b.

The placoliths present a characteristic bridge constructed by two thin and expanded elements, and a conspicuous ring of spines around the central area.

Coccosphere consists of ca. 15 coccoliths (only one specimen has been studied)

**Dimensions.** Coccosphere diameter ca. 4.5 µm (exclusive protrusions); coccolith length ca. 2.2 - 2.5 µm.

**Genus Reticulofenestra** Hay et al. 1966, emend. Gallagher 1989

Placoliths without slits between the distal shield elements or bridge; proximal side of the central area typically filled by a reticulate grid or a grill but may be filled by a more or less solid plate, or may appear open.

**Reticulofenestra parvula** (Okada et McIntyre, 1977) Biekart, 1989 var. *parvula* (Fig. 61D)

*Crenalithus parvulus* Okada et McIntyre, 1977, p. 6-7, pl. 2, figs. 1-2; Heimdal et Gaarder, 1981, p. 48, pl. 4, fig. 17.

Placoliths small (1.5 - 2 µm length) with central area filled by a reticulate grid; they differ from *Gephyrocapsa ericsonii* in not having a central bridge, and they differ from *Emiliania huxleyi* in not having slits between the distal shield elements.

Some specimens of *Gephyrocapsa ericsonii* from the NW Mediterranean have placoliths without a bridge (Cros 2001, pl. 40, figs. 2 and 3) which closely resemble the placoliths of *R. parvula* var. *parvula*. Similar specimens were figured by Heimdal and Gaarder (1981) pl. 4, figs. 20 a-b; Moreover, Okada and McIntyre (1977) point out the similarity between placoliths of *G. ericsonii* and *R. parvula* var. *parvula*. A very close relationship between these species is evident and indeed the possibility exists that *R. parvula* var. *parvula* consists in fact of specimens of *G. ericsonii* which lack the distal bar in all of their placoliths.

Coccosphere consists of 20 coccoliths (1 coccosphere).

**Dimensions.** Coccosphere diameter ca. 3.7 µm; coccolith length 1.4-1.9 µm.

**Order COCCOSPHAERALES** Haeckel, 1894 emend. Young and Bown, 1997

Monomorphic coccospheres with placoliths, usually without structures in the central area and with curved and overlapped shield elements. Alternations with holococcolith-bearing phases have been reported for two representatives of this order, *Coccolithus* and *Calcidiscus*.

**Family CALCIDISCACEAE** Young et Bown 1997b

Placoliths have the rim structure characteristic of *Calcidiscus*: large distal shields with sutures that typically show levogyral curvature.

In this family, specimens of *Calcidiscus leptoporus* have been shown to form combination coccospheres with holococcoliths (Kleijne, 1991; Cortés, 2000; Renaud and Klaas, 2001; and Geisen et al. 2000).

**Genus Calcidiscus** Kamptner, 1950

Placoliths subcircular with the central area closed or narrow and having shields with strong levogyral curvature; they are tightly interlocked to form a robust spherical to subspherical coccosphere.

**Calcidiscus leptoporus** (Murray et Blackman, 1898) Loeblich and Tappan, 1978 (Fig. 62)

*Coccosphaera leptopora* Murray and Blackman, 1898, pp. 430, 439, pl. 15, figs. 1-7.

*C. leptoporus* (Murray and Blackman) Loeblich et Tappan, Hallegaard, 1984, p. 233, fig. 6; Kleijne, 1993, p. 185-189, pl. 1, figs 1-6, pl. 2, figs. 1-3, pl. 5 figs. 5-8.

*Crystallolithus rigidus* Gaarder in Heimdal et Gaarder, 1980, pp. 6-7, pl. 2, figs. 10-12.

*Calcidiscus leptoporus* f. *rigidus* (Gaarder) stat. nov. Kleijne, 1991, p. 17, 19, 21, pl. IV, figs. 4-6.

**Combination coccospheres of Calcidiscus leptoporus with Crystallolithus rigidus** Gaarder, 1980 (in Heimdal and Gaarder, 1980), have been repeatedly found and it is clear that the former *C. rigidus* is the holococcolithophore phase of *C. leptoporus* (Kleijne, 1991, 1993; Cortés, 2000; Renaud and Klaas 2001). Moreover, Geisen et al. (2000) presented a well formed combination coccosphere with holococcoliths of *Syracolithus quadriperforatus* (Kamptner) Gaarder surrounding a complete coccosphere of *C. leptoporus* and suggested a cryptic speciation of the heterococcolithophore morphology, as a possible explanation for these very different

NW MEDITERRANEAN COCCOLITHOPHORES 47
associated holococcoliths. Nevertheless three different morphotypes of *C. leptoporus* (Kleijne, 1993; Knappertsbusch *et al.* 1997) have been recognized and these different holococcoliths could correspond to different *C. leptoporus* morphotypes. Until more details are known, we report here *C. rigidus* as the well recognized holococcolith-bearing phase of *C. leptoporus* and we leave *S. quadriperforatus* inside the Calyptrosphaeraceae group.

The cell is either non-motile with the coccosphere consisting of placoliths (heterococcoliths) or motile with the coccosphere consisting of holococcoliths (Kleijne, 1991, 1993).

The measured coccospheres have 14, 19(2), 20, 22, 23, 24 and 26 placoliths; the holococcolith coccospheres of the former *Crystallolithus rigidus* have 54, 70, 90, 92 and 160 holococcoliths.

**Dimensions.** Heterococcolith coccospheres diameter (14.5-) 18.5-19.0 (-19.5) µm; placolith diameter (8.4-) 9-10 (-11.7) µm; holococcolith coccospheres (collapsed) approximate diameter 8-15 µm; holococcolith length (1.6-) 1.9-2.3 (-2.4) µm.

Genus *Oolithotus* Reinhardt, in Cohen and Reinhardt 1968.

Placoliths have their central area and tube asymmetrically placed on the distal shield, giving the characteristically non-concentric shields.

*Oolithotus antillarum* (Cohen), Reinhardt, in Cohen and Reinhardt, 1968 (Fig. 63A)

- *Discolithus antillarum*, (in part) Cohen 1964, p. 236, pl. 2, fig. 2a, b (non pl. 3, fig. 3a-e).
- *Oolithotus fragilis* subsp. *cavum*, Okada and McIntyre 1977, pp. 11-12, pl. 4, figs. 4-5; Nishida 1979, pl. 5, figs. 4a, b; Winter *et al.* 1979, p. 206, pl. 2, fig. 2; Reid, 1980, p. 155, pl. 1, fig. 10.
- *Oolithotus antillarum* (Cohen), Reinhardt, in Cohen and Reinhardt, Kleijne, 1993, pp. 195-196, pl. 2, figs. 4-7

The placoliths have the proximal shield considerably smaller than the distal shield (less than half the diameter) and have very small depressions in both ends of the eccentric narrow tube.

The specimens found in the course of the present study have a smooth surface and a very small depression on the distal face instead of a real pore as seen in the specimens figured by Okada and McIntyre (1977), Hallegraeff (1984), and Kleijne (1993).

The measured four coccospheres possess 21, 24, 34 and 38 coccoliths.

**Dimensions.** Coccosphere diameter 10-13 µm; coccolith length 4.5-6.5 µm.

**Oolithotus fragilis** (Lohmann 1912) Martini *et* Müller, 1972 (Fig. 63B)

*Coccolithus fragilis*, Lohmann 1912, pp. 49, 54, text-fig. 11.

*Oolithotus fragilis* (Lohmann), Martini *et* Müller 1972, p. 67, pl. 1, fig. 8, pl. 2, fig. 6; Kleijne, 1993, p. 196, pl. 3, figs. 1, 2a, b.

*Oolithotus fragilis* (Lohmann) Okada *et* McIntyre 1977, p. 11, pl. 4, fig. 3; Borsetti and Cati 1979, p. 159, pl. 14, figs. 5-6.

This species differs from *O. antillarum* in having larger coccospheres and placoliths which have closer sized proximal and distal shields and a less asymmetrically placed tube.

The coccosphere consists of around 30 coccoliths.

**Dimensions.** Coccosphere diameter ca. 20 µm; coccolith length 6.7-8.7 µm.

Genus *Umbilicosphaera* Lohmann, 1902

Placoliths with large central opening and distal shield showing complex kinked sutures.

*Umbilicosphaera hulburtiana* Gaarder, 1970 (Figs. 63C, D)

*Umbilicosphaera hulburtiana*, (in part) Gaarder 1970, pp. 121-126, figs. 7a-d, 9a, b (non figs. 7e-h, 8a-d)

*Umbilicosphaera hulburtiana* Gaarder, Okada and McIntyre, 1977, p. 12, pl. 3, fig. 12; Kleijne, 1993, p. 197, pl. 3, figs. 5-6; Winter and Siesser, 1994, p. 121, fig. 18.

Placoliths elliptical with an elliptical opening in the central area which is surrounded by a ring of small nodes.

**Dimensions.** Coccosphere diameter ca. 8-10 µm; coccolith length ca. 4 µm.

*Umbilicosphaera sibogae* (Weber-van Bosse 1901) Gaarder 1970 var. *sibogae* (Figs. 64A, B)

*Umbilicosphaera sibogae* Weber-van Bosse 1901, pp. 137, 140, pl. 17, fig. 7a, b.

*Umbilicosphaera sibogae* (Weber-van Bosse) Gaarder, Okada and McIntyre, 1977, p. 13, pl. 4, fig. 2; Kleijne, 1993, p. 197-198, pl. 4, figs. 1-2.

The coccosphere consists of a large number of coccoliths. Placoliths circular with a large circular central opening; distal shield equal to, or slightly narrower than the proximal shield.

The three collapsed coccospheres have 84, 94 and 124 coccoliths.

**Dimensions.** (Collapsed) coccosphere diameter 20-30 µm; coccolith diameter (3-) 4.5-5.5 (-7) µm.

*Umbilicosphaera sibogae* var. *foliosa* (Kamptner, 1963) Okada *et* McIntyre 1977 ex Kleijne, 1993 (Figs. 64C, D)
**Cycloplacolithus foliosus** Kamptner, 1963, pp. 167-168, pl. 7, fig. 38.

*Umbilicosphaera sibogae* var. *foliosa* (Kamptner), Okada and McIntyre, 1977, p. 13, pl. 4, fig. 1; Reid 1980, pp. 155-156, pl. 2, figs. 3-4.

*Umbilicosphaera sibogae* var. *foliosa* (Kamptner), Okada and McIntyre ex Kleijne, Kleijne 1993, p. 198-199, Plate 4, figs. 3-4, pl. 5, fig. 4; Winter and Siesser 1994, p. 121, fig. 21, phot. from J. Alcober.

This variety differs from *U. sibogae* var. *sibogae* in having smaller coccospheres with less coccoliths, and in having coccoliths with: a) the distal shield larger than the proximal shield; b) a narrower central opening; and c) in usually possessing a small spine inside the central opening protruding from the tube.

**Dimensions.** Coccosphere diameter 12-13 µm; coccolith diameter (4.7-) 5.0-5.5 (-6.3) µm.

**Coccoliths of uncertain affinities**

**Family PAPPOSPHAERACEAE Jordan et Young, 1990**

Family of minute, lightly-calcified coccolithophores, mainly known from high-latitudes, with holo-and heterococcolith phases (Thomsen et al., 1991; Thomsen and Buck, 1998). The characteristic heterococcolith of this family is the pappolith (Tangen, 1972; Norris, 1983), a coccolith with a narrow murolith rim of non-overlapping elements, which may have a central spine supporting a calyx of four plates (Young and Bown, 1997). In the genus *Papposphaera*, all of the pappoliths on the coccosphere have a spine, whereas in the genus *Pappomonas*, the coccosphere also possesses pappoliths without a central spine (Manton et al., 1976a). Nevertheless, it has been pointed out that these two genera are similar and eventually might be merged if and when more species are discovered (Thomsen et al., 1988). The known Papposphaeraceae species have been described and studied essentially from high-latitude sea waters, and this is possibly the reason for the large number of undescribed species observed in this NW Mediterranean study, and for the absence of most of the known species. Of the formally described species, only *Papposphaera lepida* Tangen, 1972, was recognized in NW Mediterranean waters.

**Genus Papposphaera** Tangen, 1972

The heterococcospheres have pappoliths with processes and with pentagonal plates that form the rim. The shape of the process and the morphology of the base plate are used to separate the different species. Thomsen *et al.* (1991) showed that species of *Papposphaera* and species placed in the genus *Turrisphaera* are life history stages of a single organism.

**Papposphaera lepida** Tangen, 1972

**Dimensions.** Coccosphere diameter 4.5-8 µm; coccolith base length (0.5-) 0.7-1.0 (-1.5) µm, spine length (0.5-) 0.7-1.7 (-2.7) µm; distal structure (0.4-) 0.8-1 (-1.6) µm.

**Papposphaera sp. type 1**

(Figs. 66A, B)

A single coccolith described and figured as *Deflandrius* cf. *intercisus* (Deflandre) Bramlette and Martini, 1964, by Norris (1983), p. 165, fig. 5 (the coccolith was found in the gut of a salp collected in the Indian Ocean, 31º08'S, 78º23'E, July 4 1963). *Papposphaera* sp. 1 Thomsen and Buck (1998), p. 34, Fig. 17. (The *Papposphaera* phase specimen was from the Sea of Cortez, Mexico).

The coccosphere has clearly varimorphic pappoliths with larger shafts at one pole and very short shafts in other parts of the coccosphere. The pappoliths have an elliptical base plate with a crown-shaped rim and axial crossbars which appear to act...
as struts to support the central stem; there are no visible collar around the distal part of the stem, below the central calyx, and the calyx structure is formed of “four quasi-rectangular, diverging plates”. The number of specimens studied from NW Mediterranean waters was 8. Coccospheres possess around 60-110 coccoliths.

**Dimensions.** Coccosphere diameter 4.1-5.6 µm; coccolith base length 0.5-0.8 µm; coccolith height (0.4-) 0.7-1.0 (-1.6) µm.

**Papposphaera** sp. type 2
(Figs. 66C, D)

Coccosphere with dimorphic coccoliths, having at one pole pappoliths with larger shafts and a distal structure composed of four small rod-shaped elements perpendicular to the shaft; the other pappoliths have shorter shafts that end in four small diverging rods.

The studied specimen consists of 8 coccoliths with long spines and about 34 coccoliths with small central process.

**Dimensions.** Coccosphere diameter ca. 5 µm; coccolith base length 0.5-1.0 µm; spine height 0.5-1.5 µm.

**Papposphaera** sp. type 3
(Figs. 67A, B)

Coccosphere with varimorphic coccoliths having at one pole pappoliths with larger stems and a distal structure composed of four diverging sepal-like elements; the other pappoliths mostly have smaller sepal-like elements, but some are tipped by four petaloid elements resembling the distal structure a flower (further specimens are required to clearly establish the extent of variability of the coccoliths).

**Papposphaera** sp. 3 resembles the described **Papposphaera bourrelly** Thomsen et Buck, 1998, differing mainly in having varimorphic coccoliths and in having different sepal-like structures, with no collar at the base.

Coccospheres possess around 50-60 coccoliths.

**Dimensions.** Coccosphere diameter ca. 10 µm; coccolith base length 0.6-0.8 µm, height of long spines ca. 3 µm; distal structure 0.6 to 1.2 µm.

**Papposphaera** sp. type 4
(Figs. 67C, D)

Coccosphere with varimorphic coccoliths. The proximal side of the coccoliths is typical of **Papposphaera**, but the distal side is not a typical calyx; in the studied specimen the distal part of the stem splits into four triangular lamina, joined on their long side and with the distal part serrated.

The studied specimen consists of ca. 50 coccoliths.

**Dimensions.** Coccosphere diameter ca. 6 µm; coccolith base length 0.7-0.8 µm; stem height 0.7-2.0 µm.

**Papposphaera** sp. type 5 (only three elements compose the distal structure) (Figs. 68A, B)

Coccosphere with varimorphic coccoliths, which have stems of different sizes and diverse distal structures; the proximal side of the coccoliths is typical of **Papposphaera** (elliptical base plates with crown-shaped rims and an axial crossbar), but the distal side does not have the typical calyx-like structure with four elements, but rather a distal structure resembling a propeller composed of three triangular elements.

The two studied coccospheres have ca. 90 to 120 coccoliths.

**Dimensions.** Coccosphere diameter 6-7 µm; coccolith base length ca. 0.7 µm; coccolith height (including stem) 0.6-1.5 µm.

**Papposphaera** sp. type 6 (only three elements compose the distal structure) (Figs. 68C, D)

Coccosphere with varimorphic coccoliths. The distal structure is characteristically composed of three elements in the form of large triangular blades which start near the base plate, leaving no space for a real stem.

The studied coccosphere consists of ca. 62 coccoliths.

**Dimensions.** Coccosphere diameter 5-6 µm; coccolith base length 0.7-1.1 µm; coccolith height 1.0-2.5 µm.

**Papposphaera** holococcolithophore (“**Turrisphaera**”) phase (Thomsen et al., 1991; Thomsen et Buck, 1998) (Formerly genus **Turrisphaera** Manton, Sutherland et Oates, 1976b)

The former genus **Turrisphaera** Manton, Sutherland et Oates, 1976 has tower-shaped coccoliths constructed of small hexagonal crystallites.

**Papposphaera** holococcolithophore (“**Turrisphaera**”) phase sp. type A
(Figs. 69A, B)
The holococcoliths are “apple-core” shaped structures similar to the holococcoliths of *Papposphaera sarion* (formerly *Turrisphaera borealis*), but shorter and wider.

The studied coccosphere consists of ca. 60 coccoliths.

*Dimentions. Coccosphere diameter ca. 5 µm; coccolith base diameter ca. 0.8 µm; coccolith height 0.8-1.6 µm.*

*Papposphaera* holococcolithophore (*“Turrisphaera”*) phase sp. type B (Figs. 69C, D)

The proximal part of the holococcoliths is typically “apple-core” shaped, but they become flattened distally, ending in a very characteristic distal structure which resembles a leaf.

The studied coccosphere consists of ca. 45 coccoliths.

*Dimentions. Coccosphere diameter ca. 8 µm; coccolith base diameter ca. 0.7 µm; coccolith height 1-2 µm.*

Genus *Pappomonas* Manton *et* Oates, 1975

The heterococcospheres have pappoliths with and without central spine; the rim of all coccoliths is constructed of pentagonal plates.

Thomsen *et al.* (1991) reported that species of *Pappomonas* and species of the holococcolithophore *Trigonaspis* Thomsen (Thomsen, 1980) sometimes form combination cells, and concluded that the taxa involved (*P. flabellifera* var. *borealis* and *Trigonaspis* cf. *diskoensis* Thomsen, 1980) are different phases of the same life-cycle. However, preliminary results indicated that *P. virgulosa* forms combination cells with *Balaniger balticus* Thomsen and Oates (results referred from Ostergaard in Thomsen and Oates, 1978).

*Pappomonas* sp. type 1 (Fig. 70A)

Body coccoliths with central area structure of two concentric rings and a conspicuous bar across the minor axis. The pappoliths with spine have a long central stem tipped by four small rods. *Pappomonas* sp. type 1 resembles *P. virgulosa* in having the apical pappoliths tipped by four rods, but differs from it in having longer stems, with much shorter ends and in having body coccoliths with higher and more developed rims.

*Dimensions. Coccoliths without spines length ca. 1.2 µm; coccoliths with spines length 0.6-1.2 µm, stem height ca. 2.5 µm.*

*Pappomonas* sp. type 2 (Fig. 70B)

Body coccoliths elliptical with plate elements covering the entire base plate. Apical pappoliths having a rounded base plate with a cross-bar, a long central stem and a large obpyramidal distal calyx. The rim is characteristically low in all the coccoliths, showing no clear pentagonal plates.

The calyx of coccoliths of *Pappomonas* sp. type 2 resembles that of *Papposphaera obpyramidalis*, but the stems of the latter species are shorter, the base plates are different, and moreover *Pappomonas* sp. type 2 possesses elliptical coccoliths without a central process.

The coccosphere consists of ca. 16 coccoliths with calicate spines (spines with calyx); 32-42 coccoliths without central process.

*Dimensions. Coccosphere diameter 6-8 µm; coccoliths without spines length 0.5-1.5 µm; coccoliths with spines length 0.6-0.8 µm, distal structure ca. 1.5 µm wide, coccolith height (including stem) ca. 2.3 µm.*

*Pappomonas* sp. type 3 (Figs. 70C, D)

Body coccoliths with a cross-bar in the base plate and a small nodular central structure. The pappoliths with calicate spine have a long central stem and a distal structure composed of four varimorphic sepal-like elements.

The studied specimens (3 coccospheres) have 23, 30 and 37 coccoliths with calicate spines; 52, 58 and 80 coccoliths without spines.

*Dimensions. Coccosphere diameter 12-15 µm; coccoliths without spines length ca. 1 µm; coccoliths with spines length base 0.5-1.0 µm, height 3.5-5.0 µm.*

*Pappomonas* sp. type 4 (Fig. 71A)

The coccosphere consists of three different types of coccoliths. The body coccoliths consist of elements that form two concentric rows and a bar across the minor axis. Apical pappoliths have a long circular central spine with no calyx. There is another coccolith type which has a shorter circular spine.

NW MEDITERRANEAN COCCOLITHOPHORES 51
Note that it would be necessary to redefine the genus *Pappomonas* if this species was to be included; by definition, members of this genus have two types of coccoliths, both with a caliculate spine, but this species has three types of coccoliths and those with a spine have no calyx. Nevertheless, the structure of the central area and the rim of both types of coccoliths (with and without spine) are clearly typical of this genus.

The studied coccosphere consists of ca. 112 coccoliths.

*Dimensions.* Coccosphere diameter ca. 6 µm; coccoliths length ca. 1 µm; spine height 0.5-2.5 µm.

*?Pappomonas* sp. type 5  
(Fig. 71B)

Body coccoliths have elements that form two concentric rows and a bar across the minor axis. Apical pappoliths have a long, bent, circular central rod. A few antapical coccoliths have a shorter circular rod.

This specimen resembles *?Pappomonas* sp. type 4, but has smaller coccoliths with longer and bent spines.

The studied coccosphere consists of ca. 105 coccoliths; 4 with short spine, about 21 with long bent spine, and 80 without spine.

*Dimensions.* Coccosphere diameter ca. 7 µm; coccoliths without spine length 0.5-0.8 µm; coccoliths with short spine length ca. 1 µm, spine length 1 µm; apical coccoliths with long, bent spines base diameter ca. 0.5 µm, spine length 2.5-3 µm.

Genus *Picarola* Cros et Estrada (in press)

This genus, which resembles to *Papposphaera*, has some characteristics that suggest affinities with *Vexillarius cancellifer* Jordan et Chamberlain, 1993b.

Coccoliths have a curved four-sided process and a rim consisting of quadrilateral elements.

