Preface

The main objective of the present Atlas is to illustrate, using SEM micrographs, the great diversity of the coccolithophore forms present in NW Mediterranean waters. The idea of this study was conceived, several years ago, by Dr. Ramon Margalef, who highlighted the interest of a thorough examination of the Mediterranean coccolithophores. Dr. Marta Estrada provided the necessary support to collect the samples and to implement the research.

In the course of examining the samples, many problems of species identification were encountered. One of the authors (L. C.) undertook the task of surveying the relevant literature and clarifying the taxonomic problems that had emerged from the collected material. The result was a Ph. D. thesis (Cros, 2001), directed by Dr. Ramon Margalef and recently published in a limited edition (Cros, 2002).

The present book is based on the above mentioned Ph. D. thesis (especially on its chapters 3 and 4), but updated with recent findings and with the material ordered according to the last taxonomic developments. It must be pointed out that, after the extensive incorporation of electron microscopy techniques, coccolithophore systematics is in a state of constant flux.

We wish to thank *Scientia Marina* for the opportunity to print the present Atlas and to expose the beauty of these delicate organisms. The funds that made possible the publication of this book were provided by the EU project CODENET (Coccolithophorid Evolutionary Biodiversity and Ecology Network).

The **Introduction** of the Atlas contains an overview of the state of the art of the current knowledge on coccolithophores. The **Material and Methods** section presents the cruises and stations sampled and the techniques used to collect the samples, to measure coccospheres and coccoliths, and to obtain the SEM photomicrographs. The chapter on **Classification of living species**, begins with a review of the basic nomenclature used, including some illustrative drawings, and continues with the classification, systematics and description of the studied forms, which are represented in 411 SEM photomicrographs (Figs. 9-112).

This Atlas does not intend to be a comprehensive survey of all the NW Mediterranean coccolithophores. However, we believe that it contains a representative number of them, specially of the forms inhabiting sub-superficial summer waters, which were the most extensively sampled.

We hope this Atlas will be helpful to both coccolithophore workers and interested public.

THE AUTHORS

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Atlas of Northwestern Mediterranean Coccolithophores*

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SUMMARY: The present Atlas contains a detailed study, based in scanning electron microscopy (SEM) observations, of living coccolithophores from NW Mediterranean waters. The study contains 103 figures with 411 micrographs, which correspond to 168 coccolithophores (including different taxonomic and morphotypic entities). The figured specimens were collected during different cruises carried out from 1995 to 1999. Classification of the organisms follows modern taxonomy of living calcareous nannoplankton. Measures of the specimens and notes on their taxonomy are given in addition to abridged descriptions of the studied taxa. The atlas contains a large number of previously undescribed forms, specially in the genera *Syracosphaera, Papposphaera, Polycrater, Anthosphaera, Corisphaera* and *Sphaerocalyptra*. Several species never illustrated in the literature are presented here for the first time. Coccospheres having coccoliths of different recognized species are presented. These combination coccospheres are nowadays considered as transitional steps between different phases in the cellular life-cycle. An introduction with a brief overview of the actual coccolithophore knowledge and an abridged glossary with figures of the basic terminology are included.

Key words: coccolithophores, calcareous nannoplankton, living, Haptophyta, Prymnesiophyceae, NW Mediterranean Sea, SEM photomicrographs.

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 paleoceanographic purposes; they have been extensively used as stratigraphic fossils in sediments of Jurassic to Quaternary age (Perch-Nielsen, 1985a, b; Bown, 1998) and detailed chronostratigraphic and paleoecological 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

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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 coccospheres 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 coccospheres 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 pelagicus* 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 *et* 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 phase may form naked swarmers 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-calcifying 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 *Coronosphaera mediterranea* (Lohmann) Gaarder) and *Zygosphaera wettsteinii* Kamptner (now *Calyptrolithina wettsteinii* (Kamptner) Norris). He noted the similarity of his observation of *Calyptrosphaera 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 *Calyptrosphaera quadridentata*. Moreover he described the association of two holococcolithophores: *Corisphaera gracilis* Kamptner with *Zygosphaera hellenica* 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 pulchra* Lohmann and *Calyptrosphaera pirus* Kamptner (now, *Daktylethra 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 *Calyptrosphaera 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 *Acanthoica acanthos* Schiller with *Syracosphaera aperta* Schlauder.

Among natural specimens examined by SEM, Kleijne (1991) found a composite cell of the heterococcolithophore *Calcidiscus 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 *Calcidiscus 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 zygolith-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 *Calciarcus* 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, Sprengel and Young (2000) represented the combination of *Ceratolithus cristatus, Neosphaera coccolithomorpha* coccoliths and hoop-like cocccoliths (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 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 Fans cruises

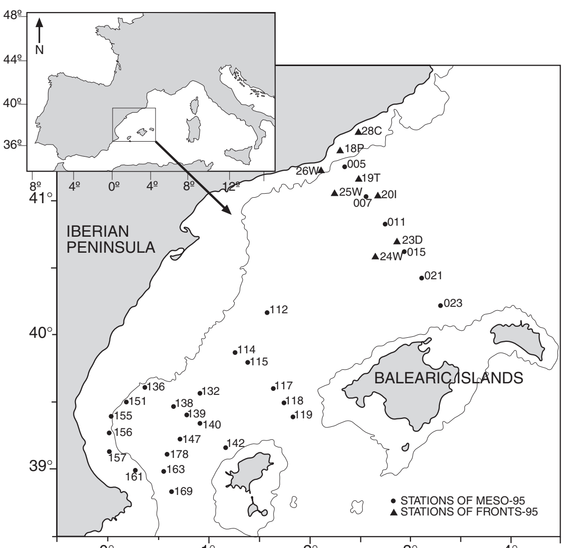

FIG. 1. – Position of the sampled stations during the year 1995 (Cruises Meso-95 and Fronts-95). It is enclosed the general map of the western Mediterranean showing the location of the studied area.

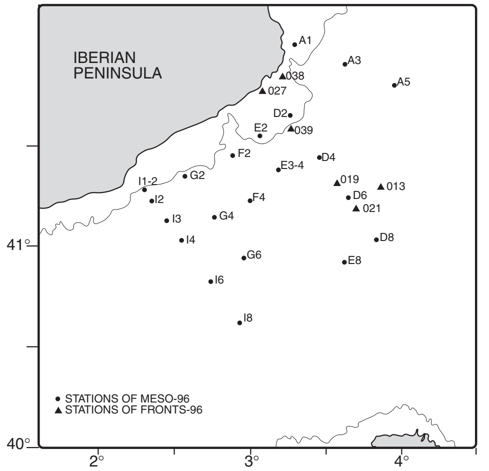

FIG. 2. – Position of the sampled stations during the cruises Meso-96 and Fronts-96.

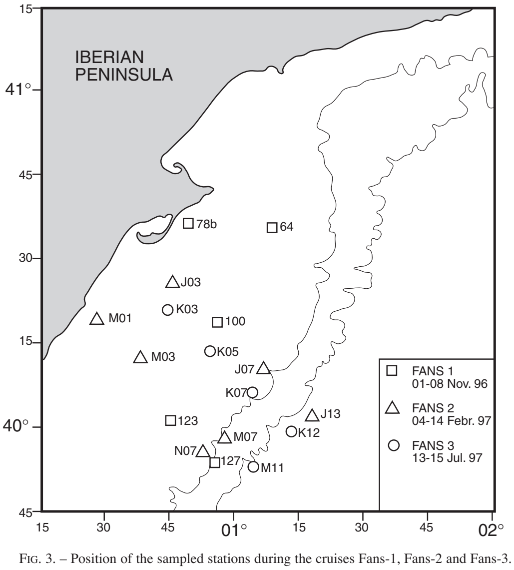

FIG. 3. – Position of the sampled stations during the cruises Fans-1, Fans-2 and Fans-3.

TABLE 1. – Spatial and temporal position of samples collected during the 1995 cruises (Fig. 1).

Stations	Date	Latitude	Longitude	Sampled depths (m)
Series	**Meso-95**			
005	31-05-95	41º13.8'N	2º20.5'E	0, 40
007	01-06-95	41º01.5'N	2º32.2'E	0, 40
011	01-06-95	40º49.3'N	2º44.1'E	0, 40
015	02-06-95	40º36.8'N	2º55.2'E	0, 40
021	02-06-95	40º24.9'N	3º06.8'E	0, 40
023	02-06-95	40º12.6'N	3º18.4'E	0, 40
112	11-06-95	40º09.4'N	1º34.6'E	0, 40
114	12-06-95	39º51.9'N	1º15.0'E	0, 40
115	12-06-95	39º47.5'N	1º22.9'E	0, 40
117	12-06-95	39º35.4'N	1º38.2'E	0, 40
118	12-06-95	39º29.2'N	1º44.1'E	0, 40
119	12-06-95	39º22.9'N	1º50.0'E	0, 40
132	13-06-95	39º33.7'N	0º54.5'E	0, 40
136	13-06-95	39º36.3'N	0º22.1'E	0, 40
138	13-06-95	39º27.6'N	0º38.5'E	0, 40
139	13-06-95	39º23.3'N	0º46.3'E	0, 40
140	13-06-95	39º19.0'N	0º54.7'E	0, 40
142	14-06-95	39º09.4'N	1º09.9'E	0, 40
147	14-06-95	39º13.1'N	0º42.7'E	0, 40
151	14-06-95	39º29.7'N	0º10.6'E	0, 40
155	14-06-95	39º23.4'N	0º01.4'E	0, 40
156	14-06-95	39º16.3'N	0º01.0'E	0, 40
157	14-06-95	39º08.2'N	0º00.4'E	0, 40
161	15-06-95	38º59.6'N	0º16.5'E	0, 40
163	15-06-95	38º59.0'N	0º33.4'E	0, 40
169	15-06-95	38º49.8'N	0º37.3'E	0, 40
178	16-06-95	39º06.4'N	0º34.6'E	0, 40
Series	**Fronts-95**			
18P	21-06-95	41º21.2'N	2º17.8'E	5, 10, 20, 30, 40, 50, 60, 65
19T	21-06-95	41º08.8'N	2º28.0'E	5, 10, 20, 30, 40, 50, 60, 70, 85
20I	21-06-95	41º01.5'N	2º40.6'E	5, 10, 20, 30, 40, 50, 60, 70, 80
23D	22-06-95	40º40.3'N	2º52.0'E	5, 10, 20, 30, 40, 50, 60, 70, 80
24W	22-06-95	40º33.9'N	2º38.7'E	5, 10, 20, 30, 40, 50, 60, 70, 80
25W	22-06-95	41º02.3'N	2º14.7'E	5, 10, 20, 30, 40, 50, 60, 70, 80
26W	22-06-95	41º11.9'N	2º06.5'E	5, 10, 20, 30, 40, 50, 60, 70, 80
28C	23-06-95	41º29.1'N	2º29.0'E	5, 10, 20, 30, 35

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

Stations	Date	Latitude	Longitude	Sampled depths (m)
Series	**Meso-96**			
A1	18-06-96	42º00.0'N	3º17.3'E	5, 40, 70, 100
A3	19-06-96	41º54.0'N	3º37.1'E	5, 40, 70, 100
A5	19-06-96	41º48.0'N	3º56.9'E	5, 40, 70, 100
D2	21-06-96	41º38.9'N	3º15.0'E	5, 40, 70, 100
D4	21-06-96	41º26.6'N	3º26.5'E	5, 40, 70, 100
D6	20-06-96	41º14.3'N	3º38.0'E	5, 40, 70, 100
D8	20-06-96	41º02.0'N	3º49.5'E	5, 40, 70, 100
E2	30-06-96	41º33.0'N	3º03.0'E	5, 40, 70, 100
E3-4	01-07-96	41º23.0'N	3º10.2'E	5, 40, 70, 100
E8	02-07-96	40º55.1'N	3º36.6'E	5, 70, 100
F2	23-06-96	41º27.2'N	2º52.0'E	5, 40, 70, 100
F4	24-06-96	41º13.7'N	2º59.7'E	5, 40, 70, 100
G2	24-06-96	41º20.9'N	2º33.7'E	5, 20, 40, 50, 70, 100
G4	24-06-96	41º08.6'N	2º45.2'E	5, 40, 70, 100
G6	25-06-96	40º56.3'N	2º56.7'E	5, 40, 70, 100
I1-2	29-06-96	41º17.0'N	2º17.8'E	5, 40, 70, 100
I2	24-06-96	41º13.9'N	2º20.7'E	5, 40, 70, 100
I3	28-06-96	41º07.7'N	2º26.5'E	5, 40, 70, 100
I4	25-06-96	41º01.6'N	2º32.2'E	5, 40, 70, 100
I6	25-06-96	40º49.3'N	2º43.7'E	5, 40, 70, 100
I8	27-06-96	40º37.0'N	2º55.2'E	5, 40, 70, 100
Series	**Fronts-96**			
013	16-09-96	41º17.8'N	3º51.2'E	10, 30, 60, 66, 75, 90
019	17-09-96	41º19.3'N	3º33.5'E	5, 30, 57, 100
021	17-09-96	41º11.7'N	3º41.6'E	20, 30, 50, 68, 90
027	18-09-96	41º46.7'N	3º03.9'E	5, 10, 20, 30, 45
038	20-09-96	41º51.0'N	3º12.0'E	15, 35, 45, 60
039	21-09-96	41º35.3'N	3º15.8'E	10, 30, 40, 50, 70, 160

TABLE 3. – Spatial and temporal position of samples collected during FANS 1-2-3 (Fig. 3).

Stations	Date	Latitude	Longitude	Sampled depths (m)
Series	**Fans-1**			
64	04-11-96	40º35.7'N	1º07.6'E	5, 25, 40, 60, 75, 81
78b	06-11-96	40º35.7'N	0º48.0'E	5, 12
100	07-11-96	40º17.0'N	0º55.2'E	5, 25, 40, 60, 75, 85
123	07-11-96	39º59.6'N	0º44.4'E	5, 25, 40, 60, 75, 88
127	08-11-96	39º52.8'N	0º54.0'E	5, 25, 40, 60, 75, 100
Series	**Fans-2**			
J03	10-02-97	40º24.7'N	0º44.5'E	5, 10, 25, 40, 58
J07	11-02-97	40º09.6'N	1º05.9'E	5, 25, 40, 60, 75, 100
J13	11-02-97	40º01.3'N	1º17.4'E	5, 25, 40, 60, 75, 100
M01	12-02-97	40º17.9'N	0º26.8'E	5, 10, 25, 30
M03	12-02-97	40º11.3'N	0º36.9'E	5, 10, 25, 40, 66
M07	13-02-97	39º57.1'N	0º56.9'E	5, 25, 40, 60, 75, 150
N07	13-02-97	39º54.6'N	0º51.7'E	5, 10, 25, 40, 60, 75
Series	**Fans-3**			
K03	13-07-97	40º19.4'N	0º40.4'E	5, 10, 25, 40, 60, 66
K05	13-07-97	40º12.4'N	0º53.2'E	5, 10, 25, 41, 64, 84
K07	14-07-97	40º04.8'N	1º03.1'E	5, 25, 40, 60, 75, 100
K12	14-07-97	40º00.3'N	1º10.4'E	6, 24, 40, 60, 75, 150
M11	15-07-97	39º53.9'N	1º01.0'E	5, 25, 40, 60, 75, 100

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-

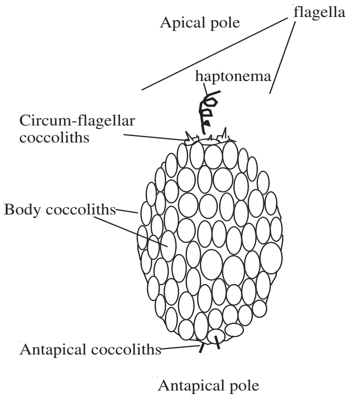

FIG. 4. – Coccolithophore cell.

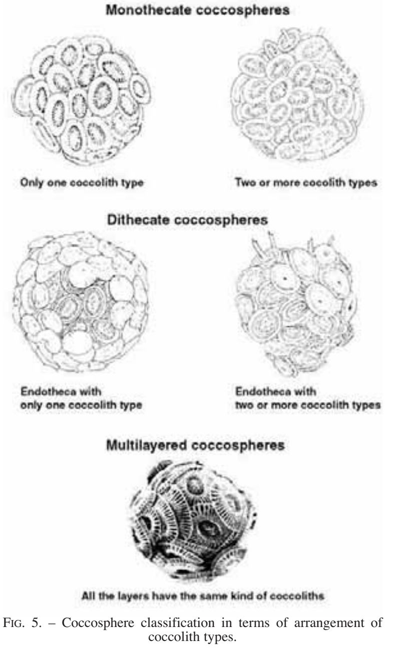

FIG. 5. – Coccosphere classification in terms of arrangement of coccolith types.

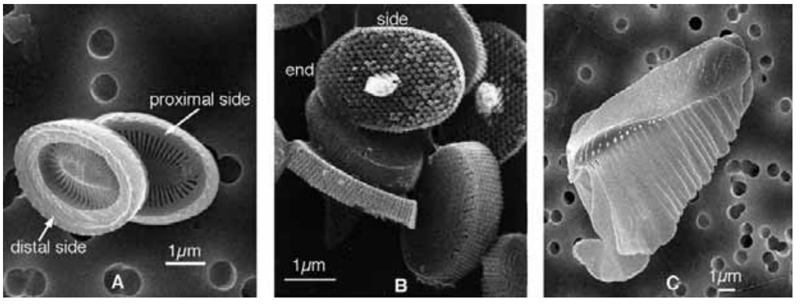

FIG. 6. – Types of coccoliths: (A) Heterococcoliths; one in distal view (left) and the other, partially obscured, in proximal view. (B) Holococcoliths, formed of numerous minute crystallites; one in distal view (upper centre) and one in latero-proximal view (lower right); (C) A ceratolith, considered to be an irregularly shaped nannolith.

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 **nannoliths** (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, 1985a, b). 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).

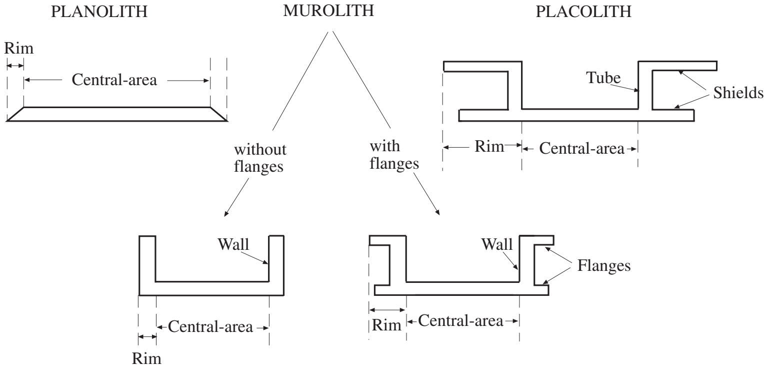

FIG. 7. – Heterococcolith types according the rim morphology. Outlined cross-sections of a planolith, a murolith without and with flanges, and a placolith. (Based on Young, 1992b and Young *et al*., 1997)

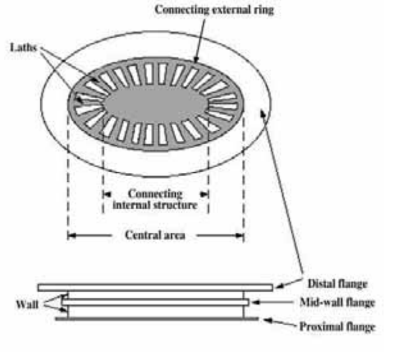

FIG. 8. – A murolith with flanges in distal view and side view. This murolith has the central area filled with laths, and hence is termed a caneolith. The connecting external ring, a character useful for the classification of caneoliths, morphologically belongs to the central area but structurally belongs to the rim corresponding to the inner rim of rhabdoliths (see coccolith structure of the Rhabdosphaeraceae in Kleijne, 1992).

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), Edvarsen *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 CHROMISTA Cavalier-Smith 1981
emend. Cavalier-Smith 1998
Subkingdom CHROMOBIOTA Cavalier-Smith 1991
Infrakingdom HAPTOPHYTA Cavalier-Smith 1995
Division HAPTOPHYTA Hibberd 1972
ex Edvardsen *et* Eikrem 2000
Class PRYMNESIOPHYCEAE Hibberd 1976
emend. Cavalier-Smith, 1996
Subclass PRYMNESIOPHYCIDAE Cavalier-Smith 1986
emend. Cavalier-Smith, 1996 (in Cavalier-Smith *et al*., 1996)

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 HELICOSPHAERACEAE 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*., 2000b).

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*., 2000b). 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*., 2000b, 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, D and 11)

Syracosphaera (Syracolithus) catillifera Kamptner, Kamptner, 1941, pp. 81, 103, pl. 4, figs. 43-45.
Syracolithus catillifera Kamptner, Deflandre, 1952, p. 453, figs. 351c, d.
Calyptrosphaera catillifera (Kamptner) Gaarder, Nishida, 1979, pl. 17, fig. 3a, b.
Calyptrolithophora catillifera (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*., 2000b, and Figs. 11C, D) we infer that this variation is ecophenotypic rather than genotypic. It may prove ecologically significance 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 catilliferus*.

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 these 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)

Coccolithophora wallichi Lohmann, 1902 (part) p. 138, pl. 5, figs 58, 58b.
Coccolithus wallichi Lohmann, in Schiller 1930, pp. 247-248, text-fig. 124c.
Helicopontosphaera wallichi Lohmann, in Boudreaux and Hay 1969, pp. 272-273, pl. 6, fig. 9.
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* var. *carteri* and *H. carteri* var. *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 subspherical and they may have highly-modified equatorial coccoliths (*Scyphosphaera*). 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 affinty 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 apsteini 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 Fortuño, 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 f. *apsteinii,* Gaarder, 1970, fig. 4e, f; Mostajo, 1985, figs. 43-45; Winter and Siesser, 1994, p. 127 fig. 66 (micrograph from J. Alcober).
Scyphosphaera apsteini Deflandre, Nishida, 1979, pl. 2, 1ab.

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 apsteini 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 Figure 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. a*psteinii*.

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. a*psteinii*, 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 STEPHANOLITHIALES 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)

Cylindrotheca brasiliensis Lohmann, 1920, p. 187, Bild 56.
Anoplosolenia brasiliensis (Lohmann) Deflandre, 1952, p. 458, Fig. 356 D, E; Halldal and Markali, 1955, pp. 14-15, Pl. 16; Gaarder and Hasle, 1971, p. 523, Fig. 3 a-c; Manton and Oates, 1985, pp. 466-469, pl. 1-3, figs. 1-12; Kleijne, 1993, p. 231-232, Pl. 1, fig. 1-2.

Throughout the present study, and following Heimdal and Gaarder (1981), "all spindle-shaped coccolith cases with scapholith-type coccoliths and tapering at both ends into long horns were included in this species".

In the quoted literature, as in the present study, differences in coccosphere and coccolith size and number and wideness of the laths, as well as presence or absence of enlargements in the pointed tip of the rhomboidal coccoliths are observed. For this reason more work is necessary on this genus to determine if the differences among the specimens could permit recognition of different species or if only one species with gradational differences exists.

The species *A. brasiliensis* was described by Lohmann (1919) under the name *Cylindrotheca brasiliensis*, a confusion based on its similarity to diatoms of the genus *Cylindrotheca*. When Halldal and Markali (1955) described the coccoliths, using TEM techniques, they remarked that the coccoliths shown by Deflandre and Fert (1953) were somewhat smaller in size than their observations. In the present study the coccoliths of *Anaplosolenia* specimens more closely resemble those described by Deflandre and Fert (1953), having less (around 40 compared to more than 50) but wider laths than the specimens observed by Halldal and Markali (1955) and Gaarder and Hasle (1971).

Coccosphere consists of 160-190 scapholiths.

Dimensions. (4 specimens) coccosphere long axis (43-) 60-80 (-86) μm, short axis (5-) 6-8 (-10.5) μm, length/width ratio 7.5-14.5; coccoliths (13 measured) major diagonal (2.9-) 3.2-3.4 (-3.9) μm, minor diagonal (1-) 1.2-1.6 (-2) μm, long side (1.1-) 1.3-1.7 (-2.7) μm, short side (1.2-) 1.25-1.45 (-1.7) μm, ratio long/short diagonals ca. 2.4; ratio long/short sides 1.67.

Genus ***Calciosolenia*** Gran, 1912

Large-sized coccosphere with tapering ends and bearing polar spine-like coccoliths. This genus differs from *Anaplosolenia* 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)

Calciosolenia sinuosa Schlauder in Halldal and Markali, 1955, p. 15, Pl. 17.
Calciosolenia murrayi Gaarder *et* Hasle, 1971, p. 529, Fig. 3, d,e.; Kleijne, 1993, p. 232, Pl. 1 fig. 4-5.
Calciosolenia aff. *murrayi* Gran in Manton *et* Oates, 1985, 185, pp. 469-471, pl. 4 figs. 13-18.

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 5.3-7.7 μm; 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 coccospheres 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 *Syracosphaera* 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*. 2000b 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. 16A, B)

Acanthoica acanthifera sp. nov. Lohmann, 1912 (nomen nudum). Validated by Lohmann, 1913, pp. 358, 359, figs. 15b, c.
Acanthoica acanthifera Lohmann, ex Lohmann, Kleijne, 1992, p. 22, 23 pl. 1 Figs. 5-7; 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. 16A, 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 coronata 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 *Sphaerocalyptra* genus (Figs. 18B-D). Moreover, Figures 114C and D show several coccoliths of *Acanthoica* aff. *A. quattrospina* with coccoliths figured here as *Sphaerocalyptra* 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 Figure 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; Giraudeau and Bailey, 1995, pl. 3, fig. 1; Probert *et al*., 2000, p. 132-133, 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)

Acanthoica 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 coccoliths 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 varimorphic 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)

Acanthoica 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)

Acantoïca cucullata, Lecal-Schlauder, 1951, p. 269-270, figs. 6a-d.
Cyrtosphaera cucullata (Lecal-Schlauder, 1951) 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. - (nomen 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.
Acanthoica aculeata Kamptner, 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)

Discosphaera tubifera (Murray *et* Blackman) Lohmann; Halldal and Markali, 1955, p. 17, pl. 22, figs. 1-3.
Discosphaera tubifera (Murray et Blackman) Ostenfeld; Norris, 1984, p. 35, figs. 1L, 11, 12: Kleijne, 1992, 36-37, pl. 7, figs. 5-7.

The coccoliths are formed by a proximal disc and a trumpet-like distal structure; the proximal disc has a well developed rim, a radial ring of laths and a lamellar ring surrounding a pore which sometimes contains a small spine-like structure (Fig. 21D) which may be organic (Kleijne, 1992); the trumpet-like distal structure, which is loosely attached, is formed of needle-shaped elements which become tile-shaped in the flaring distal part.

Dimensions. Coccosphere diameter without processes 4.5-6.5 μm; coccosphere diameter with processes 12.5-16 μm; coccolith length (3.3-) 4-5 (-5.7) μm, distal width (2.2-) 2.6-3.6 (-4.5) μm.

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 vandeli Lecal, 1965 emend. R.E. Norris, 1984 (Figs. 22A, B)

Palusphaera vandeli Lecal, 1965b, pp. 68-69, text-fig. k, pl. 2, fig. 9; Norris, 1984, p. 35, figs 1f, 9, 10; Kleijne, 1992, p. 38-39, pl. 8, fig. 1; Giraudeau and Bailey, 1995, pl. 3, fig. 3.

The rhabdoliths, in distal view, have a relatively wide rim, a smooth central area and a very thin styliform central structure formed of imbricate elongated elements and typically gradually tapering 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. vandeli* 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. vandeli* 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 clavigera,* 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)

Rhabdosphaera claviger sp. nov. Murray *et* Blackman, 1898, p. 438, pl. 15, figs. 13-15.
Rhabdosphaera stylifer sp. nov. Lohmann, 1902, p. 143, pl. 5, fig. 65.
Rhabdosphaera claviger Murray *et* Blackman, Norris, 1984, pp. 31, 33, figs. 2-5; Kleijne, 1992, p. 39-41, pl. 8, figs. 3, 4, 6, 7.

Rhabdoliths of the endotheca 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 0.4-0.5 μm; spine length (3.7-) 5.0-5.3 (-5.8) μm; exothecal coccolith length (2.7-) 3.4-3.7 (-3.9) μm, coccolith width 1.7-2.5 μm, rim width 0.2-0.3 μm.

Rhabdosphaera xiphos (Deflandre *et* Fert, 1954) Norris, 1984 (Figs. 23C, D)

Rhabdolithus 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 caneoliths, 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 varimorphism 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.* 2000b).

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 caneoliths 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 caneoliths with central laths running somewhat obliquely to the sides, whilst *C. rigidus* has narrowly elliptical caneoliths 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 caneolith with spine described in the diagnosis of the species was not observed, and only three different kinds of coccoliths have been seen. The body coccoliths 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 caneolith; 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 caneoliths, 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 caneoliths length (1-) 1.3-1.6 (-2)

μm, width (0.5-) 0.75-0.9 (-1.1) μm; whorl planoliths 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 coccosphere 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, 1912 emend. Manton *et al*., 1984

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

Michaelsarsia 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 coccosphere has a robust appearance with the body caneoliths having a wide and raised central structure; 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 caneolith 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 osteoliths; 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. 3, figs. B, E; Winter *et al*., 1979, p. 206, pl. 3, fig. 6; Manton 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 caneoliths 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, ʼl. 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)

The former *Calyptrolithina wettsteinii* (Kamptner, 1937) Norris, 1985, is now known to be the holococcolith phase of *Coronosphaera mediterranea* (Kamptner, 1941; Cros *et al*. 2000b). A combination coccosphere of *Coronosphaera mediterranea* with *Calyptrolithina wettsteinii* (Fig. 28B), very similar to the figured by Kamptner (1941), has been observed during the present study.

Heterococccolith phase (Figs. 27D and 28A)

Syracosphaera mediterranea Lohmann, 1902, p. 133, 134, pl. 4, figs. 31, 31a, 32.

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.

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

Zygosphaera wettsteinii, Kamptner (1937), pp. 306, 307, pl. 16, figs. 30-32
Zygosphaera wettsteinii Kamptner, Kamptner (1941), pp. 88, 89, pl. 10, figs. 103-106.
Zygosphaera wettsteinii (Kamptner), Halldal *et* Markali (1955), p. 9, pl. 5.
Calyptrolithina wettsteinii (Kamptner, 1937) 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)

Syracosphaera 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 coccoliths are not always present in the dithecate species and isolated caneoliths are often difficult to identify (Janin, 1987).

At present, the genus *Syracosphaera* 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 endotheca 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 *Syracosphaera*. In a near future the genus *Gaarderia* may also be placed back into *Syracosphaera (*see explanations in *Gaarderia* text).

From the study of the variability of the exothecal coccoliths in the *Syracosphaera* 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 *Syracosphaera* species according to their exothecal coccoliths type.

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

All these *Syracosphaera* species have endothecal caneoliths with proximal and distal flanges.

Species with complex undulating exothecal coccoliths

Exothecal coccoliths only around the flagellar area. The endotheca 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.
Syracosphaera sp. A, Samtleben *et* Schröder, 1990, pl.1, fig. 3.
Syracosphaera sp. type H, Kleijne, 1993, p. 258-259, pl. 5, fig. 6.

Coccosphere dithecate, with dimorphic endothecal 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 *Syracosphaera ossa*. Both species have a smooth distal flange, a high degree of size variability in body caneoliths, small circumflagelar 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. 332-333, fig. 5; Borsetti and Cati 1972, p.401, pl. 45, fig. 2 a-b; Okada and McIntyre, 1977, pp. 24, pl. 8, fig. 4-5; Samtleben and

Schröder, 1992, p. 345 pl. 1 fig. 2; Kleijne 1993 p. 238 pl. 3 fig. 10-11; Winter and Siesser 1994 p. 137 figs. 115 A, B; Samtleben *et al.*, 1995, p. 235, pl. 2, fig. 5; Cros, 2000, p. 49, Plate 5, fig. 1.
Caneosphaera molischii (Schiller) Gaarder, in Gaarder and Heimdal 1977, pp. 66-68, pl. 7, pl. 8 fig.49; Heimdal and Gaarder 1981, pp. 44-46, pl. 3; Hallegraeff 1984, p. 242 fig. 47 a-b.
Syracosphaera elatensis Winter, Winter *et al.*, 1979, p. 207 pl. 3 figs. 11-13.

Coccosphere dithecate with dimorphic endothecal coccoliths. Body caneoliths have a wide curved and ridged distal flange, sometimes with protrusions towards the central area; central structure, when present, an elongated or variably shaped mound; these caneoliths are highly variable in size and morphology, even on one coccosphere. Circum-flagellar caneoliths 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 of the coccosphere (Fig. 31A).

A disintegrated coccosphere with heterococcoliths of *S. molischii* and holococcoliths of *Anthosphaera fragaria* has been found in the studied samples (Fig. 112A).

The coccosphere consists of (24-) 34-38 (-48) body caneoliths; around 5 circum-flagellar caneoliths with spine; 4 to 8 exothecal coccoliths.

Dimensions. Coccosphere length 6-9 μm; body caneoliths length (1.7-) 2.3-2.7 (-3.4) μm; circum-flagellar caneolith spine length ca. 1.5 μm; complex undulated exothecal coccolith diameter ca. 2.5 μm.

Syracosphaera ossa (Lecal) Loeblich Jr. *et* Tappan, 1968 (Fig. 32A-D)

Syracorhabdus ossa Lecal, 1965a, p. 253-254 pl. 2 figs 5-8.
Syracosphaera ossa (Lecal) Loeblich and Tappan, Okada and McIntyre 1977, pp. 25-26, pl.10, figs. 9-10; Kleijne, 1993 p. 240 pl. 5, figs 4-5; Winter and Siesser, 1994, p. 138 fig. 119 (Phot. C. Samtleben).

Coccosphere dithecate with dimorphic endothecal coccoliths. The variable sized body caneoliths have a wide and smooth distal flange and may or may not possess a central structure, which can be very variable; it is noteworthy that near the apical and antapical poles the central structure typically becomes smaller or is absent. The circumflagellar 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 caneolith 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 morphologically to *S. molischii*, but differs in having a smooth distal flange on the body caneoliths and smooth distal 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 caneoliths 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 present. The smooth surfaced complex undulating exothecal coccoliths resemble the exothecal coccoliths of *S. ossa, S. molischii* and *S. marginaporata*.

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

Dimensions. Coccosphere long axis 6-10 μm; body caneolith length (1.3-) 1.7-1.9 (-2.2) μm; circum-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 planoliths. 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 (Halldal *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; Giraudeau 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 and has a rectilinear outline. Circum-flagellar caneoliths possess a large spine, but sometimes these coccoliths are obscured by the exothecal coccoliths. Exothecal coccoliths are characteristically large disc-shaped coccoliths (planoliths) with a hollow conical central structure.

Heimdal and Gaarder (1981) demonstrated that *Deutschlandia anthos* Lohmann, 1912 was the correct name of the species reported as *Syracosphaera variabilis* (Halldal and Markali, 1955) by various authors (Okada and McIntyre 1977; Nishida, 1979; Winter *et al*., 1979), but not of the species reported by Halldal and Markali (1955) (pl.12, fig. 1) as *S. variabilis*. Taking into consideration such past confusion, they decided to retain the specific name of *Deutschlandia anthos* Lohmann, 1912. Otherwise, the generic descriptions of *Deutschlandia* (emend. Heimdal *et* Gaarder, 1981) and *Syracosphaera* (emend. Gaarder *et* Heimdal, 1977) differ in only two points: *Deutschlandia* has no distal flange and the central part of the exothecal coccoliths has a distally raised hollow cone whilst their counterparts in *Syracosphaera* have a central depression. Other taxonomists (Okada and McIntyre, 1977; Janin, 1987) do not agree completely and assume a morphological variation inside the genus *Syracosphaera* wider than that accepted by Gaarder and Heimdal (1977) (see the former description of *Syracosphaera* genus). Hence, the genus *Deutschlandia* has been transferred to the genus *Syracosphaera* (Janin, 1987; Jordan and Young, 1990) and in later taxonomical works (Kleijne, 1993; Jordan and Kleijne, 1994, Jordan and Green, 1994) the genus *Deutschlandia* is dropped in favour of *Syracosphaera*, although some authors (e.g. Heimdal, 1993) maintain this species in the genus *Deutschlandia*.