Qualitative X-ray analysis of several specimens of this genus have proved the calcium content of the coccoliths.

*Picarola margalefii* Cros et Estrada (in press)  
(Figs. 72A, B)

*Picarola margalefii* Cros et Estrada (in press).

Cocosphere can possess three different types of coccoliths. Body coccoliths have a highly curved appendix, which finishes in a pointed end. Circumflagellar coccoliths have a straight and high wall and a large and slightly curved appendix, which finishes abruptly in a truncated end. Antapical coccoliths (only 0 to 2) have a flaring wall and a nearly straight appendix, which finishes in a pointed end.

*Dimensions.* Coccosphere diameter 6-12 µm; coccolith base length ca. 0.8 µm; spine length 1.5-5 µm (highly variable).

Genus Type A

Monomorphic coccoliths with a long central structure and a rim formed of rectangular plates.

The studied coccosphere consists of ca. 50 coccoliths.

*Dimensions.* Coccosphere diameter ca. 15 µm; coccolith base length 1 µm; spine length 5-6 µm.

Genus Type A, species type 2  
(Fig. 71D)

Coccoliths with a long, square central process that flares and bends distally, resulting in a very characteristic feather-like structure.

*Dimensions.* Coccosphere diameter ca. 10 µm; coccolith base length ca. 0.7 µm; spine length 2-5 µm (highly variable).

Family CERATOLITHACEAE Norris, 1965

Cells with two extremely different types of structure: a single horseshoe-shaped nannolith and ring-
shaped coccoliths which adhere together to form a sphere that encloses the proplast and the single horseshoe-shaped coccolith. It was recently discovered that the species has an alternate phase with another coccolith type: a subcircular planolith with an open central area.

**Genus Ceratolithus** Kamptner, 1950

The ceratoliths are the horseshoe-shaped nannoliths characteristic of this genus; they are robust and somewhat asymmetrical in form, with one arm being slightly shorter than the other. The coccosphere also bears ring-shaped coccoliths, named hoop-like coccoliths, which are numerous but delicate. Several cells, each with a ceratolith, may be present within a single sphere constructed by hoop-like coccoliths. It is now known that the species can generate another kind of coccolith, formerly known as *Neosphaera coccolithomorpha* (Alcober and Jordan, 1997; Young et al., 1998, Cros et al., 2000b; Sprengel and Young, 2000).

**Ceratolithus cristatus** Kamptner, 1950

Fig. 73.

*Ceratolithus cristatus* Kamptner, Norris, 1965, pp. 19-21, pl. 11, Figs. 1-4, Pl. 12; Borsetti and Cati, 1976, p. 224, pl. 17; Kleijne, 1993, p. 232, pl. 1, fig. 3, 6; Alcober and Jordan, 1997, p. 91-93, figs. 1-4; Young et al. 1998, p. 90, pl. 2-3. Sprengel and Young, 2000, p. 39-41, pl. 1.

The cells of **Ceratolithus cristatus** have three very different types of coccoliths: a) ceratoliths, which may be considered horseshoe-shaped nannoliths because they do not have the symmetrical characteristics of heterococcoliths and holococcoliths; b) hoop-like coccoliths which are a ring formed of connected crystal-units; c) the coccoliths belonging to the former *Neosphaera coccolithomorpha* Lecal, circular heterococcoliths with a single shield and a tube. Each one of these coccoliths can appear in at least two varieties:

a) Ceratoliths. Three types have been described: *Ceratolithus cristatus* var. *cristatus* which is the typical form; *Ceratolithus cristatus* var. *telesmus* (Norris) Jordan et Young, a form with longer arms that curve together to almost touch (morphotype first described as *Ceratolithus telesmus* Norris, 1965); *Ceratolithus cristatus* forma *rostratus* which is an ornate form with an apical beak or rostrum (this form was summarily described by Borsetti and Cati (1976), but they did not propose a formal description, so the epithet “*rostratus*” it is not yet validated).

b) Hoop-coccoliths. With at least two forms: robust hoops with a thick ring and more delicate hoops with thinner rings, but of larger size (Young et al. 1998).

c) “Neosphaera” coccoliths. They vary considerably in size and diameter of the central-opening; two main varieties are distinguished: var. *coccolithomorpha* and var. *nishidae* (Kleijne, 1993).

In NW Mediterranean waters, the **Ceratolithus cristatus** coccolith types are: **Ceratolithus cristatus** forma *rostratus*, delicate hoop-like and “*Neosphaera*” type var. *nishidae*. This appears to be a very characteristic association (Young et al., 1998), leading to the suspicion that the three coccolith types belong to the same coccolithophore taxon.

Coccospheres can have 1-2 ceratoliths, a very variable number of hoop-like coccoliths and around 21 coccoliths of the type “*Neosphaera*”.

**Dimensions.** “*Neosphaera*” type coccosphere diameter 7-10 µm; ceratolith length (14-) 17-19 (-21) µm, width (8.9-) 9-10 (-13) µm; hoop-like coccoliths very thin (ca. 0.1 µm), ring diameter (4.5-) 5-6 (-7.5) µm; “*Neosphaera*” type coccoliths diameter (3.2-) 4.5-5.0 (-6.0) µm.

**Polycrater–Alisphaera–Canistrolithus,**
provisional group of genera

Two combination coccospheres were observed from NW Mediterranean waters with coccoliths of **Polycrater** and of the genus **Alisphaera** (Cros, 2001; Plate 87, figs. 1-6). Two other combination coccospheres were observed involving **Polycrater** coccoliths and **Canistrolithus** coccoliths (Plate 88, figs. 1-6). The **Polycrater** specimens associated with **Alisphaera** and **Canistrolithus** were of different morphological types. The two genera, **Alisphaera** and **Canistrolithus**, are recognized as very close in the literature (Jordan and Chamberlain, 1993a) and it is noteworthy that these three genera, **Polycrater**, **Alisphaera** and **Canistrolithus**, present common characteristics in both, coccolith morphology and coccosphere arrangement. All three genera show a longitudinal asymmetry of their coccoliths and a general coccolith arrangement based on approximately regular meridian rows around the cell. The presence of horns, spines and extended protrusions is common in the coccoliths of **Polycrater**, **Alisphaera** and **Canistrolithus**. Inside the framework of these findings it is hypothesised that these three genera may represent an unusual sub-group of coccolithophores in which, possibly, the aragonitic
Polycrater coccoliths substitute for holococcoliths in their life-cycle (Cros et al., 2000a). At the moment, in the present Atlas, we leave the three taxa with their respective usual names, but we remove Alisphaera and Canistrolithus from the Syracosphaeraceae family to group them with the genus Polycrater, which was considered incertae sedis.

Genus Alisphaera Heimdal, 1973, emend. Kleijne et al., 2001

Alisphaera genus presents elliptical coccoliths with a short tube, a proximal flange and a distal flange. Alisphaera coccoliths are clearly asymmetrical with respect to the major axis, having one half of the distal flange wider than the other; usually the more developed part shows some characteristic spike or protrusion specific of the species. The central area usually presents a longitudinal, slightly S-shaped fissure and nodules along the inner periphery of the distal flange, specially on the narrow side.

This genus can form combination coccospheres with Polycrater (Cros et al. 2000b; Cros, 2001; Figs. 77A, B).

Until now, the genus Alisphaera has been included in the family Syracosphaeraceae, but the fact that its coccoliths are not real caneoliths is recognized in the literature, some authors referring to them as placolith-like coccoliths (Young and Bown, 1997b) or as modified caneoliths (Chrétiennot-Dinet, 1990; Jordan and Chamberlain, 1993a). A new and extensive review of this genus is giving in Kleijne et al. 2001. Following the discovery of coccospheres combining Alisphaera with the nannolith-bearing genus Polycrater, it seems advisable to group these genera with the other associated taxa.

Alisphaera capulata Heimdal, in Heimdal et Gaarder, 1981 (Figs. 74A, B)

Alisphaera capulata Heimdal, in Heimdal and Gaarder, 1981, p. 39-40, pl. 1 Fig. 3-4 ; Kleijne, 1993, p. 233, pl. 2, fig. 7; Kleijne et al., 2001, p. 587, Figs. 22-24.

The coccoliths possess an extension like a flat handle on the external part of the wider flange; this raised part is more or less inclined to the left; the central area appears to have a solid base plate without a fissure.

Coccospheres have between 68 and 90.

Dimensions. Coccospheres long axis 4.5-7.0 µm; coccolith length 1.4-1.6 µm.

Alisphaera extenta Kleijne et al., 2001. (Figs. 74C, D)

Alisphaera extenta Kleijne et al., 2001, p. 587-589, Figs. 25-29. Alisphaera unicornis Okada et McIntyre, Jordan et Chamberlain, 1993a, p. 378, figs. 8, 10 g; Samtleben et al., 1995, pl. 1, fig. 7.

The coccoliths of this species have a broad, wing-like, pointed extension on the outside part of the wider distal flange; central area with a longitudinal fissure and usually no nodules.

The studied coccosphere consists of around 88 coccoliths.

Dimensions. Coccosphere long axis ca. 8 µm; coccolith length 1.6-1.9 µm.

Alisphaera gaudii Kleijne et al. 2001. (Figs. 77C, D)

Alisphaera gaudii Kleijne et al., 2001, p. 589, 592, Figs. 30-32. Alisphaera unicornis Okada et McIntyre, 1977 p. 18, pl. 6, fig 8 (not fig. 7); Winter and Siesser, 1994, p. 132, fig. 90B (phot. from Samtleben).

Coccoliths show a variable morphology of the distal flange extension and they are considered dimorphic and even varimorphic (Kleijne et al. 2001). Most of the coccoliths have on the wider distal flange a pointed projection like a beak or asymmetrical spine, a longitudinal irregularly shaped opening in the central area and nodules. Coccoliths without the pointed protrusion occur on the coccosphere. A well formed combination coccosphere of this species with a Polycrater with holes, reminiscent of Gaudi’s architecture is figured in Figs. 77A, B.

The studied coccosphere consists of around 158 coccoliths.

Dimensions. Coccosphere diameter ca. 10 µm; coccolith length 1.6-2 µm.

Alisphaera pinnigera Kleijne et al. 2001. (Figs. 75A, B)

Alisphaera pinnigera Kleijne et al., 2001, p. 594, Figs. 40-45. Alisphaera sp. cf. A. unicornis Okada and McIntyre 1977, in Kleijne, 1993, p. 233, pl. 2, fig. 10.

The coccoliths have a longitudinal fissure in the central area and small tooth-like protrusions along their inner margin; some coccoliths have a vertical protrusion like a flat triangle with its base positioned perpendicularly on the wider flange in the direction of the short axis of the coccolith.

Most coccospheres are presumably broken, so coccolith numbers (128, 164, 174, 244 and 342) may be underestimated.
Dimensions. Coccosphere long axis 7.0-10.5 µm; coccolith length (1.3-) 1.5-1.6 (-1.8) µm.

*Alisphaera quadrilatera* Kleijne et al. 2001  
(Figs. 75C, D)

*Alisphaera ordinata* (Kamptner) Heimdal 1973, in Borsetti and Cati, 1979, p. 160, pl. 15, fig. 6; Kleijne, 1993, p. 233, pl. 2, fig. 8.

The coccoliths possess a flat and obliquely raised protrusion, which is more or less five-sided counting the wide base, with four external sides, situated in the centre of the wide distal flange, covering a slit present in the outer part of the same flange. Central area shows longitudinal fissure.

This taxa differs from *Alisphaera ordinata* mainly in possessing a polygonal protrusion instead of a very broad protrusion extended over nearly all the distal flange.

Coccospheres possess 60, 62, 80 and 112 coccoliths.

Dimensions. Coccosphere long axis 6.5-8 µm; coccolith length (1.3-) 1.4-1.7 (-2.1) µm.

*Alisphaera unicornis* Okada et McIntyre, 1977,  
emend. Kleijne, 2001 (Figs. 76A, B)

*Alisphaera unicornis* Okada et McIntyre, 1977 p. 18, pl. 6, fig 7 (not fig. 8); Borsetti and Cati, 1979, p. 160, pl. 16, figs. 1-3; Hallegraeff, 1984, p. 239, fig. 41a-b; Winter and Siesser, 1994, p. 132, fig. 90A (phot. from Winter and Friedinger).

Coccoliths have a pointed protrusion like a horn, eccentrically placed, on the wider distal flange, although a few coccoliths on the coccosphere may lack this obliquely raised tooth. Central area with a longitudinal irregularly shaped fissure. Nodules usually absent.

It is difficult to distinguish between *Alisphaera unicornis* and *A. spatula* Steinmetz, 1991, but the smaller sized coccoliths of *A. spatula* possess nodules and a flat blade-shaped element with a pointed extension on top, which is centrally placed instead of a horn, which usually is asymmetrically placed in *A. unicornis*.

Coccosphere consists of around 140 coccoliths.

Dimensions. Coccosphere diameter ca. 11 µm; coccolith length 2.4-2.7 µm.

Genus *Canistrolithus* Jordan et Chamberlain, 1993

Coccoliths are narrowly elliptical to oblong. They have a high and composite wall and are asymmetrical along the major axis, having one half of the distal flange wider than the other; usually the more developed part shows a single upright thorn and the narrower half can presents nodules along the inner periphery of the flange; an organic membrane appears to cover the proximal central area of the coccolith.

This genus includes only one formally described species, *C. valliformis* Jordan et Chamberlain, 1993a and another species figured by Reid (1980), p. 158, 160, pl. 4, fig. 8-11, with the name *Alisphaera unicornis*.

This genus has been classified inside the family Syracosphaeraceae because the authors who described it recognized the resemblance with the genus *Alisphaera* (Jordan and Chamberlain, 1993a).

In the present study only two specimens were observed, both being combination coccospheres with coccoliths of *Polycrater*. Taking into account these combinations with the nannolith bearing genus *Polycrater* (Figs. 78A, C, D and 79A, B), it seems necessary to group *Canistrolithus* with *Polycrater* and *Alisphaera*, and to define this newly emerging genus perhaps within a new higher taxon.

*Canistrolithus* sp. 1  
(Fig. 78B)

Coccoliths with and without spines; the spine is placed on the more developed part of the flange, near the outer edge; the central area is unfilled or possesses a proximal organic membrane.

This species can be associated with *Polycrater* on combination coccospheres.

*Canistrolithus* sp. 1 differs from *C. valliformis* and the species figured by Reid (1980), p. 158, 160, pl. 4, fig. 8-11, in having coccoliths with a lower wall, wider flange (particularly in its narrow part) with neither nodes nor peg-like structures and with spines placed in a less central position.

The more complete coccosphere consists of around 212 coccoliths.

Dimensions. Coccosphere diameter (one specimen) ca. 19 µm; coccolith length (2.3-) 2.6-2.9 (-3.1) µm.

Genus *Polycrater* Manton et Oates, 1980

Coccosphere with a close packed layer of delicate bowl-shaped coccoliths arranged with the concavities directed outwards; this kind of coccolith has also been defined as aragonitic square-sectioned cones.
This genus contains a single recognized species, but many different forms were found in the course of the present work. Hence the genus description must be emended in order to embrace all of the possible new species. Moreover, in the studied samples it has been found that different Polycrater taxa can form combination cocospheres with different Alisphaera and Canistro lithus species.

The coccosphere has numerous very small coccoliths of angular architecture wedged together with the short coccolith axis presumably in a polar direction. The coccoliths are asymmetrical in relation to the major axis, with one half broader than the other; they may or may not have a bowl-like distal side, but all of them present a cross-like proximal side.

The special coccoliths have two well differentiated parts comparable to a flower, as clearly represented in fig. 5 of Manton and Oates (1980): a proximal part with sepal-like components and a distal part with petal-like components. Usually the specimens have four petal-like components that build a bowl or cone of squared section; on the external part of the angular joins there are buttress-like extensions that connect with the sepal-like proximal structures.

**Polycrater galapagensis** Manton et Oates, 1980

(Figs. 80A, B)

*Polycrater galapagensis* Manton et Oates, 1980, p. 102, 103, figs. 1, 3, 4, 5, 6.; Thomsen et al. 1994, figs. 10.6, 10.7.

*Polycrater* sp. Chrétiennot-Dinet, 1990, p. 104, fig. 500

This species has bowl-shaped coccoliths with distal concavities and a cruciform external thickening that define the four petal-like lobes and four sepal-like structures with undulate edges overlaying the cruciform thickenings on the proximal side. Coccoliths composed of aragonite (Manton et Oates, 1980).

Coccospheres possess 600 to 1000 coccoliths (more precise counts gave 628, 796 and 994).

**Dimensions.** Coccosphere diameter (9.4-) 9.8-10.8 (-11.5) µm; coccolith length (0.55-) 0.60-0.7 (-0.75) µm.

**Polycrater galapagensis** var. A (with nodes)

(Figs. 79C, D)

Winter and Siesser, 1994, p. 141, fig. 128.

This coccosphere closely resembles *P. galapagensis*, but the distal part of the smaller half of coccoliths has small nodes and usually a v-shaped incision in the higher corner. This *Polycrater* taxa can form associations with *Canistro lithus* sp. 1 (Figs. 78A, C, D and 79A, B).

Coccosphere possesses between 1000 and 1300 coccoliths (estimated numbers 1088 and 1286).

**Dimensions.** Coccosphere diameter 13.8-15.8 µm; coccolith length (0.7-) 0.80-0.85 (-0.95) µm.

**Polycrater** sp. (with holes, reminiscent of Gaudí’s architecture) (Figs. 77C, D)

*Polycrater galapagensis* auct. non Manton et Oates, Giraudeau and Bailey, 1995, pl. 3, fig. 11.

This coccosphere resembles *P. galapagensis*, but coccoliths have two lenticular holes in the larger half, near the centre, on each large petal-like element; upper corner shows a slender leaf-like extension. This *Polycrater* taxa can form associations (Figs. 77A, B) with *Alisphaera gaudii* and should be considered as a “*Polycrater*” form of the *Alisphaera gaudii*.

This *Polycrater* has a characteristic appearance reminiscent of the shapes created by Gaudí.

The studied coccospheres possess from 200 to 750 coccoliths (separate counts 208, 456 and 740).

**Dimensions.** Coccosphere diameter (5.6-) 7.9 (-10.6) µm; coccolith length (0.63-) 0.72-0.82 (-0.86) µm.

**Polycrater** sp. (with slit)

(Figs. 80C, D)

This coccosphere resembles *P. galapagensis*, but coccoliths have a distal slit near the lower corner, in sinistral position, and usually have a v-shaped incision in the higher corner.

**Dimensions.** Coccosphere diameter ca. 9 µm; coccolith length (0.61-) 0.65-0.75 (-0.91) µm.

**Polycrater** sp. (with lip-like borders)

(Figs. 81A, B)

Genus and species indeterminable, Nishida, 1979, pl. 21 fig. 6.

This coccosphere resembles *P. galapagensis*, but coccoliths have a distal slit near the lower corner, in sinistral position, and usually have a v-shaped incision in the higher corner. This *Polycrater* taxa can form associations with *Canistro lithus* sp. 1 (Figs. 78A, C, D and 79A, B).

Coccosphere possesses between 1000 and 1300 coccoliths (estimated numbers 1088 and 1286).

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This coccosphere resembles *P. galapagensis*, but coccoliths have two lenticular holes in the larger half, near the centre, on each large petal-like element; upper corner shows a slender leaf-like extension. This *Polycrater* taxa can form associations (Figs. 77A, B) with *Alisphaera gaudii* and should be considered as a “*Polycrater*” form of the *Alisphaera gaudii*.

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**Dimensions.** Coccosphere diameter ca. 9 µm; coccolith length (0.61-) 0.65-0.75 (-0.91) µm.

**Polycrater** sp. (with lip-like borders)

(Figs. 81A, B)

Genus and species indeterminable, Nishida, 1979, pl. 21 fig. 6.

This coccosphere resembles *P. galapagensis*, but coccoliths are smaller (0.3 to 0.5 µm along the major axis) and have the borders of the larger half bent like lips; the sepal-like parts (proximal side) are small with a very simple structure.

**Dimensions.** Coccosphere diameter (6-) 8.5-9.5 (-11.5) µm; coccolith length (0.35-) 0.44-0.48 (-0.55) µm, with very simple sepal-like part ca. 0.4 µm.
**Polycrater** sp. (minimum, the smallest coccoliths) (Figs. 81C, D)

The coccosphere has very small coccoliths, with the sepal-like structures formed of a very little cross. The size of each coccolith is around 0.2 µm.

The studied coccosphere consists of ca. 1870 coccoliths.

*Dimensions.* Coccosphere diameter ca. 6 µm; coccolith length (0.25-) 0.3-0.4 (-0.5) µm.

**Polycrater** sp. (two petal-like structures very modified; ladle-like coccoliths) (Figs. 82A, B)

The coccosphere has an unusual spiny shape. The coccoliths have the sepal-like structure similar to the other *Polycrater* species, whilst the petal-like structure is highly modified: two petal-like elements are very reduced with the corner highly extended forming a tall rod; the other two petal-like elements are normally constructed, the entire structure thus resembling a ladle.

*Dimensions.* Coccosphere diameter ca. 4.5 µm; coccolith width 0.4-0.5 µm, height of the spiny part 0.5-0.6 µm.

**Polycrater** sp. (two petal-like structures very modified, two others absent). (Figs. 82C, D)

The coccosphere has a spiny shape. The coccoliths have the sepal-like structure similar to the other *Polycrater* species, whilst the petal-like structure is completely modified: two petal-like elements are very reduced with the corner highly extended forming a stick of variable width; there are no more petal-like elements.

The species *Erciolus spiculiger* Thomsen (Thomsen *et al.* 1995) appears morphologically related with this *Polycrater* sp., but the coccoliths of *Erciolus spiculiger* do not show the cross sepal-like proximal structures that possess *Polycrater* sp. coccoliths.

*Dimensions.* Coccosphere diameter 4-6 µm; coccolith length 0.4-0.7 µm, width in distal part variable (up to 0.3 µm)

**Genera Incertae Sedis**

Genus *Umbellosphaera* Paasche in Markali *et al.* Paasche, 1955 emend. Gaarder 1981 (in Heimdal and Gaarder, 1981)

The coccoliths have a placolith-like morphology with the distal shield greatly extended; some authors have called them umbelloliths (Kleijne, 1993).

*Umbellosphaera* spp. appears in the Late Pliocene (Perch-Nielsen, 1985b).

**Umbellosphaera tenuis** (Kamptner, 1937) Paasche in Markali *et Paasche, 1955* (Figs. 83A, B)

*Coccolithus tenuis* Kamptner 1937, pp. 311-312, pl. 17, figs. 41-42. *Umbellosphaera tenuis* (Kamptner) Paasche, McIntyre and Bé, 1967, pp. 566-567, pl. 3; Borsetti and Cati, 1972, pp. 406, 407, pl. 53, fig. 3, pl. 54, fig. 1 and 2; Heimdal and Gaarder 1981, pp. 62-63, pl. 11, fig. 59 a, b; Samtleben and Schröder 1990, pl. 4, fig. 1; Kleijne, 1993, pp. 202-205, pl. 6, figs. 1-2; pl. 7, figs. 5-6; pl. 8, figs. 1-6; pl. 9, figs 1-6.

The coccosphere consists of coccoliths of diverse size which can be separated in two main types: (a) small umbelloliths or micrococcoliths with an elliptical central area; (b) umbelloliths or macrococcoliths which are larger with a subcircular central area. Both types have a very short tube, a practically nonexistent proximal shield, and a greatly extended distal shield with highly variable ornamentation. Micrococcoliths are usually present in a proximal layer on large coccospheres; macrococcoliths are always present and the different ornamentation of their distal shield could be of considerable ecological interest (Kleijne, 1993).

Coccospheres consist of between 14 and 30 coccoliths.

*Dimensions.* Coccospheres long axis (8-) 10-11 (-12) µm; micrococcolith length 2.5-3.0 µm; macro-coccolith length 2.6-6.8 µm.

Genus *Gladiolithus* Jordan *et Chamberlain, 1993*

Coccosphere with dimorphic coccoliths: tubular coccoliths and lepidoliths. The tubular coccoliths are hollow and tightly arranged around the cell; the lepidoliths are flat and arranged at the base of the tubular coccoliths.

**Gladiolithus flabellatus** (Halldal and Markali, 1955) Jordan *et Chamberlain, 1993* (Figs. 83C, D)

Thorosphaera flabellata Halldal and Markali, 1955, p. 19, pl. 26, Figs. 1-4; Winter and Siesser, 1994, p. 141, figs. 129A-B; Hagino and Okada, 1998, p. 249, fig. 8.

The tubular coccoliths have six sides and presents spine-like projections; the lepidoliths are elliptical disc-like planoliths consisting of two elements separated by a suture perpendicular to the long axis of the coccolith.
**Dimensions.** Cocosphere long axis ca. 12 µm; tubular coccoliths length 5-8 µm, width ca. 2 µm; lepidolith length 1.5-2.0 µm.

**Genus Turrilithus** Jordan et al. 1991

Cocosphere with monomorphic coccoliths which are tower-shaped, each with a four-sided appendix composed of quadrangular plates.

**Turrilithus latericioides** Jordan et al. 1991 (Figs. 84A, B)

*Coccocosphere* with *monomorphic* coccoliths which are tower-shaped, each with a four-sided appendix composed of quadrangular plates.

**Tu rrilithus** Jordan et al. 1991, p. 176, 178, 181, 182, 183, figs. 2-12; Winter and Siesser, 1994, p. 141, fig. 130.

Coccoliths elliptical, subtended by a thin base plate with a proximal, central perforation, with a low and flaring wall and a central upright, hollow, tower-shaped appendix which widens distally and is partially occluded at its tip.

**Dimensions.** Cocosphere long axis from 8 to 11 µm; coccolith height from 1.3 to 1.5 µm; coccolith base length ca. 1 µm.

**Genus Florisphaera** Okada and Honjo, 1973

Coccospheres in the form of a multi-petaled flower. Coccoliths in the shape of polygonal plates, classified as nannoliths; to form the coccosphere, these nannoliths are arranged all in the same direction and show a concentric pattern in top view, forming a rosette when spread open in apical view.

**Florisphaera profunda** Okada and Honjo, 1973 (Figs. 84C, D and 85A-C)

*Coccoliths* are small irregular plates formed of single calcite units. A peg-like structure on the base of some specimens may indicate a second crystal unit.

Okada and Honjo (1973) separated the species in two varieties (A and B) on the basis of the differences in coccolith shape and size. Later, the varieties were validated as var. *profunda* and var. *elongata* (Okada and McIntyre, 1977; 1980), var. *profunda* being smaller, more quadrangular and having a zigzag pattern of lines at the base and top (Fig. 85B), while var. *elongata* is larger in size, with side profiles tapered towards the bottom, and the top profile straight with an outstanding peak (Fig. 85A).

Among NW Mediterranean specimens, some possess clearly identifiable coccoliths of both reported varieties. Other specimens possess coccoliths very different from both recognized varieties, e.g. the specimen figured in Fig. 85D, the coccoliths of which are notably different in shape and have a conspicuous distal spine. More observations are required in order to be able either to distinguish varieties or to acknowledge that they are not consistently separable, as suggested by Young (1998).

**Dimensions.** Cocosphere diameter (5.4-) 7.5-8.5 (-11) µm; coccoliths length (1.7-) 2.2-2.6 (-3.0) µm, coccolith width (1.0-) 1.5-1.8 (-3.0) µm.

**Family CALYPTROSPHAERACEAE**

Boudreaux et Hay, 1969

This family embraces all the holococcolithophores, which have only holococcoliths in their known life cycle. Holococcoliths are composed of microcrystals arranged in an ordered manner. Parke and Adams (1960) reported that a culture of a heterococcolithophore, *Coccolithus pelagicus*, had given rise to cells of a holococcolithophore, the former *Crystallolithus hyalinus*, on the shaking of heterococcolith associations, the family Calyptrosphaeraceae at present only includes the holococcolithophore species for which no heterococcolith stage is known. The number of such species is rapidly diminishing as research advances. Several species and even genera (*Crystallolithus* Gaarder and Markali, emend. Gaarder 1980 (in Heimdal and Gaarder, 1980); *Turrisphaera* Manton, Sutherland and Oates, 1976b) have been taken out of this family in recent literature (Kleijne, 1991; Jordan and Kleijne, 1994; Jordan and Green, 1994; Young and Bown, 1997b) and are included among their heterococcolithophore counterparts.

The following descriptions of genus, species and coccolith morphology are mainly based on the revision work of Kleijne (1991); but here the species are alphabetically ordered following Jordan and Green (1994) and not separated by their monomorphism or dimorphism, since in some genera it is difficult to identify if they have mono- or dimorphic coccospheres.

**Genus Anthosphaera** Kampfner emend. Kleijne, 1991

Coccosphere with calyptrolith-like body coccoliths and circum-flagellar fragarioliths. The calyp-
trolith-like body coccoliths have characteristic proximal rims of one crystal thickness; the circum-flagellar fragarioliths have the same characteristic proximal rim and a single layered leaf-like structure making up the rest of the coccolith. The crystals are cubiform.

**Anthosphaera fragaria** Kamptner, 1937 emend. Kleijne, 1991 (Figs 86A, B)

*Anthosphaera fragaria* Kamptner, 1937, p. 304, pl. 15, fig. 20.
*Helladosphaera fragaria* (Kamptner), Gaarder, 1962, pp. 47, 48, pl. 11.
*Anthosphaera fragaria* Kamptner emend. Kleijne, 1991, p. 304, pl. 15, fig. 20.

Body holococcoliths have a dome-shaped distal part and a proximal baseplate with the rim three crystals wide and with pores. The large fragarioliths have a rim three crystals wide and bear a very large and broad, single layered process.

A single “hybrid” collapsed coccosphere showing dimorphic endothecal coccoliths of *Syracosphaera molischii* with both body and circumflagellar coccoliths of *Anthosphaera fragaria* (Fig. 112A) was found in the studied samples. This collapsed coccosphere was not considered a conclusive combination due to the observed bad condition of the specimen.

The specimens studied (4 coccospheres) have 8, 7, 8 and 10 fragarioliths, and 54, 44, 60 and 66 body coccoliths.

**Dimensions.** Coccosphere diameter (5-) 6.5-7.0 (-8) µm; fragariolith height (2.1-) 2.2-2.6 (-2.9) µm; body coccolith length (1.0-) 1.15-1.30 (-1.8) µm.

**Anthosphaera cf. fragaria** Kamptner, 1937 emend. Kleijne, 1991 (Fig. 86C)

Two specimens studied are similar to *A. fragaria*, but differ in that both calyptrolith-like coccoliths and fragarioliths are smaller in size and have larger pores.

The coccospheres possess between 6 and 8 fragarioliths and 50 to 80 body coccoliths.

**Dimensions.** Coccosphere diameter ca. 5.5 µm; fragariolith height 1.7-2.0 µm; body coccolith length (0.75-) 0.85-0.95 (-1.1) µm.

**Anthosphaera lafourcadii** (Lecal 1967)
Kleijne, 1991 (Fig. 86D)

*Coccoliths smaller than those of* *A. fragaria.* Body coccoliths with a narrow rim connected to the distal dome by rows of one or two crystals separated by perforations. Circum-flagellar coccoliths with a broad, but very short, process.

Coccospheres consists of ca. 10 fragarioliths; 72, 62 and 48 body coccoliths.

**Dimensions.** Coccosphere diameter 4.1-5.1 µm; fragariolith height (0.77-) 0.85-0.95 (-1.1) µm; body coccolith length (0.76-) 0.8-1.0 (-1.1) µm.

**Anthosphaera periperforata** Kleijne, 1991 (Fig. 87)

*Anthosphaera periperforata* Kleijne, 1991, p. 60, 61, 63, pl. 9 figs. 3-6.

Body coccoliths with a narrow rim connected to the distal dome by ca. 16 radial rows of crystals separated by perforations. Circum-flagellar fragarioliths are constructed by a rim of crystals connected to a pointed leaf-like process by long rows of one crystal width. Three different types: 1, 2 and 3 can be recognized within this species.

- *A. periperforata* type 1 (Figs. 87A, B).

Kleijne, 1991, figured this type 1 in pl. 9, figs. 5-6

The body coccoliths of this type have the shortest connecting rows between the rim and the distal dome; this dome is highly vaulted and in some antapical coccoliths bears a small spine. Circum-flagellar coccoliths with pointed distal process and no central rows.

Coccospheres possess 10 to 14 fragarioliths and 64 to 80 body coccoliths.

**Dimensions.** Coccosphere diameter ca. 6-7 µm; fragariolith height (1.2-) 1.3-1.4 (-1.6) µm; body coccolith length (1.0-) 1.15-1.30 (-1.4) µm.

- *A. periperforata* type 2 (Figs. 87C).

Kleijne, 1991, figured this type 2 in pl. 9, figs. 3-4

The body coccoliths have rows of 4 to 5 crystals that connect the rim with the distal dome which is highly vaulted; in some antapical coccoliths the dome bears a small spine. Circum-flagellar coccoliths have a pointed distal process and usually central rows of one crystal width.

Coccospheres possess 5 to 8 fragarioliths and 52 to 96 body coccoliths.

**Dimensions.** Coccosphere diameter 4.8 - 6.5 µm; fragariolith height (1.25-) 1.35-1.65 (-1.75) µm; body coccolith length (0.95-) 1.10-1.35 (-1.40) µm.
- *A. periperforata* type 3 (Figs. 87D).

This type differs from types 1 and 2 in having nearly flat body coccoliths, with long rows of about 6 crystals connecting the rim with the reduced distal dome.

Coccospheres possess 54 to 100 coccoliths.

**Dimensions.** Coccosphere diameter 4.5 - 6.5 µm; fragario lith height ca. 1.5 µm; body coccolith length (0.95-) 1.10-1.20 (-1.25) µm.

**Anthosphaera** sp. type A (origami art) (Fig. 88A)

The body coccoliths have a very characteristic structure in the shape of a small origami paper boat, instead of the simple dome. Circum-flagellar fragario liths heavily ornamented.

Coccospheres have 6 to 8 fragario liths and 42 to 60 body coccoliths.

**Dimensions.** Coccosphere long axis ca. 5 µm; body coccolith length (1.0-) 1.10-1.20 (-1.35) µm; fragario lith height ca. 1.2 µm.

**Anthosphaera** sp. type B (Fig. 88B)

The body coccoliths have a thin rim constituted of a ring, one crystal wide, and a simple dome formed by only some crystals. Circum-flagellar fragario liths have a flat leaf-like process with nearly straight sides.

The studied specimen consists of ca. 8 fragario liths and ca. 80 body coccoliths.

**Dimensions.** Coccosphere long axis ca. 4.5 µm; body coccolith length ca. 0.6 µm; circum-flagellar coccolith height ca. 1.3 µm;

**Anthosphaera** sp. type C (Fig. 88C, D)

The small body coccoliths of this species appear to be very simple calyptroliths which, in some cases, have lost the central part leaving only the rim; circum-flagellar coccoliths can appear as very simple and slender fragario liths. This holococcolithophore might thus be considered to be a very simple representative of the genus *Anthosphaera.*

Coccospheres have from 10 to 12 circum-flagellar coccoliths; 170 to 268 body coccoliths.

**Dimensions.** Coccosphere long axis 5.8 µm; body coccolith length (0.4-) 0.6-0.7 (-0.8) µm; circum-flagellar coccolith height 1.3-1.5 µm.

**Genus Calicasphaera** Kleijne, 1991

Monomorphic coccospheres without obvious flagellar opening. The coccoliths, called calicaliths, are chalice-shaped; they consist of a tube, with or without constrictions, widening towards the distal end and always without any distal process.

**Calicasphaera concava** Kleijne, 1991 (Figs 89A, B)

*Calicasphaera concava* Kleijne, 1991, p. 42, pl. 1 fig. 5, 6.

The calicaliths have a proximal ring of crystallites and a concave wall, which widens broadly towards the distal end.

Coccospheres possess around 32 coccoliths.

**Dimensions.** Coccosphere diameter ca. 6 µm; coccolith height ca. 1.3 µm, proximal diameter ca. 0.9 µm, distal length ca. 1.6 µm.

**Calicasphaera blokii** Kleijne, 1991 (Figs 89C, D)

*Calicasphaera blokii* Kleijne, 1991, p. 42, pl. 2 fig. 1-3.

The calicaliths have a characteristic elliptical-oval shaped proximal side and have a short tube. Kleijne (1991) points out the strong resemblance of this species with some specimens of *Calyptrosphaera sphaeroidea* Schiller in terms of the size of the holococcoliths and of the crystallites.

Coccospheres possess around 62 coccoliths.

**Dimensions.** Coccosphere diameter ca. 6 µm; coccolith proximal length ca. 1.1 µm; distal length 1.0-1.3 µm.

**Genus Calyptrolithina** Heimdal, 1982

Coccosphere with dimorphic coccoliths. Body coccoliths are calyptroliths. Circum-flagellar coccoliths are zygololiths with a pointed bridge parallel to the long axis of the coccolith. The crystallites are arranged in an hexagonal pattern.

**Calyptrolithina divergens** (Halldal et Markali 1955) Heimdal 1982 var. *divergens* (Figs. 90A, B)

*Zygosphaera divergens* Halldal et Markali 1955 p. 8 pl. 2.

*Zygosphaera divergens* Halldal et Markali 1955 emend. Heimdal, in: Heimdal and Gaurder (1980), p. 12, pl. 3, fig. 24a, b.

*Calyptrolithina divergens* (Halldal et Markali 1955), Heimdal (1982), p. 54; Kleijne, 1991, p. 45, pl. 10, fig. 1-3.

60 L. CROS and J.-M. FORTUÑO
Body calyptroliths with a short and distally widening tube that surrounds and protrudes over the distal surface, which has the form of a highly vaulted roof. Circum-flagellar zygoliths with a broad process ending in a sharply pointed protrusion.

Coccospheres possess around 60 body coccoliths.

**Dimensions.** Body coccolith length (1.4-) 1.6-1.7 (-1.9) µm.

*Calyptrolithina divergens* var. *tuberosa* (Heimdal) Jordan et al., 1993(Figs. 90C, D)

Sphaerozoaerapyra graecilina* (Kamptner) Thornsden, 1972, p. 54, figs. 10-15; Nishida, 1979, pl. 4a-b.

*Calyptrolithophora gracieilina* (Kamptner) Heimdal 1980, p. 2; Winter and Siesser, 1994, p. 150, fig. 171 (phot. from S. Nishida).

The body calyptroliths have a rounded distal protrusion. The protrusion of circum-flagellar calyptroliths is larger, sometimes forming a bridge crossing the short axis of the coccolith.

Coccospheres have 6 to 8 circumflagellar coccoliths; 64 to 120 body coccoliths.

**Dimensions.** Coccosphere major axis 10-14 µm; coccolith length (2.1-) 2.2-2.3 (-2.5) µm.

*Calyptrolithophora papillifera* (Halldal) Heimdal in Heimdal et Gaarder, 1980 (Fig. 91)

*Calyptrosphaera papillifera* Halldal, 1953, p. 48, fig. 14; Halldal and Markali, 1954a, p. 118, pl. 2.

*Calyptrolithophora papillifera* (Halldal) Heimdal in Heimdal et Gaarder, 1980, p. 2-3, pl. 1, fig. 2-3; Kleijne, 1991, p. 50, pl. 12, figs. 1-2.

Body calyptroliths with a flat distal surface with perforate hexagonal pattern. The circum-flagellar calyptroliths have a convex distal side with characteristic parallel rows of crystallites. A collapsed coccosphere of *C. papillifera* surrounded by several coccoliths of *Syracosphaera histrica* (Fig. 112B) was found in the studied samples, but this collapsed coccosphere was not considered a conclusive combination (Cros et al. 2000b).

Coccospheres possess from 118 to 152 coccoliths.

**Dimensions.** Coccosphere major axis ca. 12–14 µm; coccolith length (1.5-) 1.7-1.9 (-2.0) µm.

Genus *Calyptrosphaera* Lohmann, 1902.

This genus bears dome-shaped calyptroliths, and is usually considered to have monomorphic coccoliths; nevertheless, some coccoliths near the flagellar area may be higher than the others and may even possess a papilla or a short distal spine.

*Calyptrosphaera cialdii* Borsetti et Cati, 1976

Figs. 92C, D.

Sphaerozoaerapyra cialdii Borsetti et Cati, 1976, p. 210-211, pl. 12, figs. 3-5.

The coccosphere bears monomorphic coccoliths with the central area slightly depressed; the crystal-
lites have characteristic arrangement (Fig. 92D). The coccoliths appear to be laminoliths rather than calyptroliths; should this be the case, this taxon should be placed in the genus *Syracolithus*, which is monomorphic and bears laminoliths.

The three studied specimens have 64, 116 and 130 coccoliths.

**Dimensions.** Coccosphere major axis 15-17 µm; coccolith length (2.3-) 2.5-2.7 (-2.9) µm.

*Sphaerocalyptra cf. papillifera* Halldal, in Borsetti and Cati, 1976, p. 213, pl. 14, fig. 1; *Sphaerocalyptra aff. S. papillifera* (Halldal) Halldal, Okada and McIntyre, 1977, pl. 11, fig. 6.

Calyptrosphaera dentata Kleijne, 1991, p. 26-28, pl. 3, figs. 1-2

The calyptroliths have a distal surface with the usual hexagonal pattern and six-sided regularly arranged perforations; the rim is very characteristic, protruding from the distal plate with several centripetal rings of microcrystals and a conspicuous tooth-like protrusion.

Coccospheres possess between 46 and 70 coccoliths.

**Dimensions.** Coccosphere major axis 11-15 µm; coccolith length (2.5-) 2.9-3.0 (-3.3) µm.

*Calyptrosphaera heimdaliae* R.E. Norris, 1985, orth. emend. Jordan et Green, 1994 (Figs. 93A, B)

*Sphaerocalyptra* (Kamptner) Halldal and Markali, 1955, p. 10, pl. 6; Okada and McIntyre 1977, pl. 13, fig. 11; Winter et al. 1979, pl. 4, fig. 12.

*Calyptrosphaera heimdaliae* R.E. Norris, 1985, p. 628, fig. 35; Winter and Siesser, 1994, fig. 144 (phot. from A. Kleijne).

Calyptroliths consisting of a broad rim and a dome-shaped central area with one central pore and 7 large pores surrounding the base of the dome area; these latter pores are characteristically straight on the proximal side of the coccolith and arched distally. Some calyptroliths, presumably from the circum-flagellar area, are higher and can bear a conspicuous spine.

Coccospheres possess from 30 to 44 coccoliths.

**Dimensions.** Coccosphere major axis 10-11 µm; coccolith length (2.0-) 2.5-2.9 (-3.2) µm.

*Calyptrosphaera oblonga* Lohmann, 1902

*C. oblonga* is now considered as the holococcolith phase of *Syracosphaera pulchra* (p.Figs. 51C, D).

**Calyptrosphaera sphaeroidea** Schiller 1913 (Figs. 94C, D)

*Calyptrosphaera sphaeroidea* Schiller 1913, p. 606, pl. 3, figs. 18 a, b; Klaveness, 1973, pp. 152, 154, 157, 158; Kleijne, 1991, p. 28, pl. 2, figs. 4-7.

*Calyptrosphaera aff. globosa* Lohmann, in Borsetti and Cati, 1976, p. 211, pl. 12, fig. 6, 7.

Spherical coccosphere built up of dome shaped calyptroliths; these are constituted of relatively large crystallites. Calyptroliths with a proximal rim, one crystallite thick, a widening tube and a rounded distal part. The distal part is sometimes incompletely constructed (Fig. 94D).

Coccospheres possess from 48 to 182 coccoliths (7 specimens).

**Dimensions.** Coccosphere major axis (5.5-) 6-7 (-12) µm; coccolith length (0.9-) 1.1-1.3 (-1.5) µm.

**Calyptrosphaera** sp. (smaller *heimdaliae*) (Figs. 93C, D)

The specimens closely resemble *C. heimdaliae*, but have smaller coccoliths with lower tubes and a larger number of pores (around 20) which are smaller and square-shaped. An added character is that the microcrystallites are packed more closely.

It is remarkable that some specimens appear to be more similar to *C. heimdaliae* than others; this might be a taxon possibly related with *C. heimdaliae*, or be morphological variants of this latter species.

Coccospheres possess from 54 to 78 coccoliths.

**Dimensions.** Coccosphere major axis 7-12 µm; coccolith length (1.9-) 2.2-2.5 (-2.7) µm.

**Genus Corisphaera** Kamptner 1937

Coccospheres with dimorphic coccoliths. Body coccoliths are zygoliths. The circum-flagellar coccoliths are enlarged zygoliths with an expanded, pointed bridge.

This genus is recorded in the recent check-lists of the extant coccolithophores and Haptophyta (Jordan and Kleijne, 1994; Jordan and Green, 1994) with only three species (*C. gracilis*, *C. strigilis* and *C. tyrrheniensis*), while in the extensive holococcolithophore revision of Kleijne (1991), this genus includes two more species described in open nomenclature (*C. sp. type A* and *C. sp. type B*). In the present NW Mediterranean study, the *Corisphaera* specimens display a high diversity of morphologies, but only three of the five above enumerated species...
can clearly and repeatedly be recognized. A deeper study of *Corisphaera* should be carried out, including a review of the old literature of LM studies and further detailed observation of LM and parallel SEM samples, to properly clarify this genus. Plate 62 includes only the clearly classified *Corisphaera* species and Plate 63 represents the high diversity of *Corisphaera* morphologies.