Dimensions. Coccosphere diameter (7-) 9.0-11.0 (-13) μm; caneolith length (2-) 2.2-2.5 (-2.8) μm, width 1.4-1.9 μm; circum-flagellar caneolith central spine length ca. 1 μm; exothecal coccolith diameter 3.0-5.5 μm.

Holococcolith phase, formerly *Periphyllophora mirabilis* (Schiller) Kamptner, 1937 (Fig. 35B)

Periphyllophora mirabilis (Schiller) Kamptner, Halldal and Markali, 1955, p. 9, pl. 3, figs. 1-4; Kleijne, 1991, p. 33, 34, pl. 14, fig. 1, 2; Winter and Siesser, 1994, p. 146, fig. 156 (phot. from Samtleben).

Coccosphere consisting of ca. 100 helladoliths which possess clear double-layered protrusions.

Dimensions. Coccosphere diameter 11-13 μm; coccolith length (1.5-) 1.9-2.2 (-2.5) μm.

Species with oval exothecal coccoliths

The endotheca 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* Cati, 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 endothecal 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*., 2000b).

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 caneoliths 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 zygolith-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)

Coccosphere dithecate with dimorphic endothecal caneoliths. 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. Circum-flagellar 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. Coccospheres 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 endotheca 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 endothecal 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 caneoliths 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*. 2000b (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 Kamptner 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*. 2000b, Plate VII, fig. 1; 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) Kamptner, Hallegraeff (1984), p. 242, fig. 50.
Corisphaera sp. type A Kleijne, 1991, p. 54, pl. 13, figs. 1-2.

Body zygoliths 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*. 2000b. (Figs. 42A-D)

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

Coccosphere dithecate with dimorphic endothecal 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 coccoliths 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.

Syracosphaera 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.

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

? *Syracosphaera variabilis* Verbeek, 1989, fig. 23.
? *Syracosphaera 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 connecting 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 with 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 Kamptner, 1967, pp. 136-137, plate 5 figs. 30-31.
Syracosphaera ribosa (Kamptner) 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 endothecal 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. (Kamptner) 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 dithecatism 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 coccospheres studied consisted of 36, 48, 50 and 58 body caneoliths and indeterminate numbers of exothecal caneoliths (more than 10-15 in several studied coccospheres; they are very loosely attached to the coccosphere and in consequence they are easily lost).

Dimensions. Coccosphere long axis 10-20 μm; body caneoliths 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 coccosphere with monomorphic endothecal caneoliths; these coccospheres 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 coccospheres 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 coccosphere and hence easily lost).

Dimensions. Coccosphere 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.

Coccosphere 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 coccosphere of *S. nodosa* with *Helladosphaera cornifera* was found (Fig. 113D).

The coccospheres 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. Coccosphere long axis (6.0-) 6.5-7.5 (-9.5) μm; body caneoliths 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*
(Fig. 47)

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 coccosphere with dimorphic endothecal coccoliths. 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*.

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 presents body caneoliths with proximal and distal flanges, and has no differentiated spinous caneoliths.

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

Syracosphaera rotula Okada *et* McIntyre, 1977, p. 27, Plate 9 fig. 12; Borsetti and Cati, 1979, p. 161, pl. 17, figs. 1-2; Kleijne, 1993, p. 241, pl. 5 fig. 9; Winter and Siesser, 1994, p. 140, fig. 123 (phot. J. Alcober).

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 caneoliths; (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 coccolith length (2.1-) 3.0-3.2 (-3.6) μm.

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

Combination coccospheres of *Syracosphaera pulchra* with *Calyptrosphaera 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 cocospheres found in the studied samples.

Geisen *et al*. (2000) presented a combination coccosphere with heterococcoliths of *S. pulchra* and holococccoliths 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, 1977, p. 55 pl. 1 figs. 1-8; Borsetti and Cati, 1972, p. 402, pl. 46 figs. 2 a-b; Nishida, 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 Siesser, 1994, p. 139, fig. 122 (phot. J. Alcober).
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 endothecal caneoliths. The rim of body caneoliths has a corrugated 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 coccoliths have a thick spine forked at the end. The vaulted exothecal coccoliths have a central depression in the shape of an inverted cone, which is sometimes flattened laterally.

S. pulchra is the best known of the *Syracosphaera* 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 coccoliths, a feature which he was the first to record (1939, p. 120). Gaarder and Heimdal (1977) showed that the proximal coccoliths 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 Mediterranean water contained some flower-shaped coccoliths with an extended wing or petal-like rim which seem related to *S. pulchra*, possibly representing malformed specimens of coccoliths of this species (Fig. 50B); such kind of *S. pulchra* coccoliths 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 *Calyptrosphaera oblonga* Lohmann, 1902. (Figs. 51C, D)

Calyptrosphaera 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 coccoliths (6 specimens).

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

Syracosphaera species having caneoliths (muroliths) as exothecal coccoliths

Species having elliptical caneoliths, with flanges, as exothecal coccoliths

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 circum-flagellar 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 circum-flagellar 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.
Syracosphaera 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 *Syracosphaera* sp. type D coccoliths with *Homozygosphaera arethusae* holococcoliths; but these associations could be a random product, as discussed in Cros *et al*. (2000b).

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 (-12) 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 double-ended long spines around the flagellar area.

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

Syracosphaera sp. type E, Kleijne (1993), p. 242, pl. 6, fig. 4.
Syracosphaera noroiticus Knappertsbusch, 1993, p. 71-72, pl. 1 fig. 1-3

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 coccoliths 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.

Syracosphaera sp. type G of Kleijne, 1993 (Fig. 55)

Syracosphaera sp. type G, Kleijne 1993, p.243, pl.6, figs. 6, 9.

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 characteristically 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 coccoliths

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, 1913 *sensu* Throndsen, 1972 (Fig. 56)

Syracosphaera prolongata Gran ex Lohmann, 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 Halldal *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 coccoliths are sub-circular caneoliths; wider gaps are present between the laths than on the body coccoliths 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 coccoliths 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 coccoliths 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 caneoliths 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); Giraudeau and Bailey, 1995, Plate 5, figs. 2-3.

The coccosphere is dithecate with dimorphic endothecal coccoliths; 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 coccoliths 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. 2 μm; 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 aff. *ossa* Lecal Borsetti *et* Cati, 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)

Syracosphaera mediterranea Lohmann *sensu* Halldal and Markali, 1954b, p. 330, figs 2 a-d.
Syracosphaera halldalii Gaarder in Gaarder and Hasle, 1971, p. 536; Borsetti and Cati, 1976, p. 215 plate 14 figs. 11-12; Okada and McIntyre, 1977, p. 23, 26, plate 10, figs. 1-2.
Syracosphaera halldalii Gaarder f. *halldalii* in Kleijne, 1993, p. 237-238, plate 4 figs. 4-6; Winter and Siesser, 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.
Syracosphaera protrudens Okada *et* McIntyre, 1977, pp. 26-27, plate 10 fig. 3.
Syracosphaera 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, around 6 apical spine-bearing caneoliths, coccosphere diameter 7-12 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 *Chrysotila* (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 *et* 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 *et* 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. protohuxleyi* McIntyre or *G. ornata* Heimdal may represent different morphotypes of the species *G. ericsonii* McIntyre *et* Bé (Kleijne, 1993). In the present study, *G. protohuxleyi* 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 *et* Tappan, 1978 (Fig. 62)

Coccosphaera leptopora Murray and Blackman, 1898, pp. 430, 439, pl. 15, figs. 1-7.
Calcidiscus leptoporus (Murray and Blackman) Loeblich *et* Tappan, Hallegraeff, 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.
Calcidiscus leptoporus (Murray *et* Blackman, 1898) Loeblich and Tappan, f. *leptoporus* Kleijne, 1991, pl. IV, fig. 3.

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 holococccoliths 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 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, 1968.
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)

Coccosphaera 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.

The coccospheres possess around 25 coccoliths.

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
(Fig. 65)

Papposphaera lepida Tangen, 1972, pp. 172, 175, 176, 177, Figs. 1-13.
Papposphaera lepida Tangen, in Manton *et* Oates, 1975, pp. 94, 96, Figs, 3-4; Thomsen *et* Buck, 1998, pp. 32-33, figs 2-8.

The basal part of the pappoliths is from elliptical to subcircular, the rim composed of a crown of non-overlapping, distally pointed, pentagonal elements and a proximal ring of narrow rod-shaped elements; the central spine is usually long and delicate with four ridges which diverge at the bottom plate forming a distinct axial cross-bar; at the top of the appendage there is a wide structure, the calyx, formed of four flattened lobes, most having shallow incisions giving a flower-like appearance. This calyx structure can be highly variable in shape and can even appear completely square, as described and figured by Thomsen and Buck (1998) from Mexico (Bahia de los Angeles, Sea of Cortez). In addition to the rim and the central area, the length and width of the spine can also be very variable.

Coccospheres possess around 45-90 coccoliths (coccospheres usually collapsed, making estimations difficult).

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)

Deflandrius cf. *intercisus* (Deflandre) Bramlette and Martini, 1964, by Norris (1983), p. 165, fig. 5 (a single 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. 3μm; 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.

Dimensions. 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.

Dimensions. 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 Șstergaard 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.

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 calicate 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. 1μm, 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).

Coccosphere 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; central process length 1-3 μm.

Picarola sp.
(Figs. 72C, D)

Coccosphere with different types of coccoliths. Coccoliths with a curved central process that gradually flares distally, resulting in a characteristically hollow distal structure with pointed endings. The central area of the base appears to have a diagonal rather than an axial cross-bar, and the rim consists of different sized rectangular plates which give a characteristic side profile to the coccolith base.

Dimensions. Coccosphere diameter 7-11 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.

Genus Type A, sp. type 1
(Fig. 71C)

Coccoliths having long and sharp spines without distal structure.

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, sp. 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 protoplast 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 cocccolithomorpha* (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; ceratoliths 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 (Cros, 2001, 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*. 2000a; 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).

Cocccoliths 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. Cocccoliths without the pointed protrusion occur on the coccosphere. A well formed combination coccosphere of this species with a *Polycrater* with holes, reminiscent of Gaudí'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 cocoliths 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, 1993 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 (Cros *et al*., 2000a).

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 *Canistrolithus* 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 and 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-) 0.6-0.7 (-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 *Canistrolithus* 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. 5, fig. 11.

This coccosphere resembles *P. galapagensis*, but coccoliths have two lenticular holes in the larger half, near the centre, one 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 resemble *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)

? Coccolithophorid sp. 2, Thomsen *et al*., 1988 p. 433, figs. 48-49 (from the Weddell Sea).

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* 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; macrococcolith 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 and 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. Coccosphere 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

Coccosphere 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)

Turrilithus latericioides Jordan *et al.,* 1991, p. 176, 178, 179, 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. Coccosphere 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)

Florisphaera profunda Okada and Honjo, 1973, pp. 373-374, pl. 1, fig. 6, pl. 2, figs. 4-6; Nishida, 1979, pl. 16, fig. 3-4; Young, 1998, p. 254, pl. 8.6, fig. 20, 25.

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. Coccosphere 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*. As a result of several other observations of hetero-holococcolith 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 coccoliths.

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

Coccosphere with calyptrolith-like body coccoliths and circum-flagellar fragarioliths. The calyptrolith-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 (Cros *et al.,* 2000b).

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)

Helladosphaera (Cyclohelladosphaera) lafourcadii, Lecal, 1967, pp. 326-328, text-figs. 21, 22, figs. 28-30.
Anthosphaera lafourcadii (Lecal) Kleijne, 1991, p. 60, pl. 9, figs. 28-30.

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; fragariolith 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 fragarioliths heavily ornamented.

Coccospheres have 6 to 8 fragarioliths 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; fragariolith 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 fragarioliths have a flat leaf-like process with nearly straight sides.

The studied specimen consists of ca. 8 fragarioliths 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 fragarioliths. 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 zygoliths 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 Gaarder (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.

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)

Zygosphaera divergens Halldal *et* Markali, Borsetti and Cati, 1976, p. 223, pl. 18, fig. 1.
Zygosphaera divergens Halldal *et* Markali, f. *tuberosa* Heimdal, in: Heimdal and Gaarder, 1980, pp. 12, 13. pl. 3, fig. 25a, b.
Calyptrolithina divergens f. tuberosa (Heimdal), Heimdal, 1982, p. 54.
Calyptrolithina divergens (Halldal *et* Markali) Heimdal cf. *C. divergens* f. *tuberosa* (Heimdal) Heimdal, Kleijne, 1991, p. 45, pl. 10, fig. 4.
Calyptrolithina divergens var. *tuberosa* (Heimdal) Jordan *et al*., 1993, p. 18.

The body calyptroliths have a nearly flat distal surface with a pronounced convexity (*tuber*). Both the calyptroliths and the zygoliths usually have regularly shaped pores. In some coccoliths (Fig. 90C) areas with and without clear perforations are present. The coccoliths figured in Heimdal and Gaarder (1980) have masked perforations whilst the coccoliths figured in Borsetti and Cati (1976) and Kleijne (1991) are clearly perforated with large pores, like those in Fig. 90D.

The three studied specimens possess 62, 100 and 122 body coccoliths.

Dimensions. Body coccolith length (1.5-) 1.8-2.1 (-2.4) μm.

Calyptrolithina wettsteinii (Kamptner, 1937) Norris, 1985

C. wettsteinii is now considered to be the holococcolith phase of *Coronosphaera mediterranea* (see p. 28 and Figs. 28B-D).

Genus **Calyptrolithophora** Heimdal in Heimdal *et* Gaarder, 1980

Coccosphere with dimorphic coccoliths. Both body and circumflagellar coccoliths are calyptroliths with straight sides and a straight rim, which has a distal prominence. The body calyptroliths have a nearly flat distal side, while circum-flagellar calyptroliths show a highly convex distal part.

The name, from the Greek *kalyptra* (cap-shaped covering), *lithos* (stone) and *phor* (carrier) is fitting.

Calyptrolithophora gracillima (Kamptner, 1941) Heimdal, 1980 (Figs. 92A, B)

Calyptrosphaera gracillima Kamptner, 1941, pp. 77, 98, pl. 1, figs. 13-16.
Sphaerocalyptra gracillima (Kamptner) Throndsen, 1972, p. 54, 56, figs. 10-15; Nishida, 1979, pl. 4a-b.
Calyptrolithophora gracillima (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 histri*ca (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)

Calyptrosphaera 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 crystallites 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.

Calyptrosphaera dentata Kleijne, 1991
(Figs. 94A, B)

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)

Homozygosphaera tholifera (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. 40, Fig. 51).

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. Figure 95 includes only the clearly classified *Corisphaera* species and Figures 96 and 97 represent 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 tyrrheniensis Kleijne, 1991 (Figs. 95C, D)

Corisphaera tyrrheniensis 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. 35, Fig. 40 and 41A, B).

Corisphaera cf. ***gracilis*** Kamptner, 1937 (Fig. 96A)

Corisphaera gracilis Kamptner, 1937, pp. 307, 308, pl. 16, fig. 33-35; Kamptner, 1941, pp. 90, 107, 108, pl. 11, figs. 113-116; Heimdal and Gaarder, 1980, p. 3, pl. 1, fig. 6 a, b; Kleijne, 1991, p. 52, pl. 12, fig. 3-5.

The body coccoliths are rather robust zygoliths that have a low bridge. Circum-flagellar zygoliths have a small pointed leaf-like protrusion.

Coccosphere consists of ca. 60 coccoliths (1 specimen).

Dimensions. Coccosphere long axis ca. 6 μm; coccolith length 1.4-1.6 μm.

Corisphaera sp. (ornamented circum-flagellar coccoliths) (Fig. 96B)

Body zygoliths with a very low wall. Circum-flagellar zygoliths with characteristically high leaf-like extended bridge.

Dimensions. Coccosphere diameter ca. 6 μm (1 collapsed specimen); body coccolith length 1.3-1.4 μm.

Corisphaera sp. (aff. type A of Kleijne, 1991) (Figs. 96C, D)

Body zygoliths closely resembling those of *Corisphaera* sp. type A (Kleijne, 1991), but without the well-formed low, one crystal thick, marginal rim. Circum-flagellar coccoliths without the double-layered wall showed in *Corisphaera* sp. type A. The specimens appear to have larger crystallites than those of *Corisphaera* sp. type A. Some specimens appear more fragile, possibly representing a variety of the species.

Coccospheres possess from 70 to 140 coccoliths.

Dimensions. Coccosphere long axis 5.5-9.2 μm; coccolith length (1.2-) 1.4-1.5 (-1.7) μm.

Corisphaera sp. (aff. type A of Kleijne, 1991, and *C. gracilis*) (Fig. 97A)

? *Corisphaera gracilis* Kamptner, Kleijne, 1991, pl. 12, fig. 4.

Body zygoliths with a rather high and flaring wall which ends in a row of regularly arranged angular crystallites; they posses a relatively wide, high and thin bridge.

Coccosphere consists of ca. 80 coccoliths (1 collapsed specimen).

Dimensions. Coccolith length 1.5-1.8 μm.

Corisphaera sp. (body zygoliths with pointed bridge) (Fig. 97B)

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 p. 47-48 and 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)

Calyptrosphaera pirus Kamptner, Throndsen, 1972, pp. 53-56, figs. 2-9; Reid, 1980, p. 164, pl. 7, figs. 2,3; Steinmetz, 1991, pl. 6, figs. 6-8 and pl. 7, figs. 1-2.
Daktylethra pirus (Kamptner), Norris, 1985, p. 631, figs. 10, 38, 39; Kleijne, 1991, p. 28-29, pl. 3, fig. 5-6.

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 (Throndsen, 1972; Heimdal, 1993; Fig. 98A).

Geisen *et al*. (2000) and Saugesgat and Heimdal (2002) presented combination coccospheres with heterococcoliths of *S. pulchra* and holococcoliths of *Daktylethra pirus*. Geisen *et al*. (2000) 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 *Helladosphaera cornifera* is illustrated in Fig. 113D. However, this collapsed coccosphere was not considered as a conclusive combination coccosphere (Cros *et al.,* 2000b).

Coccospheres possess 10-12 circum-flagellar coccoliths and (40-) 54-84 (-106) body zygoliths.

Dimensions. Coccosphere 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, 1941) 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 coccospheres (see discussion in Cros *et al*., 2000b)

Coccospheres possess from 54 to 96 coccoliths.

Dimensions. Coccospheres 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.

Coccospheres possess from 86 to 88 coccoliths.

Dimensions. Coccosphere 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 coccospheres 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. 32, 33 and Fig. 35).

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 *et* 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. 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 Fig. 101D).

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 poritectus (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 *Poritectolithus 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. 18), 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 protrusion 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.,* 2000b)

Syracolithus catilliferus (Kamptner, 1937) Deflandre, 1952

S. catilliferus is now considered as the holococcolith phase (solid) of *Helicosphaera carteri* (p. 18-19, Figs. 9D, 10, 11A, C and D).

Syracolithus confusus Kleijne, 1991

S. confusus is now considered as the holococcolith phase (perforate) of *Helicosphaera carteri* (p. 19, Fig. 11B).

Syracolithus dalmaticus (Kamptner) Loeblich *et* Tappan, 1966 (Fig. 107A)

Syracosphaera dalmatica, Kamptner 1927, p. 178, fig. 2.
Syracosphaera (Syracolithus) dalmatica Kamptner, Kamptner 1941, pp. 81, 104, pl. 4, figs. 46-48.
Syracolithus dalmaticus (Kamptner) Loeblich *et* Tappan, 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.

Coccospheres 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.
Homozygosphaera 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.

Coccosphere 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

Coccosphere 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 zygoliths as circum-flagellar coccoliths.

Zygosphaera amoena Kamptner, 1937 (Figs. 108A, B)

Zygosphaera amoena Kamptner, 1937, p. 305, pl. 16, figs. 24-26.
Calyptrolithina poritectum (Heimdal), Norris 1985, p. 625, fig. 32.
Zygosphaera amoena Kamptner, Kleijne, 1991, p. 65, 67, pl. 18, fig. 2; Winter and Siesser, 1994, p. 154, Fig. 188.

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.

Coccospheres 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 *et* Cati, 1976) Heimdal, 1980

Zygosphaera bannockii is now considered as the holococcolith phase (solid) of *Syracosphaera bannockii* (p. 35, Figs 40C, D and 41C, D).

Zygosphaera hellenica Kamptner, 1937 (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).

Coccospheres 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 *et* 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 microcrystals, usually with the form of a transverse ridge. Circum-flagellar zygoform laminoliths have a high transverse ridge.

Coccospheres 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. Coccosphere 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. Coccosphere 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 rigth). 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. 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. 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.

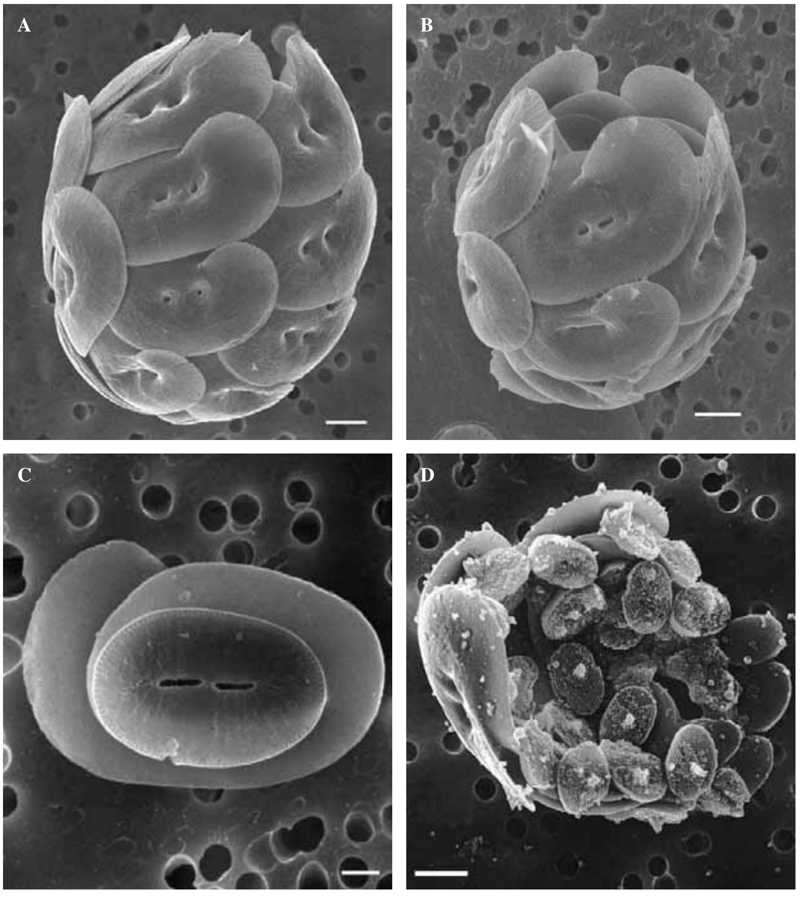

FIG. 9. – ***Helicosphaera carteri*** (Wallich) Kamptner var. ***carteri***: **A**, complete coccosphere of helicoliths [Fronts-96, 021, 68 m]; **B**, coccosphere showing coccoliths with two central pores and one coccolith with a longitudinal slit (lower middle) [Fans-1, 127, 25 m]; **C**, helicolith 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.

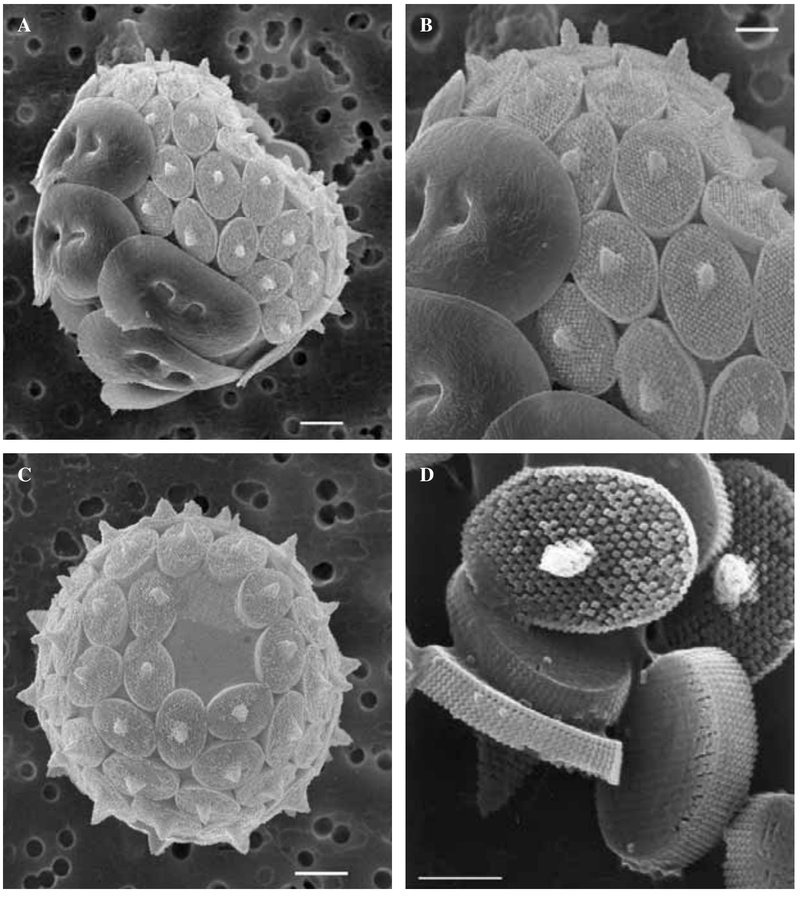

FIG. 10. – ***Helicosphaera carteri*** (Wallich) Kamptner var. ***carteri***: **A**, a well-formed combination coccosphere of *H. carteri* (heterococcoliths) and the former *Syracolithus catilliferus* (holococcoliths) [Meso-96, G4, 70 m]; **B**, detail of Fig. A; **C**, coccosphere of the former *S. 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.

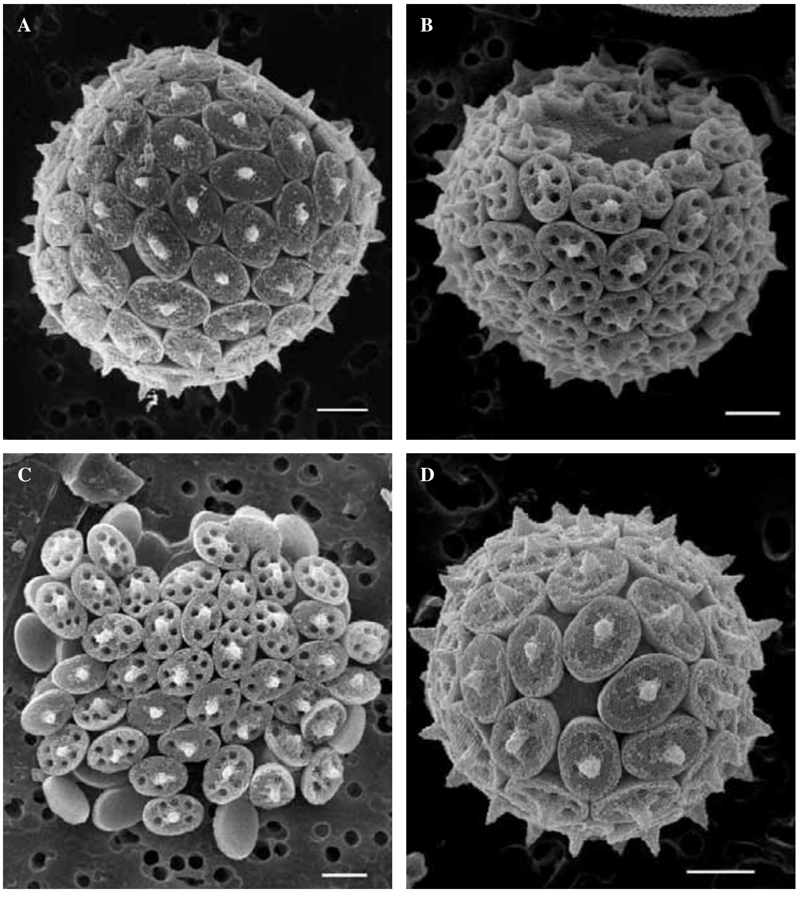

FIG. 11. – ***Helicosphaera carteri*** (Wallich) Kamptner var. ***carteri***: **A**, *Helicosphaera carteri* (holococcolith phase, solid), formerly *Syracolithus catilliferus* [Meso-96, A3, 5 m]; **B**, *H. carteri* (holococcolith phase, perforate), formerly *Syracolithus confusus* Kleijne. Coccosphere 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.

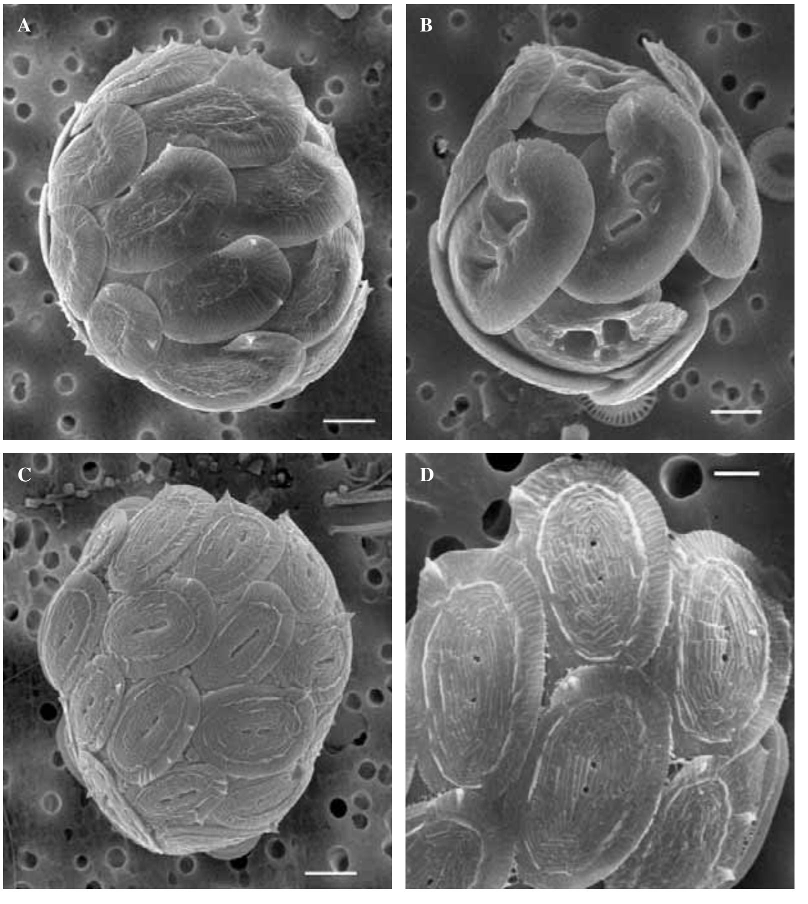

FIG. 12. – **A**, ***Helicosphaera carteri*** var. ***hyalina*** (Gaarder) Jordan *et* Young: complete coccosphere [Fans-3, K03, 60 m]. **B**, ***Helicosphaera carteri*** var. ***wallichii*** (Lohmann) Theodoridis: complete coccosphere [Fans-1, 123, 60 m]. C-D, ***Helicosphaera pavimentum*** Okada *et* McIntyre: **C**, complete coccosphere showing coccoliths with one or two aligned central slits; note the narrow flange of the helicoliths [Meso-96, I6, 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.

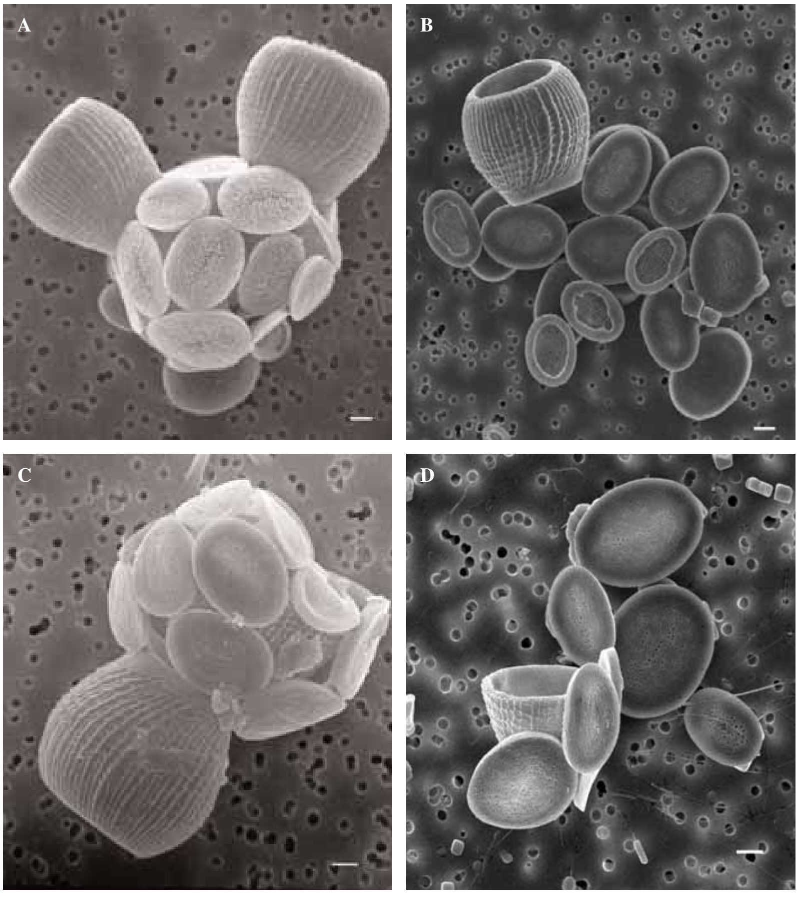

FIG. 13. – A-C, ***Scyphosphaera apsteinii*** Lohmann: **A**, coccosphere with cribriliths and two lopadoliths [Fronts-95, 18P, 30 m]; **B**, disintegrated coccosphere with one lopadolith and cribriliths [Fans-1, 123, 40 m]; **C**, well formed coccosphere with one lopadolith in an equatorial position 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.