Representatives of this genus have been found forming associations with coccospheres of the genus *Syracosphaera* (see *S. bannockii* and *S. delicata*).

**Corisphaera strigilis** Gaarder, 1962
(Figs. 95A, B)

*Corisphaera strigilis* Gaarder, 1962, p. 43, pl. 6; Heimdal and Gaarder, 1980, p. 4, pl. 1, fig. 8; Kleijne, 1991, p. 52, pl. 13, fig. 3, 4. *Homozygosphaera strigilis* (Gaarder), Norris, 1985, p. 636.

The zygolith-like body coccoliths have a flat, one crystal thick basal layer, with a central opening which is crossed by a low and broad bridge which sometimes resembles a small cap (Kleijne, 1991, pl. 13, fig. 3). The circum-flagellar zygolith-like coccoliths are similarly constructed, but have a small pointed leaf-like process instead of the broad bridge. Some authors (Norris, 1985; Kleijne, 1991) point out the resemblance of this species to certain species in different genera (e.g. with *Anthosphaera* species) and consider that a further revision of the present species is necessary.

Coccospheres possess from 62 to 90 coccoliths.

*Dimensions*. Coccosphere long axis 5-7 µm; coccolith length (0.9-) 1.15-1.25 (-1.33) µm.

**Corisphaera tyrreniensis** Kleijne, 1991
(Figs. 95C, D)

*Corisphaera tyrreniensis* Kleijne, 1991, p. 71-72, pl. 12, fig. 6; Winter and Siesser, 1994, p. 151, fig. 176 (phot. from Kleijne).

The body zygoliths as well as the larger circum-flagellar zygoliths are constructed of loosely connected rows of microcrystallites, resulting in a characteristic perforated appearance.

Coccospheres possess from 28 to 60 coccoliths.

*Dimensions*. Coccosphere long axis 4.5-7.5 µm; coccolith length (1.25-) 1.50-1.60 (-1.75) µm.

**Corisphaera** sp. type A of Kleijne, 1991

*Corisphaera* sp. type A of Kleijne is now considered the Holococcolithophore phase (perforate) of *Syracosphaera bannockii* (see p. and Figs. 41A, B).
Body zygoliths have a high wall and a wide, high and thin bridge which is pointed distally; this bridge forms a real mid-wall inside the zygolith.

Coccospheres possess from 60 to 80 coccoliths.

**Dimensions.** Coccosphere long axis 7-9 µm; coccolith length 1.3-1.6 µm.

**Corisphaera** sp. (double-layered body zygoliths with S-shaped bridge) (Fig. 97C, D)

? Okada and McIntyre, 1977, p. 28, pl. 13, fig. 4.

? Corisphaera gracilis Kamptner, Kleijne, 1991, pl. 12, fig. 5.

Body zygoliths having a characteristic S-shaped bridge, double-layered wall and no crystallites extending into the central area of the base plate. Circum-flagellar coccoliths with double-layered wall and a broad pointed protrusion.

Coccospheres possess from 38 to 48 coccoliths.

**Dimensions.** Coccosphere long axis 7-8 µm; coccolith length (1.8-) 1.9-2.0 (-2.2) µm.

Genus **Crystallolithus** Gaarder et Markali 1956, emend. Gaarder 1980 (in: Heimdal et Gaarder, 1980)

The **Crystallolithus** genus was described as having coccospheres of monomorphic crystalloliths. This genus had three species: **Crystallolithus braarudii**, **C. hyalinus** and **C. rigidus**. **C. braarudii** and **C. hyalinus** are now considered as the holococcolithophore phases of **Coccolithus pelagicus** (Parke and Adams, 1960; and Rowson et al. 1986), and **C. rigidus** is considered the holococcolith phase of **Calcidiscus leptoporus** (Kleijne, 1991).

**Crystallolithus rigidus** Gaarder 1980, in: Heimdal and Gaarder, 1980

**Crystallolithus rigidus** is now considered to be the holococcolith phase of **Calcidiscus leptoporus** (Kleijne, 1991). The former **Crystallolithus rigidus** is presented in Figs. 62C, D.

Genus **Daktylethra** Gartner 1969 (in: Gartner and Bukry, 1969)

This genus bears coccoliths named aeroliths. The aeroliths are described as calyptrolith-like holococcoliths with an areolate interior comprised of thickened ridges of calcite elements.

**Daktylethra pirus** (Kamptner, 1937) Norris, 1985 (Figs. 98A, B)

The coccosphere is formed of characteristic calyptrolith-like holococcoliths (Fig. 98B show such coccoliths in distal view). The internal thickened ridges distinctive of this species (Norris, 1985) were not visible in these studied specimens.

Although this species is considered to have monomorphic coccoliths, presumed circum-flagellar coccoliths with a short conical extension protruding from the central area are observed (Thron- sen, 1972; Heimdal, 1993; Fig. 98A).

Geisen et al. (2000) presented combination coccospheres with heterococcoliths of **S. pulchra** and holococcoliths of **Daktylethra pirus** (Kamptner) Norris, and suggested a cryptic speciation, not clearly recognizable from the heterococcolithophore morphology, as a possible explanation for these very different holococcoliths associated to Syracosphaera pulchra. More work in this matter is necessary to ascertain whether **Daktylethra pirus** is part of the life-cycle of **S. pulchra**; in the meantime it seems better to consider **Daktylethra pirus** as independent of **S. pulchra**.

Coccosphere consists of ca. 180 coccoliths (1 specimen).

**Dimensions.** Coccospheres major axis 6-18 µm; coccolith length (2.2-) 2.4-2.7 (-3.2) µm.

Genus **Helladosphaera** Kamptner, 1937

Coccosphere with dimorphic coccoliths. Body coccoliths are zygoliths. Circum-flagellar coccoliths are helladoliths which are characterized by having a large, double-layered process.

**Helladosphaera cornifera** (Schiller, 1913)

Kamptner, 1937 (Figs. 98C, D)

**Helladosphaera cornifera** (Schiller) Kamptner, 1937, p. 308, pl. 17, figs. 36-38. **Helladosphaera cornifera** (Schiller) Kamptner, Kleijne, 1991, p. 37-39, pl. 14, fig. 3-6; Winter and Siesser, 1994, p. 151, fig. 177.

The body zygoliths have a high bridge that is considerably wider than the coccolith tube, which does not have crystallites extending to the central area. Circum-flagellar helladoliths have a large angular process with a pointed upper rim and a small pore near the basal tube.

A group of coccoliths which appeared to be a mixed collapsed coccosphere of **Syracosphaera**
nodosa and Helladosphera cornifera is illustrated in Fig. 113D. However, this collapsed coscosphere was not considered as a conclusive combination coscosphere (Cros et al., 2000b).

Coscospheres possess 10-12 circum-flagellar coccoliths and (40-) 54-84 (-106) body zygoliths.

Dimensions. Coscosphere major axis (6-) 7-8 (-11.5) µm; body coccolith length (1.1-) 1.4-1.5 (-1.6) µm.

Genus Homozygosphaera Deflandre, 1952

This genus bears zygoliths, and is considered to contain species with monomorphic coccoliths; nevertheless, some coccoliths near the flagellar area may be higher than the others and may even possess a papilla.

Homozygosphaera arethusae (Kamptner) Kleijne 1991 (Figs. 99A, B)

Corisphaera arethusae Kamptner, in Borsetti and Cati, 1972, p. 403, pl. 48, fig. 3a,b.

Homozygosphaera arethusae (Kamptner) Kleijne, 1991, p. 31, pl. 5, fig. 3,4; Winter and Siesser, 1994, p. 145, fig. 151 (phot. from Alcober).

The zygoliths have a proximal tube that seems double-layered and also a distal, robust bridge, which sometimes is very broad. The circum-flagellar coccoliths have a higher bridge topped by a small protrusion.

Two coccolith heaps with heterococcoliths of Syracosphaera sp. type D and holococcoliths of Homozygosphaera arethusae were found (Figs. 113A, B), but they were not considered conclusive combination coscospheres (see discussion in Cros et al., 2000b)

Coscospheres possess from 54 to 96 coccoliths.

Dimensions. Coscospheres major axis (6-) 9-10 (-15) µm; coccolith length (1.2-) 1.6-1.8 (-2.0) µm, coccolith height ca. 0.8 µm increasing near apical pole up to 1.8 µm.

Homozygosphaera triarcha Halldal et Markali, 1955 (Figs. 99C, D)

Homozygosphaera triarcha Halldal et Markali, 1955, p. 9, pl. 4, figs. 1-4.

Homozygosphaera triarcha Halldal et Markali, in Borsetti and Cati, 1972, p. 404, pl. 50, fig. 2; Kleijne, 1991, p. 31, 33, pl. 5, figs. 5-6.

The zygoliths have a proximal tube with 3 distally protruding arches, two of which rise from one side of the tube and the other from the opposite side; a conical process protrudes where the arches meet.

Several coccoliths, presumably from the circum-flagellar area, have a more elevated protrusion with a higher conical process that has a spine-like appearance at the tip.

Coscospheres possess from 86 to 88 coccoliths.

Dimensions. Coscosphere major axis 10-13 µm; coccolith length (1.7-) 1.9-2.2 (-2.4) µm.

Genus Periphyllophora Kamptner, 1937

Periphyllophora was considered as a monospecific genus having coscospheres consisting of monomorphic helladoliths. Recently, Cros et al. (2000b) demonstrated the association of the only species in this genus with the heterococcolithophore Syracosphaera anthos.

Periphyllophora mirabilis (Schiller) Kamptner, 1937

P. mirabilis is now considered as the holococcolith phase of Syracosphaera anthos (p. and Fig. 35B.

Genus Poricalyptra Kleijne, 1991

Coccosphere with dimorphic coccoliths. Body coccoliths are calyptroliths with a perforated tube wall and a flat distal surface with slits or pores and a prominent rim. Circum-flagellar coccoliths are helladoliths.

Poricalyptra aurisinae (Kamptner 1941) Kleijne, 1991 (Figs. 100A, B)

Helladosphaera aurisinae, Kamptner, 1941, p. 91, pl. 11, figs. 121-124. Helladosphaera aurisinae Kamptner, in Borsetti and Cati, 1972, p. 403, pl. 49, fig. 1a,b; Nishida, 1979, pl. 20, fig. 2a,b; Heimdal and Gaarder, 1980, p. 7, pl. 2, fig. 14; Reid, 1980, p. 166, pl. 7, fig. 5,6. Poricalyptra aurisinae, Winter and Siesser, 1994, p. 152, fig. 179 (phot. from Alcober).

The body calyptroliths present, on the distal side, four oblong transverse pores and, following the minor axis, one row of extra crystallites. Circum-flagellar helladoliths with no extra pores.

Coccospheres possess from 60 to 64 coccoliths.

Dimensions. Coccosphere major axis 7-12 µm; coccolith length (2.1-) 2.3-2.4 (-2.6) µm.

Poricalyptra isselii (Borsetti and Cati, 1976) Kleijne, 1991 (Figs. 100C, D)

Helladosphaera isselii, Borsetti and Cati, 1976, pp. 220-221, pl. 16, figs. 1-3. Poricalyptra isselii (Borsetti and Cati) Kleijne, 1991, p. 62, pl. 15, figs. 5,6; Winter and Siesser, 1994, p. 152, fig. 181 (phot. from Samtleben).
The body calyptroliths have large pores (usually 6) in the distal side, and, following the minor axis, one very short row of extra crystallites. Circum-flagellar helladoliths with no extra pores.

Coccospheres possess from 68 to 92 coccoliths.

**Dimensions.** Coccosphere major axis 9.5-11.5 µm; coccolith length (1.7-) 1.9-2.1 (-2.4) µm.

**Genus** *Poritectolithus* Kleijne, 1991

Coccosphere with dimorphic coccoliths. Body holococcoliths with characteristic strings of crystallites on the distal face. Circum-flagellar coccoliths are helladoliths. Within *Poritectolithus* there are two clearly distinguishable groups; one with body coccoliths like calyptroliths and the other with body coccoliths like zygoliths. N.B. Kleijne (1991) described this genus as possessing zygolith-like body coccoliths.

*Poritectolithus* taxa bearing calyptrolith-like body coccoliths

This group contains the *Poritectolithus* species with calyptrolith-like body coccoliths which have a closed roof. These calyptroliths can be flat like laminoliths, e.g. *Poritectolithus* sp. 1, or with the central area of the distal side slightly convex, e.g. *Poritectolithus tyronus*, or like real calyptroliths with a distally widening wall, e.g. *Poritectolithus poritectus*.

*Poritectolithus* sp. 1

(Figs. 101A, B)

The coccosphere consists of flat body calyptroliths having a rim two crystallites high. Circum-flagellar helladoliths with a basal part similarly constructed and a straight and flat leaf-like protrusion. Coccosphere possesses ca. 100 coccoliths.

**Dimensions.** Body coccolith length 1.5-1.6 µm, width 0.95-1.05 µm, height 0.16-0.22 µm; circum-flagellar coccolith height 1.4-1.7 µm.

*Poritectolithus tyronus* Kleijne, 1991

(Figs. 101C, D)

Body calyptroliths with a slightly convex central distal part which has crystals arranged in rows, leaving narrow, elongate openings (Kleijne, 1991). Circum-flagellar helladoliths with a basal part similarly constructed and a straight and flat leaf-like protrusion. The circum-flagellar coccoliths have a very sharply pointed protrusion, which ends in a peak of one crystal width (see upper right corner of Plate 67, fig. 4).

Coccosphere consists of ca. 92 coccoliths.

**Dimensions.** (Collapsed) coccosphere diameter ca. 9 µm; body coccolith length 1.25-1.75 µm, width 0.9-1.0 µm, height ca. 0.3 µm; circum-flagellar coccolith height 1.5-2.0 µm.

*Poritectolithus* poritectum (Heimdal 1980) Kleijne, 1991 (Figs. 102A, B)

*Helladosphaera poritectum* Heimdal, in Heimdal and Gaarder, 1980, p. 7, pl. 2, fig. 15 a.b.

*Non* *Poritectolithus poritectum* (Heimdal) Kleijne, 1991, p. 62, 63, pl. 16, fig. 1-3, neither in Winter and Siesser, 1994, p. 153, fig. 184.

The body holococcoliths are more calyptrolith-like than zygolith-like; they are constructed of relatively large crystallites which form a wall and a distal side with characteristic rows and a conspicuous rim; several neighbouring rows appear to present some kind of symmetry which is also clearly shown in the micrographs of Heimdal and Gaarder (1980); the wall slightly widens distally and protrudes the neighbouring distal roof. Circum-flagellar helladoliths with a flared wall and a large protrusion.

Coccosphere consists of ca. 66 coccoliths.

**Dimensions.** Coccosphere diameter ca. 9 µm; body coccolith length 1.3-1.8 µm, width 1.1-1.3 µm, height 0.2-0.5 µm; circum-flagellar coccolith height ca. 2 µm.

*Poritectolithus* taxa bearing zygolith-like body coccoliths

This group includes the *Poritectolithus* with zygolith-like body coccoliths which have a bridge consisting of several irregularly placed rows of crystals. These zygolith-like holococcoliths can have a slightly vaulted bridge, e.g. *Poritectolithus* sp. 2, or possess a very high and vaulted bridge, e.g. *Poritectolithus maximus* Kleijne, 1991.

*Poritectolithus* sp. 2.

(Figs. 102C, D)

Body holococcoliths are zygolith-like coccoliths with convex rows of crystallites, irregularly placed, forming a bridge. Circum-flagellar helladoliths have a triangular-shaped leaf-like protrusion, which is wider than high. The coccoliths are constructed of microcrystals separated by perforations.
The studied specimen closely resembles the specimen figured in Kleijne (1991) as *Poritectolitus poritectum* and that figured, with the same name, in Winter and Siesser (1994), fig. 185.

Coccosphere consists of ca. 80 coccoliths.

*Dimensions.* Coccosphere long axis ca. 14 µm; body coccolith length 1.7-1.9 µm, width ca. 1.3 µm; circum-flagellar coccolith height ca. 1.8 µm.

**Genus Sphaerocalyptra** Deflandre, 1952

Coccosphere with dimorphic coccoliths. Body and circum-flagellar holococcoliths are calyptroliths with a tapered shape, resembling campanulate coccoliths without a tube; circum-flagellar coccoliths clearly higher than body coccoliths.

Species of this genus appear to have relationships with species of the family Rhabdosphaeraceae.

*Sphaerocalyptra quadridentata* (Schiller, 1913) Deflandre, 1952 (Figs. 103A, B)

*Calyptrosphaera quadridentata* Schiller, Kamptner, 1941, pp. 78, 99, pl. 2, figs. 20-23.
*Sphaerocalyptra quadridentata* (Schiller), Borsetti et Cati, 1972, p. 398, pl. 41, fig. 1.
*Sphaerocalyptra quadridentata* (Schiller) Deflandre, Kleijne, 1991, p. 65, pl. 17, fig. 3.

Body calyptroliths taper abruptly distally and are tipped by a small protrusion which usually forms a short elongated ridge along the long axis. Circum-flagellar calyptroliths are notably higher than body calyptroliths and taper more gradually. The microcrystallites are irregularly arranged, separated by small perforations.

This species was found as part of a combined, but collapsed, specimen with *Rhabdosphaera clavigera* (Fig. 114A) and coccoliths of the same species were found (Fig. 114B) in an apparently random grouping (see discussion in *R. clavigera* text).

Coccospheres have from 30 to 56 coccoliths (6 specimens).

*Dimensions.* Coccosphere diameter 5-8.5 µm; body coccolith length (1.3-) 1.6-1.8 (-2.3) µm.

*Sphaerocalyptra cf. adenensis* Kleijne, 1991 (Figs. 103C, D)

*Sphaerocalyptra adenensis* Kleijne, 1991, p. 65, pl. 17, fig. 4-6; Winter and Siesser, 1994, p. 154, fig. 186.

Body calyptroliths taper abruptly from the base. Circum-flagellar calyptroliths are notably higher than body calyptroliths, tapering slightly towards near the base and more abruptly distally, forming a pointed protrusion that sometimes appears bent. The microcrystallites are closely packed and appear arranged in concentric rows.

The specimens studied have smaller coccoliths than the described *S. adenensis* Kleijne, 1991.

Coccospheres have from 58 to 74 coccoliths (3 specimens).

*Dimensions.* Coccosphere diameter 5.5-8.5 µm; body coccolith length (1.2-) 1.55-1.75 (-2.0) µm.

*Sphaerocalyptra* sp. 1.

(Figs. 104A, B)

Body coccoliths are of small size and steeply tapered, with a thin central protrusion tipped by one crystallite. Circum-flagellar calyptroliths are notably higher than body calyptroliths and are tipped by a thin and acute protrusion.

Some *Sphaerocalyptra* specimens, morphologically very related to *Sphaerocalyptra* sp. 1, with few crystallites on the distal side (Fig. 18A), are now considered as the holococcolithophore phase of *Acanthoica quattrospina* (Cros et al., 2000b).

Coccospheres possess from 62 to 134 coccoliths.

*Dimensions.* Coccosphere diameter 6-10 µm; body coccolith length (1.2-) 1.35-1.55 (-1.9) µm.

*Sphaerocalyptra* sp. 2 (cone-shaped body coccoliths) (Fig. 105A)

Body coccoliths are small cone-shaped calyptroliths tipped by a thin, acute spine-like protrusion. Circum-flagellar calyptroliths are notably higher and thinner than those covering the body and they possess a long and thin distal projection.

Figs. 114C, D, illustrates a collapsed *Sphaerocalyptra* sp. 2 with odd coccoliths of *Acanthoica*. Coccosphere consists of ca. 44 coccoliths.

*Dimensions.* Coccosphere collapsed; body coccolith length 0.7-0.9 µm, height (0.65-) 0.8-0.9 (-1.05) µm; circum-flagellar coccolith proximal diameter ca. 1 µm, height ca. 1.7 µm.

*Sphaerocalyptra* sp. 3 (string-formed calyptroliths) (Figs. 105B-D)

Body calyptroliths consist of a thin basal ring of crystals connected to about six strings of one crystallite width which form the perforate calyptrolith; where these strings meet, a thin central distal pro-
troch is formed. Circum-flagellar calyptroliths are notably higher (i.e. with longer strings).

Coccosphere consists of ca. 84 coccoliths (1 specimen).

**Dimensions.** Coccosphere diameter ca. 5 µm; body coccolith length (0.7-) 1.0-1.2 (-1.3) µm, height ca. 0.5 µm; circum-flagellar coccolith height 1.2-1.7 µm.

*Sphaerocalyptra* sp. 4 (circum-flagellar coccoliths having a stick-like protrusion) (Figs 104C, D)

The body calyptroliths have a basal rim two crystals thick and the distal side is formed by arches (usually three, but sometimes two forming a bridge). Circum-flagellar calyptroliths, usually three arched, have a characteristic thick sharp-pointed stick-like protrusion.

Coccosphere consists of ca. 30 coccoliths (1 collapsed specimen).

**Dimensions.** Body coccolith diameter (1.4-) 1.6-1.8 (-1.9) µm, height ca. 1.2 µm; circum-flagellar coccolith diameter 1.8-1.9 µm, height 2.4-2.7 µm.

*Sphaerocalyptra* sp. 5 (arch-shaped calyptroliths with irregularly filled distal side) (Figs. 106A, B)

The body calyptroliths appear to have a basal rim two crystals thick and the calyptroform side is formed of rounded irregularly widened arches. Circum-flagellar calyptroliths tipped by a long spine-like protrusion composed of three rows of crystallites.

Coccospheres possess 34-60 coccoliths (2 specimens).

**Dimensions.** Coccosphere long axis 6-7 µm; body coccolith length (1.1-) 1.4-1.7 (-2.1) µm; circum-flagellar coccolith diameter 1.3-1.9 µm, height ca. 1.5 µm.

*Sphaerocalyptra* sp. 6 (rings-shaped residual calyptroliths) (Figs. 106C, D)

The small body calyptroliths are formed of a basal ring with some crystallites that appear to be the residual part of the calyptrolith. Circum-flagellar calyptroliths have a rim two crystals high and a long and straight spine.

Coccosphere consists of ca. 8 circum-flagellar coccoliths; ca. 100 body coccoliths.

**Dimensions.** Coccosphere long axis 5-6 µm; body ring coccoliths length (0.5-) 0.7-0.9 (-1.1) µm; circum-flagellar coccolith diameter 0.8-1.1 µm, spine height (1.5-) 1.8-2.2 (-2.5) µm.

Genus *Syracolithus* (Kamptner, 1941) Deflandre, 1952.

Monomorphic coccosphere consisting of laminoliths. Certain representatives of this genus form associations with *Helicosphaera* (Cros et al. 2000)

*Syracolithus catilliferus* (Kamptner, 1937) Deflandre, 1952

*S. catilliferus* is now considered as the holococcolith phase (solid) of *Helicosphaera carteri* (p., Figs. 10C, D and Fig. 11A.

*Syracolithus confusus* Kleijne, 1991

*S. confusus* is now considered as the holococcolith phase (perforate) of *Helicosphaera carteri* (p., Fig. 11B).

*Syracolithus dalmaticus* (Kamptner) Loeblich et Tappan, 1966

Fig. 107A.

*Syracosphaera dalmatica* (Kamptner) Kamptner 1927, p. 178, fig. 2.

*Syracosphaera (Syracolithus) dalmatica* Kamptner, Kamptner 1941, pp. 81, 104, pl. 4, figs. 46-48.

*Syracolithus dalmaticus* (Kamptner) Kleijne 1991, p. 37, pl. 7, fig. 1; Winter and Siesser 1994, p. 147, fig. 160 (phot. from J. Alcober).

The coccoliths are constructed of a rim and a cover which is centrally thick and has finger-like lateral protrusions which rest on the rim; the central part of the coccolith is hollow.

*Syracolithus dalmaticus* resembles *S. confusus*, differing mainly in possessing hollow holococcoliths with real holes in the cover instead of having real laminoliths with superficial pits.

In the studied coccospheres were counted around of 45 coccoliths.

**Dimensions.** Coccosphere long axis 10-11 µm; coccolith length 2.7-2.9 µm.

*Syracolithus schilleri* (Kamptner)

Kamptner, 1956 (Fig. 107B)

*Syracosphaera (Syracolithus) schilleri* (Kamptner) Kamptner 1941, p. 82, pl. 5, figs. 52-54; Lecal-Schlauder, 1951, p. 323, pl. 10, figs. 1-2. *Homozygosphaera schilleri* (Kamptner) Okada and McIntyre, 1977, p. 32, pl. 12, fig. 7.
Large-sized laminoliths with, on their distal side, 8 to 16 pores (large holes) and a blunt protrusion tipped with some crystals, which form small spines in several specimens. Cocospheres possess from 60 to 98 coccoliths.

**Dimensions.** Coccosphere long axis 10.5-14.0 µm; coccolith length 2.7-3.7 µm.

**Syracolithus quadriperforatus** (Kamptner 1937)
Gaarder 1980 (Figs. 107C, D)

Syracosphaera (Syracolithus) quadriperforata Kamptner, Kamptner, 1941, pp. 81, 82, pl. 4, fig. 49; pl. 5, fig. 50, 51.
Homozygosphera quadriperforata (Kamptner) Gaarder, 1962, pp. 48-50, pl. 12; Borsetti and Cati, 1976, p. 222, pl. 16, figs. 7-10; Winter et al., 1979, pl. 5, fig. 5.

Syracolithus quadriperforatus (Kamptner) Gaarder, in: Heimdal and Gaarder, 1980, pp. 10, 12; Norris, 1985, p. 638, figs. 9, 42, 51, 52; Kleijne, 1991, p. 37, 38, pl. 7, figs. 3, 4.

The laminoliths are relatively high and have 4 to 7 large openings, separated by thin septa inside the coccolith tube; the distal surface is irregular and possesses small protrusions, especially where the septa meet with the rim or with other septa in the centre.

Geisen et al. (2000) presented a combination coccosphere with heterococcoliths of *Calcidiscus leptoporus* and holococcoliths of *Syracolithus quadriperforatus*, and suggested a speciation, not clearly recognizable from the heterococcolithophore morphology.

Cocosphere possess from 78 to 108 coccoliths (3 specimens).  
**Dimensions.** Coccosphere long axis 10.5-12.5 µm; coccolith length (1.6-) 1.9-2.2 (-2.4) µm.

Genus *Zygosphaera* Kamptner, 1937, emend. Heimdal, 1982

Cocosphere consisting of laminoliths as body coccoliths, and zygoform circum-flagellar coccoliths.

The original description of *Zygosphaera* defines zygoform laminoliths as circum-flagellar coccoliths. Some *Zygosphaera* species have real zygoform laminoliths but others (e.g. *Z. amoena* and the former *Z. bannockii*) appear to have real zygloliths as circum-flagellar coccoliths.

**Zygosphaera amoena** Kamptner, 1937  
(Figs. 108A, B)

Body laminoliths have an oval elevated central part that follows the main axis. Circum-flagellar coccoliths are zygoform coccoliths with a double-layered wall and a large pore.

Cocospheres have 64 to 86 body coccoliths; ca. 6 circum-flagellar coccoliths.

**Dimensions.** Coccosphere long axis 5-7 µm; coccolith length (0.9-) 1.15-1.25 (-1.4) µm.

**Zygosphaera bannockii** (Borsetti and Cati, 1976)
Heimdal, 1980

Zygosphaera bannockii is now considered as the holococcolith phase (solid) of *Syracosphaera bannockii* (p. Figs 41C, D).

**Zygosphaera hellenica** Kamptner  
(Fig. 109)

Zygosphaera hellenica, Kamptner, 1937, p. 306, pl. 16, figs. 27-29.  
Zygosphaera hellenica Kamptner, Reid, 1980, pp. 166, 168, pl. 8, figs. 1, 2; Heimdal, 1982, p. 53; Kleijne, 1991, p. 69, pl. 18, fig. 3-5.

Body coccoliths are elliptical laminoliths with a central protrusion; these laminoliths are either unperforated or they have a pore on one or both sides of the central protrusion. Circum-flagellar coccoliths are zygoform laminoliths with a pointed protrusion. The microcrystallites, which make up the coccoliths, usually appear to be aligned in concentric rows, but this arrangement is not observed in some specimens (Fig. 109D).

Cocospheres possess from 88 to 140 coccoliths (5 specimens).  
**Dimensions.** Coccosphere long axis 8-11 µm; coccolith length (1.9-) 2.0-2.2 (-2.5) µm.

**Zygosphaera marsilii** (Borsetti and Cati 1976)  
Heimdal 1982 (Figs. 108C, D)

Sphaerocalyptra marsilii, Borsetti and Cati, 1976, pp. 212, 213, pl. 13, figs. 7-10.  
Zygosphaera marsilii (Borsetti and Cati) Heimdal, 1982, p. 53; Kleijne, 1991, p. 69, 71, pl. 18, fig. 6; Winter and Siesser, 1994, p. 155, fig. 191 (photo from Alcober).

Body laminoliths with four concentric distal rows of crystallites, which are surmounted by a central structure of microcrysts, usually with the form of a transverse ridge. Circum-flagellar zygoform laminoliths have a high transverse ridge.

Cocospheres possess from 76 to 102 coccoliths (3 specimens).  
**Dimensions.** Coccosphere long axis 6.5-8.5 µm; coccolith length (1.2-) 1.30-1.45 (-1.6) µm.
Species Incertae sedis

Holococcolithophore sp. 1
(coccoliths have two small pores in the proximal side) (Figs. 110A, B)

Elliptical holococcoliths with a central protrusion surrounded by pores on the distal surface and two small pores aligned obliquely to the major axis in the proximal side; the basal plate seems to be solid.

Coccospheres possess from 80 to 98 coccoliths (4 specimens).

Dimensions. Cocosphere long axis 6.5-8.5 µm; coccolith length (1.3-) 1.5-1.7 (-2.0) µm.

Coccolithophore sp. 1 (affinity to Rhabdosphaeraceae?) (Figs. 110C, D)

The coccosphere appears to have three types of coccoliths: a) long elliptical with laterally flattened protrusion; b) long elliptical with whaleback protrusion; c) broadly elliptical with tall cylindrical protrusion. Each type of coccolith shows a highly variety of sizes and have affinities with Algirosphaera and Cyrtosphaera coccoliths. This new species differs, however, from Algirosphaera and Cyrtosphaera because its elements are somewhat structureless (e.g. it is not possible to see radial laths or a differentiated rim).

Coccospheres possess from 102 to 140 coccoliths (4 specimens).

Dimensions. Cocosphere long axis 4.5-6.5 µm; coccolith length 0.9-1.5 µm.

Coccolithophore sp. 2 (affinity to Syracosphaera?) (Figs. 111A)

The single collapsed specimen has coccoliths which slightly resemble those of Syracosphaera, especially since certain coccoliths have a small central spine. This species differs from Syracosphaera, however, in not having clear radial laths and in having a covered rim.

Coccosphere consists of ca. 36 coccoliths.

Dimensions. (Collapsed) coccosphere diameter ca. 5 µm; coccolith length 1.4-1.65 µm.

Coccolithophore sp. 3 (affinity to Sphaerocalyptra?) (Fig. 111B)

Very small calyptrolith-like coccoliths consisting of a ring with a bridge forming the cover of the calyptrolith; certain coccoliths are larger and appear to be circum-flagellar calyptroliths (upper right). These forms appear to be closer to calyptroliths than zygoliths, which are the typical forms having a bridge. They differ from the holococcoliths, however, in not having clear crystallites. Observation at a higher magnification is necessary to determine whether or not these actually are holococcoliths.

The two studied specimens have around 72 and 77 coccoliths.

Dimensions. Coccolith diameter (0.55-) 0.61-0.66 (-0.75) µm, height 0.3-0.6 µm.

Unidentified sp. no. 1
(Fig. 111C)

Specimens that appear to have an external alveolate theca, but under high magnification it is sometimes possible to distinguish individual pieces composing this theca which could be compared to small coccoliths.

The three studied specimens have 456 to 896 small pieces (coccoliths?).

Dimensions. (Collapsed) sphere diameter 5-8 µm; component (coccolith?) diameter (0.15-) 0.45-0.65 µm.

Unidentified sp. no. 2
(Fig. 111D)

This specimen presents a hard theca composed of pieces, which, if made by calcium compounds, might be related to the genus Papposphaera. In distal view, these structures resemble four pointed stars and are clearly variable in shape; the stars seem to be central structures attached to a basal ring with cross bars.

The studied specimen consists of ca. 70 pieces (coccoliths?).

Dimensions. Collapsed specimen (diameter around 8 µm); component (coccolith?) basal length 0.8 to 1.1 µm; distal length 0.9 to > 1.6 µm.
Fig. 9. – *Helicosphaera carteri* (Wallich) Kamptner var. *carteri*: A, complete coccosphere of helicoliths [Fronts-96, 021, 68 m]; B, coccosphere showing coccoliths with two central pores and one coccolith with a longitudinal slit (lower middle) [Fans-1, 127, 25 m]; C, helicolith in proximal view (Catalano-Balearic Sea, 1990); D, collapsed combination coccosphere with *H. carteri* and the former *Syracolithus catilliferus* (Kamptner) Deflandre holococcoliths [Fronts-95, 24W, 70 m]. Scale bars: A, B, D = 2 µm; C = 1 µm.
Fig. 10. — *Helicosphaera carteri* (Wallich) Kamptner var. *carteri*: A, a well-formed combination coccosphere of *H. carteri* (heterococcoliths) and the former *Syracolithus catilliferus* (holococcoliths) [Meso-96, G4, 70 m]; B, detail of Fig. A; C, coccosphere of the former *S. catilliferus* with a notable flagellar area [Meso-96, G6, 5 m]; D, detail of the former *S. catilliferus* showing solid holococcoliths with a sharply pointed distal protrusion (see the coccolith in lateral view in the lower left corner) [Meso-95, 147, surface]. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 11. – Helicosphaera carteri (Wallich) Kamptner var. carteri. A. Helicosphaera carteri (holococcolith phase, solid), formerly Syracolithus catilliferus [Meso-96, A3, 5 m]; B. H. carteri (holococcolith phase, perforate), formerly Syracolithus confusus Kleijn. Coccosphere with a large flagellar area (top); the coccoliths have 5 to 8 pits in the distal surface and a pointed central protrusion [Fans-3, K03, 5 m]; C. collapsed coccosphere of the former S. confusus including coccoliths of the former S. catilliferus (middle left); transitional forms can be seen [Meso-96, F2, 5 m]; D. coccosphere of the former Syracolithus consisting of coccoliths of both S. catilliferus and S. confusus [Meso-96, F2, 5 m]. Scale bars = 2 µm.
FIG. 12. – A, *Helicosphaera carteri* var. *hyalina* (Gaarder) Jordan et Young: complete coccosphere [Fans-3, K03, 60 m]. B, *Helicosphaera carteri* var. *wallichii* (Lohmann) Theodoridis: complete coccosphere [Fans-1, 123, 60 m]. C-D, *Helicosphaera pavimentum* Okada et McIntyre: C, complete coccosphere showing coccoliths with one or two aligned central slits; note the narrow flange of the helicoliths [Meso-96, 16, 90 m]; D, detail showing coccoliths with two central pores. Meso-95, 178, 40 m. Scale bars: A, B, C = 2 µm; D = 1 µm.
Fig. 13. – A-C, *Scyphosphaera apsteinii* Lohmann: A, coccosphere with cribriliths and two lopadoliths [Fronts-95, 18P, 30 m]; B, disintegrated coccosphere with one lopadolith and cribriliths [Fans-1, 123, 40 m]; C, well formed coccosphere with one lopadolith in an equatorial position and another located internally [Catalano-Balearic Sea, 1992]. D, *Scyphosphaera apsteinii* f. *dilatata* Gaarder: some cribriliths and one lopadolith without distal decrease in width [Fronts-96, 027, 45 m]. Scale bars = 2 µm.
FIG. 14. – *Anoplosolenia brasiliensis* (Lohmann) Deflandre: A, complete coccosphere [Fronts-95, 25W, 30 m]; B, apical zone of another coccosphere with tapering end [Meso-96, G4, 5 m]; C, detail of Fig. B (note the few but wide laths that characterize the *Anoplosolenia* scapholits found in these samples). Scale bars: A, B = 5 µm; C = 1 µm.
Fig. 15. *Calciosolenia murrayi* Gran: A, complete cocolithophore with few apical spines [Fans-3, M11, 75 m]; B, detail showing the apical area [Fans-3, K03, 66 m]; C, detail of Fig. A (note the apical spines which appear to be transformed scapholiths); D, detail of Fig. A showing scapholiths with overlapping laths (upper middle) and other coccoliths with highly transformed plate-like laths (lower part of the figure). Scale bars: A = 5 μm; B, C = 2 μm; D = 1 μm.
FIG. 16. – A-B, *Acanthoica acanthifera* Lohmann, ex Lohmann: A, collapsed coccosphere [Fans-1, 123, 5 m]; B, detail of Fig. A showing tilted radial laths and slightly compressed sacculiform protrusion. C-D, *Anacanthoica acanthos* (Schiller) Deflandre: C, complete coccosphere [Hivern-99, 25, 60 m]; D, detail of Fig. C showing body coccoliths with a relatively wide rim. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 17. – *Acanthoica quattrospina* Lohmann: A, complete coccosphere having body coccoliths and coccoliths with spines at the poles [Fans-2, J3, 10 m]; B, complete coccosphere with spines in the most characteristic disposition: one long and three short spines at one pole and two long spines at the other pole [Fans-3, K03, 40 m]; C, coccosphere in apical view showing all the spines at the same pole (notice that the base of the shorter spines is similar to that of the body coccoliths while the two long spines have small laterally flattened bases) [Meso-95, 163, 40 m]; D, detail of the body coccoliths [Fans-1, 100, 40 m]. Scale bars: A, B, C = 2 µm; D = 1 µm.
Fig. 18. — *Acanthoica quattrospina* Lohmann: A, disintegrated coccosphere consisting of body and two circum-flagellar holococcoliths of an undescribed species of *Sphaerocalyptra* [Fans-2, N7, 10 m]; B, collapsed mixed coccosphere with body rhabdoliths of *A. quattrospina* (heterococcoliths) which appear to surround the holococcoliths [Fans-2, J3, 10 m]; C, collapsed coccosphere of the undescribed holococcolithophore with several heterococcoliths of *A. quattrospina* [Fans-2, N7, 5 m]; D, detail of Fig. C. Scale bars: A, B, C = 2 µm; D = 1 µm.
Fig. 19. – *Algirosphaera robusta* (Lohmann) Norris: A, complete coccosphere in apical view showing three joined circum-flagellar petaloid coccoliths, closing the flagellar opening [Fronts-95, 23D, 60 m]; B, complete coccosphere in apical view showing three circum-flagellar petaloid coccoliths separated, leaving an open flagellar area (notice the remains of two flagella emerging from the opening, on the body coccoliths) [Fronts-95, 23D, 60 m]; C, detail of some coccoliths showing the large central protrusion and a radial cycle of laths in the basal part [Fronts-95, 23D, 60 m]; D, complete coccosphere in lateral view showing variable sized coccoliths, most with a pore in the central protrusion [Fans-1, 100, 5 m]. Scale bars: A, B, D = 2 µm; C = 1µm.
Fig. 20. – A-B, *Cyrtosphaera aculeata* (Kamptner) Kleijne: A, complete coccosphere [Fans-3, K03, 40 m]; B, detail showing coccoliths with relatively short laths, a clear lamellar cycle, a narrow cycle with needle-shaped elements and a central small papilla of cuneate elements [Hivern-99, 25, 60 m]. C-D, *Cyrtosphaera lecaliae* Kleijne: C, complete coccosphere with the varimorphic coccoliths [Fronts-96, 039, 10 m]; D, detail of Fig. C showing several coccoliths with slender laths and the highly sloped protrusion topped by a small central papilla. Scale bars: A, C = 2 µm; B, D = 1 µm.
FIG. 21. – A-B, *Cyrtosphaera cucullata* (Lecal-Schlauder) Kleijne: A, coccosphere with two detached coccoliths (upper right) showing their proximal side [Meso-96, G6, 40 m]; B, detail of some coccoliths showing the bowler hat shape, with the rim and a cycle of short laths forming the hat brim; the large sacculiform central protrusion is constructed of needle-shaped elements [Meso-95, 156, surface]. C-D, *Discosphaera tubifera* (Murray et Blackman) Ostenfeld: C, complete coccosphere showing the rhabdoliths with trumpet-like central structure [Hivern-99, 25, 20 m]; D, detail with coccoliths having detached central structures (note the small spine inside the central pore) [Meso-95, 132, surface]. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 22. – A-B, *Palusphaera vandeli* Lecal, emend. R.E. Norris: A, collapsed coccosphere [Meso-96, D4, 40 m]; B, detail with a rhabdolith showing thin styliform central structure [Hivern-99, 25, 60 m]. C-D, *Palusphaera sp.* 1 (type robusta): C, coccosphere with coccoliths having thick styliform spines [Fans-3, M11, 75 m]; D, detail of several rhabdoliths in proximal view with several small nodes around the central pore [Fronts-95, 23D, 60 m]. Scale bars: A, C = 2 µm; B, D = 1 µm.
FIG. 23. – A-B, *Rhabdosphaera clavigera* Murray et Blackman: A, coccosphere with endothecal rhabdoliths having styliform central structure which is characteristic of the specimens originally described as *R. stylifera* [Meso-95, 023, surface]; B, coccosphere with endothecal rhabdoliths having styliform central structures ending in small “wings”; this morphotype was originally described as *R. stylifera* var. *capitellifera* (notice one detached endothecal rhabdolith showing the proximal side with central pore) [Fronts-96, 027, 15 m]. C-D, *Rhabdosphaera xiphos* (Deflandre and Fert) Norris: C, complete coccosphere [Fans-3, K03, 40 m]; D, detail with endothecal and exothecal coccoliths (the base of endothecal rhabdoliths is smaller and more rounded than that of exothecal coccoliths) [Fans-3, K03, 40 m]. Scale bars: A, B, C = 2 µm; D = 1 µm.
Fig. 24. – A-B, *Calciopappus rigidus* Heimdal in Heimdal et Gaarder: A, complete coccosphere [Picasso workshop, Barcelona harbour, surface]; B, detail of the apical area, showing a partially covered whorl coccolith in distal view (upper middle), several overlapping whorl coccoliths in proximal view with the central opening partially filled by flat bands (middle right), and body caneoliths (bottom); the whorl caneoliths partially cover the base of the spine-like appendages [Fans-1, 78b, 5 m]. C-D, *Calciopappus sp.* 1 (very small): C, coccosphere with lightly calcified body caneoliths, curved spines and characteristic whorl caneoliths each with two spines [Meso-96, E8, 100 m]; D, detail showing the central opening on the proximal side of whorl caneoliths not covered and the two conspicuous spines located on the margin of the whorl caneoliths with an angular separation of about 70° [Fronts-95, 24W, 70 m]. Scale bars: A = 2 µm; B, C, D = 1 µm.
FIG. 25. – *Michaelsarsia elegans* Gran, emend. Manton *et al.*: A, coccosphere with appendages [Fans-1, 123, 60 m]; B, detail of Fig. A showing body caneoliths with robust wall and central structure; C, detail of the apical area of the coccosphere, showing open central areas of both whorl and link coccoliths and body caneoliths with a thick central structure (all of these characteristics are specific for *Michaelsarsia elegans*) [Fans-3, K03, 66 m]; D, detail showing body caneoliths and three small rhomboid circum-flagellar muroliths (lower left) with central protrusion [Fronts-96, 038, 60 m]. Scale bars: A = 5 µm; B, D = 1 µm; C = 2 µm.
FIG. 26. – A-B, *Ophiaster formosus* Gran, sensu Gaarder 1967: A, coccospere in antapical view showing the appendages with flexible arms formed of osteoliths. Note that the most proximal osteoliths are larger than the others and have loop-like proximal ends which can overlap [Fronts-95, 20I, 80 m]; B, coccospere with circum-flagellar coccoliths with short spines (top), body caneoliths and appendages in antapical position [Fans-2, M07, 25 m]. C-D, *Ophiaster hydroideus* (Lohmann) Lohmann emend. Manton *et* Oates: C, coccospere with circum-flagellar coccoliths with long spines (centre right), body caneoliths and osteoliths mostly detached [Fans-3, K12, 75 m]; D, coccospere showing circum-flagellar caneoliths with sharply pointed spines (top), body caneoliths (centre) and the antapical appendage system with overlapping proximal osteoliths (bottom) “like the lamellae of an optical diaphragm” (Gaarder, 1967) [Fans-3, K07, 60 m]. Scale bars = 2 µm.
Fig. 27. – A-C, *Coronosphaera binodata* (Kamptner) Gaarder, in Gaarder et Heimdal: A, collapsed coccosphere [Meso-95, 147, surface]; B, complete coccosphere with circum-flagellar caneoliths with spine (top) [Meso-95, 117, surface]; C, detail with three circum- flagellar caneoliths having robust spine (top) and body caneoliths with two pointed knobs which is characteristic of the species, and with strongly imbricate rims which is characteristic of the genus [Meso-95, 147, surface]. D, *Coronosphaera mediterranea* (Lohmann) Gaarder, in Gaarder et Heimdal: detail with body caneoliths and one circum- flagellar caneolith (centre left) which has a strong squared spine; notice the central structure with two flattened parts characteristic of the species and the robust strongly anti-clockwise imbricated rims characteristic of the genus [Fronts-96, 038, 60 m]. Scale bars: A, B = 2 µm; C, D = 1 µm.
Fig. 28. – *Coronosphaera mediterranea* (Lohmann) Gaarder, in Gaarder et Heimdal: A, complete coccosphere of heterococcoliths [Fronts-95, 19T, 40 m]; B, a combination coccosphere consisting half of *C. mediterranea* (heterococcolithophore) and half of the former *Calyptrolithina wettsteinii* (Kamptner) Norris holococcoliths [Meso-96, 12, 40 m]; C, complete coccosphere of the holococcolith phase, formerly *C. wettsteinii*, showing a notable flagellar area surrounded by circum-flagellar zygoliths and body calyptroliths with a rim that encircles the distal surface which has large pores [Fans-3, M11, 5 m]; D, holococcoliths; detail with a body calyptrolith (upper left corner) and three circum-flagellar coccoliths, one of which (centre) appears to be a transitional form with the bridge and one half of the central area divided into pores; the other two are zygoliths [Meso-95, 147, surface]. Scale bars: A, B, C = 2 µm; D = 1 µm.
Fig. 29. — *Gaarderia corolla* (Lecal) Kleijne: A, coccosphere showing endothecal and exothecal caneoliths [Fans-3, K05, 40 m]; B, coccosphere with the endothea partially covered by the large exothecal caneoliths (note the considerable size variations of both endothegal and exothegal coccoliths) [Fronts-96, 039, 10 m]; C, detail showing large exothecal coccoliths in distal view (bottom of the figure), variable-sized endothecal caneoliths (centre), a partially covered exothecal coccolith in proximal side view (upper right) and an endothecal caneolith in side view having proximal and distal flanges and a beaded mid-wall flange [Fans-1, 127, 25 m]; D, exothecal coccoliths, one in proximal view and another in distal view [Fronts-96, 027, 5 m]. Scale bars: A, B = 2 µm; C, D = 1 µm.
Fig. 30. – *Syracosphaera marginaporata* Knappertsbusch: A, complete coccosphere showing variable sized body caneoliths, some circum-flagellar caneoliths with long spine and several detached complex undulating exothecal coccoliths in proximal view (top) [Fans-3, K12, 75 m]; B, detail showing body caneoliths with the characteristic row of pores between the smooth central area and the flange, one caneolith with spine, in lateral view, showing a broken margin (centre left), and exothecal coccoliths in proximal view showing the conspicuous parenthesis-like slits around the central area (top) [Fronts-96, 013, 60 m]; C, coccosphere showing an exothecal coccolith in distal view (middle left) [Hivern-99, 19, 20 m]; D, detail of body caneoliths in distal and lateral view, and circum-flagellar caneoliths with spine [Hivern-99, 19, 20 m]. Scale bars = 1 µm.
**Fig. 31.** *Syracosphaera molischii* Schiller: **A**, complete coccosphere showing body caneoliths with corrugated distal flanges and robust central structures, complex undulating exothecal coccoliths in apical position covering the circum-flagellar caneoliths, and an antapical caneolith with a short spine [Meso-96, G6, 70 m]; **B**, detail of exothecal coccoliths (top) and body caneoliths with a well developed central structure and internal protrusions of the distal flange [Hivern-99, 19, surface]; **C**, complete coccosphere showing considerable morphological variation among the body caneoliths [Fronts-95, 28C, 5 m]; **D**, detail showing the apical area with circum-flagellar caneoliths, a well developed flagellar opening and body caneoliths [Meso-96, G6, 100 m]. Scale bars = 1 µm.
FIG. 32. – *Syracosphaera ossa* (Lecal) Loeblich Jr. *et* Tappan: A, coccosphere with body caneoliths showing the characteristic smooth distal flange and circum-flagellar caneoliths with the characteristic flattened spines [Meso-95, 161, surface]; B, complete coccosphere in apical view showing the complex undulating exothecal coccoliths around the flagellar area [Fronts-96, 027, 5 m]; C, complete coccosphere showing several detached exothecal coccoliths in the apical area and spines of circum-flagellar caneoliths (top), and one antapical caneolith with a short spine (lower middle); the body caneoliths have highly variable central structures [Meso-96, G2, 20 m]; D, detail with spine-bearing caneoliths, one complex undulating exothecal coccolith (upper middle) and several body caneoliths [Fronts-96, 038, 15 m]. Scale bars = 1 µm.
Fig. 33. – A-B, *Syracosphaera* sp. (slender): A, coccosphere with body caneoliths, circum-flagellar caneoliths with long and slender spines, some complex undulating exothecal coccoliths around the apical pole and one antapical caneolith with a long spine [Fronts-96, 013, 60 m]; B, detail showing some body endothecal caneoliths (lower left), exothecal coccoliths positioned around the flagellar area, and, partially hidden, some circum-flagellar caneoliths with long spines tipped by four small wings [Fans-1, 123, 40 m]. C-D, *Syracosphaera* sp. (rods on the laths): C, coccosphere showing body caneoliths with the rods distributed in a more or less regular pattern and several simple undulating exothecal coccoliths (lower left), mostly detached [Hivern-99, 25, 60 m]; D, detail showing one simple undulating exothecal coccolith with two parenthesis-like large slits around the central area and several endothecal caneoliths [Fans-1, 123, 60 m].