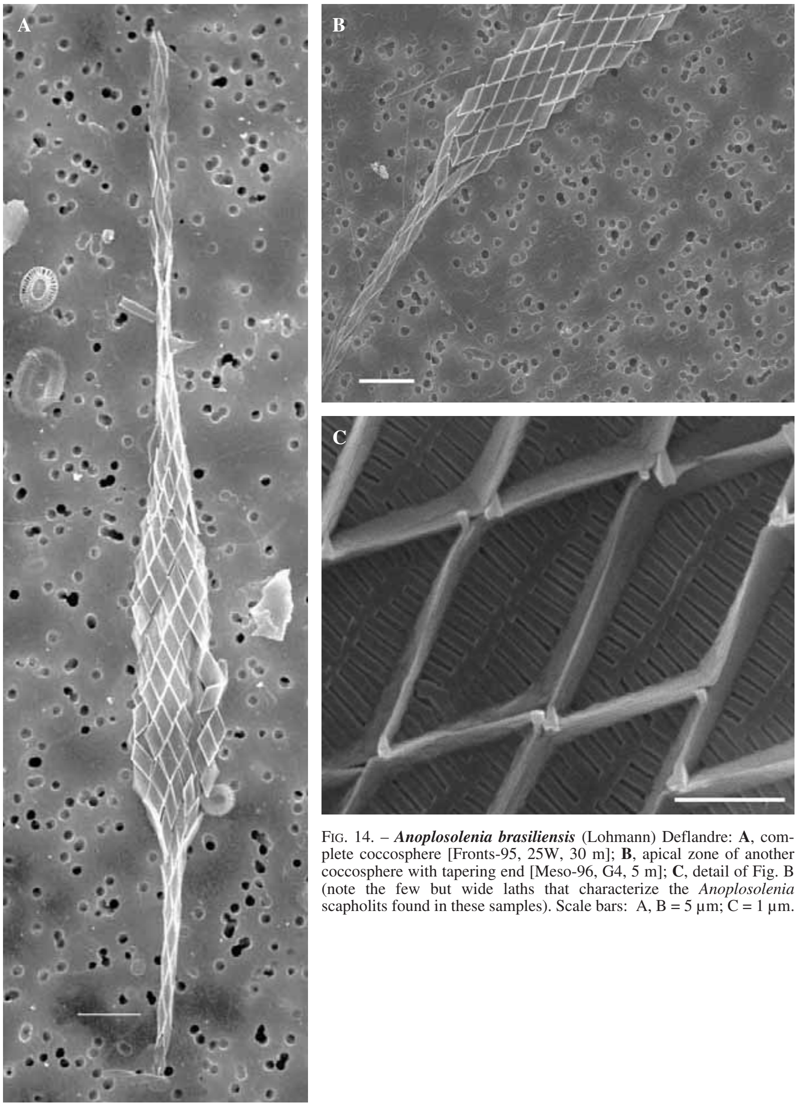

FIG. 14. – ***Anoplosolenia brasiliensis*** (Lohmann) Deflandre: **A**, complete coccosphere [Fronts-95, 25W, 30 m]; **B**, apical zone of another coccosphere with tapering end [Meso-96, G4, 5 m]; **C**, detail of Fig. B (note the few but wide laths that characterize the *Anoplosolenia* scapholits found in these samples). Scale bars: A, B = 5 µm; C = 1 µm.

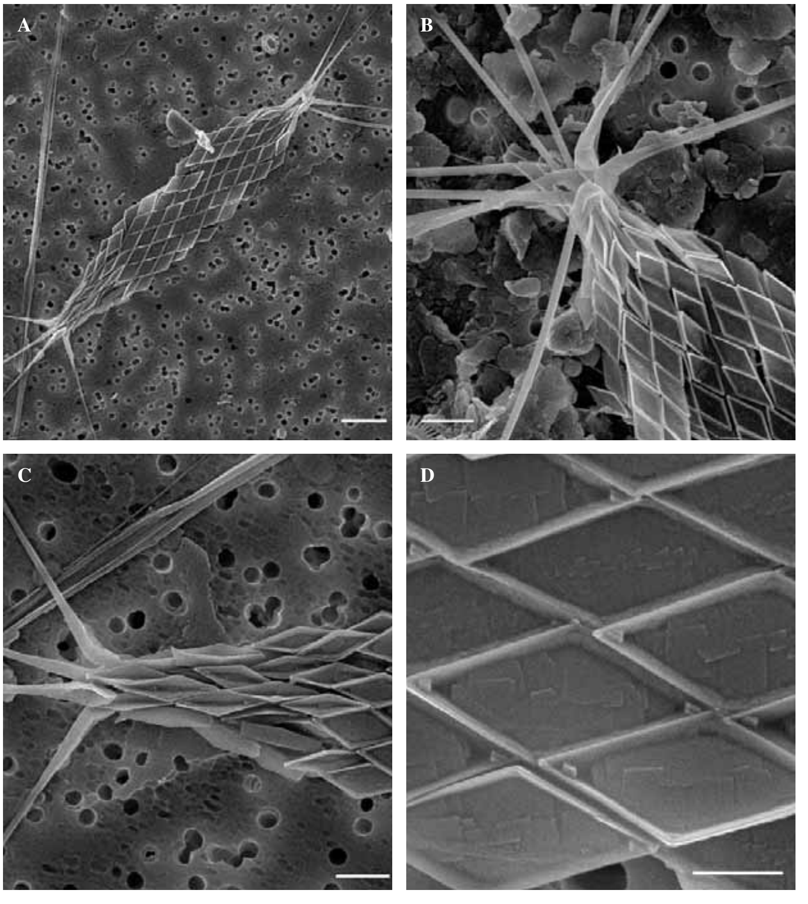

FIG. 15. – ***Calciosolenia murrayi*** Gran: **A**, complete coccosphere with few apical spines [Fans-3, M11, 75 m]; **B**, detail showing the apical area [Fans-3, K03, 66 m]; **C**, detail of Fig. A (note the apical spines which appear to be transformed scapholiths); **D**, detail of Fig. A showing 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.

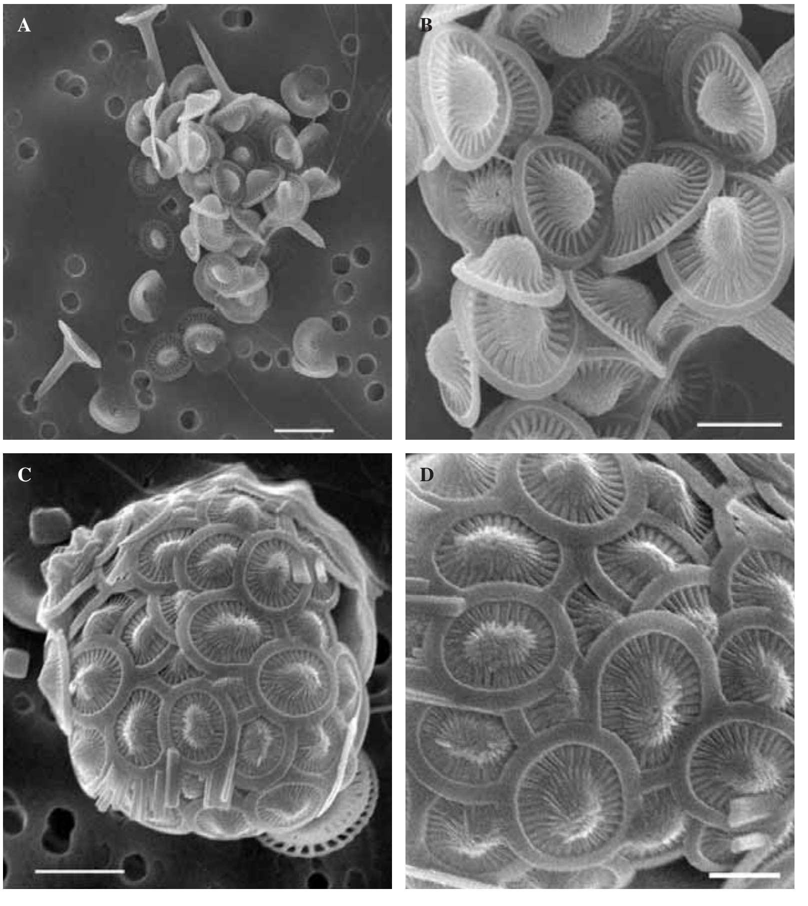

FIG. 16. – A-B, ***Acanthoica acanthifera*** Lohmann, ex Lohmann: **A**, collapsed coccosphere [Fans-1, 123, 5 m]; **B**, detail of Fig. A showing tilted radial laths and slightly compressed sacculiform protrusion. C-D, ***Anacanthoica acanthos*** (Schiller) Deflandre: **C**, complete coccosphere [Hivern-99, 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.

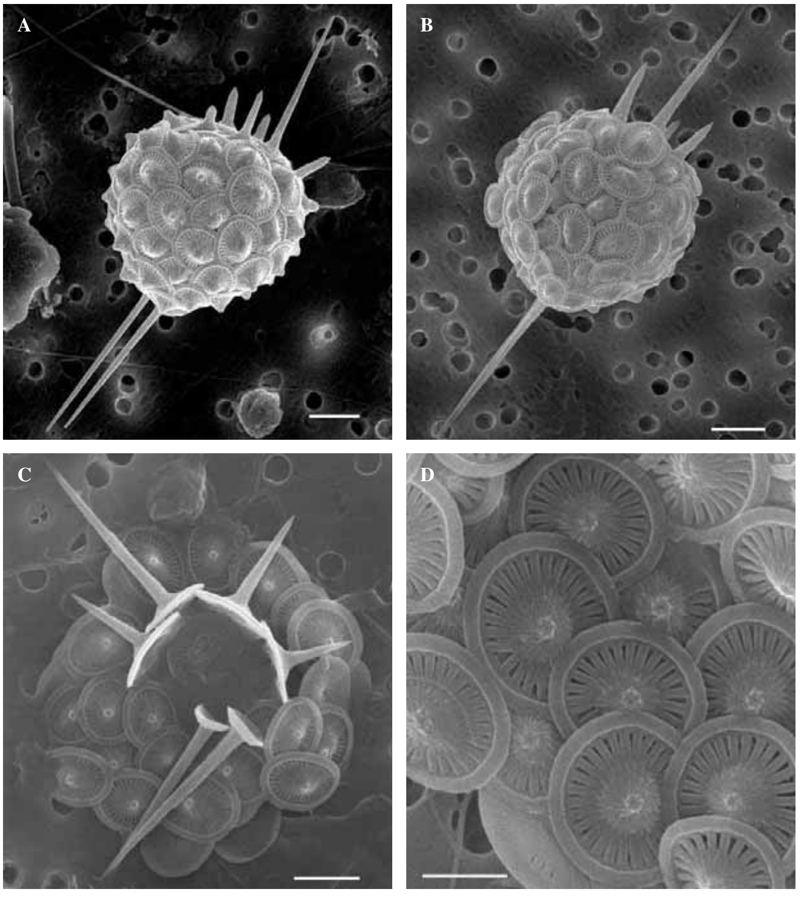

FIG. 17. – ***Acanthoica quattrospina*** Lohmann: **A**, complete coccophere having body coccoliths and coccoliths with spines at the poles [Fans-2, J3, 10 m]; **B**, complete coccosphere with spines in the most characteristic disposition: one long and three short spines at one pole and two long spines 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.

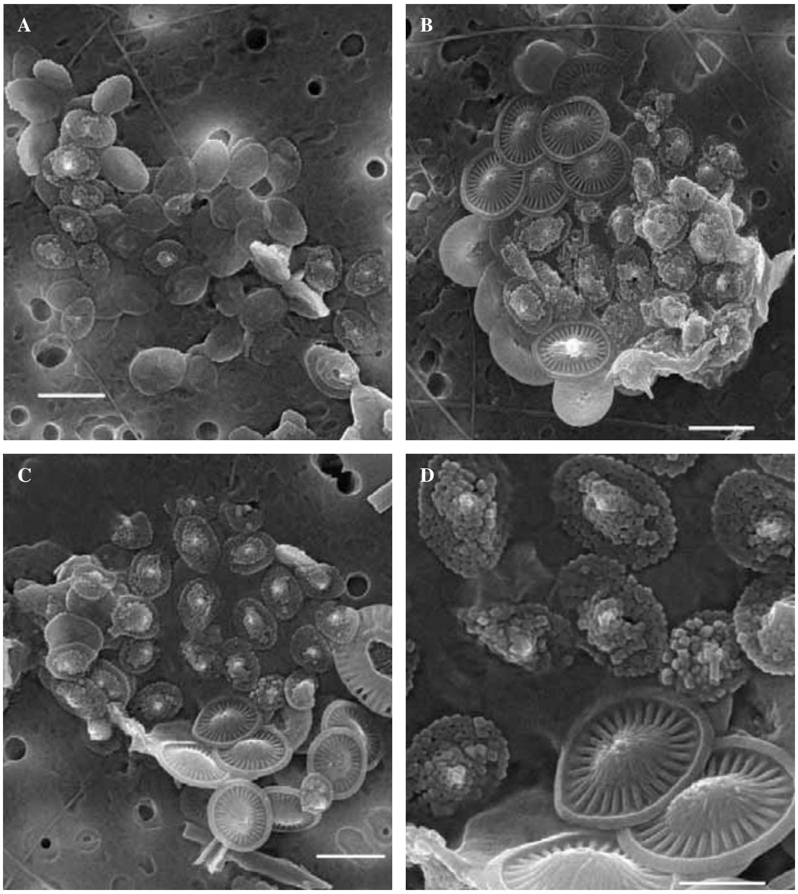

FIG. 18. – ***Acanthoica quattrospina*** Lohmann: **A**, disintegrated coccosphere consisting of body and two circum-flagellar holococcoliths of an undescribed species of *Sphaerocalyptra* [Fans-2, N7, 10 m]; **B**, collapsed mixed coccosphere with body rhabdoliths of *A. quattrospina* (heterococcoliths) 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.

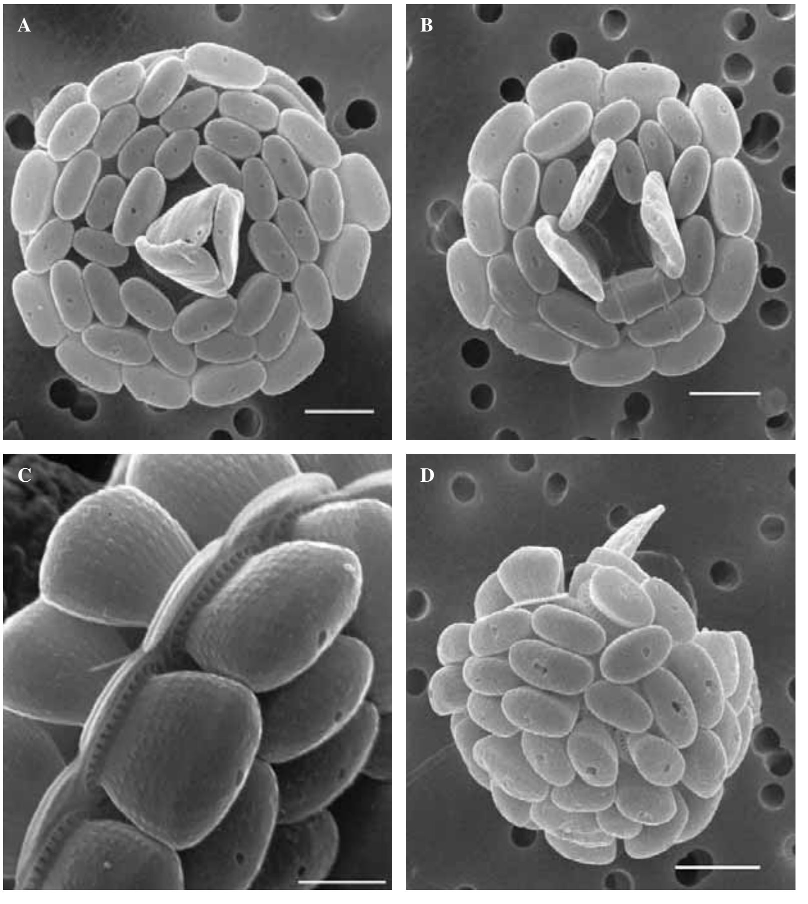

FIG. 19. – ***Algirosphaera robusta*** (Lohmann) Norris: **A**, complete coccosphere in apical view showing three joined circum-flagellar petaloid coccoliths, closing the flagellar opening [Fronts-95, 23D, 60 m]; **B**, complete coccosphere in apical view showing three circum-flagellar petaloid coccoliths 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.

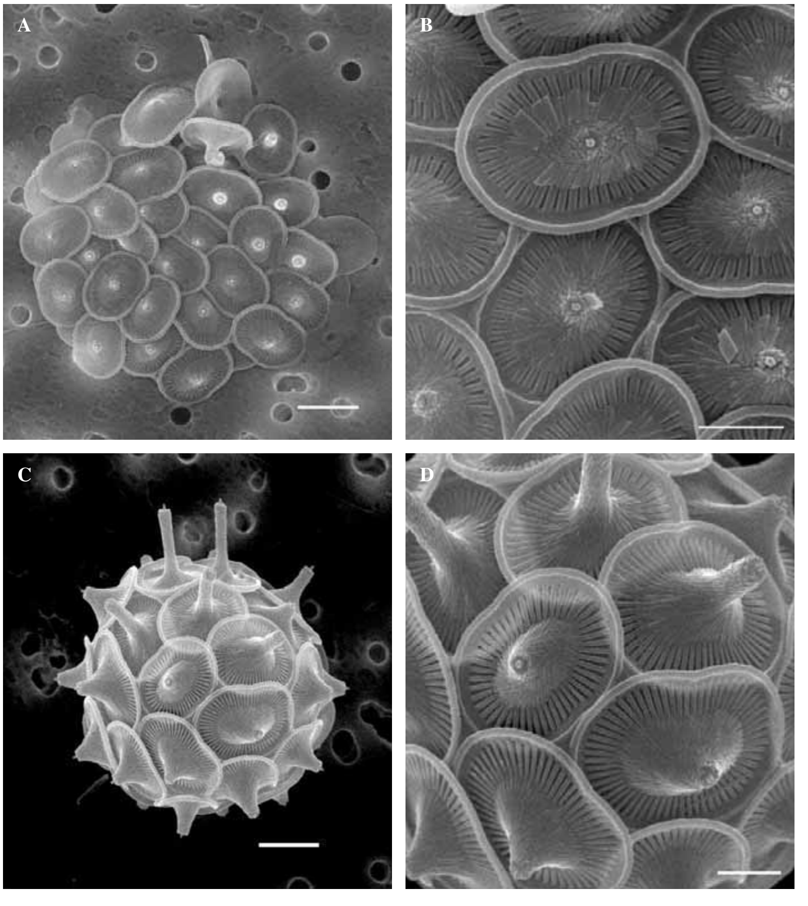

FIG. 20. – A-B, ***Cyrtosphaera aculeata*** (Kamptner) Kleijne: **A**, complete coccosphere [Fans-3, K03, 40 m]; **B**, detail showing coccoliths with relatively short laths, a clear lamellar cycle, a narrow cycle with needle-shaped elements and a central small papilla of cuneate elements [Hivern-99, 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 tipped by a small central papilla. Scale bars: A, C = 2 µm; B, D = 1 µm.

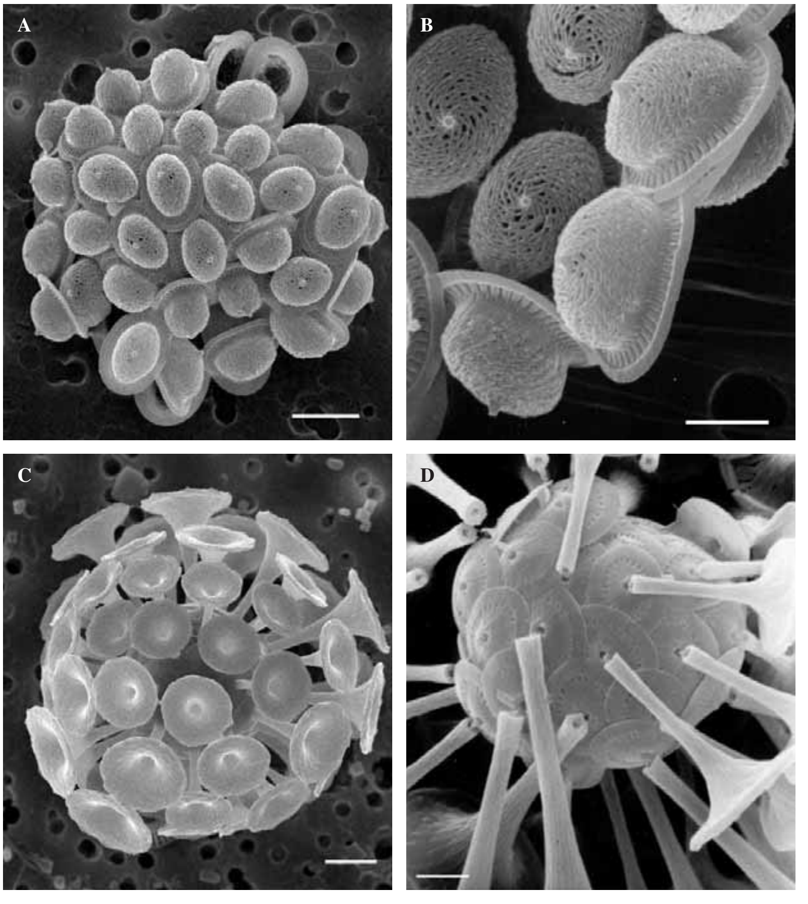

FIG. 21. – A-B, ***Cyrtosphaera cucullata*** (Lecal-Schlauder) Kleijne: **A**, coccosphere with two detached coccoliths (upper right) showing their proximal side [Meso-96, G6, 40 m]; **B**, detail of some coccoliths showing the bowler hat shape, with the rim and a cycle of short laths forming the hat 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.

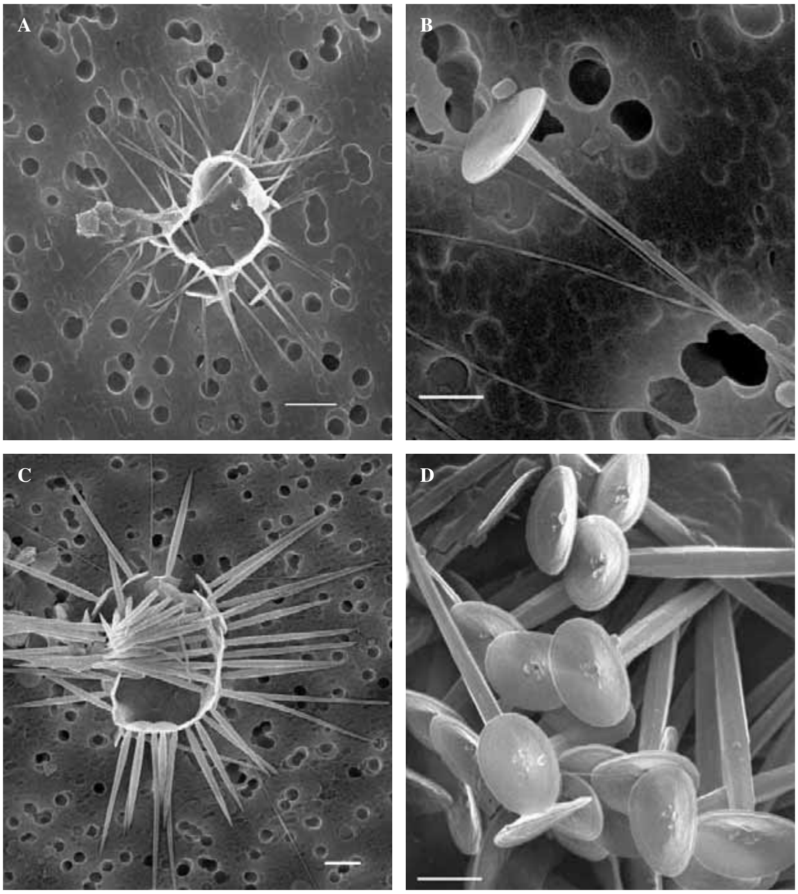

FIG. 22. – A-B, ***Palusphaera vandeli*** Lecal, emend. R.E. Norris: **A**, collapsed coccosphere [Meso-96, D4, 40 m]; **B**, detail with a rhabdolith showing thin styliform central structure [Hivern-99, 25, 60 m]. C-D, ***Palusphaera* sp. 1** (type robusta): **C**, coccosphere with coccoliths having 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.

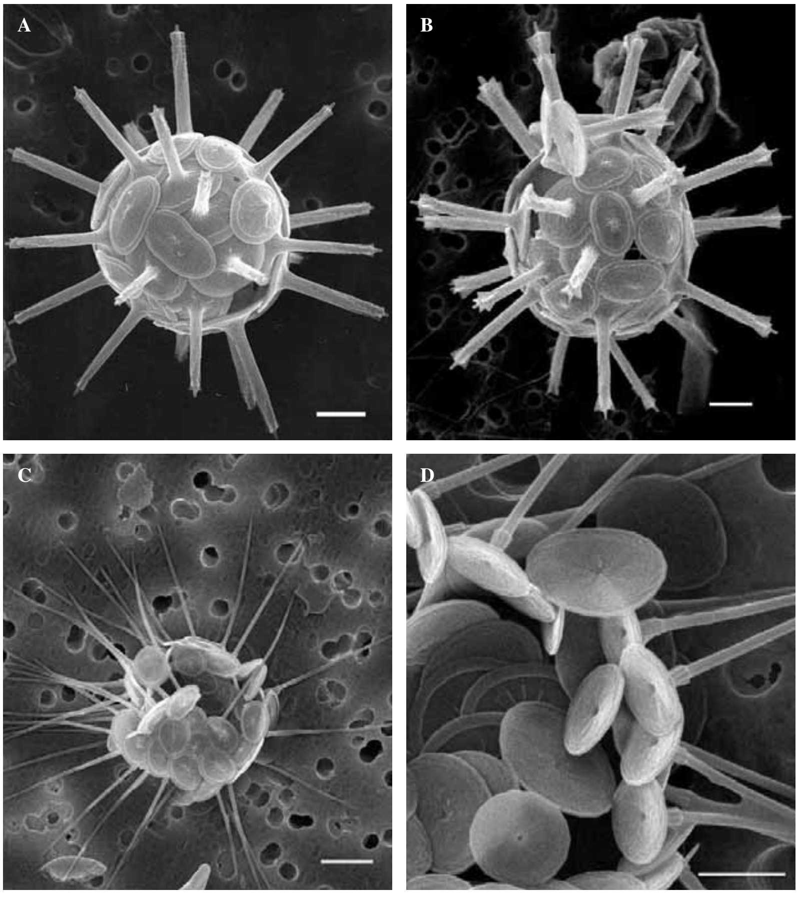

FIG. 23. – A-B, ***Rhabdosphaera clavigera*** Murray *et* Blackman: **A**, coccosphere with endothecal rhabdoliths having styliform central structure which is characteristic of the specimens originally described as *R. stylifera* [Meso-95, 023, surface]; **B**, coccosphere with endothecal rhabdoliths 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.

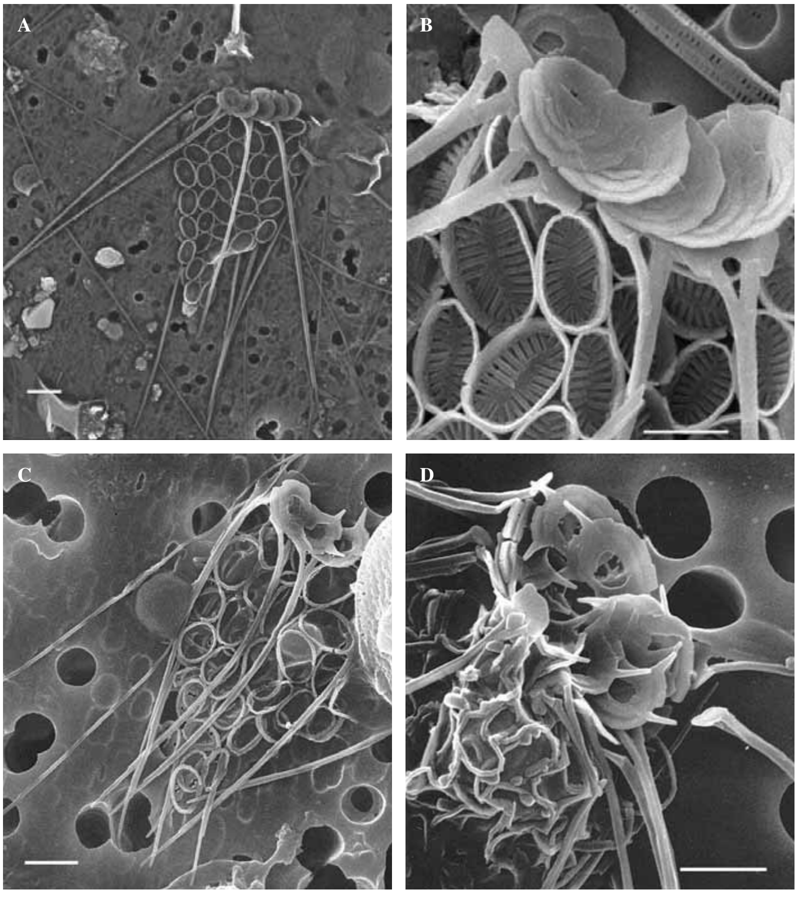

FIG. 24. – A-B, ***Calciopappus rigidus*** Heimdal in Heimdal *et* Gaarder: **A**, complete coccosphere [Picasso workshop, Barcelona harbour, surface]; **B**, detail of the apical area, showing a partially covered whorl coccolith in distal view (upper middle), several overlapping whorl coccoliths in proximal view with the central opening partially filled by flat bands (middle right), and body caneoliths (bottom); the whorl coccoliths partially cover the base of the spine-like appendages [Fans-1, 78b, 5 m]. C-D, ***Calciopappus* sp.** (very small): **C**, coccosphere with lightly calcified body coccoliths, curved spines and characteristic whorl coccoliths each with two spines [Meso-96, E8, 100 m]; **D**, detail showing the central opening on the proximal side of whorl coccoliths not covered and the two conspicuous spines located on the margin of the whorl coccoliths with an angular separation of about 70º [Fronts-95, 24W, 70 m]. Scale bars: A = 2 µm; B, C, D = 1 µm.

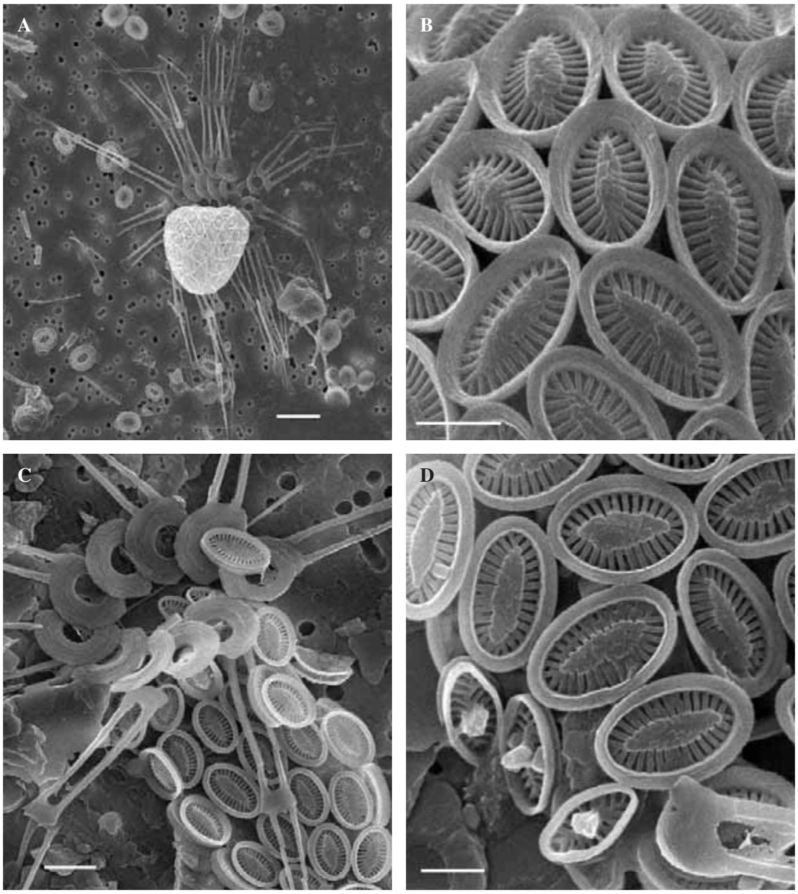

FIG. 25. – ***Michaelsarsia elegans*** Gran, emend. Manton *et al*.: **A**, coccosphere with appendages [Fans-1, 123, 60 m]; **B**, detail of Fig. A showing body caneoliths with robust wall and central structure; **C**, detail of the apical area of the coccosphere, showing open central areas of both 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.

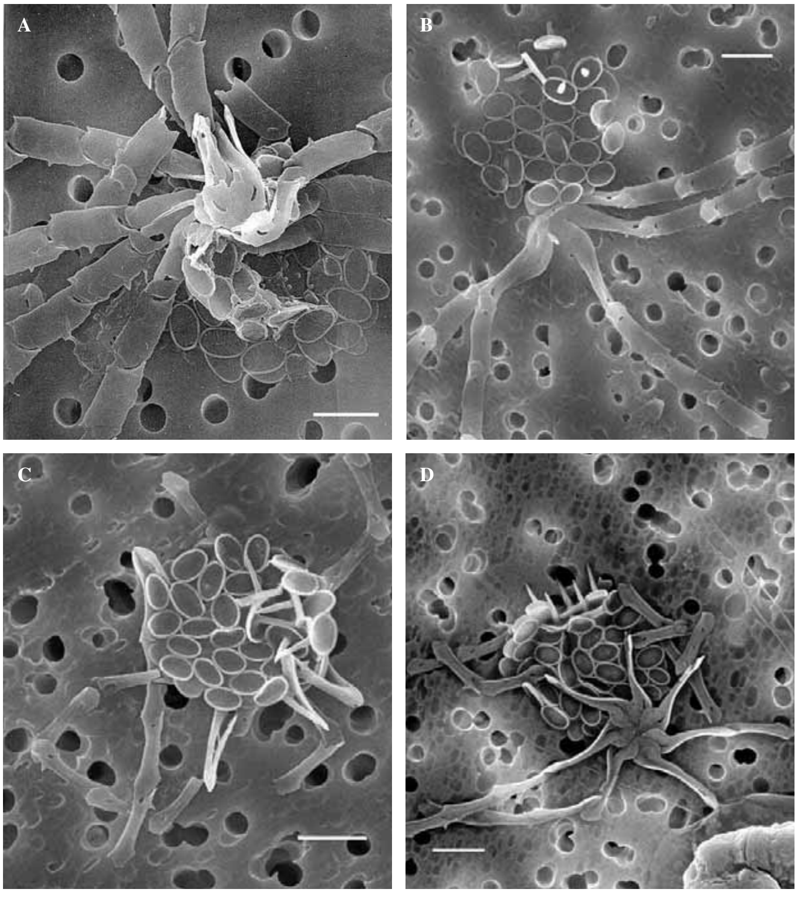

FIG. 26. – A-B, ***Ophiaster formosus*** Gran, *sensu* Gaarder 1967: **A**, coccosphere in antapical view showing the appendages with flexible arms formed of osteoliths. Note that the most proximal osteoliths are larger than the others and have loop-like proximal ends which can overlap [Fronts-95, 20I, 80 m]; **B**, coccosphere 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**, coccosphere with circum-flagellar coccoliths with long spines (centre right), body caneoliths and osteoliths mostly detached [Fans-3, K12, 75 m]; **D**, coccosphere 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.

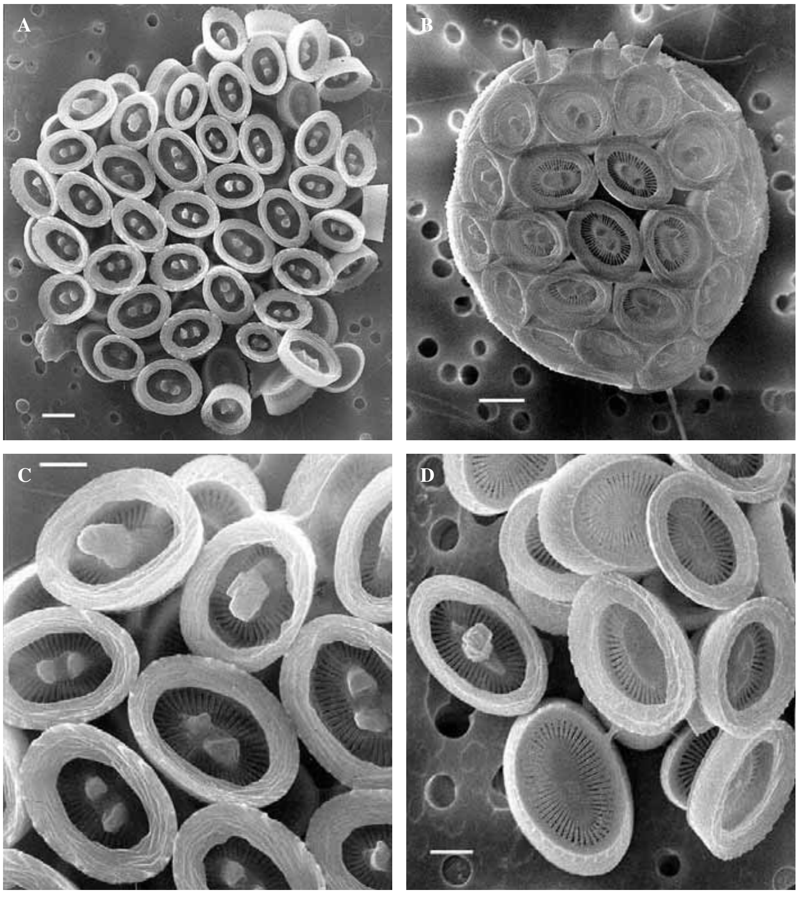

FIG. 27. – A-C, ***Coronosphaera binodata*** (Kamptner) Gaarder, in Gaarder *et* Heimdal: **A**, collapsed coccosphere [Meso-95, 147, surface]; **B**, complete coccosphere with circum-flagellar caneoliths with spine (top) [Meso-95, 117, surface]; **C**, detail with three circum-flagellar caneoliths having 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.

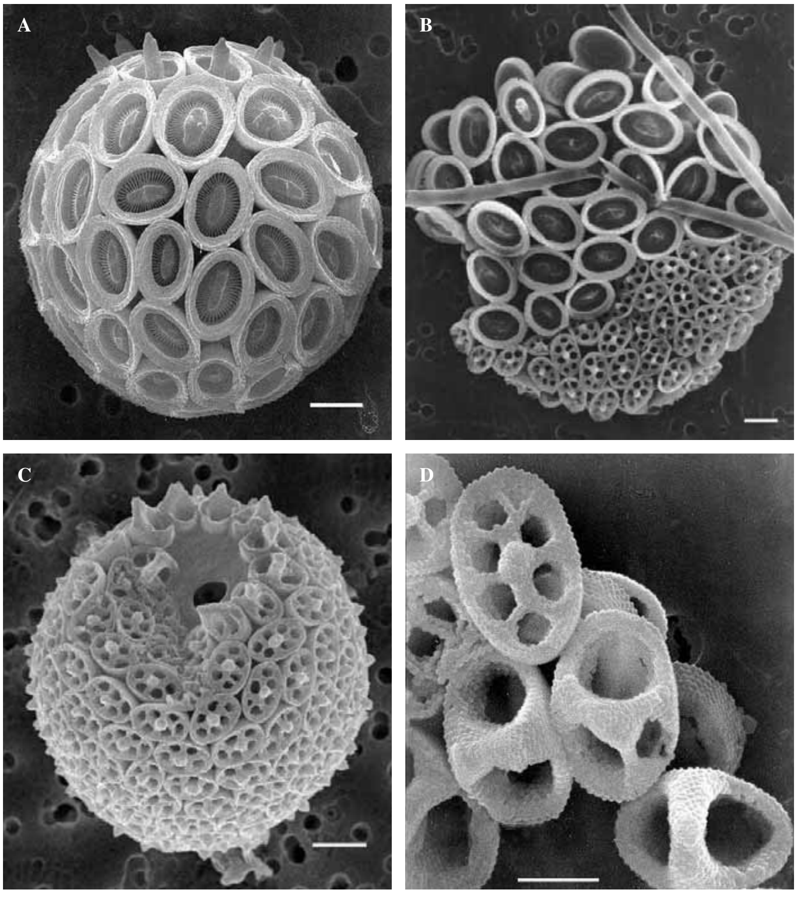

FIG. 28. – ***Coronosphaera mediterranea*** (Lohmann) Gaarder, in Gaarder *et* Heimdal: **A**, complete coccosphere of heterococcoliths [Fronts-95, 19T, 40 m]; **B**, a combination coccosphere consisting half of *C. mediterranea* (heterococcolithophore) and half of the former *Calyptrolithina wettsteinii* (Kamptner) Norris holococcoliths [Meso-96, I2, 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.

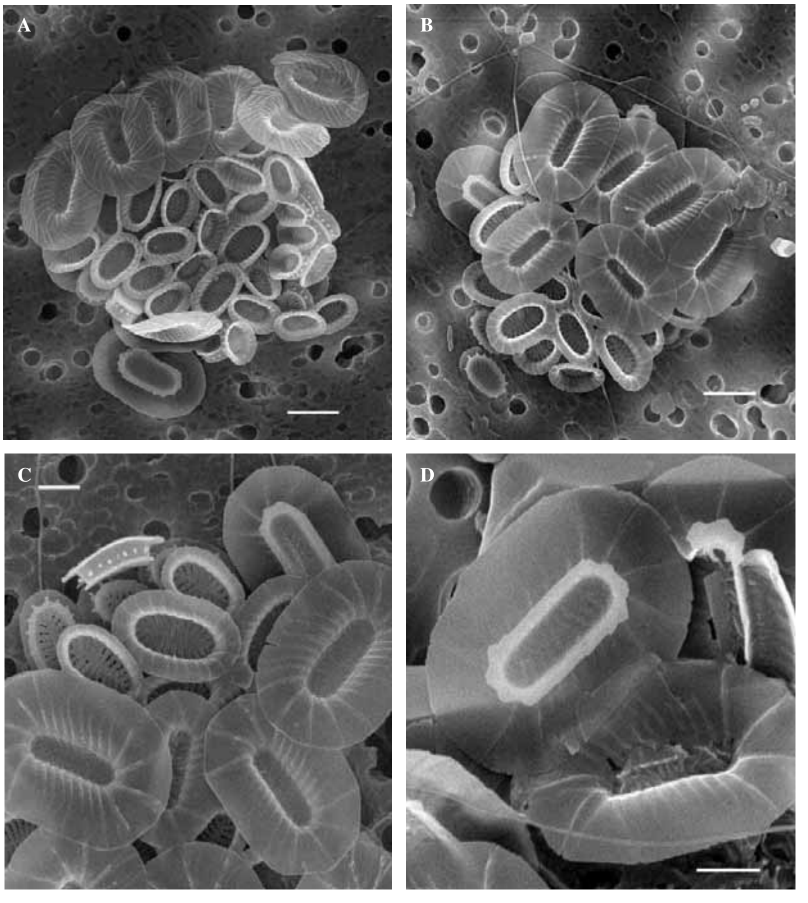

FIG. 29. – ***Gaarderia corolla*** (Lecal) Kleijne: **A**, coccosphere showing endothecal and exothecal caneoliths [Fans-3, K05, 40 m]; **B**, coccosphere with the endotheca partially covered by the large exothecal caneoliths (note the considerable size variations of both endothecal and exothecal coccoliths) [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.

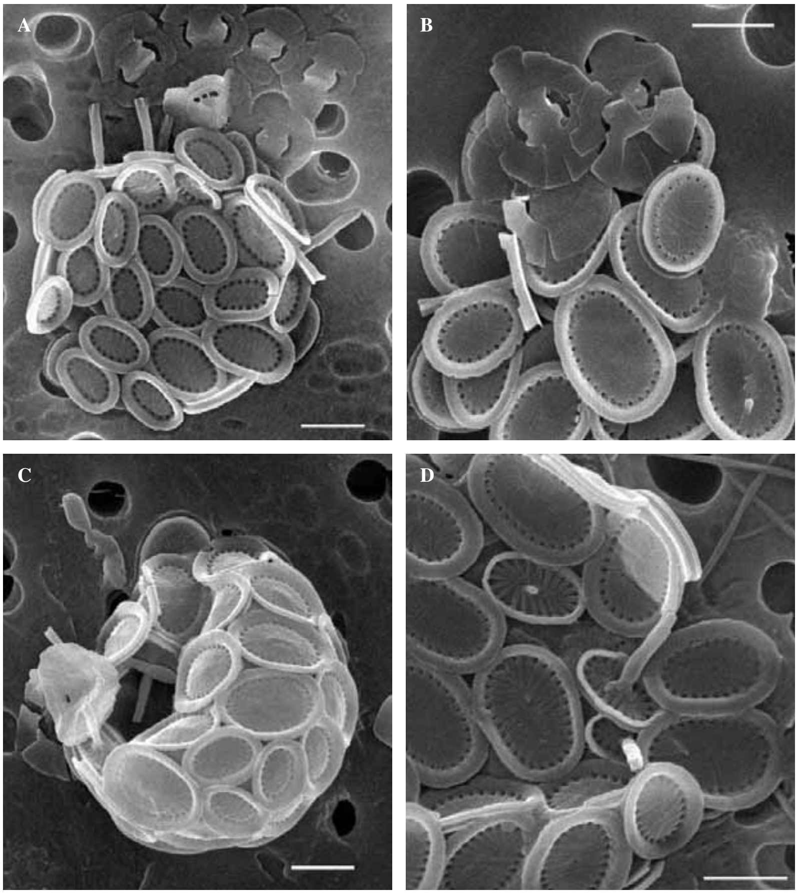

FIG. 30. – ***Syracosphaera marginaporata*** Knappertsbusch: **A**, complete coccosphere showing variable sized body caneoliths, some circum-flagellar caneoliths with long spine and several detached complex undulating exothecal coccoliths in proximal view (top) [Fans-3, K12, 75 m]; **B**, detail showing 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.

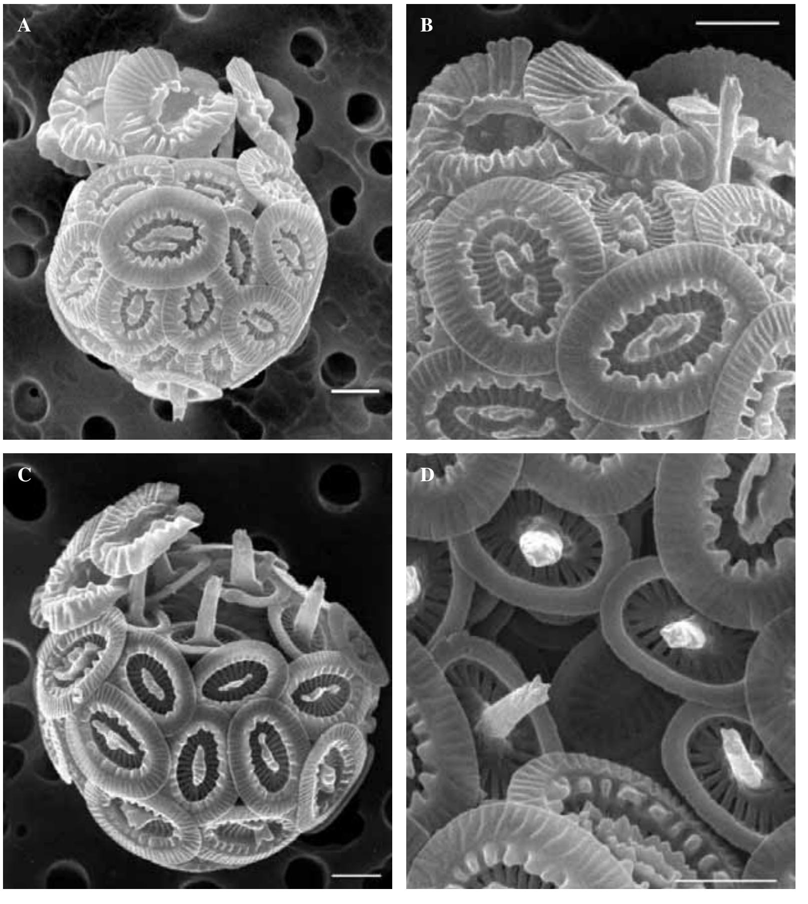

FIG. 31. – ***Syracosphaera molischii*** Schiller: **A**, complete coccosphere showing body caneoliths with corrugated distal flanges and robust central structures, complex undulating exothecal coccoliths in apical position covering the circum-flagellar caneoliths, and an antapical caneolith with a short 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.

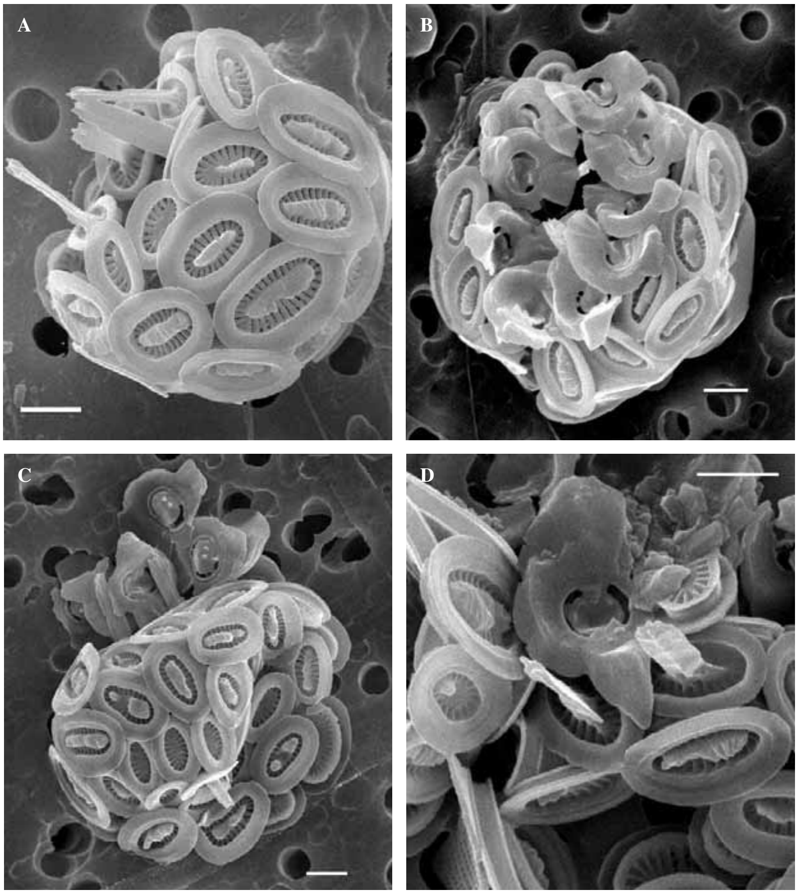

FIG. 32. – ***Syracosphaera ossa*** (Lecal) Loeblich Jr. *et* Tappan: **A**, coccosphere with body caneoliths showing the characteristic smooth distal flange and circum-flagellar caneoliths with the characteristic flattened spines [Meso-95, 161, surface]; **B**, complete coccosphere in apical view showing 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.

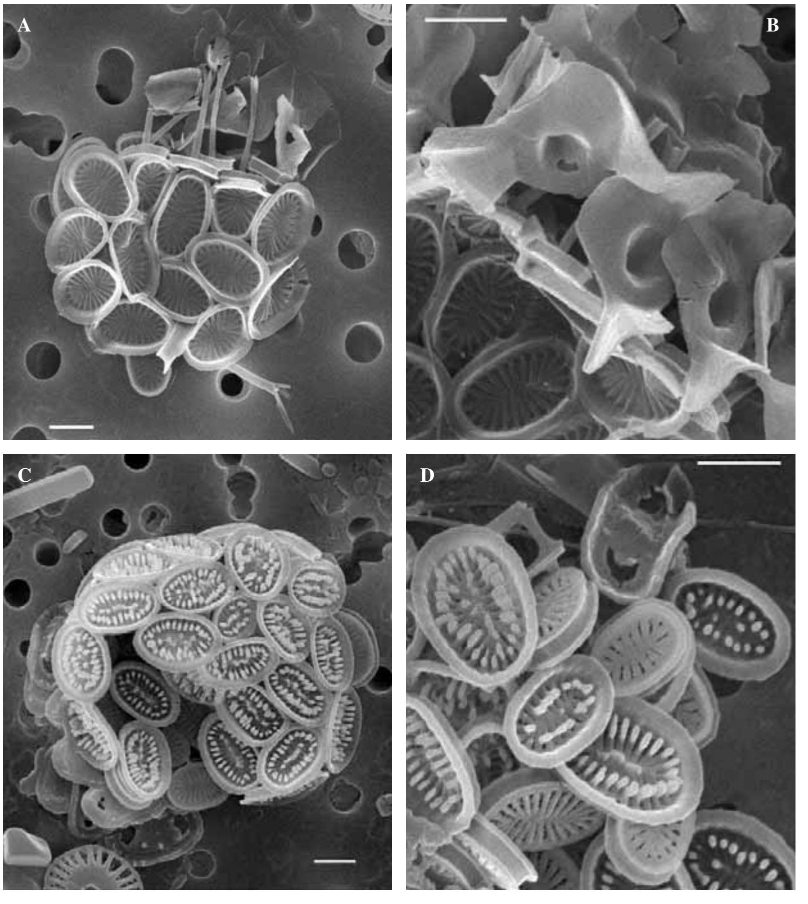

FIG. 33. – A-B, ***Syracosphaera* sp.** (slender): **A**, coccosphere with body caneoliths, circum-flagellar caneoliths with long and slender spines, some complex undulating exothecal coccoliths around the apical pole and one antapical caneolith with a long spine [Fronts-96, 013, 60 m]; **B**, detail 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.** (laths with rod protusions): **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.

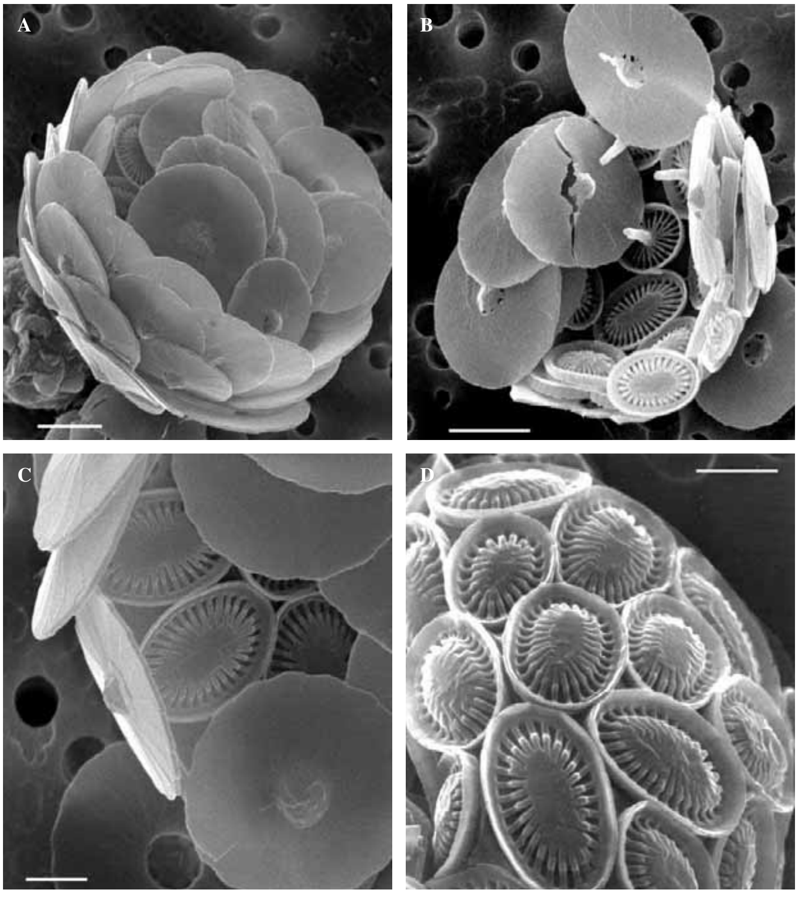

FIG. 34 – ***Syracosphaera anthos*** (Lohmann) Janin: **A**, complete coccosphere with overlapping exothecal coccoliths [Meso-96, G6, 70 m]; **B**, collapsed coccosphere with body caneoliths, circum-flagellar caneoliths with spine and exothecal coccoliths [Fronts-96, 039, 60 m]; **C**, detail with caneoliths 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 endothecal 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.

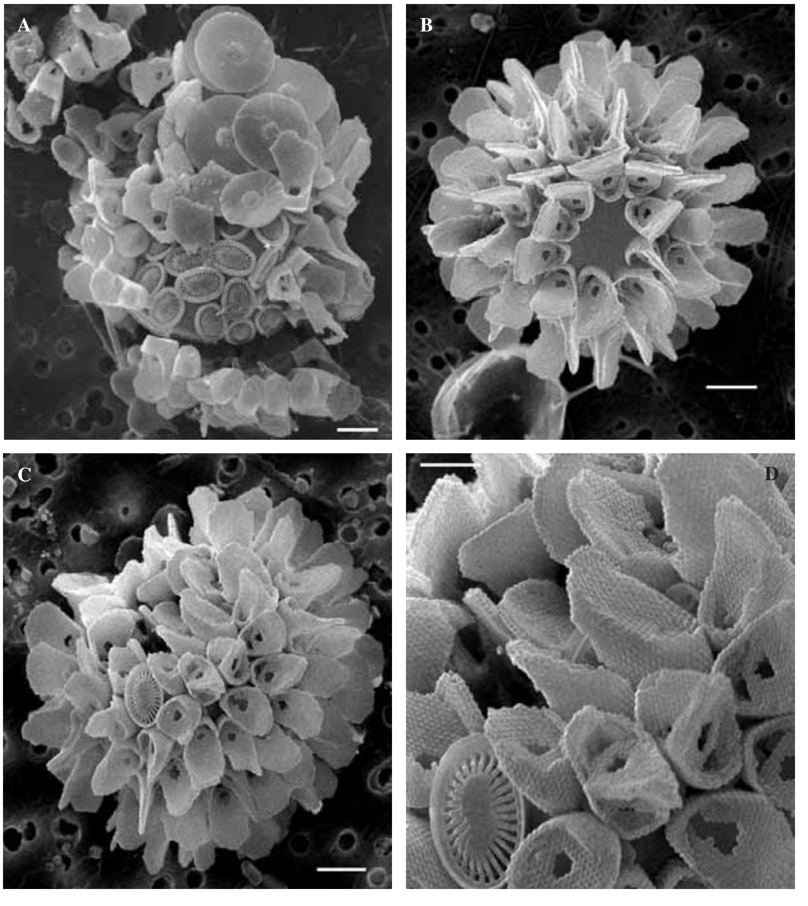

FIG. 35. – ***Syracosphaera anthos*** (Lohmann) Janin: **A**, combination coccosphere consisting of body caneoliths (upper) and exothecal coccoliths (bottom) of *S. anthos* and holococcoliths of the former *Periphyllophora mirabilis* [Meso-95, 178, 40 m]; **B**, *S. anthos* (holococcolith phase), formerly *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* (botom left). Scale bars: A, B, C = 2 µm; D = 1 µm.

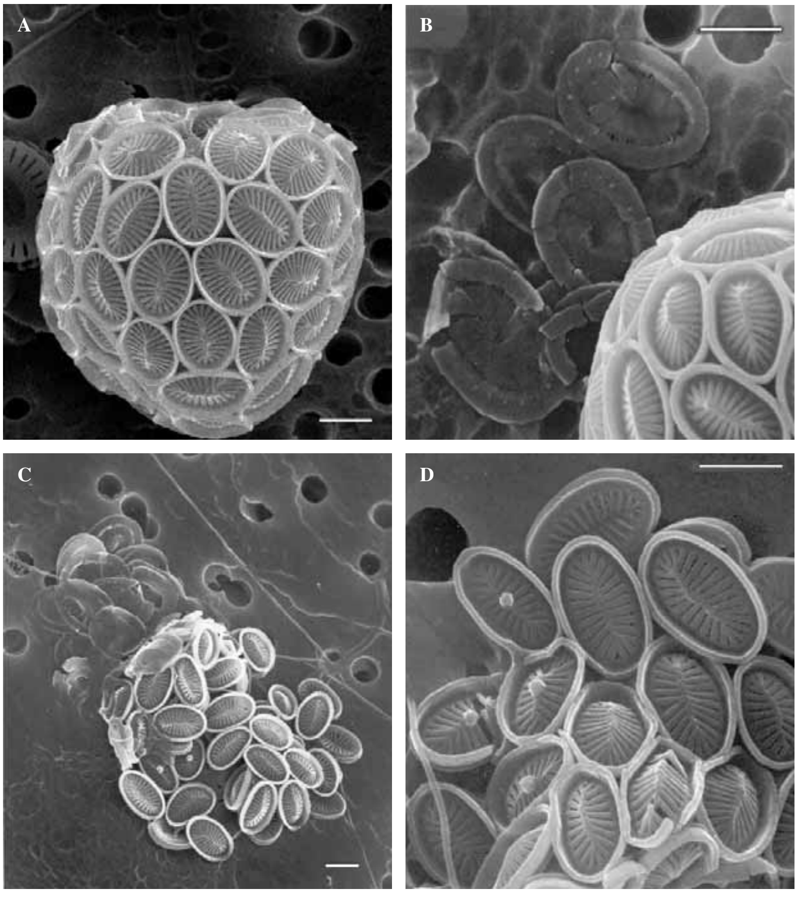

FIG. 36. – ***Syracosphaera nana*** (Kamptner) Okada *et* McIntyre: **A**, ovoid coccosphere showing body caneoliths with the central area formed like a sloping roof, and one exothecal coccolith (upper left) [Fans-3, M11, 60 m]; **B**, detail showing part of the endotheca (lower right) and several oval 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 caneoliths 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 caneoliths having small rounded spines (left) and body caneoliths showing hunch backed shape as described by Kamptner (1941) [Fronts-95, 20I, 60 m]. Scale bars = 1 µm.

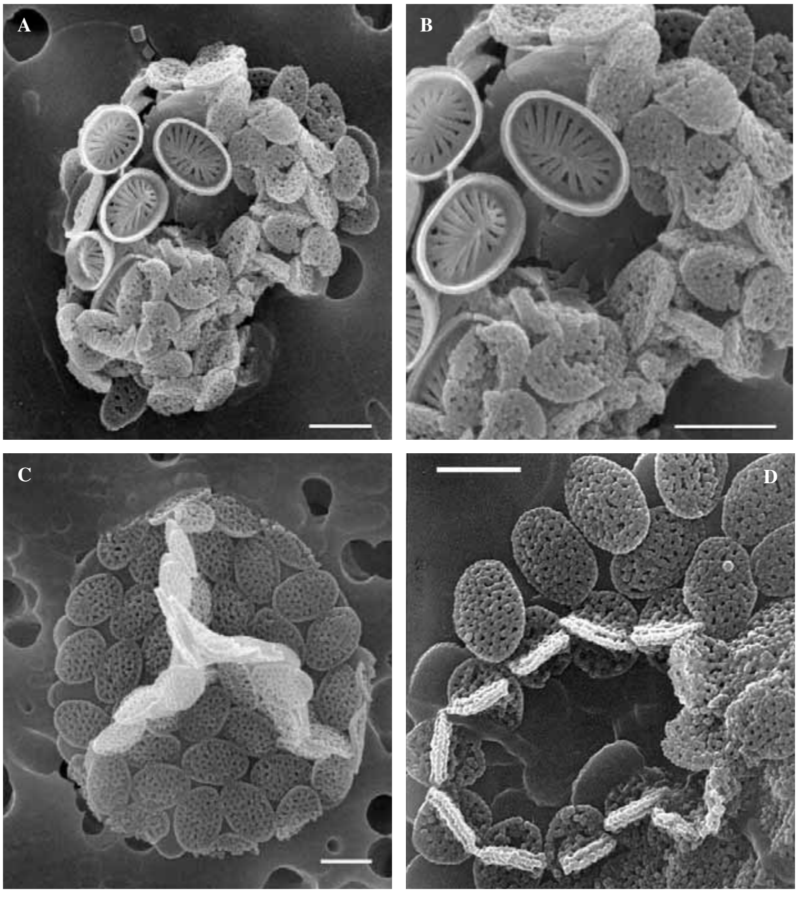

FIG. 37. – ***Syracosphaera nana*** (Kamptner) Okada *et* McIntyre: **A**, collapsed heterococcolith-holococcolith combination coccosphere [Fronts-96, 013, 75 m]; **B**, detail of Fig. A showing the holococcoliths covering heterococcoliths, including both body caneoliths and exothecal coccoliths; **C**, 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.

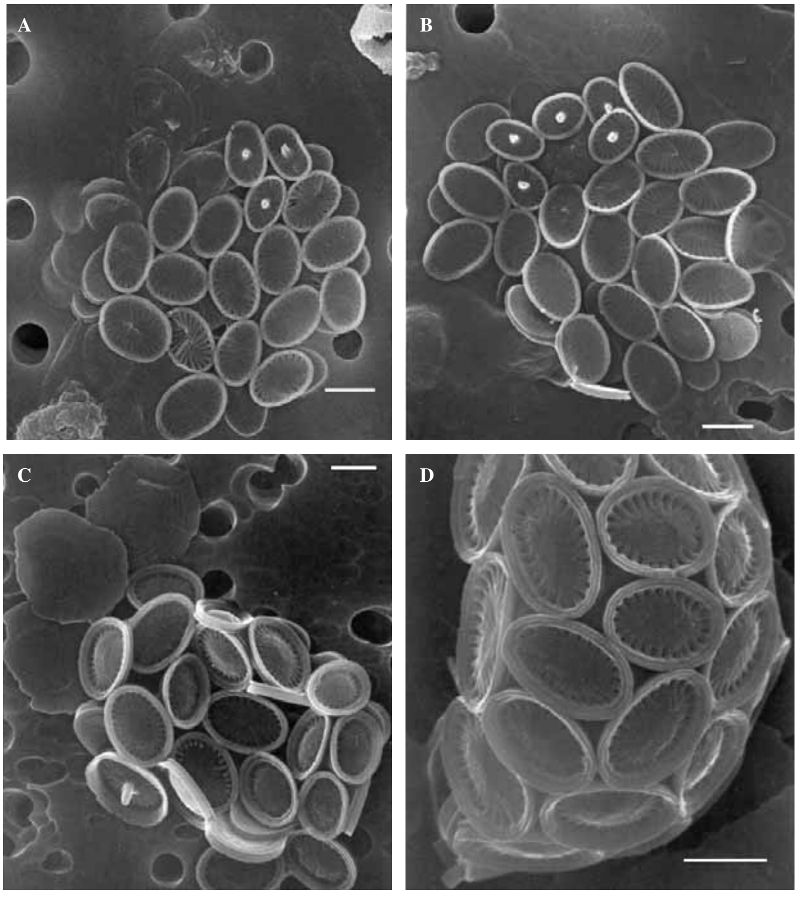

FIG. 38. – A-B, ***Syracosphaera* sp.** (aff. *S. nana*, laths with sinistral obliquity): **A**, collapsed coccosphere with body caneoliths, three circum-flagellar caneoliths and exothecal coccoliths (top) [Fronts-96, 013, 60 m]; **B**, collapsed coccosphere showing body caneoliths and five circum-flagellar caneoliths each with a small spine [Fronts-95, 23D, 50 m]. C-D, ***Syracosphaera* sp.** (with stratified exothecal coccoliths): **C**, collapsed coccosphere showing body caneoliths, one circum-flagellar caneolith with spine and three exothecal coccoliths in proximal view [Meso-96, D8, 70 m]; **D**, detail showing body caneoliths with a very thick wall and smooth central area [Meso-96, D8, 70 m]. Scale bars = 1 μm.

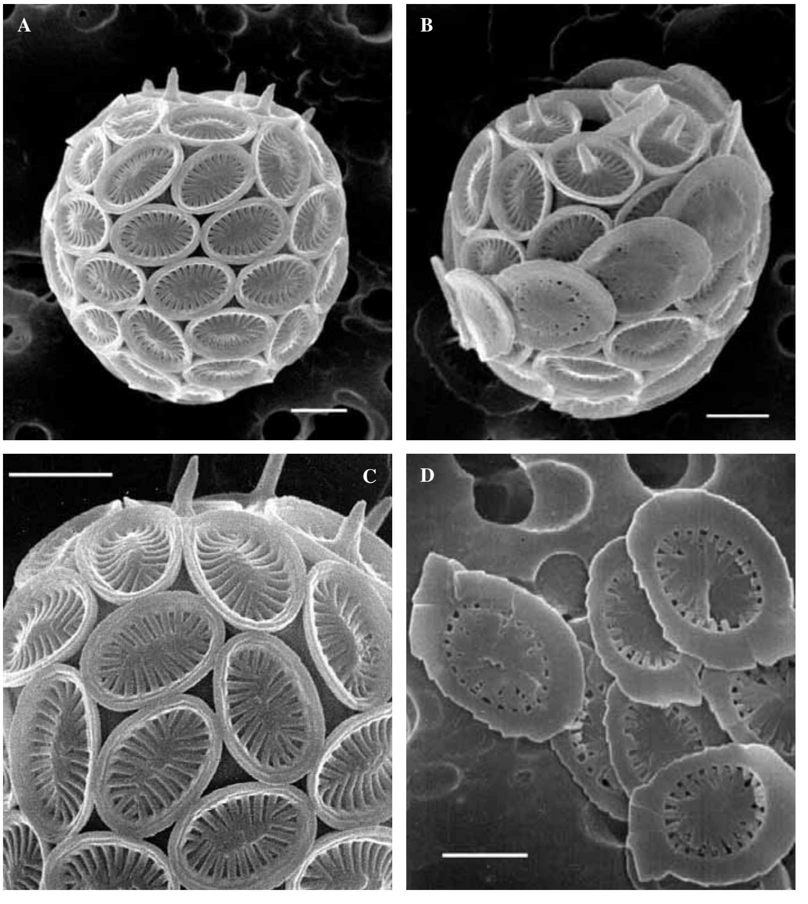

FIG. 39. – ***Syracosphaera bannockii*** (Borsetti *et* Cati) Cros *et al.*: **A**, coccosphere showing body and circum-flagellar caneoliths [Hivern-99, 25, 60 m]; **B**, complete coccosphere showing body caneoliths, four circum-flagellar caneoliths and a ribbon of exothecal coccoliths around the coccosphere [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 [Meso-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

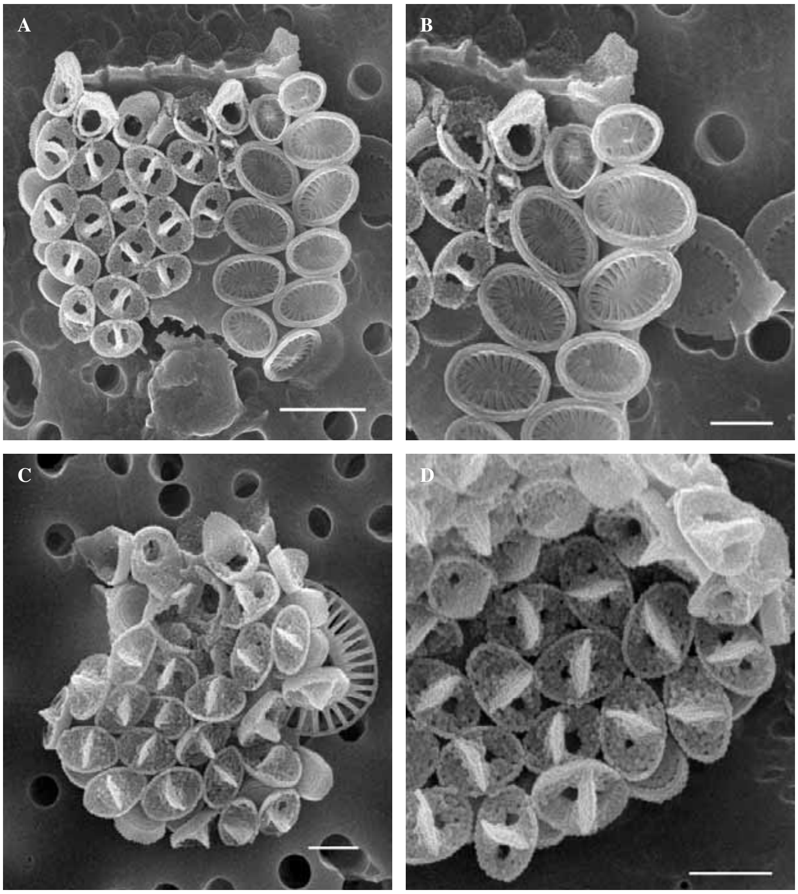

FIG. 40. – ***Syracosphaera bannockii*** (Borsetti *et* Cati) Cros *et al.*: **A**, combination coccosphere showing body and circum-flagellar holococcoliths of the former *Corisphaera* sp. type A and heterococcoliths of the former *Syracosphaera* sp. [Meso-96, G6, 40 m]; **B**, detail of Fig. A showing two detached exothecal coccoliths (rigth) 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.