Scale bars = 1 µm.
Fig. 34 – *Syracosphaera anthos* (Lohmann) Janin: A, complete coccosphere with overlapping exothecal coccoliths [Meso-96, G6, 70 m]; B, collapsed coccosphere with body caneoliths, circum-flagellar caneoliths with spine and exothecal coccoliths [Fronts-95, 039, 60 m]; C, detail with caneoliths covered by exothecal coccoliths; exothecal coccoliths can be seen in proximal (lower middle), in distal (lower right) and in latero-distal view (left) showing clearly the hollow conical shaped central structure [Meso-96, G2, 70 m]; D, detail of endotheal caneoliths showing the deeply curved laths near the wall which resemble a roof gutter, and the raised and flat central structure onto which the laths extend [Fronts-95, 19T, 60 m]. Scale bars: A, B = 2 µm; C, D = 1 µm.
FIG. 35. – *Syracosphaera anthos* (Lohmann) Janin: **A**, combination coccosphere consisting of body caneoliths (upper) and exothecal coccoliths (bottom) of *S. anthos* and holococcoliths of the former *Periphyllophora mirabilis* [Meso-95, 178, 40 m]; **B**, *S. anthos* (holococcolith phase), formerly *P. mirabilis*; complete coccosphere showing the presumed flagellar opening (centre) [Workshop Picasso, T4, July 1998]; **C**, coccosphere of the former *P. mirabilis* with caneoliths of *S. anthos* (heterococcoliths) [Meso-96, G4, 40 m]; **D**, detail of Fig. C showing a complete caneolith of *S. anthos* (bottom left). Scale bars: A, B, C = 2 µm; D = 1 µm.
FIG. 36. *Syrcosphaera nana* (Kamptner) Okada & McIntyre: A, ovoid coccosphere showing body caneololiths with the central area formed like a sloping roof, and one exothecal coccolith (upper left) [Fans-3, M11, 60 m]; B, detail showing part of the endotheca (lower right) and several oval exothecal coccoliths which have the central area filled with tile-like lamellae and the rim with small nodes on the inner perimeter [Meso-96, I3, 70 m]; C, collapsed coccosphere with two caneololiths with very small spines (centre left) and exothecal coccoliths (upper left) most of which are detached [Fronts-95, 23D, 50 m]; D, detail with four caneololiths having small rounded spines (left) and body caneololiths showing hunch backed shape as described by Kamptner (1941) [Fronts-95, 20I, 60 m]. Scale bars = 1 µm.
FIG. 37. — *Syracosphaera nana* (Kamptner) Okada & McIntyre: A, collapsed heterococcolith-holococcolith combination coccosphere [Fronts-96, 013, 75 m]; B, detail of Fig. A showing the holococcoliths covering heterococcoliths, including both body canecoliths and exothecal coccoliths; C, complete coccosphere of holococcolith phase showing laminoliths as body holococcoliths [Meso-96, G6, 5 m]; D, holococcolith phase; detail of the apical area of a coccosphere showing a large flagellar opening and zygolith-like circum-flagellar holococcoliths [Fronts-95, 26W, 30 m].

Scale bars = 1 µm.
Fig. 38. – A–B, *Syracosphaera* sp. (aff. *S. nana*, laths with sinistral obliquity): A, collapsed coccosphere with body caneololiths, three circum-flagellar caneololiths and exothecal coccoliths (top) [Fronts-96, 013, 60 m]; B, collapsed coccosphere showing body caneololiths and five circum-flagellar caneololiths each with a small spine [Fronts-95, 23D, 50 m]. C–D, *Syracosphaera* sp. (with stratified exothecal coccoliths): C, collapsed coccosphere showing body caneololiths, one circum-flagellar caneolith with spine and three exothecal coccoliths in proximal view (upper right) [Meso-96, D8, 70 m]; D, detail showing body caneololiths with a very thick wall and smooth central area [Meso-96, D8, 70 m]. Scale bars = 1 μm.
Fig. 39. – *Syracosphaera bannockii* (Borsetti et Cati) Cros *et al.:* A, coccosphere showing body and circum-flagellar caneoliths [Hivern-99, 25, 60 m]; B, complete coccosphere showing body caneoliths, four circum-flagellar caneoliths and a ribbon of exothecal coccoliths around the coccosphere [Hivern-99, 25, 5 m]; C, detail of distal side of body caneoliths which have a low and thick wall and a low elongated central structure [Mesos-96, E 3/4, 40 m]; D, detail with several asymmetrical sub-elliptical exothecal coccoliths which have an asymmetrical rim, short laths and a central area constructed of lamellae [Meso-96, D6, 40 m]. Scale bars = 1 µm
Fig. 40. – *Syracosphaera bannockii* (Borsetti et Cati) Cros *et al.*: A, combination coccosphere showing body and circum-flagellar holococcoliths of the former *Corisphaera* sp. type A and heterococcoliths of the former *Syracosphaera* sp. [Meso-96, G6, 40 m]; B, detail of Fig. A showing two detached exothecal coccoliths (right) of *S. bannockii*, formerly *Syracosphaera* sp.; C, combination coccosphere with body holococcoliths of the former *Zygosphaera bannockii* and body holococcoliths of the former *Corisphaera* sp. type A [Fans-1, 123, 40 m]; D, detail showing clearly holococcoliths of both, the former *Zygosphaera bannockii*, without holes, and the former *Corisphaera* sp. type A, with holes [Fans-1, 127, 40 m]. Scale bars: A = 2 µm; B, C, D = 1 µm.
FIG. 41. – A-B. *Syracosphaera bannockii* (holococcolith phase, perforate), formerly *Corisphaera* sp. type A of Kleijne (1991): A, slightly collapsed coccosphere. Note the possible residual parts of the flagella that appear to emerge from the flagellar area [Fronts-95, 18P, 5 m]; B, detail showing body zygoliths with the well arranged distal rim of angular crystallites and the low and narrow bridge, and circum-flagellar zygoliths (upper part of the figure) with characteristic double-layered wall [Meso-96, D6, 40 m]. C-D, *Syracosphaera bannockii* (holococcolith phase, solid), formerly *Zygosphaera bannockii* (Borsetti and Catò) Heimdal: C, coccosphere having body coccoliths with a transverse ridge; part of one apical zygolith is seen at the top of the figure [Fans-1, 100, 40 m]; D, coccosphere with circum-flagellar zygoliths having a high and broad protrusion (top) and zygof orm body laminoliths [Fans-1, 100, 25 m]. Scale bars = 1 µm.
Fig. 42. – *Syracosphaera delicata* Cros et al.: A, coccosphere of delicate appearance showing body caneoliths with flat central area, three circum-flagellar caneoliths with a very small spine and asymmetrical exothecal coccoliths having a characteristic distal ridge [Hivern-99, 25, 60 m]; B, detail of Fig. A showing two caneoliths with a small spine and a low and fragile wall (which is easily deformed and broken); C, collapsed coccosphere with exothecal coccoliths covering the endotheal caneoliths [Hivern-99, 25, 100 m]; D, detail showing exothecal coccoliths of irregular sub-elliptical shape (left) which have a rounded central area connected to the rim by a radial cycle of short laths, and some fragile body caneoliths with smooth central area (right) [Fans-2, N07, 10 m]. Scale bars = 1 µm.
FIG. 43. – A. *Syracosphaera* sp. aff. to *S. orbiculus* (ovoid): coccosphere with endothecal body caneoliths having a flat and very broad central structure, circum-flagellar caneoliths with a short but robust spine and one asymmetrical exothecal coccolith in distal view on the coccosphere (centre left) and another exothecal coccolith, in proximal view, on the filter (top) [Fans-2, M03, 10 m]; B. *Syracosphaera* sp. aff. to *S. orbiculus* (spherical): spherical coccosphere showing body caneoliths, circum-flagellar caneoliths with robust and long spines and many detached exothecal coccoliths on the filter [Hivern-99, 25, 40 m]. C-D, *Syracosphaera* sp. type L of Kleijne 1993: C, complete spherical coccosphere [Meso-95, 023, surface]; D, detail of Fig. C showing the endothecal caneoliths with smooth wall, low elongated central structure, relatively wide laths and a well developed external connecting ring; the exothecal thin subcircular coccoliths are like smooth sheets. Scale bars: A, C, D = 1 µm; B = 2 µm.
Fig. 44. – *Syracosphaera lamina* Lecal-Schlauder: A, coccosphere with remains of the exothecal coccoliths (upper middle) [Fronts-95, 23D, 70 m]; B, complete coccosphere showing the characteristic shape of this species [Fronts-95, 23D, 80 m]; C, detail of the Fig. A with body caneolths having the characteristic keel-shaped central structure and the thin (sub)circular exothecal coccoliths (centre right) covering the caneolths; D, detail with body caneolths in distal view and one in proximal view (upper right) [Meso-96, I3, 100 m]. Scale bars: A, B = 5 µm; C = 2 µm; D = 1 µm.
Fig. 45. – *Syracosphaera tumularis* Sánchez-Suárez: A, collapsed coccosphere [Fronts-95, 19T, 60 m]; B, detail of body caneolths: three caneoliths in proximal view (top); a caneolith in lateral view showing a relatively high wall with serrated distal rim (centre right); and caneoliths in distal view showing straight laths narrowing inwards and an elongated central structure irregularly constructed by transverse elements and narrow ends of the laths [Fans-3, M11, 75 m]; C, coccosphere with endothecal caneoliths and thin subcircular exothecal coccoliths (four on the coccosphere and others detached) [Fronts-96, 019, 75 m]; D, detail of Fig. A with one exothecal coccolith (upper right corner) and endothecal caneoliths; note the endothecal caneolith in proximal view (upper center) showing two central straight longitudinal ridges. Scale bars: A, C = 2 µm; B, D = 1 µm.
**FIG. 46.** *Syracosphaera nodosa* Kamptner: **A**, complete coccosphere showing the body caneoliths and two circum-flagellar caneoliths with large spines; both coccolith types have well developed walls with robust external vertical ribs [Fronts-95, 28C, 35 m]; **B**, detail of Fig. A showing the endothecal body caneoliths with straight radial laths which link the elongated central connecting structure with the well developed external connecting ring; **C**, complete coccosphere with exothecal coccoliths which show conspicuous radial cycle with sinistral obliquity [Fronts-95, 23D, 50 m]; **D**, detail with three exothecal coccoliths in proximal view showing the central flat structure constructed by two plates and bordered by a low ridge, a well developed radial cycle and a wide rim [Fronts-96, 038, 45 m]. Scale bars = 1 µm.
**Fig. 47.** *Syracosphaera aff. nodosa*: A, coccosphere showing endotheical coccoliths; both body and circum-flagellar caneoliths with spine are large and have a high wall which is vertically ribbed externally, long laths, an elongated connecting central structure and no visible connecting external ring [Meso-95, 132, surface]; B, detail of Fig. A with body and circum-flagellar caneoliths; C, complete coccosphere strongly resembling *S. nodosa* but with larger coccosphere and coccolith (both body caneoliths and exothecal coccoliths) size [Hivern-99, 25, 60 m]; D, detail with exothecal coccoliths showing a wide rim with narrow slits between the elements and a radial cycle with a larger number of laths than in *S. nodosa*; the three exothecal coccoliths in distal view (bottom) show the angular central structure and the others in proximal view (centre upper) show the central area bordered by a low ridge as in *S. nodosa* [Hivern-99, 25, 60 m]. Scale bars = 1 µm.
**Fig. 48.** – *Syracosphaera rotula* Okada et McIntyre: A, collapsed cocsphere with endothecal caneololiths and larger wheel-shaped exothecal coccoliths [Hivern-99, 19, surface]; B, detail of Fig. A with endothecal caneololiths in distal and lateral view; C, detail of Fig. A showing the exothecal coccolith with the flaring disposition of the radial laths (left); D, detail of one exothecal coccolith in proximal view showing the central flat structure constructed by two plates and bordered by a low ridge (as in *S. nodosa* group) and the bent rim [Hivern-99, 25, 20 m]. Scale bars: A = 2 µm; B, C, D = 1 µm.
Fig. 49. – *Syracosphaera histricha* Kamptner: A, complete coccosphere with body and circum-flagellar caneoliths and exothecal coccoliths [Meso-95, 161, surface]; B, detail with body caneoliths, some exothecal vaulted coccoliths (lower and centre right) showing their characteristic distal side, and two circum-flagellar caneoliths with spine in side view (top) [Fans-3, M11, 5 m]; C, complete coccosphere with exothecal coccoliths covering the coccosphere [Hivern-99, 30, surface]; D, detail of exothecal coccoliths covering body endothecal caneoliths [Fans-3, K07, 25 m]. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 50. – *Syracosphaera pulchra* Lohmann: A, detail of the apical area showing six circum-flagellar caneoliths with robust, bifurcate ended spines [Fans-1, 100, 25 m]; B, detail showing one malformed body caneolith with overgrown flanges (upper right), two well-formed body caneoliths in proximal view (right), several in distal view (center), two circum-flagellar caneoliths with spines in latero-distal view (bottom); the central area of these body caneoliths is almost filled with thin laths [Meso-95, 114, surface]; C, obpyriform coccosphere showing body caneoliths, five circum-flagellar caneoliths with spine, and exothecal coccoliths, mostly on the left side [Meso-95, 005, surface]; D, coccolith in proximal view showing the central hollow spine [Meso-96, G4, 40 m]. Scale bars: A, B, C = 2 µm; D = 1 µm.