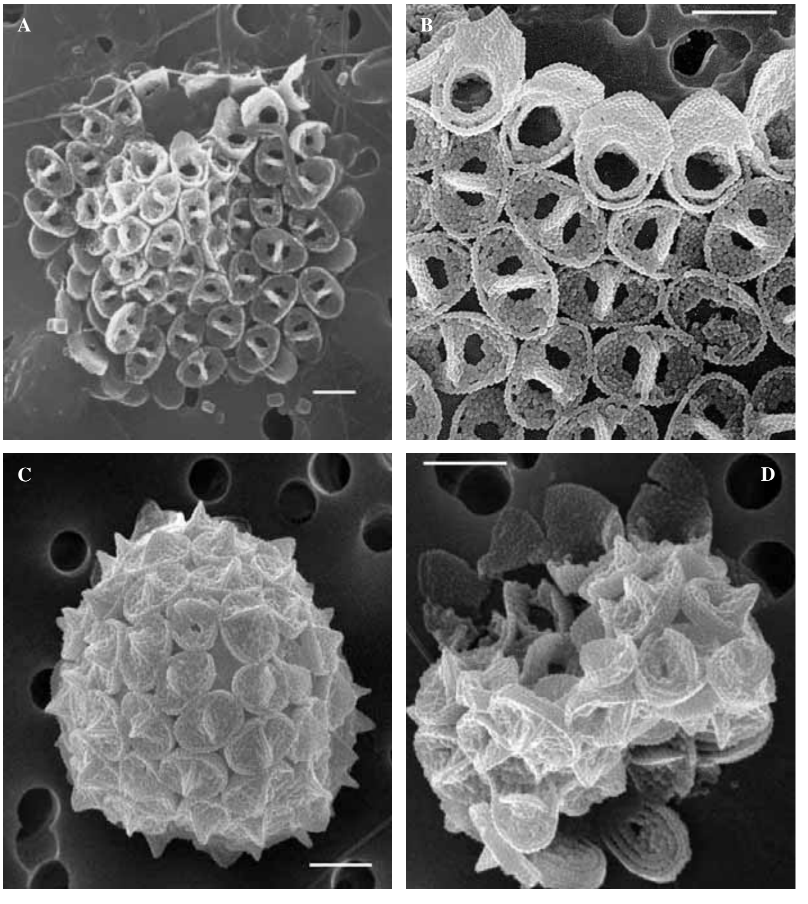

FIG. 41. – A-B. ***Syracosphaera bannockii*** (holococcolith phase, perforate), formerly ***Corisphaera* sp. type A** of Kleijne (1991): **A**, slightly collapsed coccosphere. Note the possible residual parts of the flagella that appear to emerge from the flagellar area [Fronts-95, 18P, 5 m]; **B**, 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 *et* Cati) 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 zygoform body laminoliths [Fans-1, 100, 25 m]. Scale bars = 1 µm.

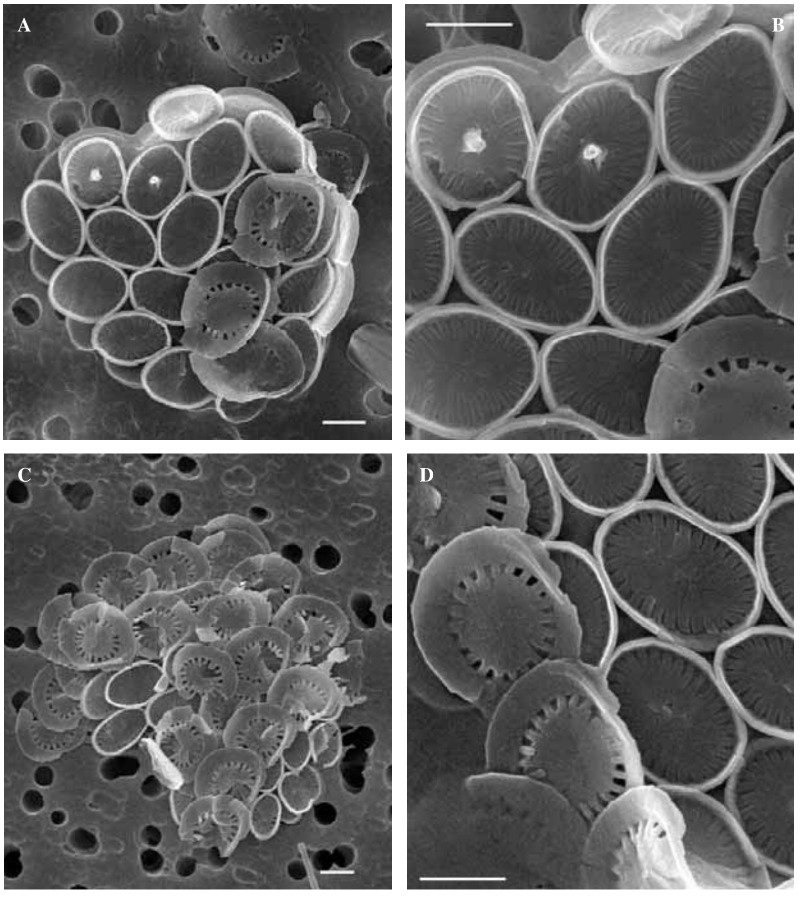

FIG. 42. – ***Syracosphaera delicata*** Cros *et al.*: **A**, coccosphere of delicate appearance showing body caneoliths with flat central area, three circum-flagellar caneoliths with a very small spine and asymmetrical exothecal coccoliths having a characteristic distal ridge [Hivern-99, 25, 60 m]; **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 endothecal 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.

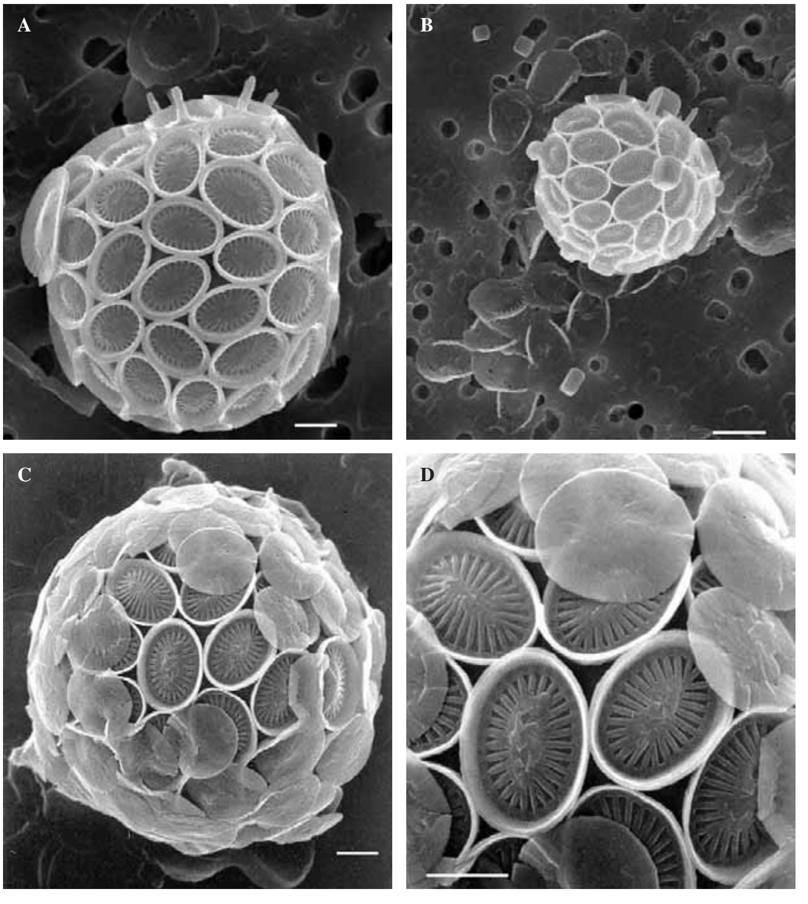

FIG. 43. – **A**, ***Syracosphaera* sp.** aff. to *S. orbiculus* (ovoid): coccosphere with endothecal body caneoliths having a flat and very broad central structure, circum-flagellar caneoliths with a short but robust spine and one asymmetrical exothecal coccolith in distal view on the coccosphere (centre 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.

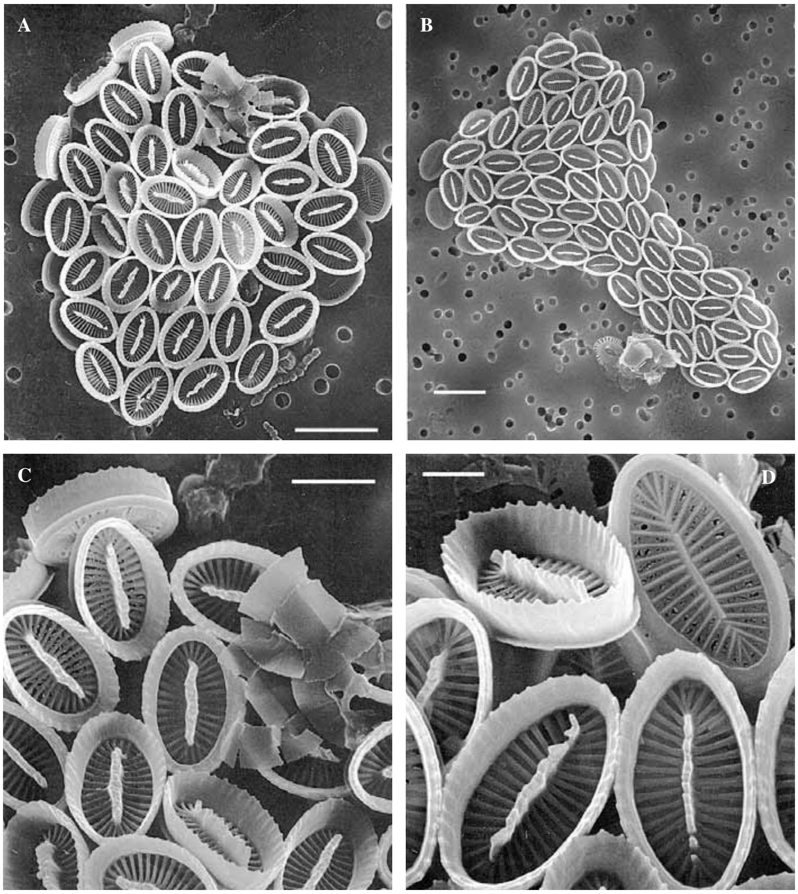

FIG. 44. – ***Syracosphaera lamina*** Lecal-Schlauder: **A**, coccosphere with remains of the exothecal coccoliths (upper middle) [Fronts-95, 23D, 70 m]; **B**, complete coccosphere showing the characteristic shape of this species [Fronts-95, 23D, 80 m]; **C**, detail of the Fig. A with body caneoliths having the characteristic keel-shaped central structure and the thin (sub)circular exothecal coccoliths (centre right) covering the caneoliths; **D**, detail with body caneoliths 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.

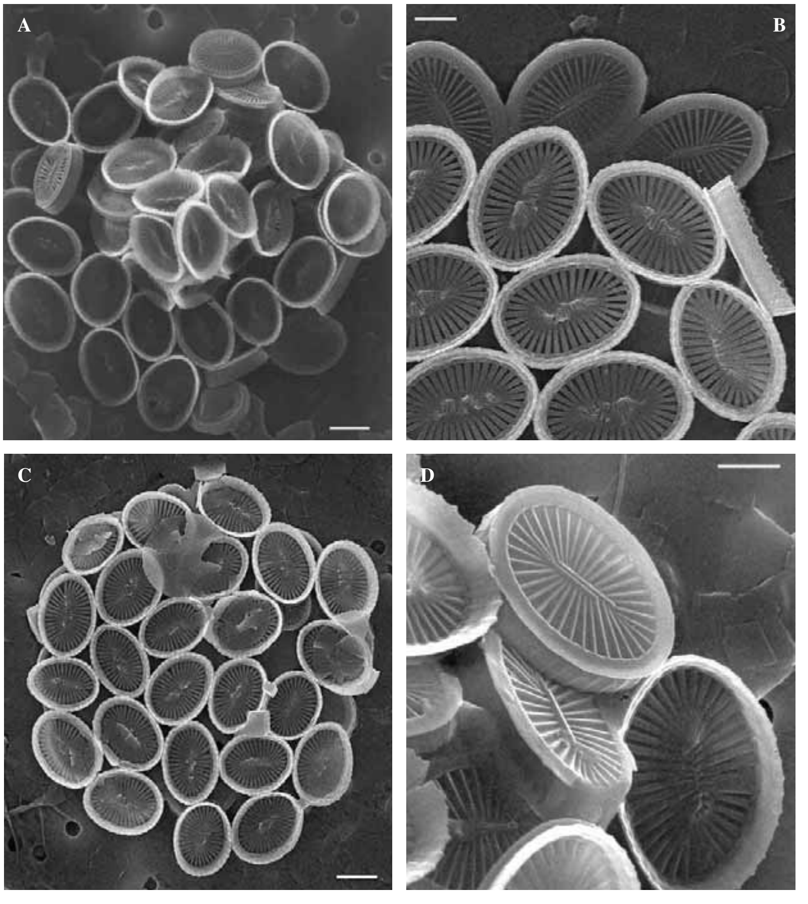

FIG. 45. – ***Syracosphaera tumularis*** Sánchez-Suárez: **A**, collapsed coccosphere [Fronts-95, 19T, 60 m]; **B**, detail of body caneoliths: three caneoliths in proximal view (top); a caneolith in lateral view showing a relatively high wall with serrated distal rim (centre right); and caneoliths in 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.

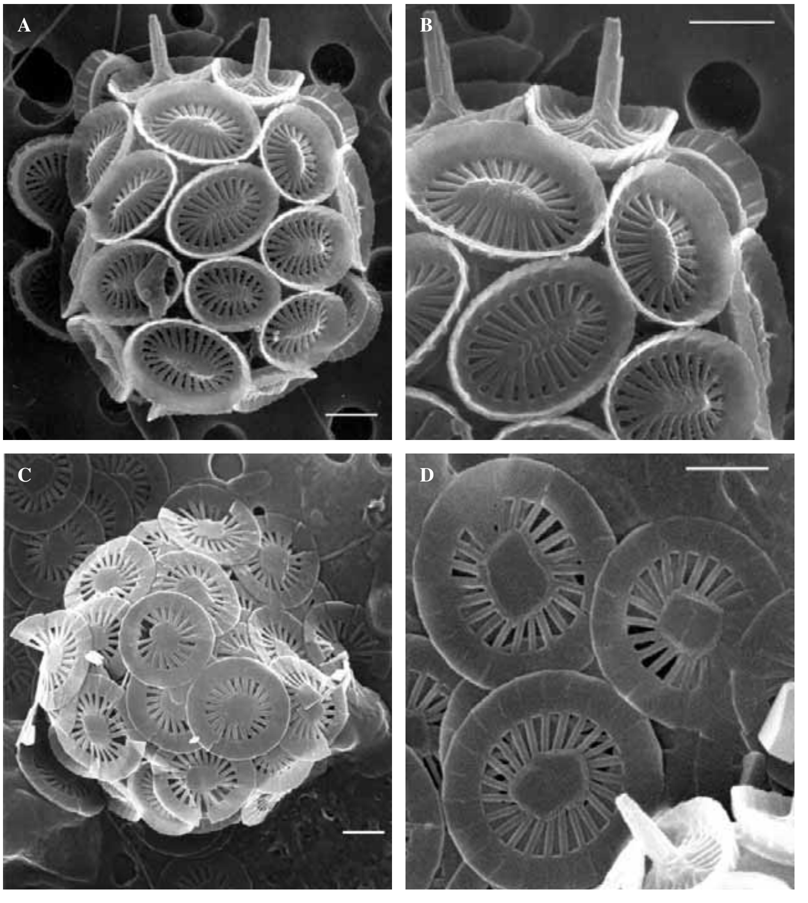

FIG. 46. – ***Syracosphaera nodosa*** Kamptner: **A**, complete coccosphere showing the body caneoliths and two circum-flagellar caneoliths with large spines; both coccolith types have well developed walls with robust external vertical ribs [Fronts-95, 28C, 35 m]; **B**, detail of Fig. A showing the 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.

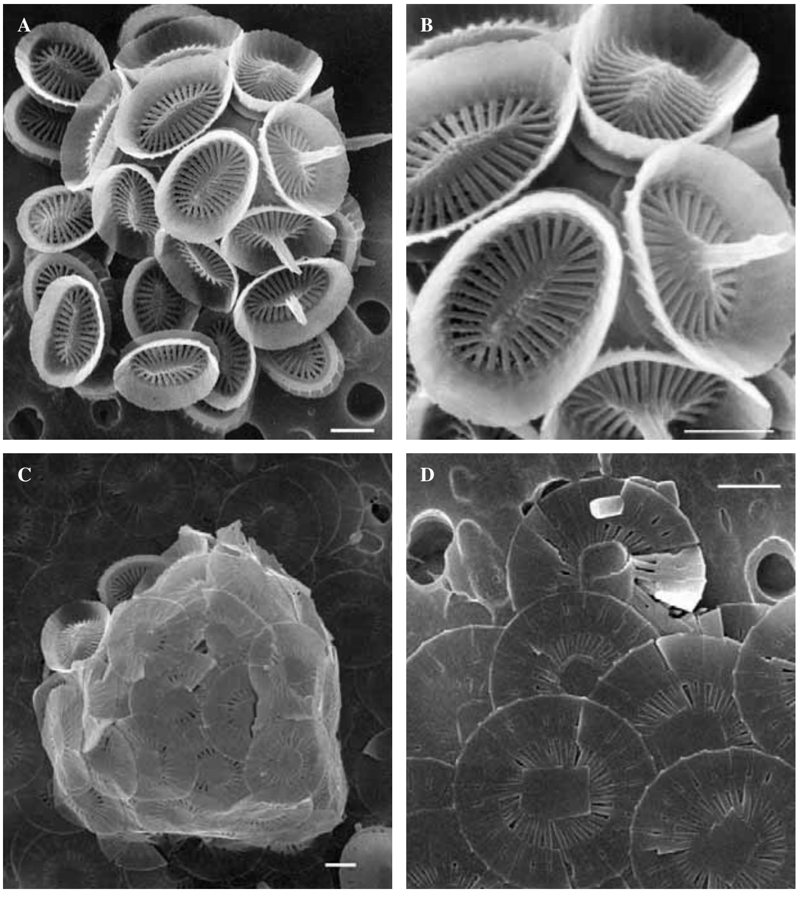

FIG. 47. – ***Syracosphaera* sp.** aff. ***S. nodosa***: **A**, coccosphere showing endothecal coccoliths; both body and circum-flagellar caneoliths with spine are large and have a high wall which is vertically ribbed externally, long laths, an elongated connecting central structure and no visible connecting external ring [Meso-95, 132, surface]; **B**, detail of Fig. A with body and cicum-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.

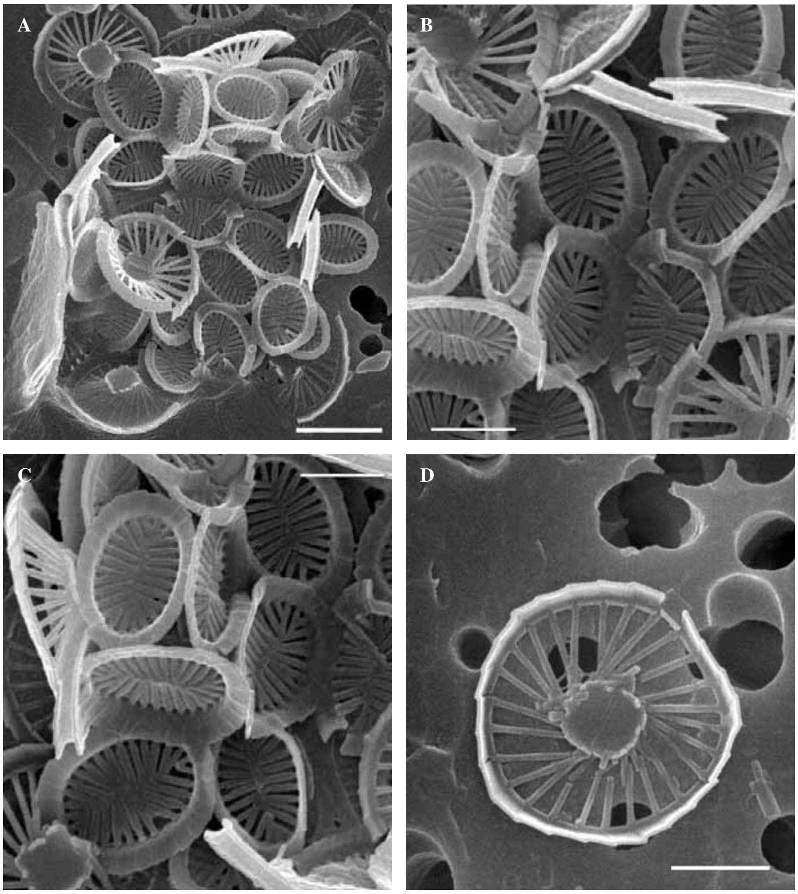

FIG. 48. – ***Syracosphaera rotula*** Okada *et* McIntyre: **A**, collapsed coccosphere with endothecal caneoliths and larger wheel-shaped exothecal coccoliths [Hivern-99, 19, surface]; **B**, detail of Fig. A with endothecal caneoliths in distal and lateral view; **C**, detail of Fig. A showing the 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.

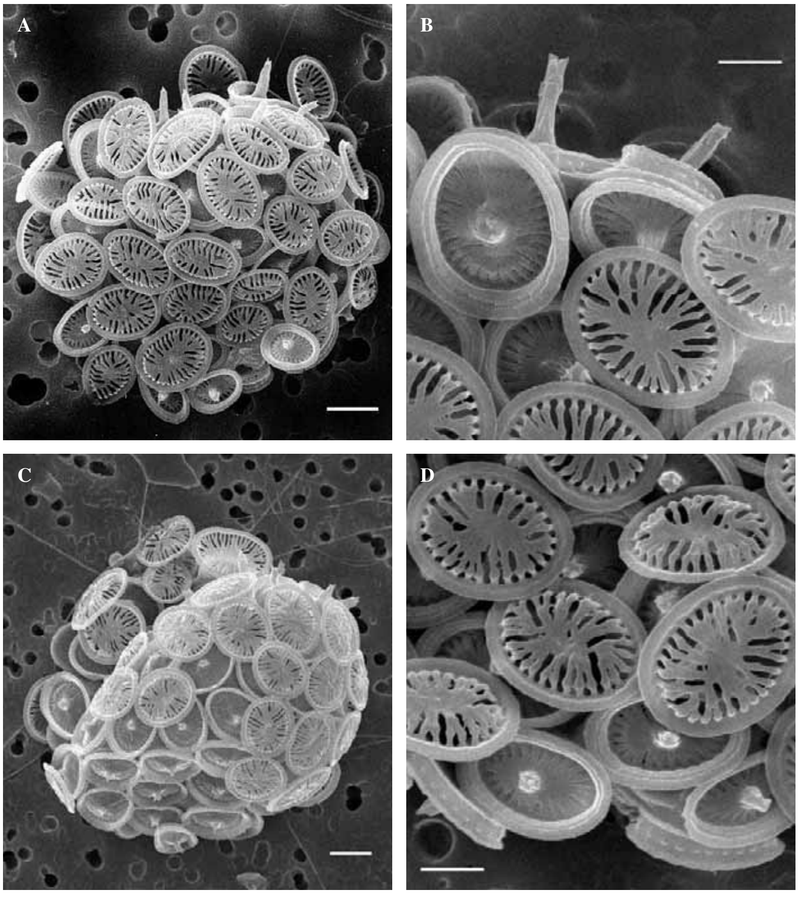

FIG. 49. – ***Syracosphaera histrica*** Kamptner: **A**, complete coccosphere with body and circum-flagellar caneoliths and exothecal coccoliths [Meso-95, 161, surface]; **B**, detail with body caneoliths, some exothecal vaulted coccoliths (lower and centre right) showing their characteristic distal 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.

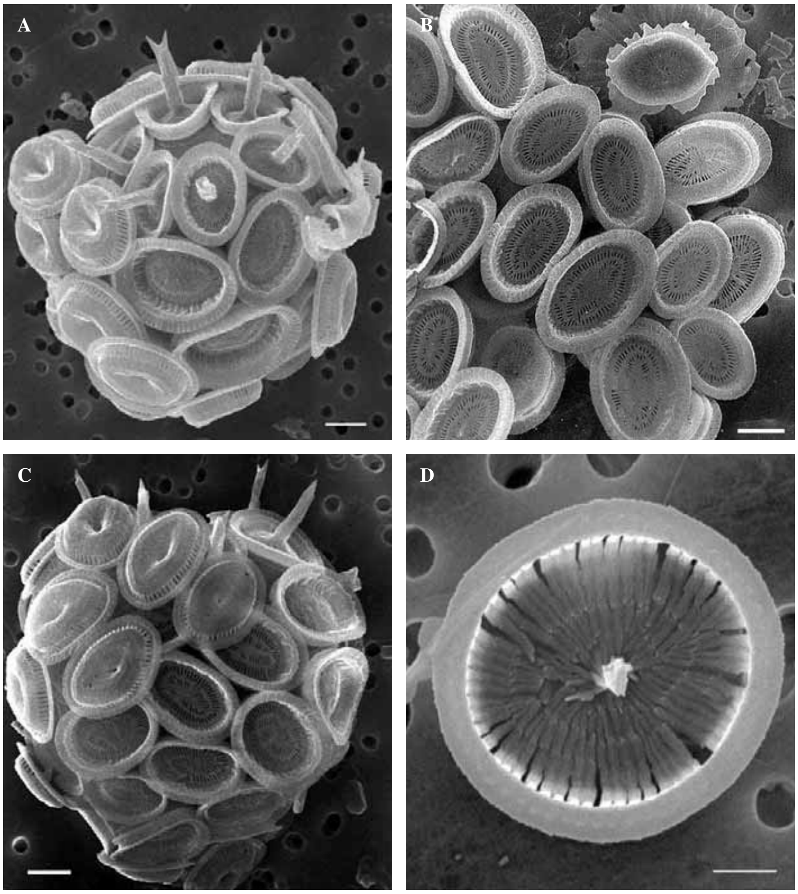

FIG. 50. – ***Syracosphaera pulchra*** Lohmann: **A**, detail of the apical area showing six circum-flagellar caneoliths with robust, bifurcate ended spines [Fans-1, 100, 25 m]; **B**, detail showing one malformed body caneolith with overgrown flanges (upper rigth), two well-formed body caneoliths in proximal view (rigth), several in distal view (center); 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.

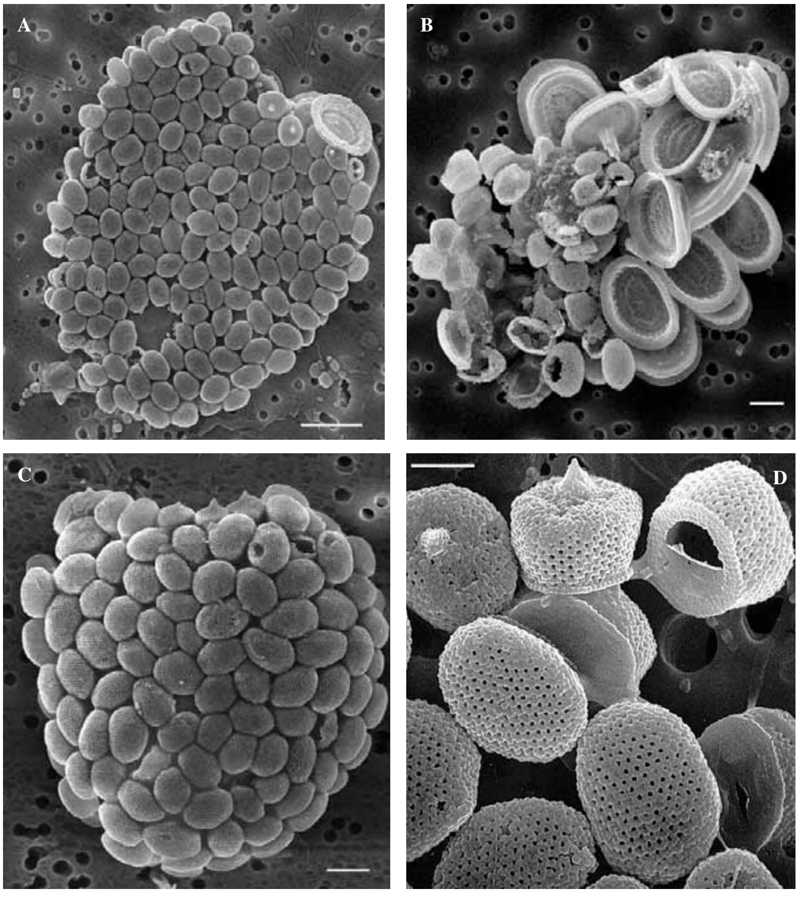

FIG. 51. – ***Syracosphaera pulchra*** Lohmann: **A**, combination coccosphere of *S. pulchra* (holococcolithophore), formerly *Calyptrosphaera oblonga*, with some body heterococcoliths of *S. pulchra* (upper right) [Fronts-96, 021, 20 m]; **B**, combination coccosphere of *S. pulchra*, with heterococcoliths 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.

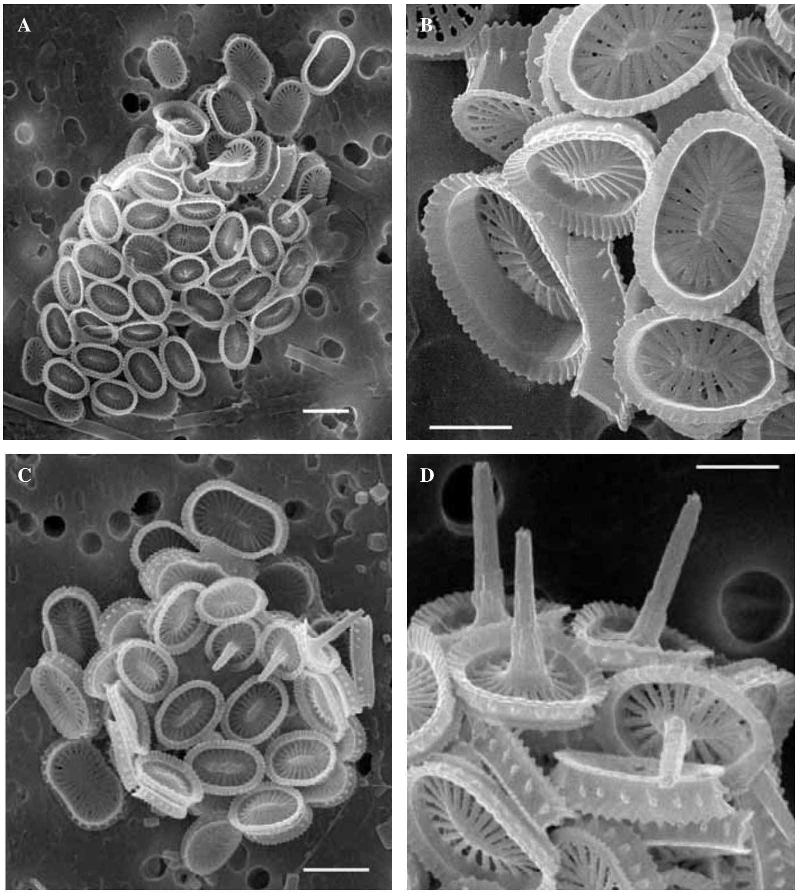

FIG. 52. – ***Syracosphaera*** cf. ***dilatata*** Jordan, Kleijne and Heimdal: **A**, whole coccosphere showing detached apical exothecal caneoliths, near the circum-flagellar caneoliths with spine [Meso-96, I2, 40 m]; **B**, detail with body caneoliths (right) and exothecal caneoliths (left); the exothecal caneoliths have higher and thinner walls [Meso-96, D4, 40 m]; **C**, coccosphere 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.

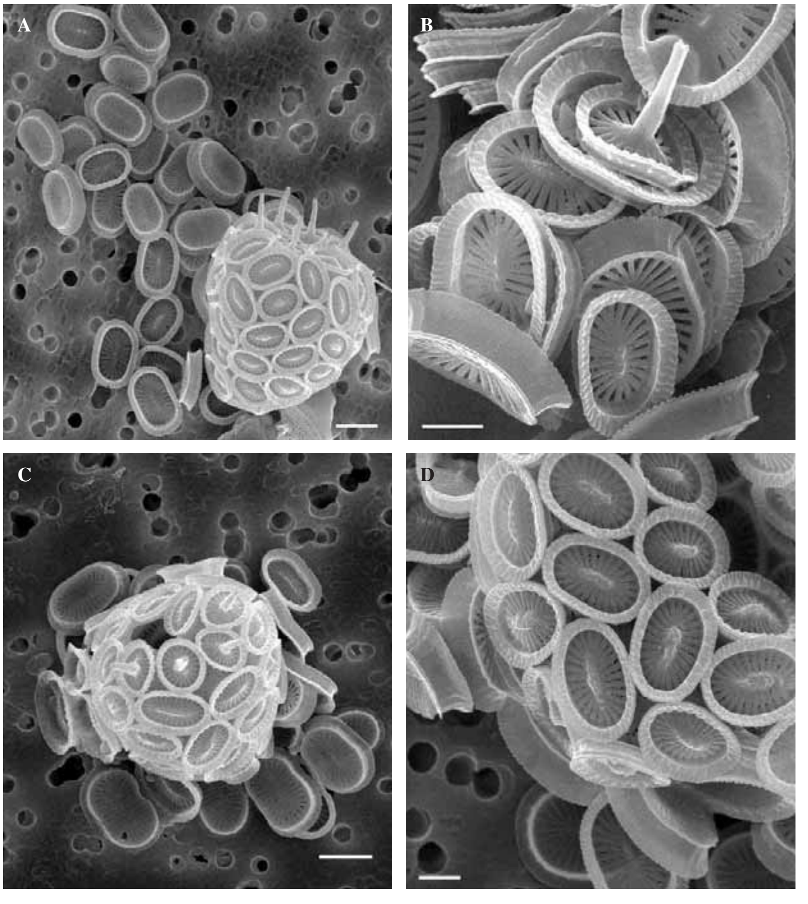

FIG. 53. – ***Syracosphaera* sp. type D** of Kleijne 1993: **A**, complete coccosphere showing the well-formed obpyriform endotheca (lower right) with five circum-flagellar spinous caneoliths and many detached large exothecal caneoliths (left) [Meso-96, I4, 70 m]; **B**, detail with the three types of 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.

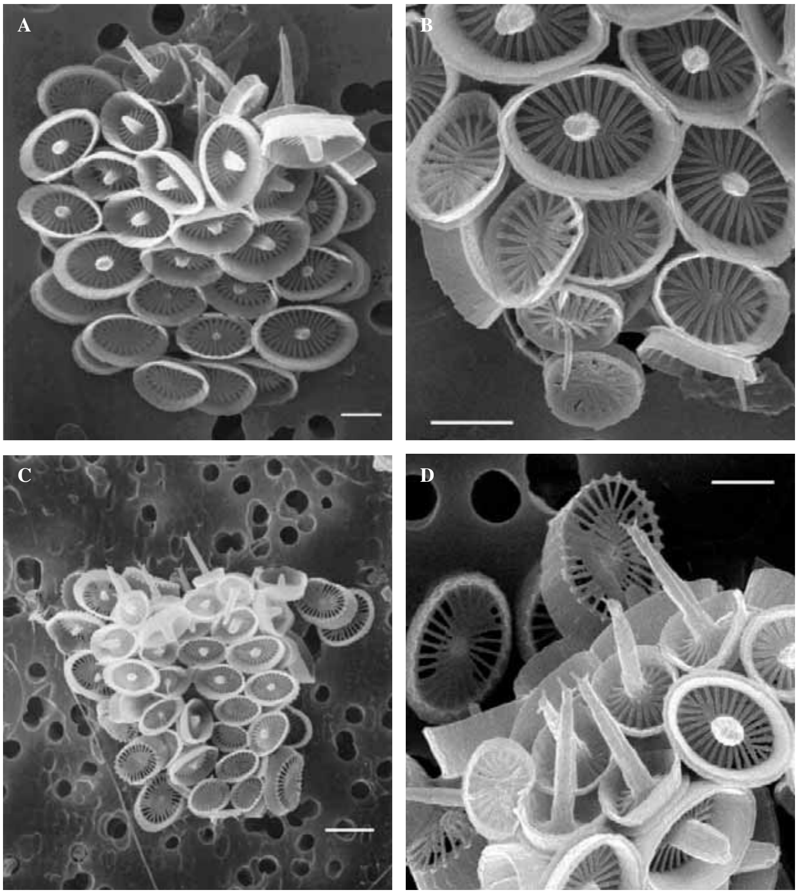

FIG. 54. – ***Syracosphaera noroitica*** Knappertsbusch: **A**, coccosphere showing apical circum-flagellar caneoliths with long spine, varimorphic body caneoliths with robust spine near the apical pole and with no central spine at the antapical pole [Fronts-95, 19T, 40 m]; **B**, detail of the antapical 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.

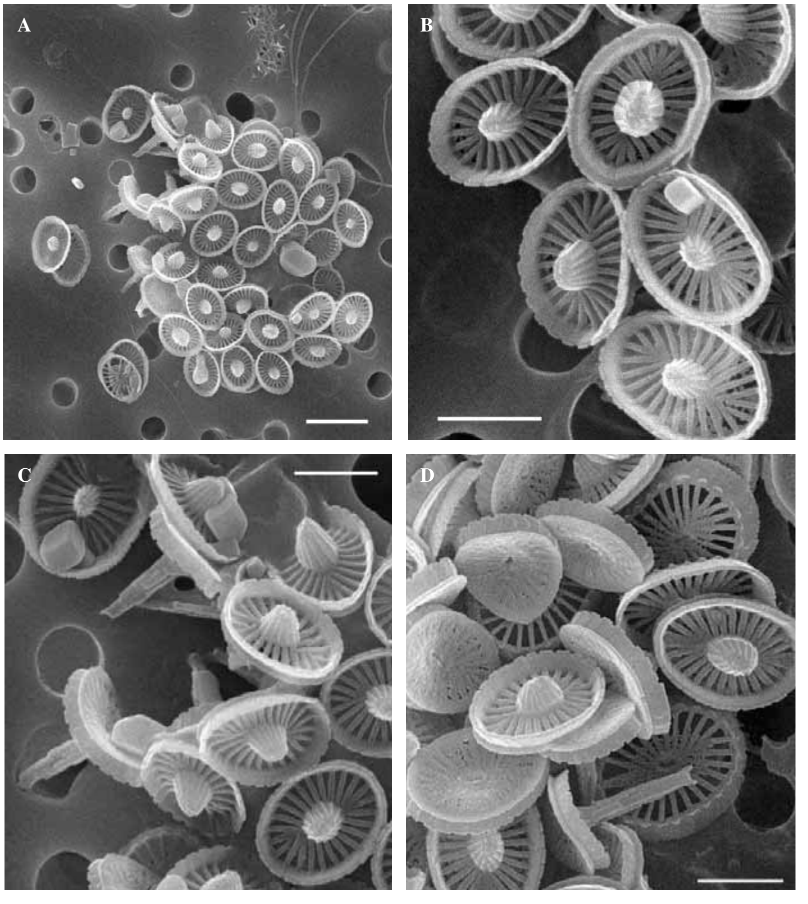

FIG. 55. – ***Syracosphaera* sp. type G** of Kleijne 1993: **A**, collapsed coccosphere with varimorphic body caneoliths, some circum-flagellar caneoliths in apical position and some detached exothecal caneoliths (left) [Fronts-96. 013, 75 m]; **B**, detail of Fig. A showing the varimorphic endothecal 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]. Sacale bars: A = 2 µm; B, C, D = 1 µm.

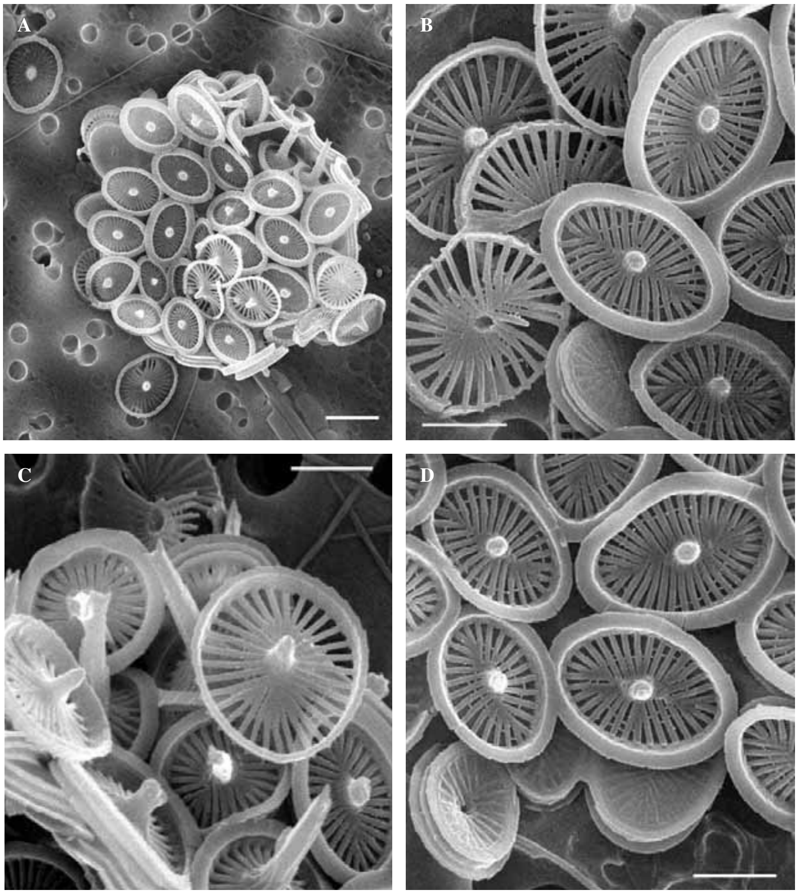

FIG. 56. – ***Syracosphaera prolongata*** Gran ex Lohmann *sensu* Throndsen: **A**, spherical coccosphere with five long-spined apical caneoliths and several exothecal caneoliths around the coccosphere; three of them (centre) remain attached to the coccosphere [Fronts-96, 039, 10 m]; **B**, detail of body caneoliths in distal view (right); one body caneolith, partially covered, in proximal view showing the three flanges (centre bottom); four exothecal caneoliths (left), two in proximal and two in distal view [Meso-96, A3, 40 m]; **C**, detail with body caneoliths with a robust node, circum-flagellar caneoliths 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 caneoliths 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.

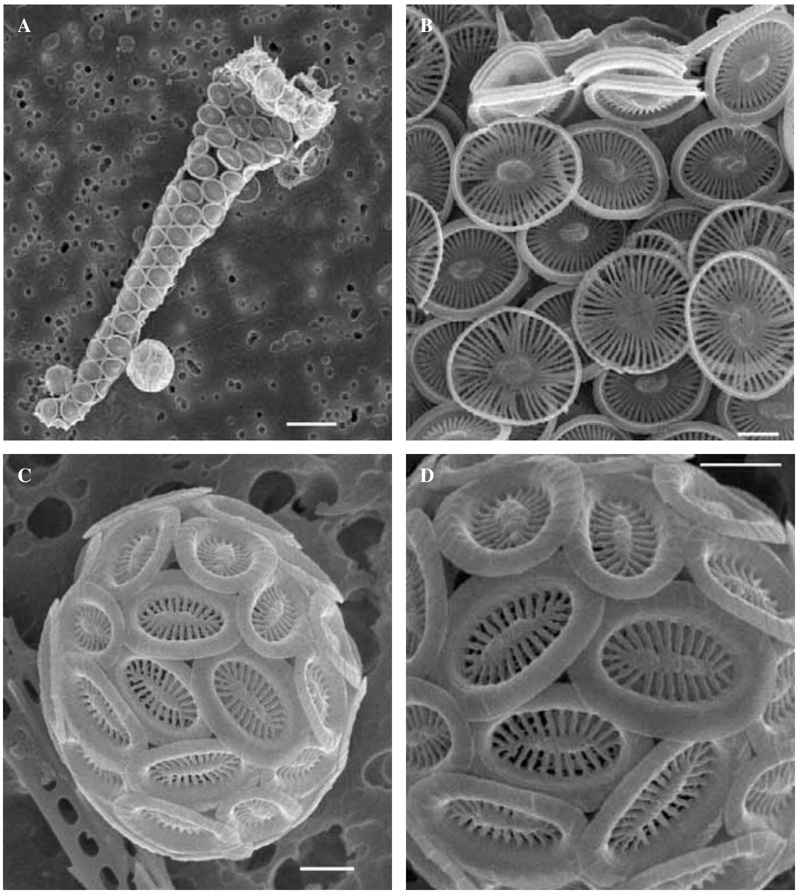

FIG. 57. A-B, ***Syracosphaera prolongata*** Gran ex Lohmann *sensu* Heimdal *et* Gaarder: **A**, complete coccophere showing body coccoliths, cicum-flagellar coccoliths with spine, and larger exothecal coccoliths near the apical area; there is one small diatom and one *Emiliania* coccosphere next to 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.

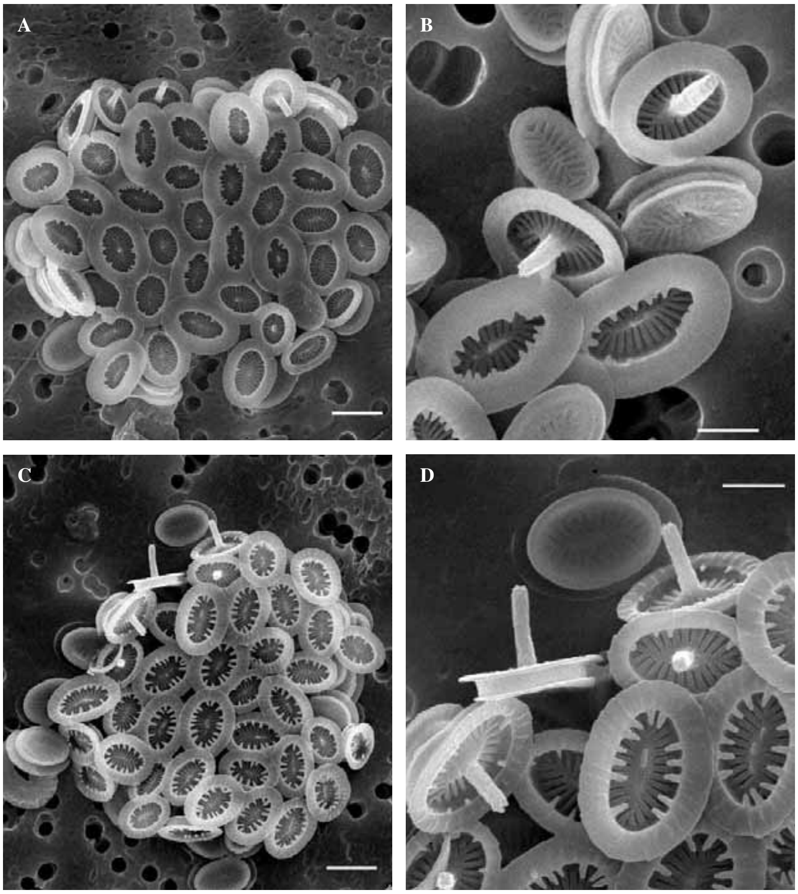

FIG. 58. – ***Syracosphaera halldalii*** Gaarder ex Jordan *et* Green: **A**, monothecate coccosphere of the "tooth-like form" showing several circum-flagellar caneoliths with spine (top); notice that some body caneoliths lack the tooth-like protrusions and therefore resemble the ordinary form of *S. 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.

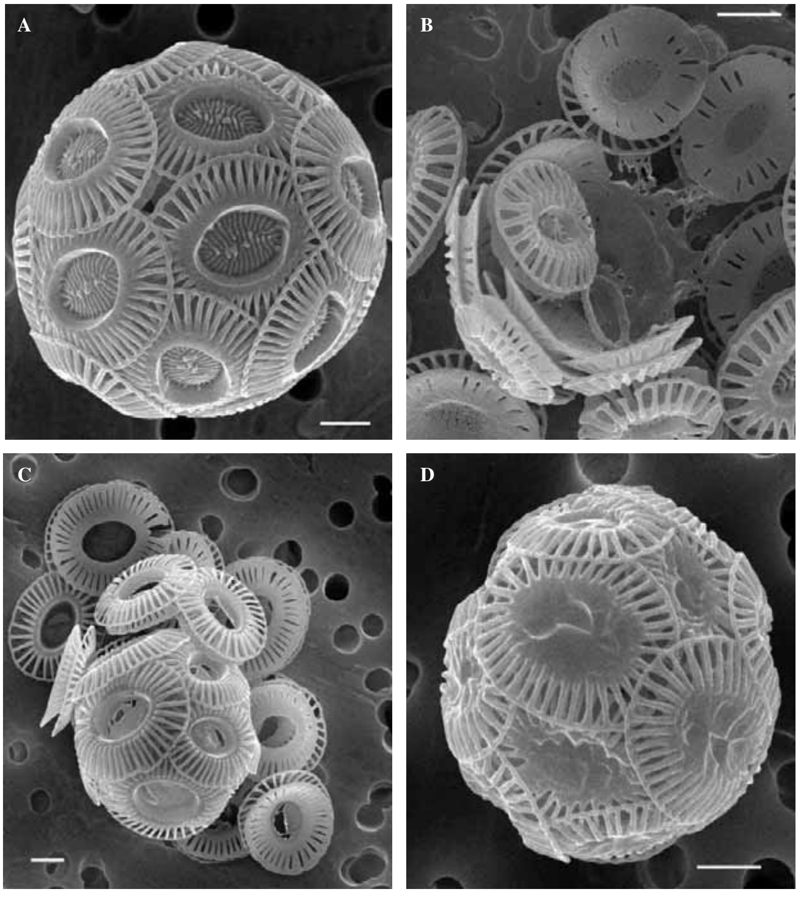

FIG. 59. – ***Emiliania huxleyi*** Hay *et* Mohler in Hay *et* al.: **A**, complete type A coccosphere showing placoliths with a central area constructed of curved rods [Fronts-96, 021, 20 m]; **B**, collapsed coccosphere showing lateral views of joined placoliths and, inside the concave remains of the 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.

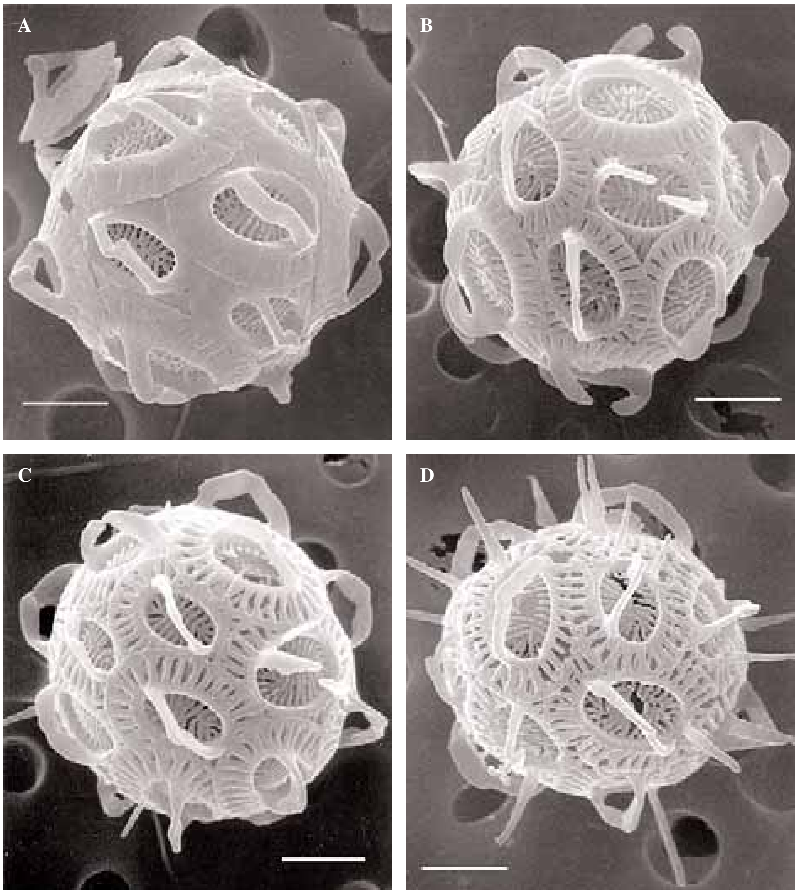

FIG. 60. – ***Gephyrocapsa ericsonii*** McIntyre *et* Bé: **A**, complete coccosphere with one detached placolith, near the top left corner; the coccoliths are small and the high bridge crosses the central area diagonally [Meso-95, 163, surface]; **B**, complete coccosphere of the type *protohuxleyi* 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.

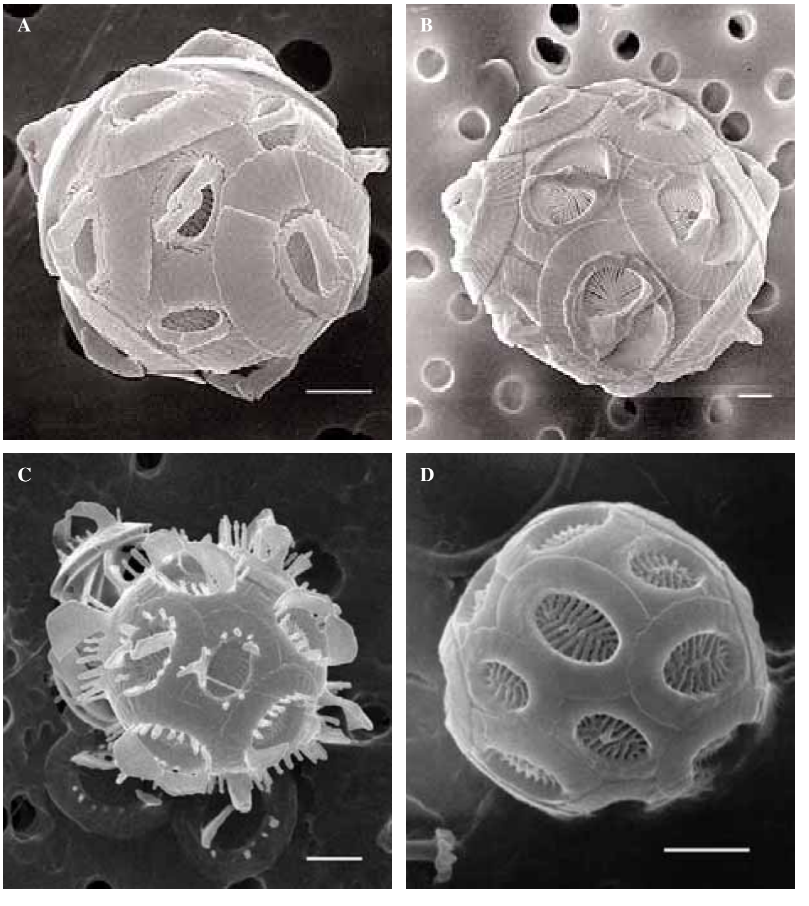

FIG. 61. – **A**, ***Gephyrocapsa muellerae*** Bréhéret: complete coccosphere with medium sized coccoliths which have a bridge that diagonally crosses the central area [Meso-95, 119, 70 m]. **B**, ***Gephyrocapsa oceanica*** Kamptner: complete coccosphere with large coccoliths which have a wide central 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.

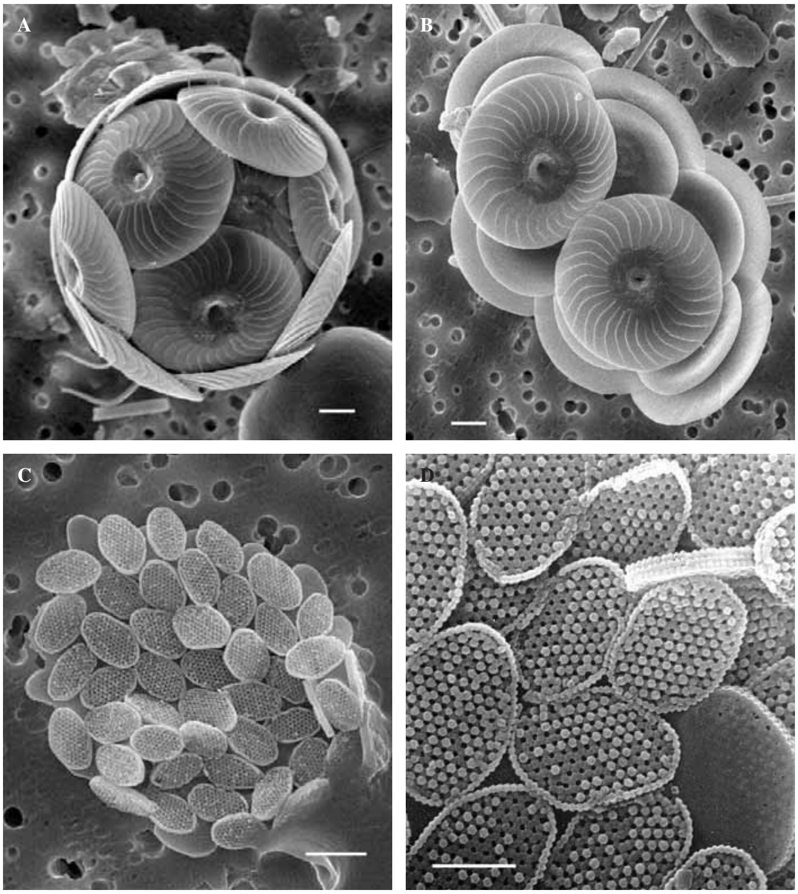

FIG. 62. – ***Calcidiscus leptoporus*** (Murray *et* Blackman) Loeblich *et* Tappan: **A**, heterococcolith phase; subcircular coccosphere showing the tightly interlocked coccoliths [Fans-2, N07, 25 m]; **B**, detail with two placoliths (heterococcoliths) in distal view and six in proximal view which 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.

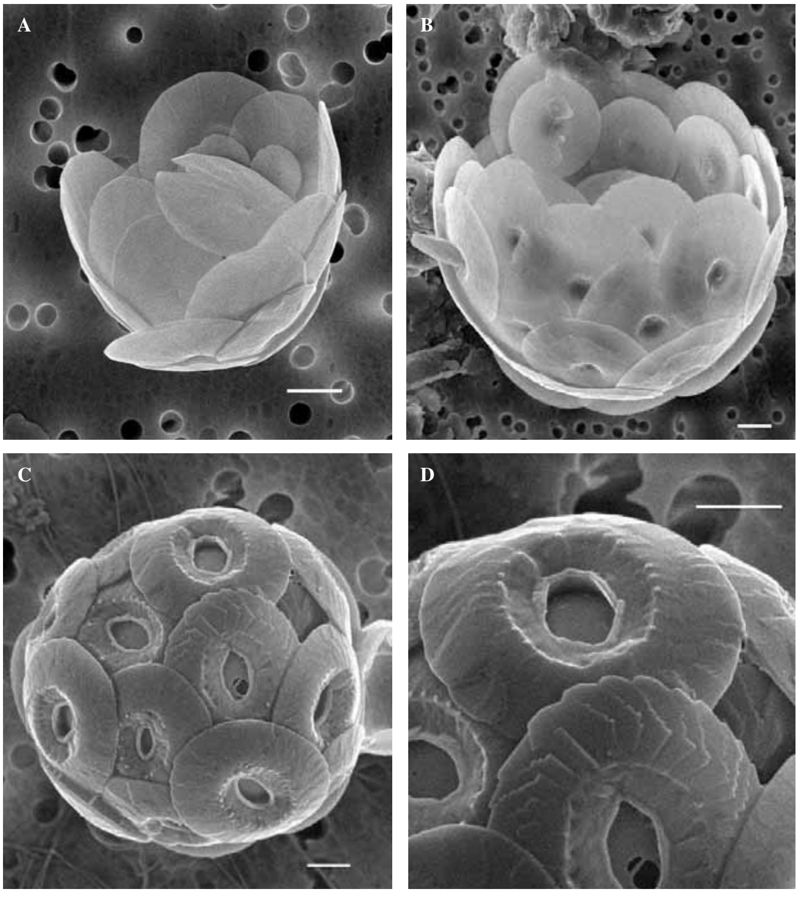

FIG. 63. – **A**, ***Oolithotus antillarum*** (Cohen) Reinhardt, in Cohen *et* Reinhardt: collapsed coccosphere with two partially covered placoliths in proximal view showing the small eccentrically placed proximal shield [Fronts-96, 021, 90 m]. **B**, ***Oolithotus fragilis*** (Lohmann) Martini *et* 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.

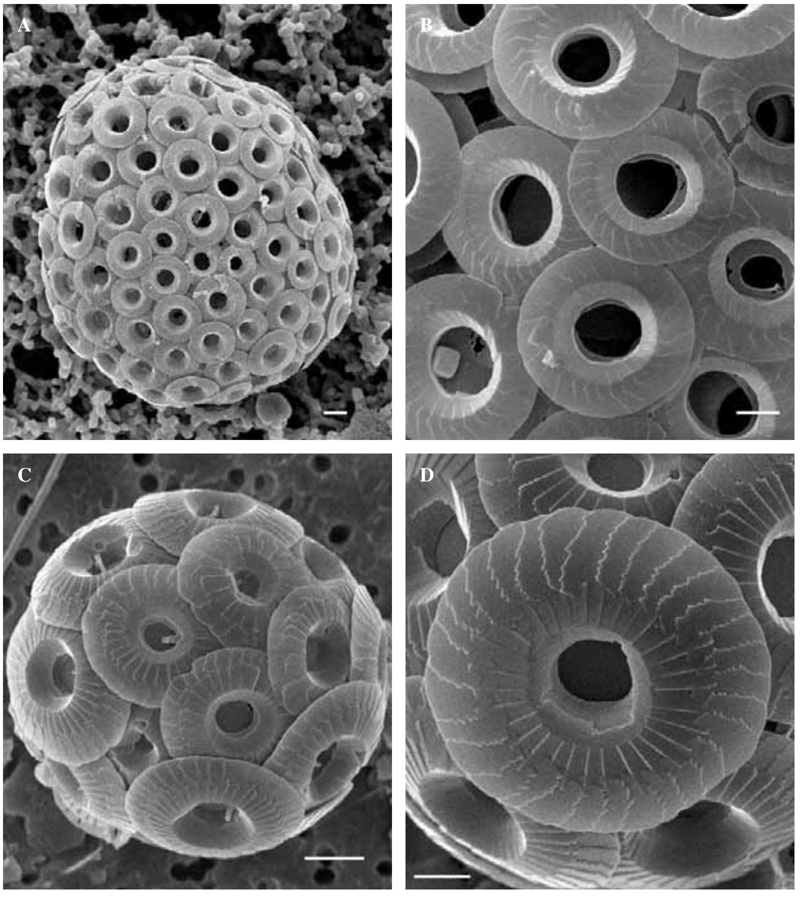

FIG. 64. – A-B, ***Umbilicosphaera sibogae*** var. ***sibogae*** (Weber-van Bosse) Gaarder: **A**, complete coccophere [Hivern-99, 25, surface]; **B**, detail with placoliths showing a distal shield slightly smaller than the proximal shield [Hivern-99, 25, 60 m]. C-D, ***Umbilicosphaera sibogae*** var. ***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.

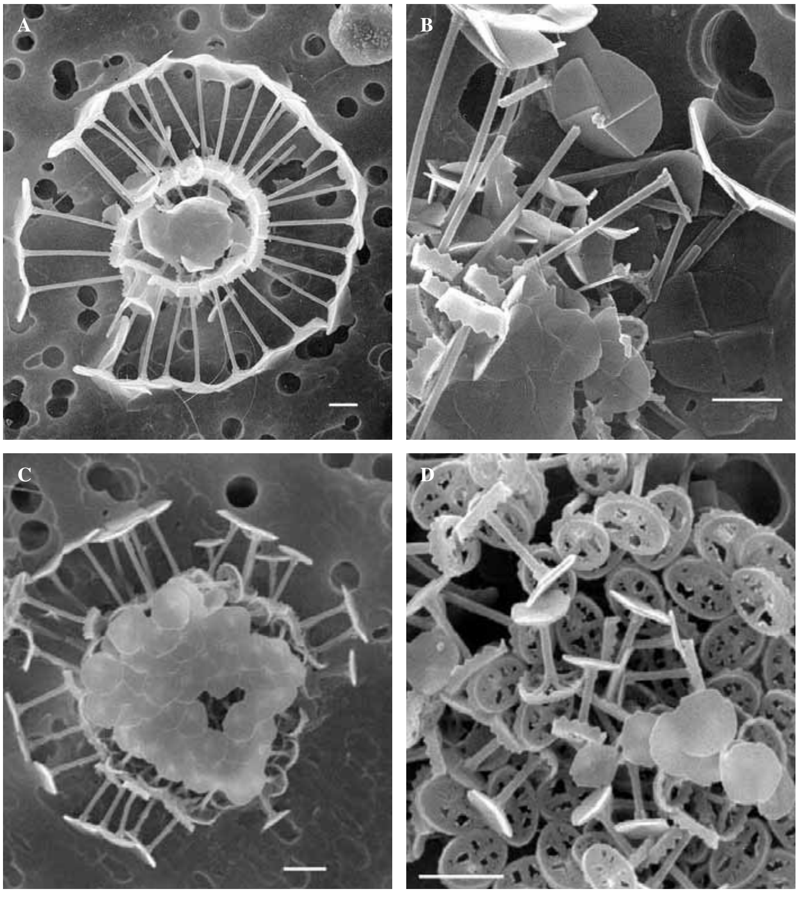

FIG. 65. – ***Papposphaera lepida*** Tangen: **A**, complete coccosphere, slightly collapsed [Meso-96, D6, 70 m]; **B**, detail with pappoliths: some basal parts with the crown-like outer rim, composed of pointed elements (lower left); distal structures, in distal view, showing the four flattened lobes (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.

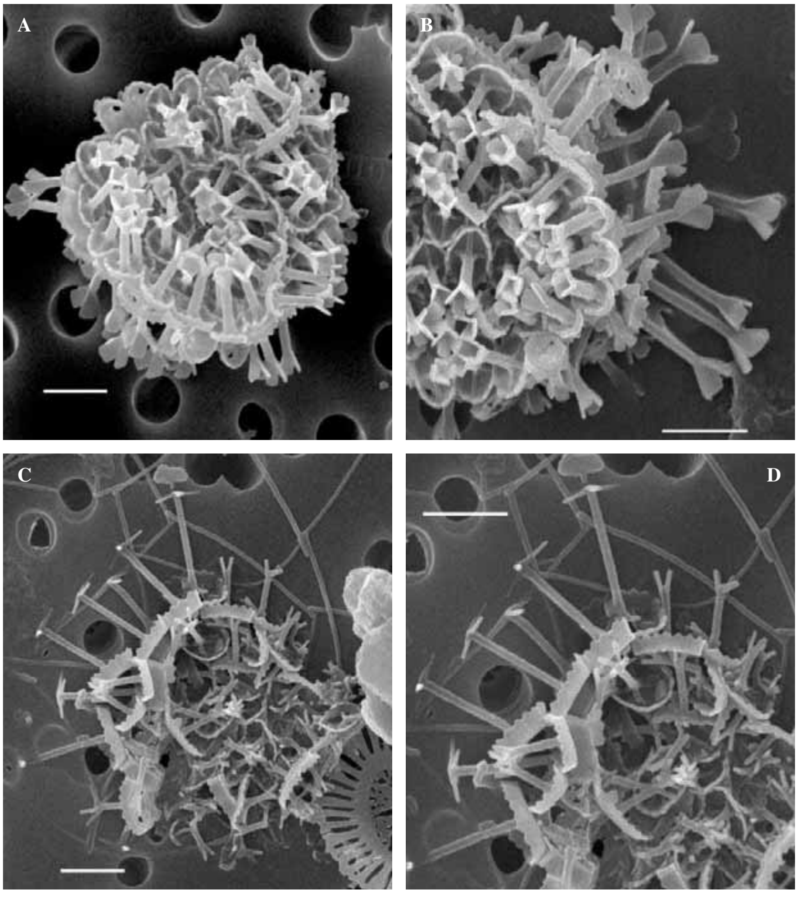

FIG. 66. – A-B, ***Papposphaera* sp. type 1**: **A**, complete coccosphere showing small varimorphic pappoliths [Meso-96, I4, 100 m]; **B**, detail with pappoliths which consist of a spine without collar and a distal structure composed of four small rectangular elements [Fans-1, 127, 75 m]. C-D, ***Papposphaera* 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.