112 L. CROS and J.-M. FORTUÑO
**Fig. 51.** – *Syracosphaera pulchra* Lohmann: A, combination coccosphere of *S. pulchra* (holococcolithophore), formerly *Calyptrosphaera oblonga*, with some body heterococcoliths of *S. pulchra* (upper right) [Fronts-96, 021, 20 m]; B, combination coccosphere of *S. pulchra*, with heterococcoliths and holococcoliths of the former *C. oblonga* [Medea-98, Masnou off-shore]; C, complete coccosphere of the holococcolith phase (formerly *C. oblonga*) [Picasso workshop, T1, surface]; D, detail of calyptroliths (holococcolith phase): the basal part consists of a ring three crystallites wide and only one crystallite high, and a presumably organic baseplate; the body calyptroliths (bottom) show the hexagonal meshwork arrangement of crystallites; the circum-flagellar calyptroliths (top) are higher and have a central protrusion [Fronts-95, 18P, 5 m]. Scale bar: A = 5 µm; B, C = 2 µm; D = 1 µm.
Fig. 52. – *Syracosphera* cf. *dilatata* Jordan, Kleijne and Heimdal: A, whole cccosphere showing detached apical exothecal caneoliths, near the circum-flagellar caneoliths with spine [Meso-96, I2, 40 m]; B, detail with body caneoliths (right) and exothecal caneoliths (left); the exothecal caneoliths have higher and thinner walls [Meso-96, D4, 40 m]; C, cccosphere with three circum-flagellar caneoliths with spine and several detached exothecal caneoliths [Hivern-99, 25, 20 m]; D, detail with body coccoliths (bottom) and circum-flagellar coccoliths with spine (top); both kinds of caneoliths have conspicuous nodes forming a mid-wall flange; note that the spine ends with four small nodes [Fronts-96, 013, 10 m]. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 53. – *Syracosphaera* sp. type D of Kleijne 1993: **A**, complete coccosphere showing the well-formed obpyriform endotheca (lower right) with five circum-flagellar spinous caneoliths and many detached large exothecal caneoliths (left) [Meso-96, 14, 70 m]; **B**, detail with the three types of caneoliths: some endothecal body caneoliths in lateral view showing the mid-wall flange seemingly formed by a fold (upper left); an exothecal caneolith in lateral view with a very high wall (lower left); and a small spine-bearing circum-flagellar caneolith with nodes forming a mid-wall flange and four very small nodes at the end of the spine (centre) [Fronts-95, 20I, 80 m]; **C**, complete coccosphere with the exothecal caneoliths mostly detached surrounding the coccosphere [Hivern-99, 25, 60 m]; **D**, detail of a coccosphere showing the body caneoliths (upper right) and exothecal caneoliths with higher and thinner walls [Meso-96, G4, 70 m]. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 54. – *Syracosphaera noroitica* Knappertsbusch: A, coccosphere showing apical circum-flagellar caneoliths with long spine, varimorphic body caneoliths with robust spine near the apical pole and with no central spine at the antapical pole [Fronts-95, 19T, 40 m]; B, detail of the antapical area showing caneoliths with central spine (top), four caneoliths without spines (centre) and antapical caneoliths (bottom) which have thin lateral spines at the edge of the central area; notice the double layered walls [Fronts-96, 013, 66 m]; C, coccosphere showing varimorphic body caneoliths, circum-flagellar caneoliths with long spine and large exothecal caneoliths around the endotheca, mostly detached [Meso-96, E 3/4, 70 m]; D, detail of apical area showing body caneoliths with robust spines (lower right), five circum-flagellar caneoliths with double-ended long spines, which resemble the horns of a snail (centre), and exothecal caneoliths with nodes forming the proximal flange (upper and left) [Fronts-96, 013, 66 m]. Scale bars: A, B, D = 1 µm; C = 2 µm.
Fig. 55. – *Syracosphaera sp. type G* of Kleijne 1993: A, collapsed coccosphere with varimorphic body caneoliths, some circum-flagellar caneoliths in apical position and some detached exothecal caneoliths (left) [Fronts-96, 013, 75 m]; B, detail of Fig. A showing the varimorphic endothecal body caneoliths; C, detail of Fig. A showing endothecal body caneoliths with a thick central structure and circum-flagellar caneoliths with a robust and long spine, both with a low wall with characteristic incised upper margin; an exothecal caneolith (upper left) in distal view showing slender laths and a relatively high, distally crenalated wall; D, detail showing body caneoliths with robust wall and proximal flanges, one circum-flagellar caneolith with a long and robust process tipped by two small spines (centre bottom), and some exothecal caneoliths with nodes forming a distal flange (right corners) [Meso-96, A5, 70 m]. Scale bars: A = 2 µm; B, C, D = 1 µm.
Fig. 56. – *Syracosphaera prolongata* Gran ex Lohmann (*sensu* Throndsen): **A**, spherical coccosphere with five long-spined apical caneololiths and several exothecal caneololiths around the coccosphere; three of them (centre) remain attached to the coccosphere [Fronts-96, 039, 10 m]; **B**, detail of body caneololiths in distal view (right); one body caneolith, partially covered, in proximal view showing the three flanges (centre bottom); four exothecal caneololiths (left), two in proximal and two in distal view [Meso-96, A3, 40 m]; **C**, detail with body caneololiths with a robust node, circum-flagellar caneololiths with a long spine which is tipped by two small opposed spines and two exothecal coccoliths which possess a central hollow spine, slender laths and a smooth wall with very narrow distal flange (centre) [Fronts-96, 013, 10 m]; **D**, detail of body caneololiths in distal view which show a filament crossing the laths and smooth distal flange [Meso-96, A3, 40 m]. Scale bars: **A** = 2 µm; **B**, **C**, **D** = 1 µm.
Fig. 57. A-B, *Syracosphaera prolongata* Gran ex Lohmann (*sensu* Heimdal *et* Gaarder): A, complete coccosphere showing body coccoliths, circum-flagellar coccoliths with spine, and larger exothecal coccoliths near the apical area; there is one small diatome and one *Emiliania* coccosphere next to the antapical area [Meso-96, G4, 70 m]; B, detail showing the exothecal coccoliths covering the endothecal body caneoliths [Meso-96, G4, 70 m]. C-D, *Syracosphaera ampliora* Okada *et* McIntyre: C, complete coccosphere with monomorphic coccoliths [Fans-1, 127, 40 m]; D, detail of caneoliths with the characteristic centrally widened laths [Fans 1, 127, 40 m]. Scale bars: A = 5 µm; B, C, D = 1 µm.
FIG. 58. – *Syracosphaera halldalii* Gaarder ex Jordan et Green: **A**, monothecate coccosphere of the “tooth-like form” showing several circum-flagellar caneoliths with spine (top); notice that some body caneoliths lack the tooth-like protrusions and therefore resemble the ordinary form of *S. halldalii* [Fans-3, M11, 5 m]; **B**, detail with body caneoliths and two circum-flagellar caneoliths with spine [Fronts-96, 013, 10 m]; **C**, monothecate coccosphere of the “finger-like form” (*S. protrudens* in Okada and McIntyre, 1977) showing body coccoliths with finger like protrusions and several circum-flagellar caneoliths with spine (upper left) [Hivern-99, 25, surface]; **D**, detail of Fig. C showing several body caneoliths with finger-like protrusions (lower right) and several circum-flagellar caneoliths with spine; one of which, in side view, shows the high and straight wall. Scale bars: **A**, **C** = 2 µm; **B**, **D** = 1 µm.
**Fig. 59.** *Emiliania huxleyi* Hay et Mohler in Hay et al.: A, complete type A coccosphere showing placoliths with a central area constructed of curved rods [Fronts-96, 021, 20 m]; B, collapsed coccosphere showing lateral views of joined placoliths and, inside the concave remains of the coccosphere, a coccolith-ring which represents the primary stage of a forming coccolith [Fans-1, 127, 60 m]; C, complete type C coccosphere: the central area of the coccoliths is formed of a smooth plate; there are several placoliths, particularly the detached ones, with the central plate partially or wholly missing [Fronts-96, 021, 50 m]; D, complete coccosphere showing placoliths with a filled central area having an overcalcified appearance [Fronts-96, 013, 90 m]. Scale bars = 1 µm.
Fig. 60. – *Gephyrocapsa ericsonii* McIntyre et Bé: A, complete coccosphere with one detached placolith, near the top left corner; the coccoliths are small and the high bridge crosses the central area diagonally [Meso-95, 163, surface]; B, complete coccosphere of the type *protohuxleyi* showing distal shields built up of T-elements, like *Emiliania huxleyi* [Meso-95, 023, surface]; C, complete coccosphere of the type *protohuxleyi* with larger slits between the T-elements; some coccoliths present a thorn; this morphotype can be an intermediate form between the coccospheres of Fig. B and D [Meso-95, 015, surface]; D, complete coccosphere of the type *protohuxleyi* “with thorn” showing the T-elements in the distal shield, very high bridges and long thorns which are perpendicular to the shield and grow from the tube of the placolith [Meso-95, 178, 40 m]. Scale bars = 1 µm.
Fig. 61. – A, *Gephyrocapsa muellerae* Bréhéret: complete coccosphere with medium sized coccoliths which have a bridge that diagonally crosses the central area [Meso-95, 119, 70 m]. B, *Gephyrocapsa oceanica* Kamptner: complete coccosphere with large coccoliths which have a wide central area crossed by a bridge almost perpendicular to the long axis of the coccolith [Meso-95, 119, surface]. C, *Gephyrocapsa ornata* Heimdal 1973: complete coccosphere with small coccoliths which have two thin plates forming the bridge and a ring of protrusions around the central area [Hivern-99, 19, 20 m]. D, *Reticulofenestra parvula* (Okada et McIntyre) Biekart var. *parvula*: complete coccosphere with coccoliths having a central area similar to *Emiliania* and *Gephyrocapsa* but with neither T-elements in the distal shield nor a bridge crossing central area [Meso-95, 142, surface]. Scale bars = 1 µm.
**Fig. 62.** *Calcidiscus leptoporus* (Murray et Blackman) Loeblich et Tappan: **A**, heterococcolith phase; subcircular coccosphere showing the tightly interlocked coccoliths [Fans-2, N07, 25 m]; **B**, detail with two placoliths (heterococcoliths) in distal view and six in proximal view which show the manner in which coccoliths imbricate [Fans-2, J03, 40 m]; **C**, holococcolith phase (Kleijne, 1991); coccosphere composed of irregularly elliptical crystalloliths [Fans-3, K12, 40 m]; **D**, detail showing holococcoliths in distal view, one in proximal view (lower right) and another in lateral view (upper right) which has a rim with three rings of crystallites [Meso-95, E023, surface] (NB: this holococcolith-bearing phase (Figs. C and D) was described previously as *Crystallolithus rigidus* Gaarder (Heimdal et Gaarder, 1980)). Scale bars: **A**, **B**, **C** = 2 µm; **D** = 1 µm.
FIG. 63. – A. Oolithotus antillarum (Cohen) Reinhardt, in Cohen et Reinhardt: collapsed coccosphere with two partially covered placoliths in proximal view showing the small eccentrically placed proximal shield [Fronts-96, 021, 90 m].

B. Oolithotus fragilis (Lohmann) Martini et Müller: large coccosphere with tightly interlocked placoliths; distal shield of coccoliths shows a slightly asymmetrically placed hole; proximal shield, slightly smaller than the distal, is eccentrically placed [Fans-2, M07, 40 m].

C-D. Umbilicosphaera hulburtiana Gaarder: C, complete coccosphere with elliptical placoliths having an elliptical opening which is surrounded distally by small nodes [Hivern-99, 76, 20 m]; D, detail of Fig. C. Scale bars: A, B = 2 µm; C, D = 1 µm.
Fig. 64. – A-B, *Umbilicosphaera sibogae* var. *sibogae* (Weber-van Bosse) Gaarder: A, complete coccosphere [Hivern-99, 25, surface]; B, detail with placoliths showing a distal shield slightly smaller than the proximal shield [Hivern-99, 25, 60 m]. C-D, *Umbilicosphaera sibogae* var. *foliosa* (Kamptner) Okada et McIntyre ex Kleijne: C, complete coccosphere; several placoliths have a characteristic small spine placed inside the central opening [Hivern-99, 64, 30 m]; D, detail showing placoliths [Hivern-99, 30, 5 m]. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 65. – *Papposphaera lepida* Tangen: **A**, complete coccosphere, slightly collapsed [Meso-96, D6, 70 m]; **B**, detail with pappoliths: some basal parts with the crown-like outer rim, composed of pointed elements (lower left); distal structures, in distal view, showing the four flattened lobes (lower centre); several spines which in distal view show a small wristlet or collar, which connects with the distal structure; a distal structure (calyx) in proximal view which shows the wristlet or collar in the centre and the characteristic arrangement of the four elements or lobes (upper centre) [Fronts-95, 20I, 80 m]; **C**, complete coccosphere with slightly varimorphic pappoliths [Meso-96, G4, 70 m]; **D**, small sized pappoliths, most of which show the proximal side of the basal part with the axial cross-bar; in the centre of the figure, there is a pappolith showing the distal part of the base with the cross-bar which appears to support the spine [Meso-96, G6, 70 m]. Scale bars = 1 µm.
Fig. 66. – A-B, *Papposphaera* sp. type 1: A, complete coccosphere showing small varimorphic pappoliths [Meso-96, I4, 100 m]; B, detail with pappoliths which consist of a spine without collar and a distal structure composed of four small rectangular elements [Fans-1, 127, 75 m]. C-D, *Papposphaera* sp. type 2: C, dimorphic coccosphere with varimorphic body pappoliths [Fans-1, 127, 100 m]; D, detail of Fig. C with long pappoliths which have a distal structure composed of four small spines perpendicular to the central shaft; the body pappoliths have the shaft tipped by three small rods.

Scale bars = 1 μm.
Fig. 67. – A-B, *Papposphaera* sp. **type 3**: A, coccosphere with variformic pappoliths [Fronts-95, 23D, 50 m]; B, detail of Fig. A showing the long shafts of the pappoliths which are tipped by four more or less rhomboidal elements. C-D, *Papposphaera* **sp. type 4**: C, coccosphere showing variformism [Fans-3, M11, 75 m]; D, detail of the Fig. C with pap poliths that show a spine tipped by four distally serrated triangular elements. Scale bars = 1 µm.
FIG. 68. – A-B, *Papposphaera* sp. type 5: A, complete coccosphere [Fronts-96, 013, 75 m]; B, detail with varimorphic pappoliths, which have a propeller-like distal structure [Fans-1, 123, 75 m]. C-D, *Papposphaera* sp. type 6: C, coccosphere with varimorphic coccoliths [Fans-1, 100, 60m]; D, detail of Fig. C showing pappolith-like base, no clear shaft and a distal structure consisting of three joined distally widened blade-like elements. Scale bars = 1 µm
Fig. 69. – A-B, *Papposphaera* holococcolithophore ("Turrisphaera") **phase sp. type A**: A, collapsed coccosphere showing varimorphic holococcoliths [Meso-96, E8, 100 m]; B, detail of Fig. A showing apple-core shaped holococcoliths. C-D, *Papposphaera* holococcolithophore ("Turrisphaera") **phase sp. type B**: C, collapsed coccosphere with characteristic leaf-like holococcoliths [Meso-96, E3/4, 70 m]; D, detail of Fig. C showing holococcoliths with an apple-core like proximal side which is suddenly flattened becoming a distally spatulate leaf-like structure. Scale bars = 1 µm.
Fig. 70. – A, *Pappomonas sp. type 1*: detail showing some papoliths with a long spine tipped by four small rods, and others without the central spine [Meso-96, D6, 100 m]. B, *Pappomonas sp. type 2*: coccosphere showing papoliths with a very simple circular base, a long spine and an obpyramidal distal structure, and other elliptical coccoliths with no central structure [Fans-2, J13, 40 m]. C-D, *Pappomonas sp. type 3*: C, dimorphic coccosphere showing varimorphic papoliths with a long spine and small calyx and other coccoliths with a crossbar in the base plate and a small nodular central structure [Meso-96, A3, 70 m]; D, detail of Fig. C showing the long papoliths with a flower-like distal calyx. Scale bars = 1 µm.
FIG. 71. – A. *Pappomonas* sp. type 4: coccosphere showing three types of coccoliths; either lacking a spine, with a small spine, or with a long spine with no calyx [Fans-2, J07, 25 m]. B. *Pappomonas* sp. type 5: coccosphere showing three types of coccoliths; lacking spine, with a straight spine, or with a slightly curved long spine with no calyx [Meso-96, A5, 100 m]. C. Genus type A, sp. type 1: monomorphic coccosphere with coccoliths showing long and sharp spines [Meso-96, D8, 100 m]. D. Genus type A, sp. type 2: coccosphere with coccoliths having a long central process with a characteristic feather-like distal structure [Fronts-96, 013, 90 m]. Scale bars: A, B, D = 1 µm; C = 2 µm.
Fig. 72. – A-B, Picarola margalefii Cros et Estrada (in press): A, complete coccosphere [Fronts-95, 25W, 70 m]; B, large coccosphere with numerous body and circum-flagellar coccoliths [Meso-96, 16, 70 m]; C-D, Picarola sp.: C, coccosphere with coccoliths having the central process with pointed ends [Meso-96, 16, 70 m]; D, collapsed coccosphere showing some detached coccoliths which show a proximal base with a diagonal cross-bar and a rim of irregular height (upper left); at the bottom of the figure, in between the longest coccoliths, the remains of the two flagella can be seen [Fronts-95, 25W, 80 m]. Scale bars = 1 µm.
FIG. 73. – *Ceratolithus cristatus* Kamptner: A, detail of one ceratolith of the forma *rostratus* showing the ‘rostrum’ (lower left corner), the dentate keel next to the ‘rostrum’, and the smooth keel in the upper part of the figure [Fronts-96, 013, 30 m]; B, collapsed cocsphere of the former *Neosphaera coccolithomorpha* showing the planoliths in proximal, distal and side views [Fronts-96, 013, 10 m]; C, the large *Ceratolithus* nannolith with remains of the hoop-like coccoliths [Fans-1, 123, 25 m]; D, the hoop-like coccoliths inside a cracked cocsphere of the former *N. coccolithomorpha* coccoliths [Fronts-96, 013, 10 m]. Scale bars = 2 µm.
Fig. 74. – A-B, *Alisphaera capulata* Heimdal, in Heimdal et Gaarder: A, collapsed coccosphere showing coccoliths with a characteristic extension [Fronts-96, 013, 60 m]; B, coccoliths with a base plate filling the central area and a characteristic sinistrally inclined extension of the wider flange [Meso-96, A3, 40 m]. C-D, *Alisphaera extensa* Kleijne et al.: C, complete coccosphere in apical view (all coccolith extensions directed to the centre of the coccosphere) [Fans-2, M03, 10 m]; D, detail of Fig. C showing coccoliths with a broad pointed extension of the wide distal flange. Scale bars: A, B, D = 1 µm; C = 2 µm.
FIG. 75. – A-B, *Alisphaera pinnigera* Kleijne *et al.*: A, complete coccosphere with small coccoliths [Meso-96, E 3/4, 70 m]; B, detail showing coccoliths with a longitudinal fissure in the central area; some of these coccoliths show a characteristic small flat, triangular protrusion [Fronts-96, 013, 60 m]. C-D, *Alisphaera quadrilatera* Kleijne *et al.*: C, complete coccosphere showing coccoliths with a characteristic extension [Hivern-99, 25, 80 m]; D, detail with coccoliths having a central area with a longitudinal fissure and a wider distal flange that has a polygonal extension [Fronts-95, 23D, 50 m]. Scale bars: A = 2 µm; B, C, D = 1 µm.
Fig. 76. – A-B, *Alisphaera unicornis* Okada *et* McIntyre: A, complete coccosphere showing coccoliths with a pointed protrusion [Hivern-99, 25, 60 m]; B, detail of Fig. A showing coccoliths with a longitudinal irregularly shaped fissure and a pointed horn-like protrusion on the wider distal flange. C-D, *Alisphaera gaudii* Kleijne *et al.*: C, complete coccosphere showing coccoliths with a small pointed beak-like protrusion [Fans-1, 64, 25 m]; D, detail of Fig. C showing coccoliths with a longitudinal fissure and a wider distal flange that has a spine-like extension. Scale bars: A = 2 µm; B, C, D = 1 µm.
Fig. 77. – *Alisphaera gaudii* and *Polycrater* sp. (with holes, reminiscent of Gaudi’s architecture): A, coccosphere consisting of a combination of *Alisphaera gaudii* (Figs. 76 C and D) at upper left, and coccoliths of the form *Polycrater* sp. (with holes, reminiscent of Gaudi’s architecture) at lower right [Fans-3, M11, 5 m]; B, detail of Fig. A; C, coccosphere of *Polycrater* sp. (with holes, reminiscent of Gaudi’s architecture), which can be considered a different phase of *Alisphaera gaudii*, showing coccoliths with elongated holes [Fans-3, K03, 25 m]; D, detail of Fig. C showing the sinuous and pointed outline of the coccoliths which have two elongated openings (characteristics reminiscent of Gaudi architecture); the sepal-like proximal side has the form of a very adorned cross (upper left). Scale bars = 1 μm.
Fig. 78. – *Canistrolithus* sp. 1 and *Polycrater galapagensis* var. A (with nodes) combination: A, coccosphere of *Canistrolithus* sp. 1 with some detached coccoliths on the filter (lower right) in proximal and lateral view; to the left of the coccosphere there are several *Polycrater* coccoliths [Fans-3, K05, 84 m]; B, detail of Fig. A showing coccoliths of *Canistrolithus* with and without a lateral squared protrusion which finishes in a pointed spine; C, coccosphere of *P. galapagensis* var. A (with nodes) surrounded by coccoliths of *Canistrolithus* sp. 1 [Fans-3, K05, 84 m]; D, detail of Fig. C showing the coccoliths of *Canistrolithus* covering the coccoliths of *Polycrater*. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 79. – A-B, *Canistrolithus* sp. 1 and *Polycrater galapagensis* var. A (with nodes) combination: A, detail of Fig. 78C showing three coccoliths of *Canistrolithus* with a robust spine and the coccoliths of *Polycrater* with characteristic nodes on the smaller petal-like side; B, detail of Fig. 78C with *Canistrolithus* coccoliths next to, and covering the *Polycrater* coccoliths. C-D, *Polycrater galapagensis* var. A (with nodes): C, complete coccosphere [Meso-95, 147, surface]; D, detail of Fig. C showing coccoliths with nodes on the distal part of the smaller half. Scale bars: A, B, D = 1 µm; C = 2 µm.
**Fig. 80.** – A-B. *Polycrater galapagensis* Manton *et* Oates: A, complete coccosphere with the small coccoliths arranged in slightly curved rows [Meso-95, 015, surface]; B, detail of Fig. A showing the squared bowl-shaped coccoliths which usually have been called nannololiths due to their unusual structure. C-D, *Polycrater* sp. (with slit): C, collapsed coccosphere [Fronts-95, 20I. 20 m]; D, detail of Fig. C showing a slit in the distal bowl-shaped part of the coccoliths (e.g. lower right). Coccoliths in proximal view show the sepal-like basal structure (e.g. centre right). Scale bars = 1 µm.
Fig. 81. – A-B. *Polycrater* sp. (with lip-like borders): A, collapsed coccosphere showing small coccoliths with rounded borders on the distal flange [Fronts-95, 24W, 5 m]; B, detail of Fig. A showing the bent borders of the distal flange which resembles a pair of lips; the proximal sepal-like structure forms a small and uncomplicated cross. C-D, *Polycrater* sp. (minimum): C, coccosphere showing numerous very small coccoliths [Meso-96, E3/4, 40 m]; D, detail of Fig. C showing the very small and simple coccoliths. Scale bars = 1 µm.
Fig. 82. – A-B. *Polycrater* sp. (spinous, two petal-like structures very modified): A, coccosphere with a spiny shape like a sea urchin due to the very modified shape of the coccoliths [Meso-96, E3/4, 70 m]; B, detail of Fig. A showing the coccoliths; half of the petal-like (distal) part of the coccoliths narrows to form a rod-like extension, giving to the coccolith the appearance of a scoop or ladle. C-D. *Polycrater* sp. (two petal-like structures very modified, the other two lacking): C, coccosphere showing the spiny appearance with the very modified “polycrater” coccoliths [Meso-96, D6, 40 m]; D, detail showing the distal rods and the sepal-like proximal part of the coccoliths [Meso-96, A3, 40 m]. Scale bars = 1 µm.
FIG. 83. – A-B, *Umbellosphaera tenuis* Paasche in Markali *et* Paasche, emend. Gaarder in Heimdal and Gaarder: A, complete coccosphere showing macrococcoliths [Fronts-96, 021, 10 m]; B, coccosphere showing macrococcoliths and micrococcoliths which are smaller and have a large elliptical central area (central part of the figure) [Fronts-96, 013, 60 m]. C-D, *Gladiolithus flabellatus* (Halldal *et* Markali) Jordan and Chamberlain: C, complete coccosphere in antapical view showing the small and flat elliptical lepidoliths partially covering the base of the tubular coccoliths [Fronts-95, 23D, 80 m]; D, detail with lepidoliths composed of two platelets joined by a suture line through the short axis of the lepidolith and the tubular coccoliths with very small spines on the distal side [Fronts-95, 23D, 70 m]. Scale bars: A, D = 2 µm; B, C = 1 µm.
FIG. 84. – A-B, *Turrilithus latericioides* Jordan et al.: A, complete coccosphere with the tower-shaped coccoliths [Meso-96, F2, 100 m]; B, detail showing elliptical proximal base of the coccoliths and the characteristic hollow, tower-shaped appendix with lateral spines on the square distal end [Fronts-95, 23D, 70 m]. C-D, *Florisphaera profunda* Okada et Honjo: C, complete coccosphere in apical view showing the flower-like arrangement of the coccoliths [Fronts-96, 039, 160 m]; D, complete coccosphere in antapical view [Fronts-96, 021, 90 m]. Scale bars = 1 µm.
Fig. 85. – A-C, *Florisphaera profunda* Okada *et* Honjo: A, collapsed cccosphere of the *elongata* type [Meso-95, 119, 70 m]; B, collapsed cccosphere of the *profunda* type [Fronts-95, 23D, 80 m]; C, cccosphere of an *elongata*-related type showing very straight sides and a characteristic basal part with a conspicuous peg-like proximal structure [Meso-96, 13, 100 m]. D, *Florisphaera ?sp.*: collapsed cccosphere with more or less square cccoliths with irregular borders and a notable distal spine [Meso-96, D8, 70 m]. Scale bars: A, B, C = 1 µm; D = 2 µm.
FIG. 86. — A-B. *Anthosphaera fragaria* Kamptner, emend. Kleijne: A, complete coccosphere with dimorphic coccoliths [Fans-3, M11, 5 m]; B, detail with calyptrolith-like body coccoliths (left) and three fragarioliths showing the three crystallite-wide proximal rim and the very large single-layered leaf-like distal part [Fronts-95, 20I, 20 m]. C. *Anthosphaera* cf. *fragaria* Kamptner, emend. Kleijne: coccosphere showing small sized coccoliths with large pores in both calyptrolith-like body coccoliths and circum-flagellar fragarioliths [Fronts-95, 23D, 50 m]. D. *Anthosphaera lafourcadii* (Lecal) Kleijne: complete coccosphere showing body coccoliths with perforations and fragarioliths having a broad but short process [Fans-1, 127, 25 m]. Scale bars = 1 µm.
FIG. 87. – A-B, *Anthosphaera periperforata* Kleijne **Type 1**: A, complete dimorphic coccospere showing fragarioliths in apical position and body coccoliths with and without small distal spine (the antapical coccoliths have a distal spine) [Meso-96, E3/4, 40 m]; B, detail with body coccoliths and, in the centre of the figure, two fragarioliths with pointed endings to the distal protrusion [Meso-96, G2, 20 m]. **C**, *Anthosphaera periperforata* Kleijne **Type 2**: complete coccospere showing fragarioliths with very pointed endings and having body coccoliths with a small distal spine [Meso-96, E3/4, 40 m]. **D**, *Anthosphaera periperforata* Kleijne **Type 3**: coccospere with very perforated coccoliths [Meso-96, E3/4, 40 m]. Scale bars = 1 µm.
Fig. 88. – A, *Anthosphaera* sp. type A (origami art): cccosphere with dimorphic coccoliths having very ornamented apical fragarioliths and body coccoliths which resemble origami paper boats [Fronts-95, 23D, 50 m]. B, *Anthosphaera* sp. type B: complete cccosphere showing fragarioliths which have a leaf-like distal protrusion with straight sides and body calyptroliths which have the dome formed of few crystallites [Hivern-99, 19, 20 m]. C-D, *Anthosphaera* sp. type C: C, cccosphere with dimorphic coccoliths; characteristic circum-flagellar fragarioliths and very simple body calyptroliths [Meso-96, G4, 5 m]; D, detail showing apical fragarioliths with a slender pointed arch and body calyptroliths, some with the central mound missing [Fans-1, 64, 5 m]. Scale bars = 1 µm.
Fig. 89. – A-B, *Calicasphaera concava* Kleijne: A, coccosphere with calicaliths in distal and proximal view [Fronts-96, 039, 40 m]; B, detail of Fig. A showing the concave wall of the calicaliths widening to form a broad distal opening. C-D, *Calicasphaera blokii* Kleijne: C, coccosphere with calicaliths mostly in distal view, with two detached calicaliths showing the elliptical proximal side (lower right); one calicalith in side view (left) shows the convex distal wall [Fans-3, K03, 10 m]; D, detail of Fig. C with calicaliths in distal view showing concentric rows of large crystallites. Scale bars = 1 µm.
FIG. 90. – A-B, *Calyptrolithina divergens* (Halldal et Markali) Heimdal var. *divergens*: A, coccosphere showing only the body calyptroliths [Fronts-95, 23D, 50 m]; B, detail of Fig. A showing body calyptroliths with a distally widening tube forming the protruding rim, and the distal vaulted roof, slightly flattened in the direction of the short axis of the coccolith. C-D, *Calyptrolithina divergens* var. *tuberosa* (Heimdal) Jordan et al.: C, detail with a zygolith (upper middle) and body calyptroliths showing a notable rim that surrounds the flat and perforated distal surface which has central mound [Fans-1, 127, 25 m]; D, detail showing a transverse row of zygoliths with a bridge tipped by a central protrusion, and the perforated body calyptroliths [Fronts-95, 23D, 10 m]. Scale bars = 1 µm.
Fig. 91. *Calyptrolithophora papillifera* (Halldal) Heimdal in Heimdal et Gaarder: A, coccosphere showing a notable flagellar opening [Fans-1, 100, 25 m]; B, detail of Fig. A showing the hexagonal arrangement of crystallites in the body calyptroliths, which have a slightly protruding rim; C, coccosphere showing the circum-flagellar calyptroliths having characteristic rows of crystallites on the distal surface [Meso-96, I8, 40 m]; D, detail showing the flat body calyptroliths and a prominent hump-like square-sided circum-flagellar calyptrolith (lower left corner) which shows the characteristic parallel rows of crystallites [Meso-95, 163, 40 m]. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 92. – A-B, *Calyptrolithophora gracillima* (Kamptner) Heimdal: A, cocolspere showing a flagellar area surrounded by zygolith-like calyptroliths and body coccoliths which are calyptroliths [Fans-1, 100, 40 m]; B, detail with body calyptroliths having a straight, slightly protruding distal rim, a flat distal surface with an hexagonal meshwork of crystallites and bearing a notable rounded protrusion; there is a zygolith-like calyptrolith near the right-bottom corner of the figure [Fronts-95, 23D, 50 m]. C-D, *Calyptrosphaera cialdii* Borsetti et Cati: C, cocolspere with monomorphic coccoliths [Fans-3, K03, 25 m]; D, detail of Fig. C showing coccoliths which more closely resemble laminoliths than calyptroliths; they appear to be constructed of triangular crystallites and the rim has a laminated structure (see the coccoliths in lateral view at the top of the figure). Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 93. – A-B, *Calyptrosphaera heimdaliae* R.E. Norris, orthog. emend. Jordan *et* Green: A, coccosphere with large dome-shaped calyptroliths with one pore at the top and typically seven at the base of the dome, next to the broad rim [Fronts-96, 013, 30 m]; B, detail of perforated calyptroliths having large lateral pores with a straight base and an arched top; the distal opening is bordered by a small protusion [Meso-95, 023, surface]. C-D, *Calyptrosphaera sp.* (smaller heimdaliae): C, collapsed coccosphere with calyptroliths similar to those of *C. heimdaliae*, but smaller and having more numerous and smaller lateral pores [Fans-3, K05, 5 m]; D, coccosphere possessing the characteristics of the specimen of Fig. C, but having more calyptroliths with smaller and more numerous lateral pores [Fronts-96, 027, 10 m]. Scale bars: A, C, D = 2 µm; B = 1 µm.
Fig. 94. – A-B, *Calyptrosphaera dentata* Kleijne: A, coccosphere with monomorphic coccoliths [Fans-3, K07, 25 m]; B, detail of Fig. A showing calyptroliths with a central area surface having six-sided regularly arranged perforations and a thick rim with a tooth-like protrusion. C-D, *Calyptrosphaera sphaeroidea* Schiller: C, coccosphere with globular calyptroliths; the coccoliths in side view show a basal ring one crystallite thick [Meso-95, 023, surface]; D, detail of a coccosphere showing irregularly constructed calyptroliths which are not completely closed distally [Fans-1, 100, 5 m].