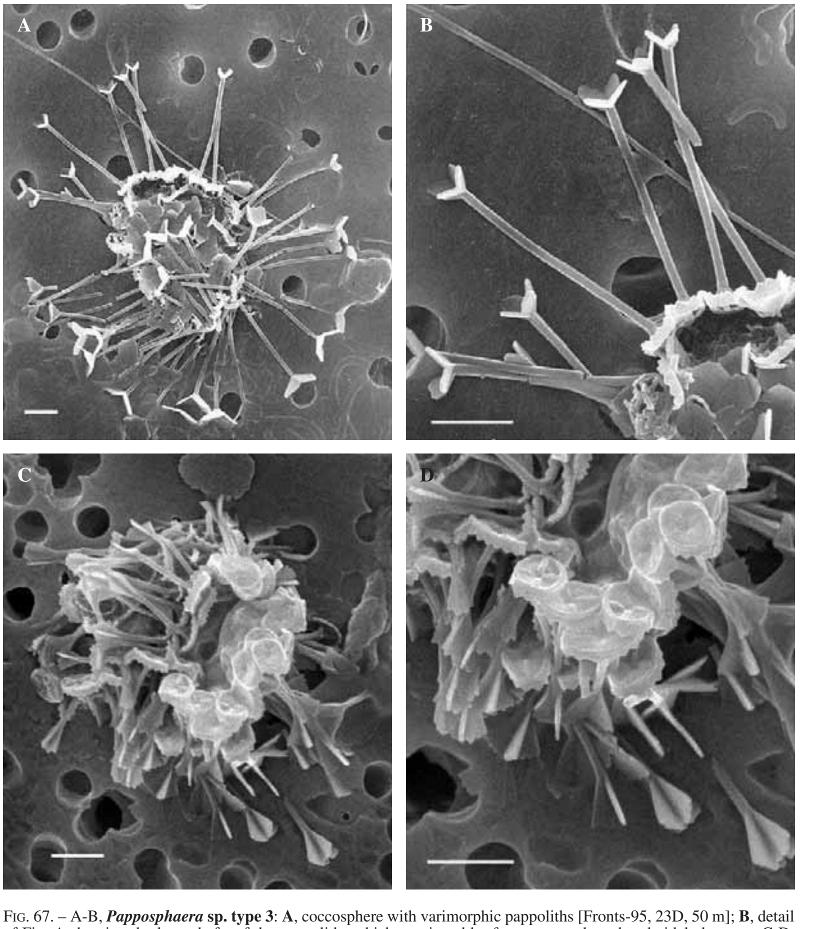

FIG. 67. – A-B, ***Papposphaera* sp. type 3**: **A**, coccosphere with varimorphic pappoliths [Fronts-95, 23D, 50 m]; **B**, detail of Fig. A showing the long shafts of the pappoliths which are tipped by four more or less rhomboidal elements. C-D, ***Papposphaera* sp. type 4**: **C**, coccosphere showing varimorphism [Fans-3, M11, 75 m]; **D**, detail of the Fig. C with pappoliths that show a spine tipped by four distally serrated triangular elements. Scale bars = 1 µm.

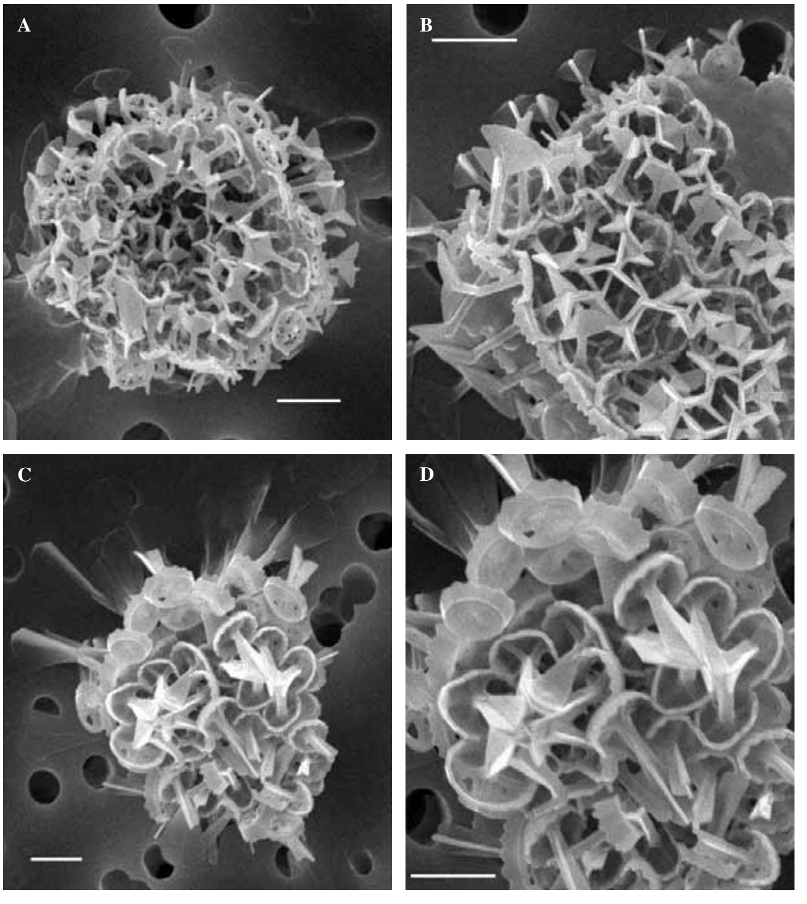

FIG. 68. – A-B, ***?Papposphaera* sp. type 5**: **A**, complete coccosphere [Fronts-96, 013, 75 m]; **B**, detail with varimorphic pappoliths, which have a propeller-like distal structure [Fans-1, 123, 75 m]. C-D, ***?Papposphaera* sp. type 6**: **C**, coccosphere with varimorphic coccoliths [Fans-1, 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

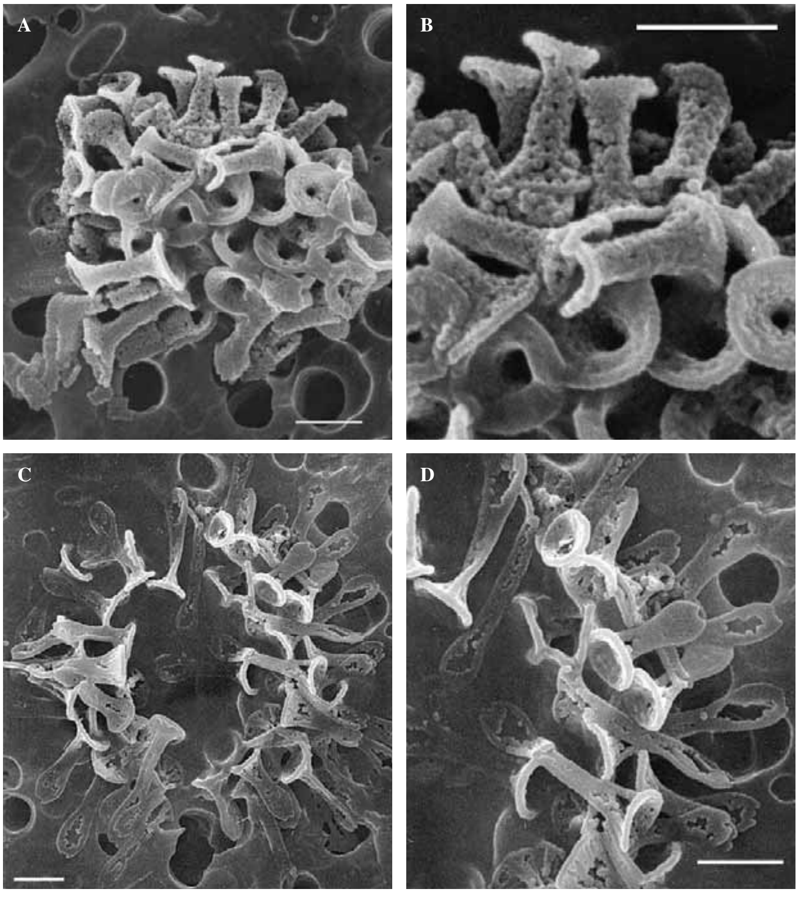

FIG. 69. – A-B, ***Papposphaera*** holococcolithophore (**"*Turrisphaera*") phase sp. type A**: **A**, collapsed coccosphere showing varimorphic holococcoliths [Meso-96, E8, 100 m]; **B**, detail of Fig. A showing apple-core shaped holococcoliths. C-D, ***Papposphaera*** holococcolithophore (**"*Turrisphaera*") 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.

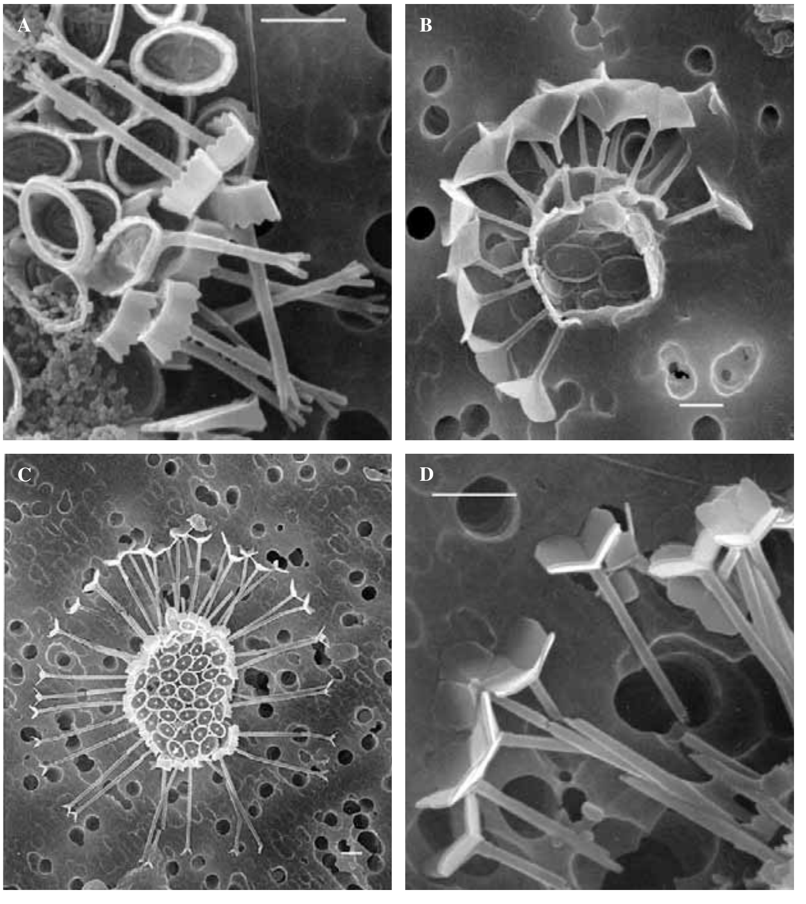

FIG. 70. – **A**, ***Pappomonas* sp. type 1**: detail showing some pappoliths with a long spine tipped by four small rods, and others without the central spine [Meso-96, D6, 100 m]. **B**, ***Pappomonas* sp. type 2**: coccosphere showing pappoliths with a very simple circular base, a long spine and a 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 pappoliths 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 pappoliths with a flower-like distal calyx. Scale bars = 1 µm.

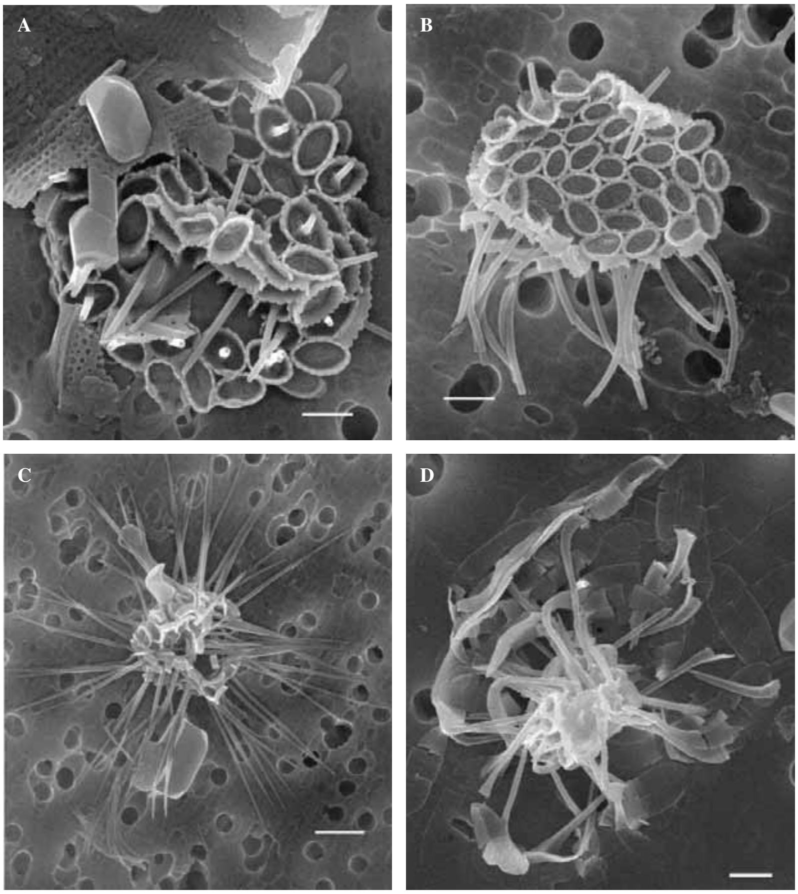

FIG. 71. – **A**, **?*Pappomonas* sp. type 4**: coccosphere showing three types of coccoliths; either lacking a spine, with a small spine, or with a long spine with no calyx [Fans-2, J07, 25 m]. **B**, **?*Pappomonas* sp. type 5**: coccosphere showing three types of coccoliths; lacking spine, with a 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.

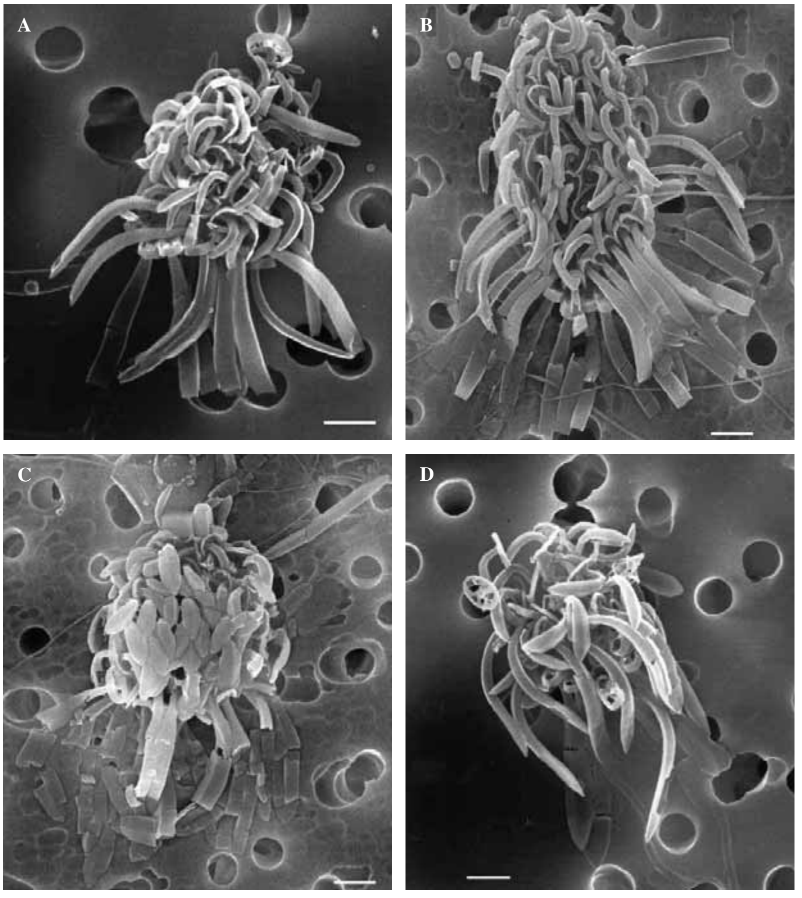

FIG. 72. – A-B, ***Picarola margalefii*** Cros *et* Estrada (in press): **A**, complete coccosphere [Fronts-95, 25W, 70 m]; **B**, large coccosphere with numerous body and circum-flagellar coccoliths [Meso-96, I6, 70 m]; C-D, ***Picarola* sp.**: **C**, coccosphere with coccoliths having the central process with pointed ends [Meso-96, I6, 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.

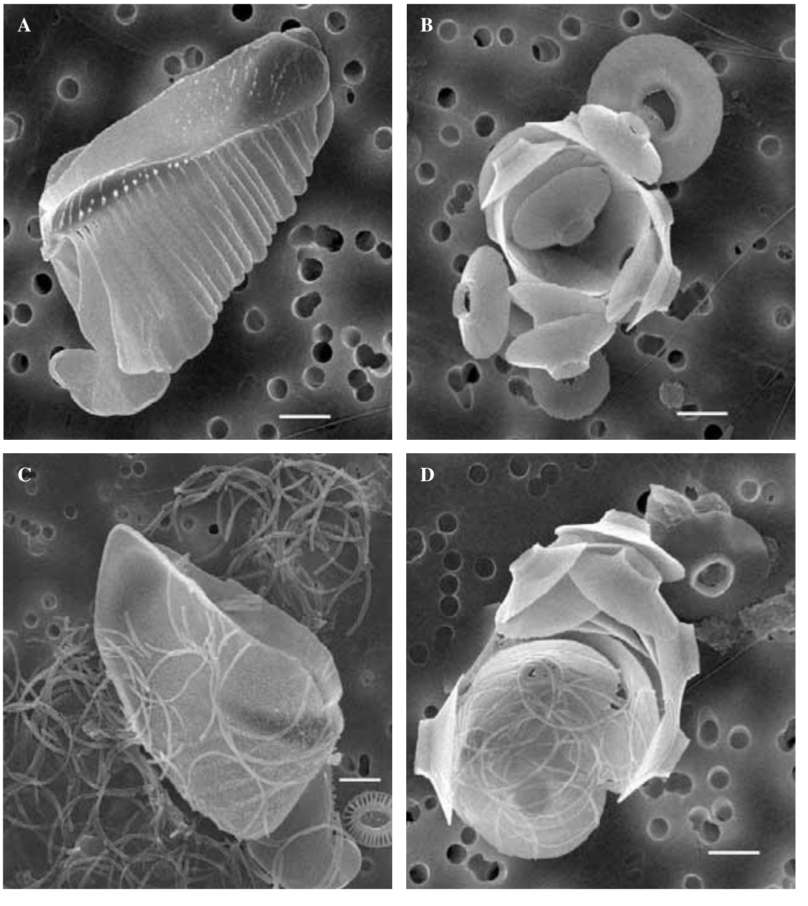

FIG. 73. – ***Ceratolithus cristatus* Kamptner**: **A**, detail of one ceratolith of the forma *'rostratus'* showing the 'rostrum' (lower left corner), the dentate keel next to the 'rostrum', and the smooth keel in the upper part of the figure [Fronts-96, 013, 30 m]; **B**, collapsed coccosphere of the 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 coccosphere of the former *N. coccolithomorpha* coccoliths [Fronts-96, 013, 10 m]. Scale bars = 2 µm.

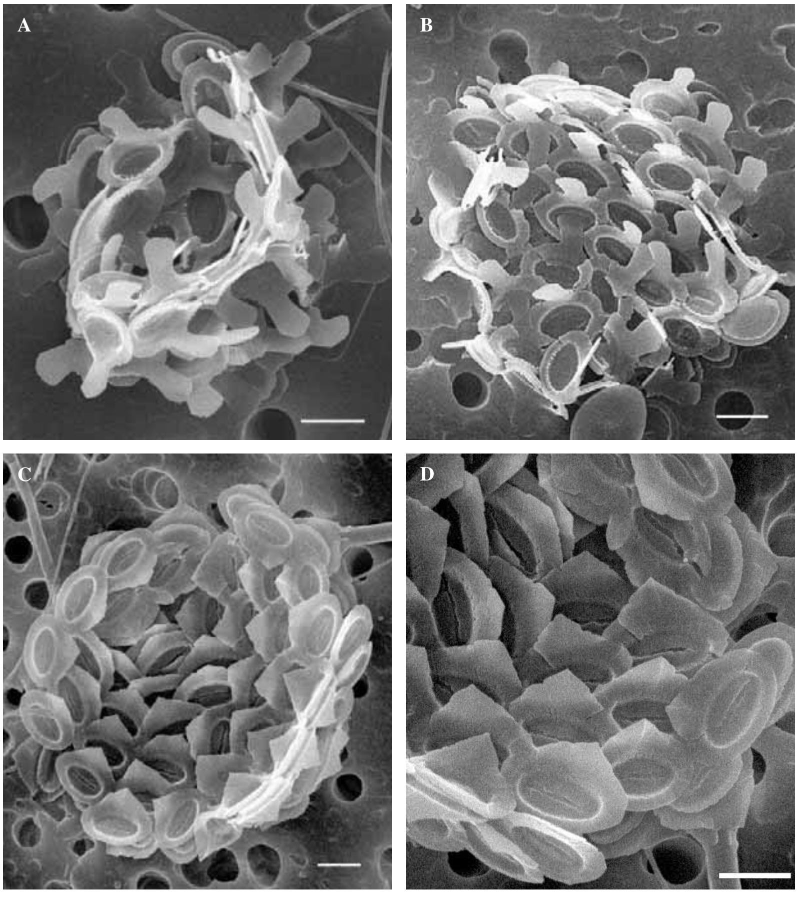

FIG. 74. – A-B, ***Alisphaera capulata*** Heimdal, in Heimdal *et* Gaarder: **A**, collapsed coccosphere showing coccoliths with a characteristic extension [Fronts-96, 013, 60 m]; **B**, coccoliths with a base plate filling the central area and a characteristic sinistrally inclined extension of the wider flange [Meso-96, A3, 40 m]. C-D, ***Alisphaera extenta*** 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.

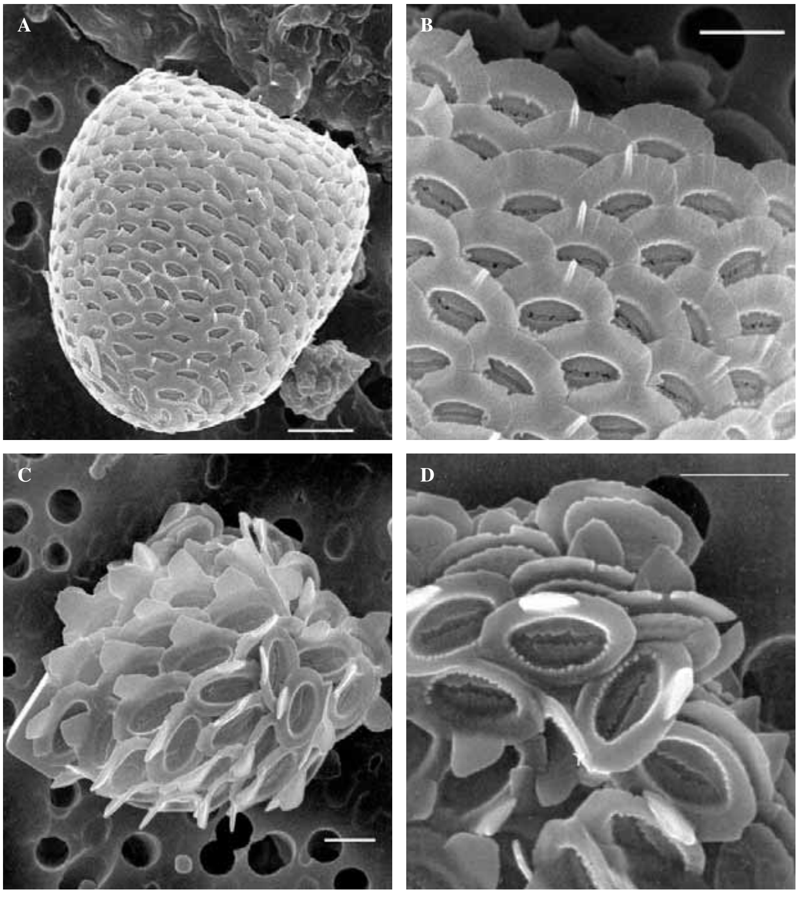

FIG. 75. – A-B, ***Alisphaera pinnigera*** Kleijne *et al.*: **A**, complete coccosphere with small coccoliths [Meso-96, E 3/4, 70 m]; **B**, detail showing coccoliths with a longitudinal fissure in the central area; some of these coccoliths show a characteristic small flat, triangular protrusion [Fronts-96, 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.

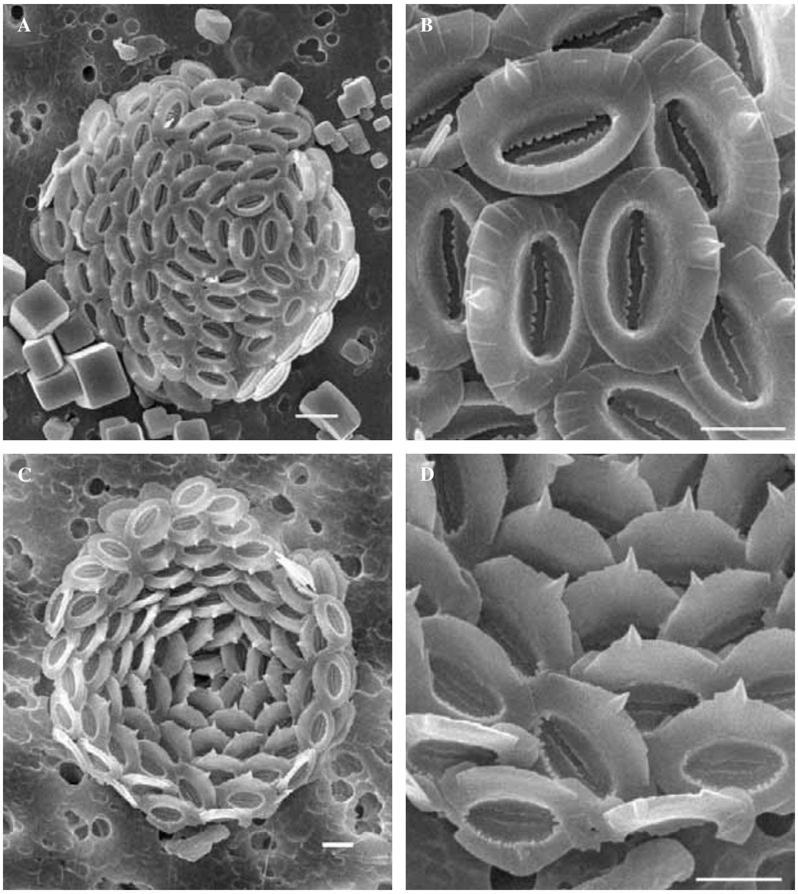

FIG. 76. – A-B, ***Alisphaera unicornis*** Okada *et* McIntyre: **A**, complete coccosphere showing coccoliths with a pointed protrusion [Hivern-99, 25, 60 m]; **B**, detail of Fig. A showing coccoliths with a longitudinal irregularly shaped fissure and a pointed horn-like protrusion on the wider distal 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.

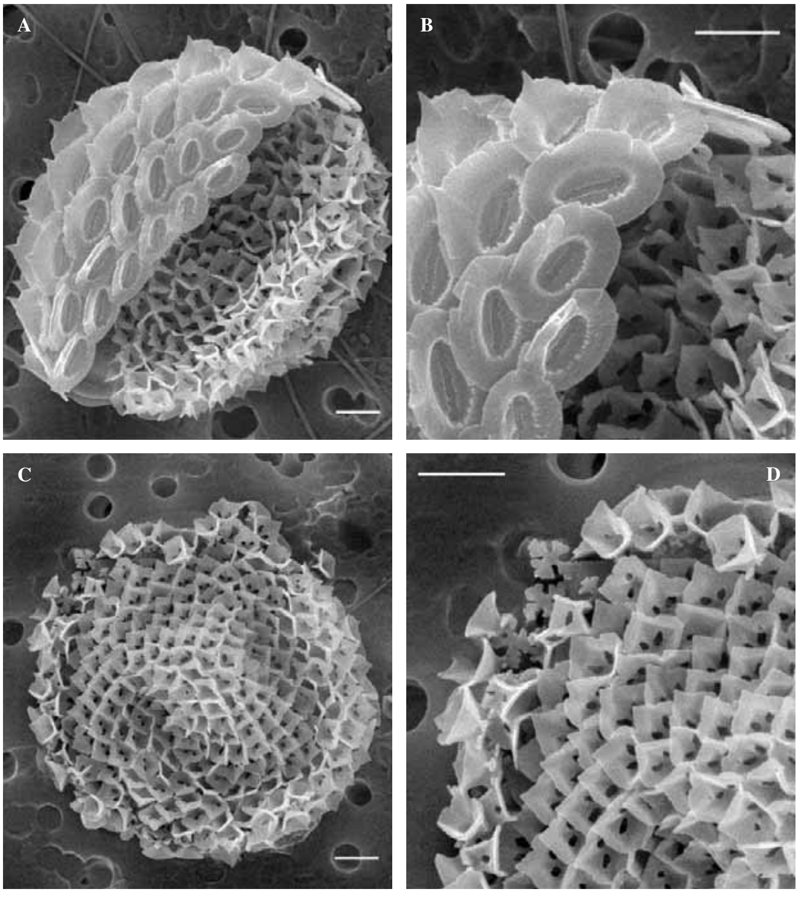

FIG. 77. – ***Alisphaera gaudii*** and ***Polycrater* sp.** (with holes, reminiscent of Gaudí's architecture): **A**, coccosphere consisting of a combination of *Alisphaera gaudii* (Figs. 76 C and D) at upper left, and coccoliths of the form *Polycrater* sp. (with holes, reminiscent of Gaudí's architecture) at lower right [Fans-3, M11, 5 m]; **B**, detail of Fig. A; **C**, coccosphere of *Polycrater* sp. (with holes, reminiscent of Gaudí'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 Gaudí architecture); the sepal-like proximal side has the form of a very adorned cross (upper left). Scale bars = 1 µm.

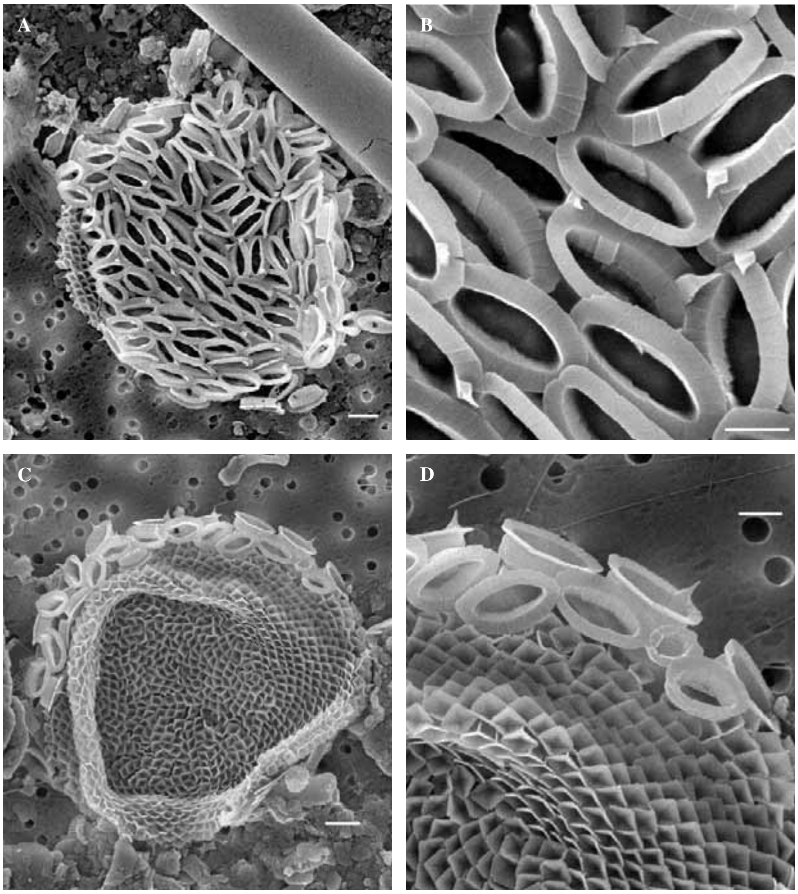

FIG. 78. – ***Canistrolithus* sp. 1** and ***Polycrater galapagensis* var. A** (with nodes) combination: **A**, coccosphere of *Canistrolithus* sp. 1 with some detached coccoliths on the filter (lower right) in proximal and lateral view; to the left of the coccosphere there are several *Polycrater* coccoliths [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.

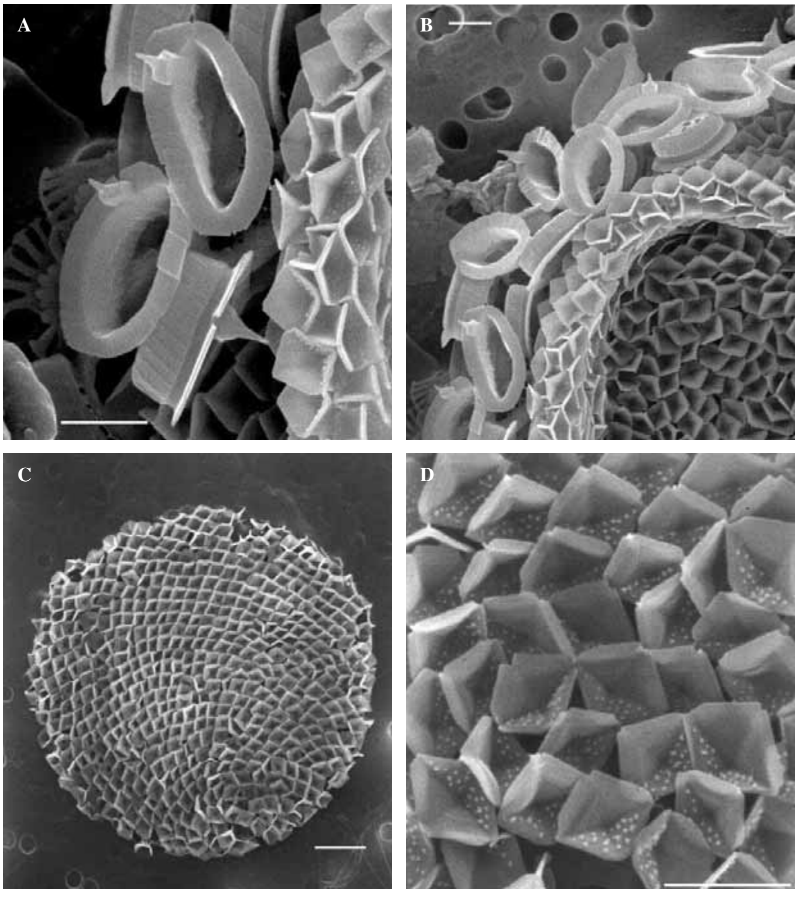

FIG. 79. – A-B, ***Canistrolithus* sp. 1** and ***Polycrater galapagensis* var. A** (with nodes) combination: **A**, detail of Fig. 78C showing three coccoliths of *Canistrolithus* with a robust spine and the coccoliths of *Polycrater* with characteristic nodes on the smaller petal-like side; **B**, 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.

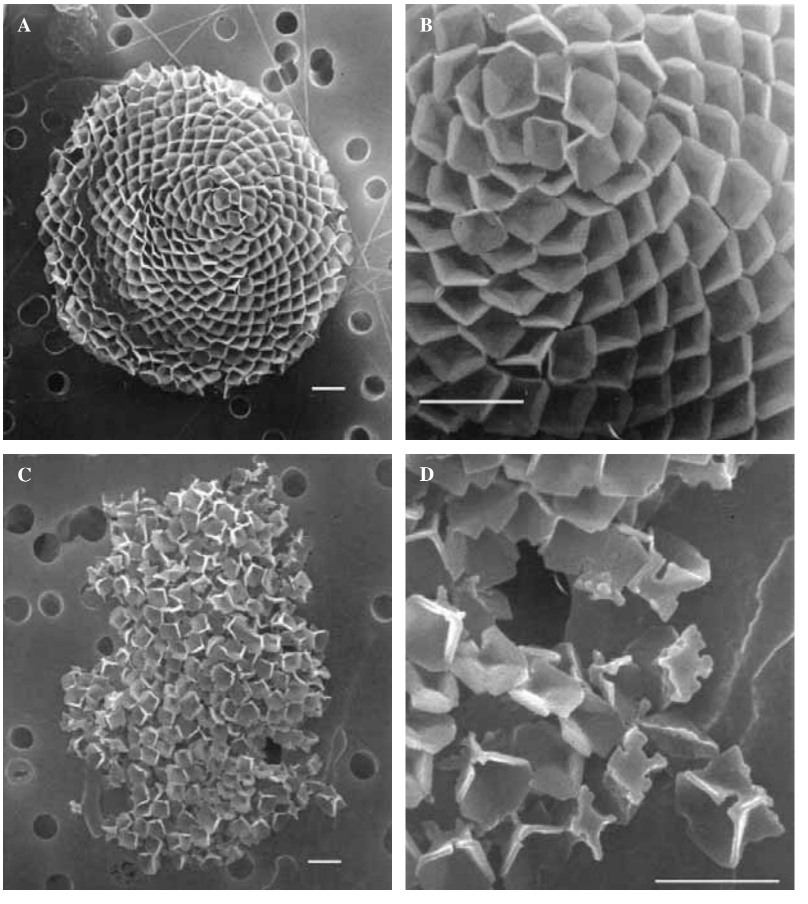

FIG. 80. – A-B, ***Polycrater galapagensis*** Manton *et* Oates: **A**, complete coccosphere with the small coccoliths arranged in slightly curved rows [Meso-95, 015, surface]; **B**, detail of Fig. A showing the squared bowl-shaped coccoliths which usually have been called nannoliths due to their unusual 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.