Scale bars = 1 µm.
Fig. 95. – A-B, *Corisphaera strigilis* Gaarder: A, coccosphere with dimorphic coccoliths [Meso-96, G6, 5 m]; B, detail showing flat body coccoliths with thick bridge (lower) and circum-flagellar coccoliths with a leaf-like pointed extension (upper) [Fronts-95, 23D, 30 m]. C-D, *Corisphaera tyrreniensi* Kleijne: C, coccosphere with several slightly disintegrated coccoliths; note the zygolith (centre left) which resembles the zygoliths of *Zygosphaera marsili* (see *Z. marsili* in Fig. 108 C and D) [Meso-96, G6, 40 m]; D, detail showing the delicate, perforated construction of the zygoliths [Fans 3, M11, 25 m]. Scale bars = 1 µm.
FIG. 96. – A, *Corisphaera* cf. *gracilis*: coccosphere with dimorphic coccoliths [Fronts-96, 013, 30 m]. B, *Corisphaera* sp. (ornamented circum-flagellar coccoliths): collapsed coccosphere with dimorphic coccoliths; body zygo liths very low and flat, circum-flagellar coccoliths have a bridge with an accentuated pointed leaf-like extension [Fronts-95, 23D, 20 m]. C-D, *Corisphaera* sp. (aff. type A of Kleijne, 1991): C, coccosphere with dimorphic coccoliths; body zygo liths have a low and very narrow bridge [Fronts-96, 039, 10 m]; D, detail of Fig. C showing the apical area of the coccosphere. Scale bars = 1 µm.
Fig. 97. – **A. Corisphaera sp.** (aff. type A of Kleijne, 1991, and *C. gracilis*): coccosphere with body zygoliths which have a well arranged distal rim of angular crystallites and a high and thin bridge spanning the wide central area [Meso-96, 14, 40 m]. **B. Corisphaera sp.** (body zygoliths with pointed bridge): collapsed coccosphere with dimorphic coccoliths; body zygoliths with rather straight walls and a thin pointed bridge, circum-flagellar zygoliths with a large bridge [Fronts-95, 23D, 20 m]. **C-D. Corisphaera sp.** (double-layered body zygoliths with S-shaped bridge): **C**, slightly collapsed coccosphere with dimorphic coccoliths; body zygoliths with double-layered wall and undulated bridge, circum-flagellar zygoliths with high and pointed bridge [Meso-96, 14, 40 m]; **D**, detail showing the body zygoliths (bottom) and circum-flagellar zygoliths (top) [Fans 1, 127, 25 m]. Scale bars = 1 µm.
FIG. 98. – A-B, *Daktylethra pirus* (Kamptner) Norris: A, collapsed coccosphere showing calyptroliths with a vaulted distal protrusion and pores around the rim [Meso-95, 178, 40 m]; B, detail of Fig. A with calyptroliths in distal view showing a prominent rim, a vaulted central protrusion which sometimes has a pore, and seven to ten openings near the rim. C-D, *Helladosphaera cornifera* (Schiller) Kamptner: C, complete coccosphere showing apical circum-flagellar helladoliths (top of the figure) and body zygoliths; the high bridge of the zygoliths becomes larger near the apical pole (see upper part of the figure, below the helladoliths) [Fans-3, K12, 5 m]; D, detail showing helladoliths (top) and body zygoliths (bottom); helladoliths present a high, double-layered process which has a pointed angular tip and a pore in the base [Meso-95, 147, surface]. Scale bars: A = 5 µm; B, C, D = 1 µm.
Fig. 99. – A-B, *Homozygosphaera arethusae* (Kamptner) Kleijne: A, complete coccosphere showing body zygoliths with broad bridges and apical circum-flagellar zygoliths with higher bridges adorned with a distal protrusion (upper middle) [Fans-1, 123, 5 m]; B, detail of body zygoliths (bottom) and circum-flagellar zygoliths with double layered tubes and very high bridges with a distal protrusion (top) [Meso-95, G6, 40 m]. C-D, *Homozygosphaera triarcha* Halldal and Markali: C, coccosphere having three-arched coccoliths; the higher coccoliths have an adorned distal tip (e.g. upper centre) [Picasso Workshop, T4, surface]; D, detail showing the disposition of the arches [Picasso Workshop, T4, surface]. Scale bars: A, C = 2 µm; B, D = 1 µm.
Fig. 100. – A-B, *Poricalyptra aurisinae* (Kamptner) Kleijne: A, complete coccosphere showing body calyptroliths with transverse slits and circum-flagellar helladoliths [Fans-3, K12, 60 m]; B, detail with body calyptroliths in latero-proximal view (left) showing the perforated wall, and in distal view showing the transverse slits and a central transverse protrusion with crystallites [Meso-95, 163, 40 m]. C-D, *Poricalyptra isselii* (Borsetti and Cati) Kleijne: C, large coccosphere with body calyptroliths only, several of which are partially disintegrated [Meso-95, 161, surface]; D, detail with two helladoliths (top) and several calyptroliths [Meso-95, 161, surface]. Scale bars = 1 µm.
Fig. 101. – A-B, Poritectolithus sp. 1: A, coccosphere having flat and thin calyptroliths and helladoliths without tube [Fronts-95, 24W, 30 m]; B, detail of Fig. A with body coccoliths distally covered by rows of crystallites and circum-flagellar coccoliths resembling helladoliths but lacking the tube and possessing a pointed protrusion. C-D, Poritectolithus tyronus Kleijne: C, coccosphere with low body calyptroliths and irregularly shaped circum-flagellar helladoliths [Fans-3, K12, 75 m]; D, detail of Fig. C with body calyptroliths having rows of big crystallites on the distal surface (upper and lower right) and helladoliths having a characteristic pointed protrusion tipped by a peak of one crystallite. Scale bars = 1 µm.
Fig. 102. – A-B, *Poritectolithus poritectus* (Heimdal) Kleijne, orthog. emend. Jordan et Green: A, coccosphere with helladoliths and varimorphic calyptroliths, higher and more vaulted near the apical area [Meso-96, E2, 70 m]; B, detail of Fig. A showing helladoliths and calyptroliths with protruding rim. C-D, *Poritectolithus* sp. 2: C, coccosphere with zygoliths as body coccoliths, the bridges of which are constructed by arches of crystallites [Fronts-95, 23D, 60 m]; D, detail of Fig. C showing body zygoliths (left) and circum-flagellar coccoliths (right) with a broad but not very high protrusion. Scale bars: A, B, D = 1 µm; C = 2 µm.
Fig. 103. – A-B, *Sphaerocalyptra quadridentata* (Schiller) Deflandre: A, coccosphere with some body calyptroliths slightly broken [Fronts-96, 013, 10 m]; B, detail with body calyptroliths and one high circum-flagellar calyptrolith (upper left); the coccoliths are constructed of irregularly arranged crystallites except the base which is one crystallite thick and has a regular structure [Meso-95, 023, surface]. C-D, *Sphaerocalyptra cf. adenensis* Kleijne: C, completely collapsed coccosphere showing high variability in the size of body calyptroliths and three large circum-flagellar calyptroliths (upper right) [Fans-3, K03, 10 m]; D, detail with calyptroliths showing the packed crystallites arranged in more or less concentric rows and the single-layered base [Meso-96, A5, 5 m]. Scale bars = 1 µm.
FIG. 104. – A-B, *Sphaerocalyptra* sp. 1: A, coccosphere showing body and circum-flagellar calyptroliths [Fans-3, K03, 10 m]; B, detail showing the angular crystallites of the calyptroliths which are distally pointed and constructed on a basal ring; circum-flagellar calyptroliths (upper left) have a very high and pointed central protrusion [Meso-95, 147, surface]. C-D, *Sphaerocalyptra* sp. 4: C, collapsed coccosphere with characteristic circum-flagellar coccoliths which possess a robust stick-like protrusion [Fronts-95, 23D, 30 m]; D, detail of Fig. C with calyptroliths which show a simple but robust construction: a baseplate with a proximal ring of crystallites is bordered by a ring of strongly packed crystallites which support robust columns that form the opened distal part; in circum-flagellar coccoliths, which are constructed in the same manner, the central area columns support a robust, slightly convex, pointed stick-like structure. Scale bars = 1 µm.
Fig. 105. – A. *Sphaerocalyptra* sp. 2: disintegrated coccosphere showing cone-shaped body calyptroliths with very thin pointed endings; circum-flagellar coccoliths are higher and more robust (top) [Meso-96, D6, 5 m]. B-D. *Sphaerocalyptra* sp. 3: B, coccosphere with very perforated and pointed coccoliths which are formed by columns of crystallites [Fronts-95, 28C, 20 m]; C, detail showing two circum-flagellar coccoliths (upper right) constructed by a basal ring and columns of crystallites; body coccoliths have a similar construction, but are lower [Fronts-95, 20I, 50 m]; D, detail with complete body calyptroliths (lower right) which have a basal ring of 1-2 rows from which rise the columns of crystallites; circum-flagellar coccoliths, larger and having a possibly organic base plate, are constructed in the same manner [Fronts-95, 23D, 40 m]. Scale bars = 1 µm.
Fig. 106. – A-B, \textit{Sphaerocalyptra sp. 5}: A, coccosphere with perforated, highly diverse-shaped calyptroliths [Meso-96, I8, 40 m]; B, detail of Fig. A showing the pointed circum-flagellar coccoliths and the rounded body calyptroliths which are constructed of large crystallites. C-D, \textit{Sphaerocalyptra sp. 6}: C, coccosphere with pointed circum-flagellar coccoliths and very simple body coccoliths, most of which have lost the cover [Meso-92, E3-4, 40 m]; D, detail with very thin and high circum-flagellar coccoliths (left) and body coccoliths which seem to be calyptroliths with the distal cover missing [Fronts-95, 20I, 20 m]. Scale bars = 1 µm.
Fig. 107. – A. *Syracolithus dalmaticus* (Kamptner) Loeblich et Tappan: coccosphere with coccoliths which show a thick cover and a hollow central part [Hivern-99, 69, 40 m]. B. *Syracolithus schilleri* (Kamptner) Kamptner: coccosphere with a flagellar opening (centre); the coccoliths have 8 to 16 pores (perforations through the laminolith) and a central protrusion [Meso-96, A5, 5 m]. C-D, *Syracolithus quadriperforatus* (Kamptner) Gaarder: C, coccosphere with very high and perforated laminoliths [Meso-95, 023, surface]; D, detail showing the perforated laminoliths [Meso-95, 023, surface]. Scale bars: A, C, D = 1 µm; B = 2 µm.
FIG. 108. – A-B, *Zygosphaera amoena* Kamptner: A, complete coccosphere showing circum-flagellar zygoliths (top) with double-layered wall and body laminoliths [Fans-3, K12, 60 m]; B, detail with zygoliths in lateral view (upper left) and laminoliths showing the longitudinal mound and the regularly arranged angular crystallites at the border [Meso-96, E3-4, 40 m]. C-D, *Zygosphaera marsilii* (Borsetti and Cati) Heimdal: C, coccosphere showing microperforate appearance of coccoliths [Hivern-99, 25, 20 m]; D, detail of body laminoliths with a small transverse ridge and circum-flagellar coccoliths which have a wider transverse ridge which gives them their zygolith appearance (upper middle/left) [Meso-95, 023, surface]. Scale bars = 1 µm.
**Fig. 109.** *Zygosphaera hellenica* Kamptner: **A**, complete coccosphere showing body laminoliths only [Meso-95, 023, surface]; **B**, complete coccosphere showing body laminoliths, several with pores, and two circum-flagellar zygof orm coccoliths (upper left) [Workshop Picasso, T4, surface]; **C**, detail with four circum-flagellar coccoliths (top) and body coccoliths with no pores (lower left), one pore (centre right), or two pores (centre, next to circum-flagellar coccoliths); all coccoliths have a central mound which is round and small on the body coccoliths [Meso-95, 157, surface]; **D**, detail with body laminoliths (left) and circum-flagellar zygolith-like laminoliths (right) showing the irregular crystallite arrangement which gives the coccosphere an unusual appearance [Fronts 95, 28C, 20 m]. Scale bars: **A, C, D** = 1 µm; **B** = 2 µm.
Fig. 110. – A-B, Holococcolithophore sp. 1 (coccoliths have two small pores in proximal side): A, holococcolithophore showing monomorphic coccoliths [Meso-96, D4, 5 m]; B, detail with holococcoliths in distal and proximal view; the proximal side of the coccoliths has two diagonally arranged pores. [Fronts-95, 23D, 5 m]. C-D, Coccolithophore sp. 1 (affinity to Rhabdosphaeraceae?): C, cccosphere with trimorphic coccoliths; this taxa may be related to Algirosphaera and Cyrtosphaera due to the shape and varimorphism of their coccoliths [Fronts-96, 019, 57 m]; D, detail of coccoliths which resemble calyptroliths but without clear crystallites [Meso-96, D8, 70 m]. Scale bars = 1 µm.
FIG. 111. – **A. Coccolithophore sp. 2** (affinity to *Syracosphaera*?): collapsed coccosphere; coccoliths resemble muroliths with a very low wall; central area might be constructed of wide laths joined together; the coccolith near the upper-right corner appears to have a central spine [Meso-96, E8, 100 m]. **B. Coccolithophore sp. 3** (affinity to *Sphaerocalyptra*?): very small and rounded coccoliths with a bridge which is higher and centrally pointed on several coccoliths [Meso-96, G4, 70 m]. **C. Unidentified sp. 1**: complete cell case showing a honeycomb aspect [Fans-3, K03, 25 m]. **D. Unidentified sp. 2**: a group of variably sized four pointed stars which appear to be joined to a rod; the stars seem to be central structures attached to a basal ring with cross bars [Meso-96, D6, 100 m]. Scale bars = 1 µm.
Fig. 112. – **Other possible heterococolith - holococolith combinations:** A, a collapsed mixed coccospere with a circum-flagellar caneolith with spine and several body caneoliths of *Syracosphaera molischii* surrounding the body and circum-flagellar holococoliths of *Anthosphaera fragaria* [Fronts-95, 20I, 20 m]; B, a collapsed coccospere of *Calypтроlithophora papillifera* surrounded by heterococoliths of *Syracosphaera histrica* [Meso-96, 14, 40 m]; C, coccospere with heterococoliths of *Syracosphaera marginaporata* (body coccoliths and circum-flagellar coccoliths in apical position) and holococoliths appearing related to *Anthosphaera* genus (body coccoliths remind *Anthosphaera* sp. type B calyptroliths) [Hivern-99, 19, sup.]; D, detail of Fig. C. with possible remains of a leaf-like distal protrusion of a fragariolith (middle right). Scale bars: A, B = 2 µm; C, D = 1 µm.
Fig. 113. – Other possible heterococcolith - holococcolith combinations: A, heterococcoliths of *Syracosphaera* sp. type D (see Kleijne, 1993) mixed with holococcoliths of *Homozygosphaera arethusae* [Fronts-96, 013, 66 m]; B, another mixed group of the same combination of coccoliths as Fig. A [Fronts-96, 013, 66 m]; C, mixed collapsed cocciosphere with body caneoliths of *Syracosphaera delicata* surrounding body holococcoliths of *Corisphaera* sp. type B (Kleijne 1991) [Fans-1, 127, 100 m]; D, a mixed collapsed cocciosphere consisting half of body caneoliths of the heterococcolithophore *Syracosphaera nodosa* (right) and half of holococcoliths of *Helladosphaera cornifera* (left); some circum-flagellar helladololiths are clearly visible in the upper-left corner [Meso-96, I8, 40 m]. Scale bars: A, B, D = 2 µm; C = 1 µm.
FIG. 114. – **Other possible heterococcolith - holococcolith combinations:** A, collapsed *Rhabdosphaera clavigera* coccosphere partially covering a coccosphere of *Sphaerocalyptra quadridentata* [Picasso workshop, T1 (off. Barcelona), surface]; B, disintegrated coccosphere of *Sphaerocalyptra quadridentata* with some exothecal coccoliths of *Rhabdosphaera clavigera* [Picasso workshop, T5 (off. Barcelona), surface]; C, collapsed coccosphere consisting of holococcoliths of *Sphaerocalyptra* sp. and heterococcoliths of an undetermined *Acanthoica* sp. [Fans-3, M11, 25 m]; D, detail of Fig. C. Scale bars: A, B, C = 2 µm; D = 1 µm.
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