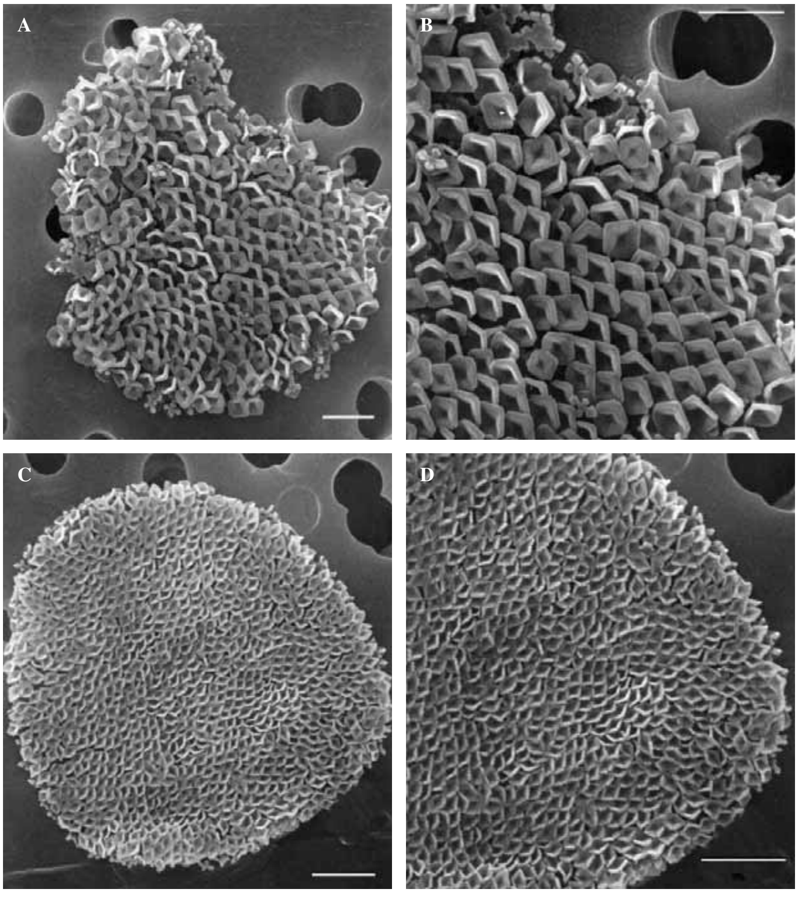

FIG. 81. – A-B, ***Polycrater* sp.** (with lip-like borders): **A**, collapsed coccosphere showing small coccoliths with rounded borders on the distal flange [Fronts-95, 24W, 5 m]; **B**, detail of Fig. A showing the bent borders of the distal flange which resembles a pair of lips; the proximal sepal-like 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.

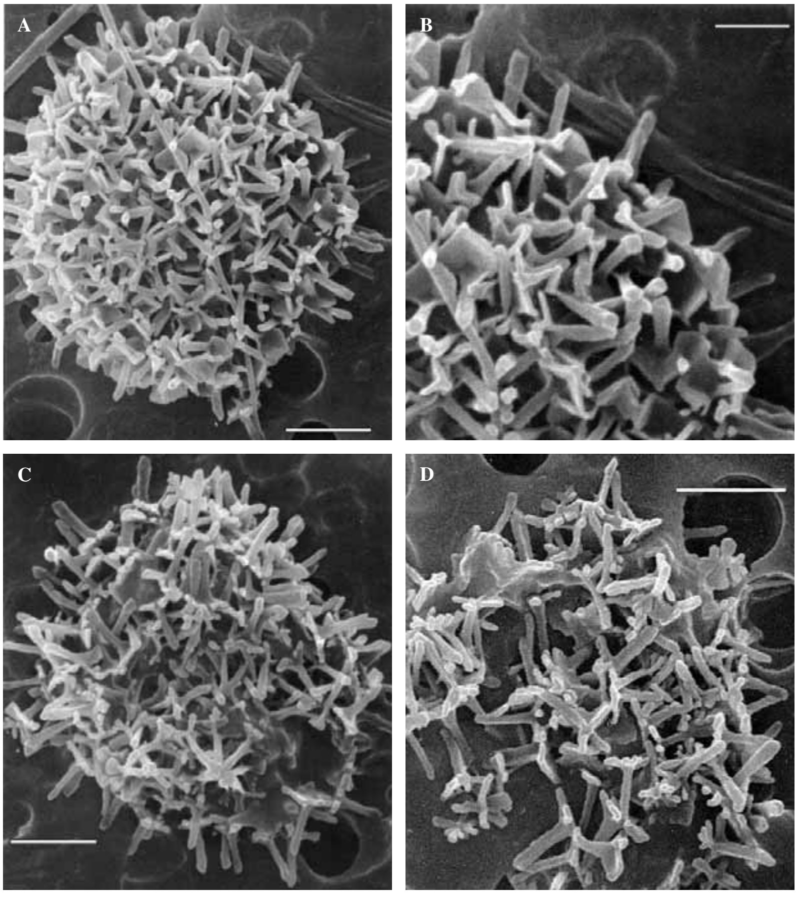

FIG. 82. – A-B, ***Polycrater* sp.** (spinous, two petal-like structures very modified): **A**, coccosphere with a spiny shape like a sea urchin due to the very modified shape of the coccoliths [Meso-96, E3/4, 70 m]; **B**, detail of Fig. A showing the coccoliths; half of the petal-like (distal) part 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, two others absent): **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.

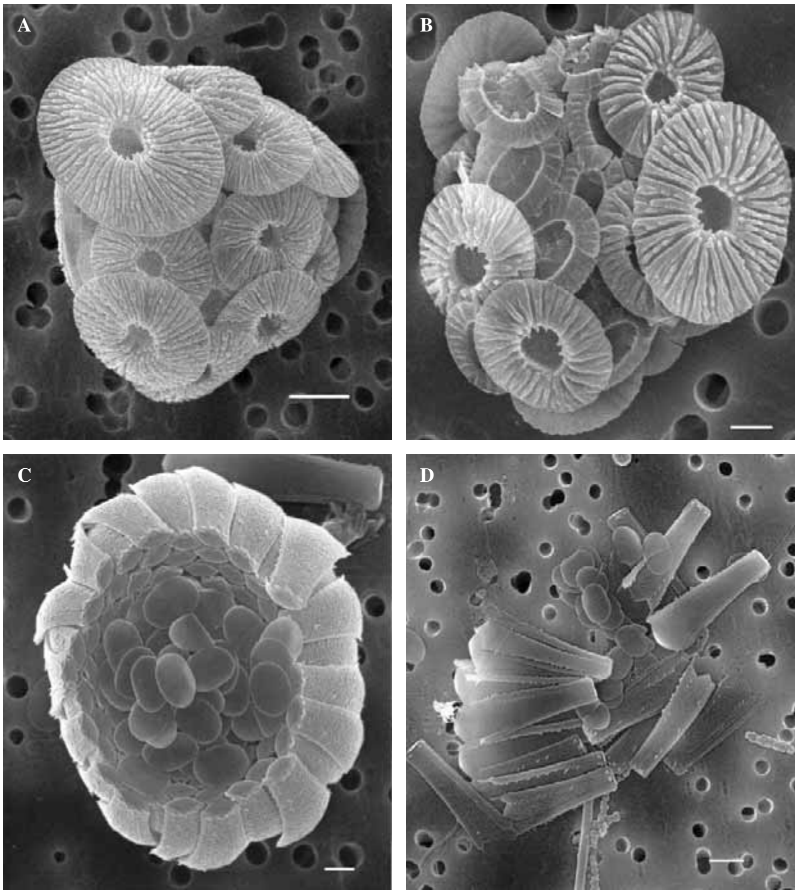

FIG. 83. – A-B, ***Umbellosphaera tenuis*** Paasche in Markali *et* Paasche, emend. Gaarder in Heimdal *et* Gaarder: **A**, complete coccosphere showing macrococcoliths [Fronts-96, 021, 10 m]; **B**, coccosphere showing macrococcoliths and micrococcoliths which are smaller and have a large elliptical 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**, 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.

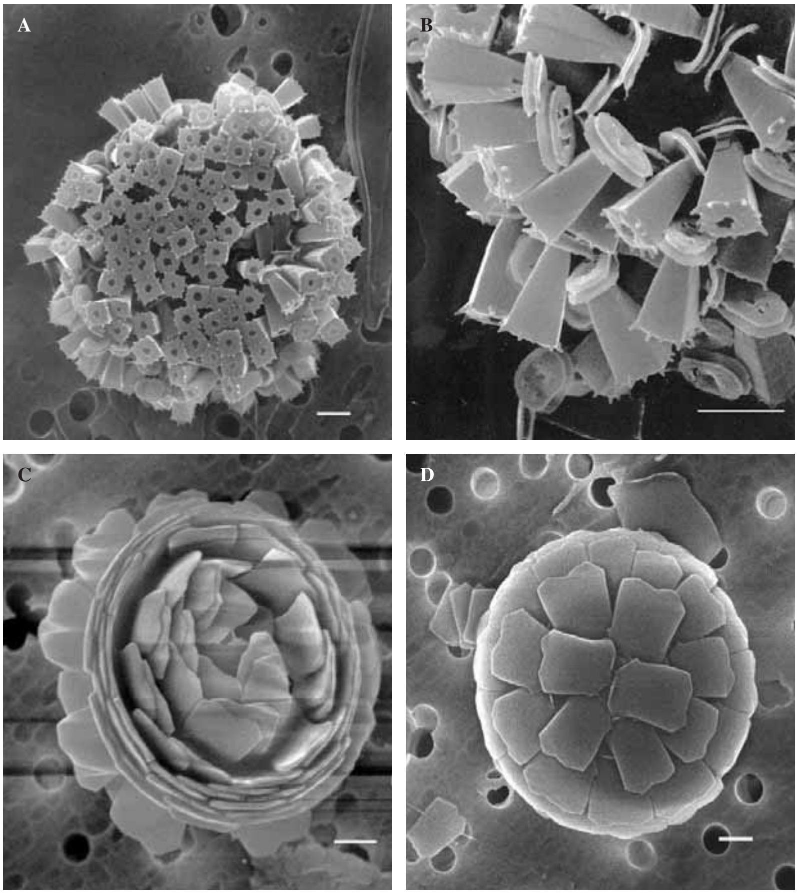

FIG. 84. – A-B, ***Turrilithus latericioides*** Jordan *et al*.: **A**, complete coccosphere with the tower-shaped coccoliths [Meso-96, F2, 100 m]; **B**, detail showing elliptical proximal base of the coccoliths and the characteristic hollow, tower-shaped appendix with lateral spines on the square distal 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.

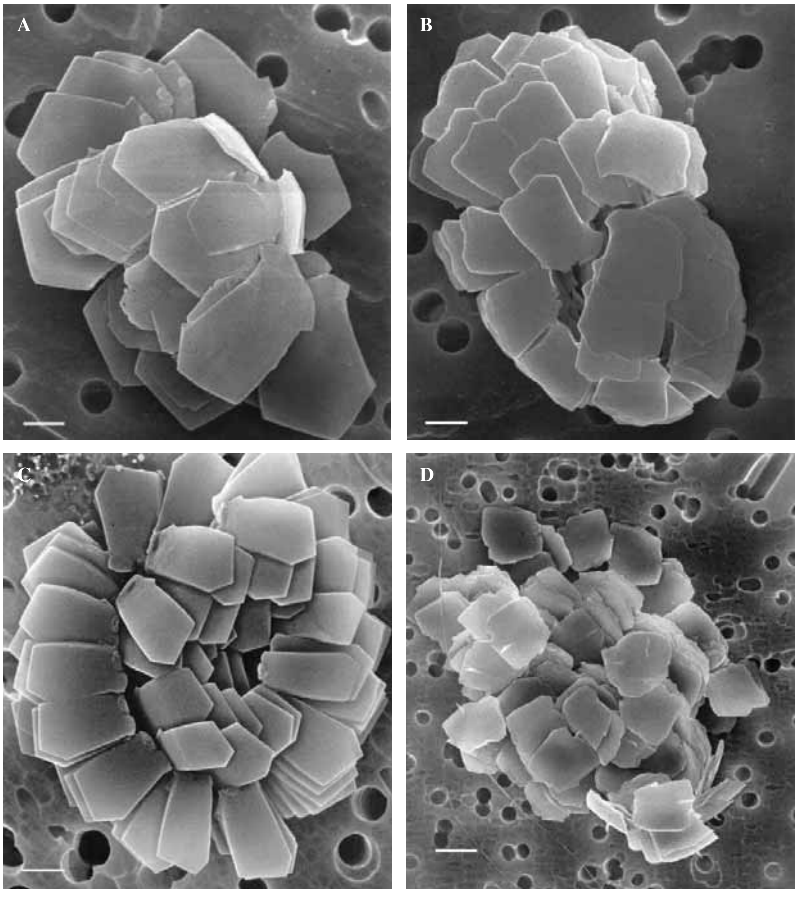

FIG. 85. – A-C, ***Florisphaera profunda*** Okada *et* Honjo: **A**, collapsed coccosphere of the *elongata* type [Meso-95, 119, 70 m]; **B**, collapsed coccosphere of the *profunda* type [Fronts-95, 23D, 80 m]; **C**, coccosphere of an *elongata*-related type showing very straight sides and a characteristic basal part with a conspicuous peg-like proximal structure [Meso-96, I3, 100 m]. **D**, ***Florisphaera*** **?sp.**: collapsed coccosphere with more or less square coccoliths with irregular borders and a notable distal spine [Meso-96, D8, 70 m]. Scale bars: A, B, C = 1 µm; D = 2 µm.

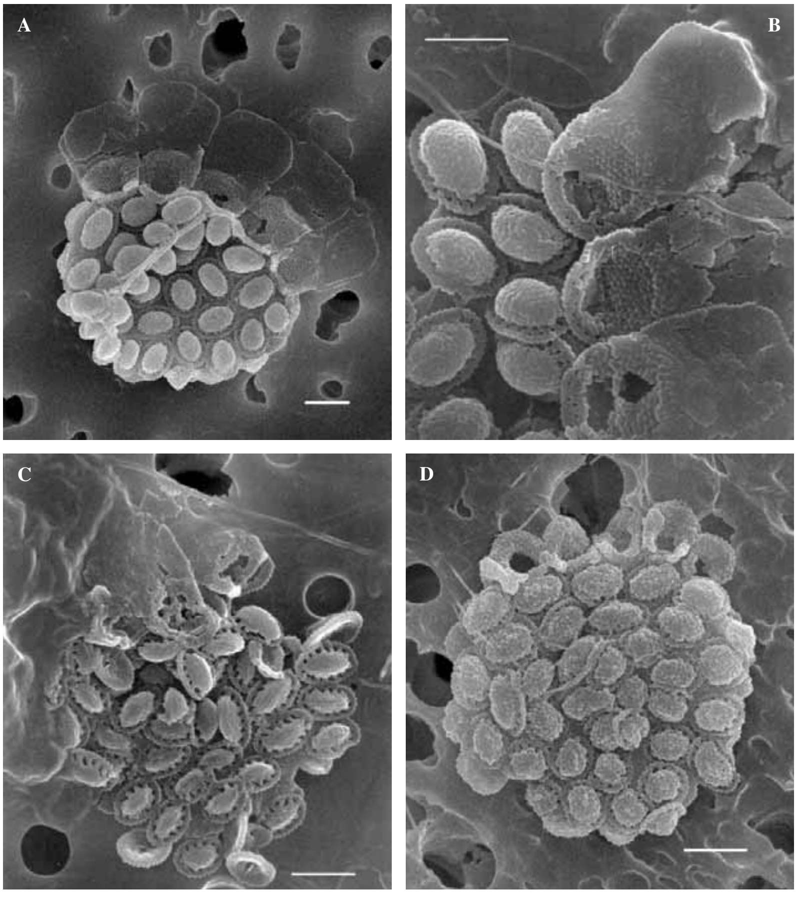

FIG. 86. – A-B, ***Anthosphaera fragaria*** Kamptner, emend. Kleijne: **A**, complete coccosphere with dimorphic coccoliths [Fans-3, M11, 5 m]; **B**, detail with calyptrolith-like body coccoliths (left) and three fragarioliths showing the three crystallite-wide proximal rim and the very large single-layered 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.

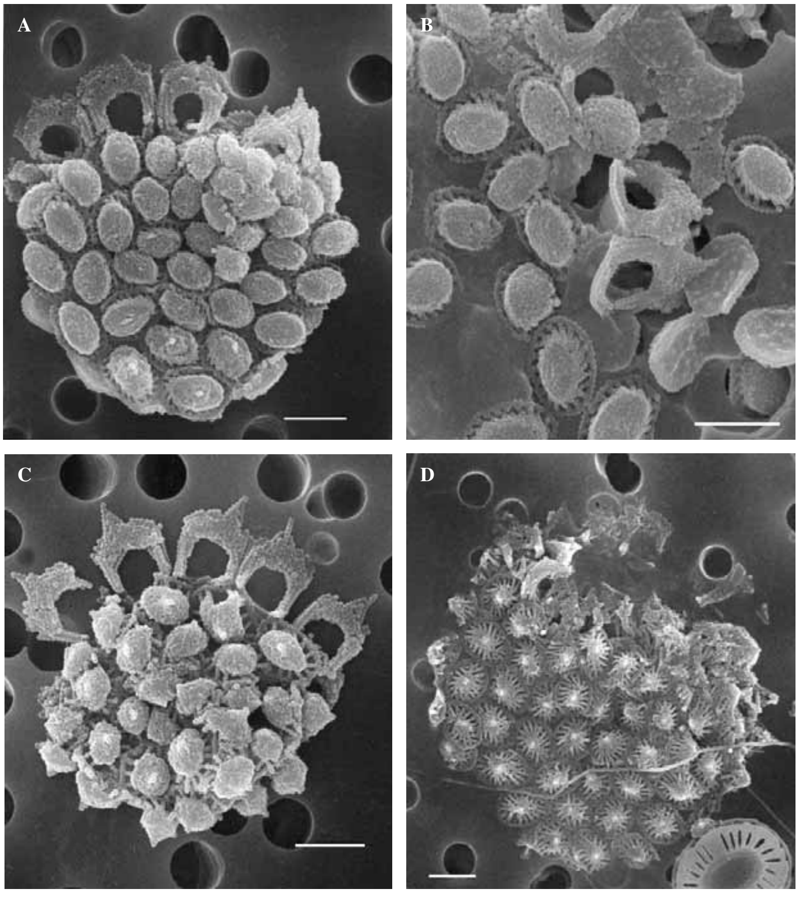

FIG. 87. – A-B, ***Anthosphaera periperforata*** Kleijne **Type 1**: **A**, complete dimorphic coccosphere showing fragarioliths in apical position and body coccoliths with and without small distal spine (the antapical coccoliths have a distal spine) [Meso-96, E3/4, 40 m]; **B**, detail with body coccoliths 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 coccosphere 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**: coccosphere with very perforated coccoliths [Meso-96, E3/4, 40 m]. Scale bars = 1 µm.

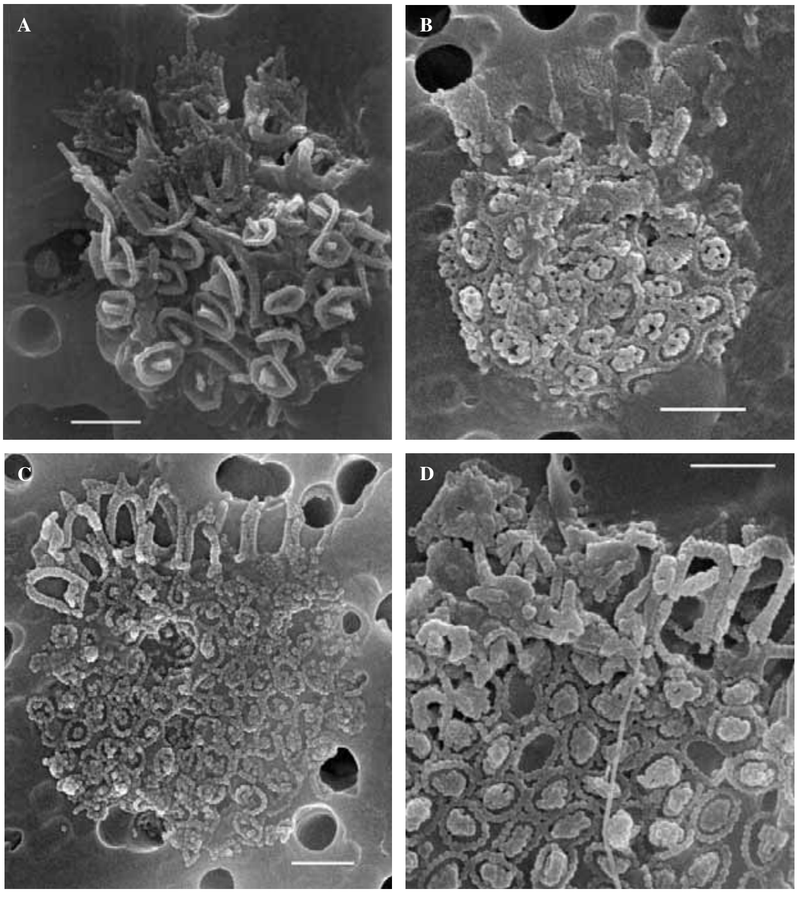

FIG. 88. – **A**, ***Anthosphaera* sp. type A** (origami art): coccosphere with dimorphic coccoliths having very ornamented apical fragarioliths and body coccoliths which resemble origami paper boats [Fronts-95, 23D, 50 m]. **B**, ***Anthosphaera* sp. type B**: complete coccosphere showing fragarioliths 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**, coccosphere 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.

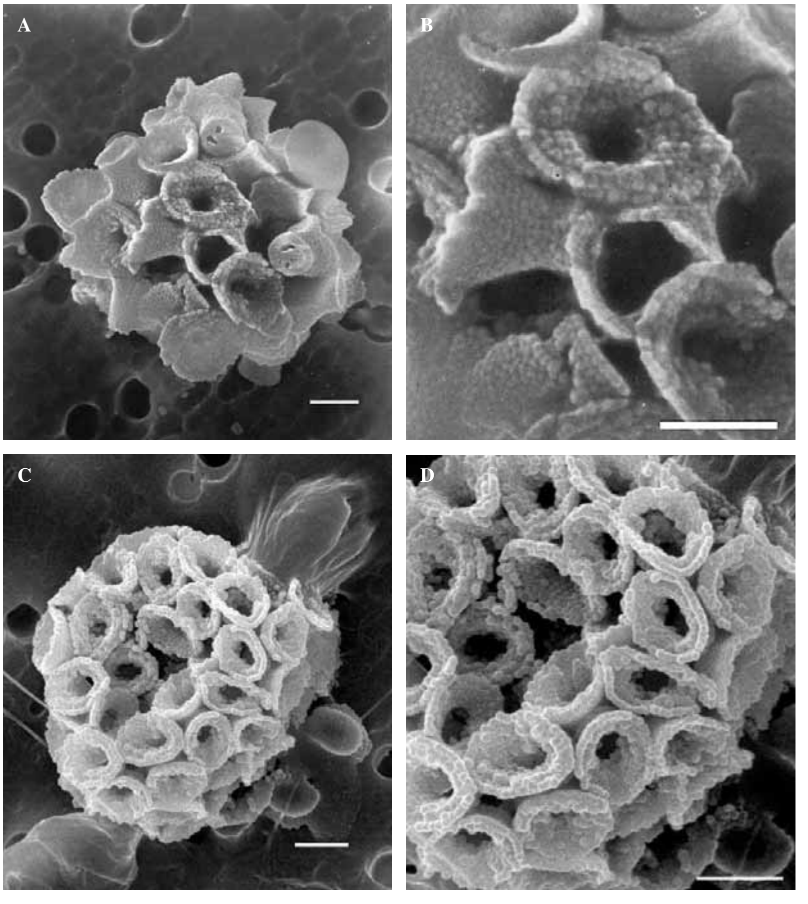

FIG. 89. – A-B, ***Calicasphaera concava*** Kleijne: **A**, coccosphere with calicaliths in distal and proximal view [Fronts-96, 039, 40 m]; **B**, detail of Fig. A showing the concave wall of the calicaliths widening to form a broad distal opening. C-D, ***Calicasphaera blokii*** Kleijne: **C**, coccosphere 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.

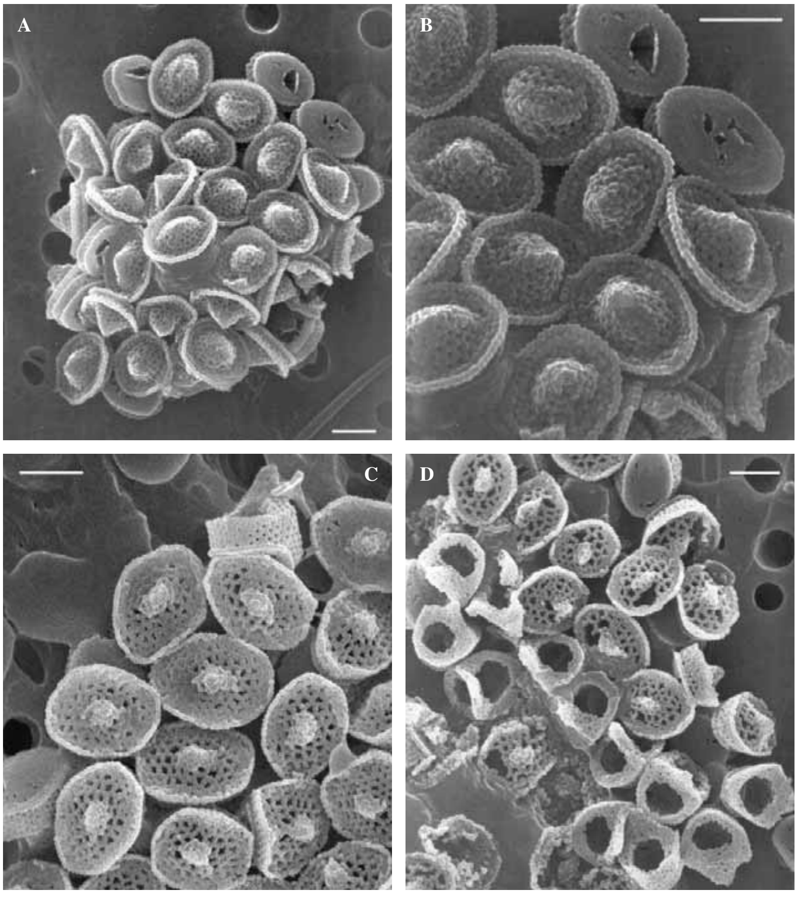

FIG. 90. – A-B, ***Calyptrolithina divergens*** (Halldal *et* Markali) Heimdal var. ***divergens***: **A**, coccosphere showing only the body calyptroliths [Fronts-95, 23D, 50 m]; **B**, detail of Fig. A showing body calyptroliths with a distally widening tube forming the protruding rim, and the distal 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.

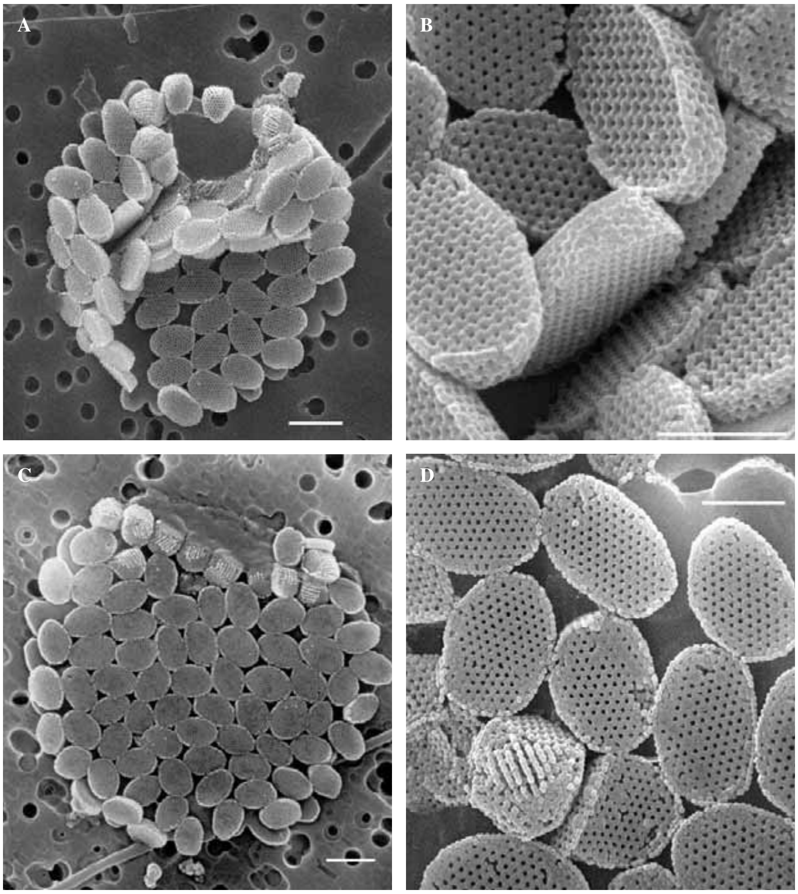

FIG. 91. – ***Calyptrolithophora papillifera*** (Halldal) Heimdal in Heimdal *et* Gaarder: **A**, coccosphere showing a notable flagellar opening [Fans-1, 100, 25 m]; **B**, detail of Fig. A showing the hexagonal arrangement of crystallites in the body calyptroliths, which have a slightly protruding 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.

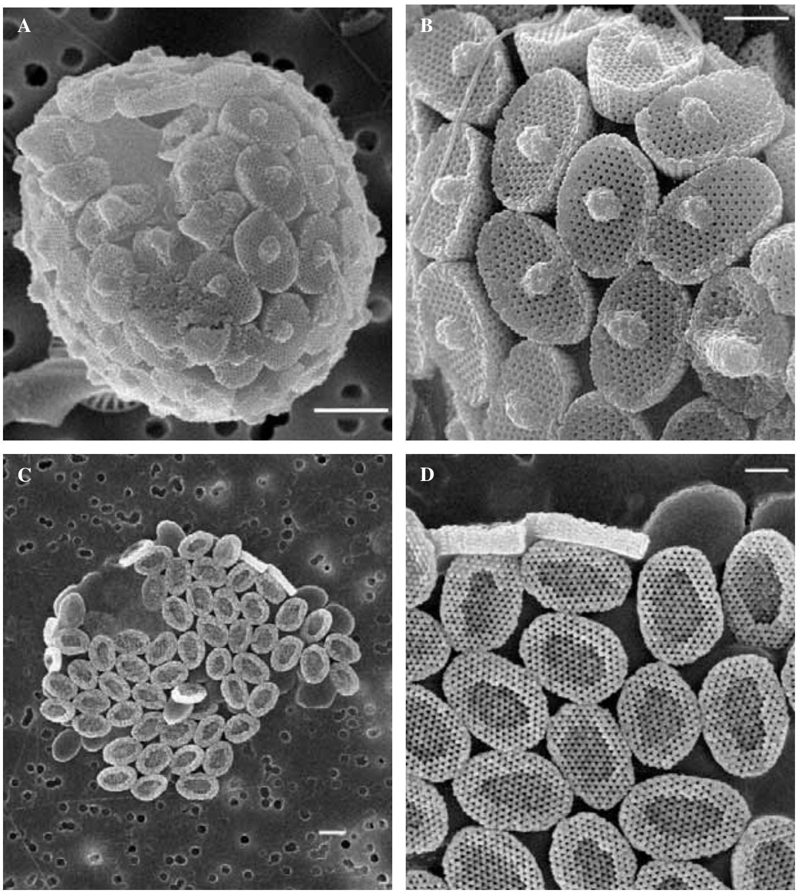

FIG. 92. – A-B, ***Calyptrolithophora gracillima*** (Kamptner) Heimdal: **A**, coccosphere showing a flagellar area surrounded by zygolith-like calyptroliths and body coccoliths which are calyptroliths [Fans-1, 100, 40 m]; **B**, detail with body calyptroliths having a straight, slightly protruding distal 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**, coccosphere 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.

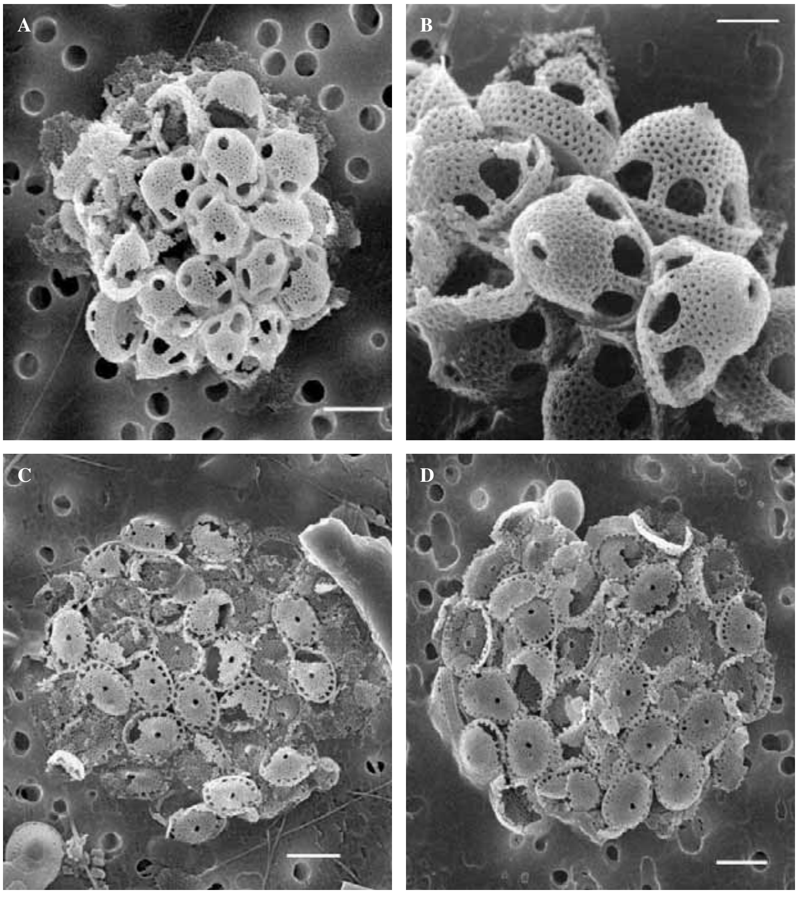

FIG. 93. – A-B, ***Calyptrosphaera heimdaliae*** R.E. Norris, orthog. emend. Jordan *et* Green: **A**, coccosphere with large dome-shaped calyptroliths with one pore at the top and typically seven at the base of the dome, next to the broad rim [Fronts-96, 013, 30 m]; **B**, detail of perforated calyptroliths having large lateral pores with a straight base and an arched top; the distal opening is bordered by a small protrusion [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.

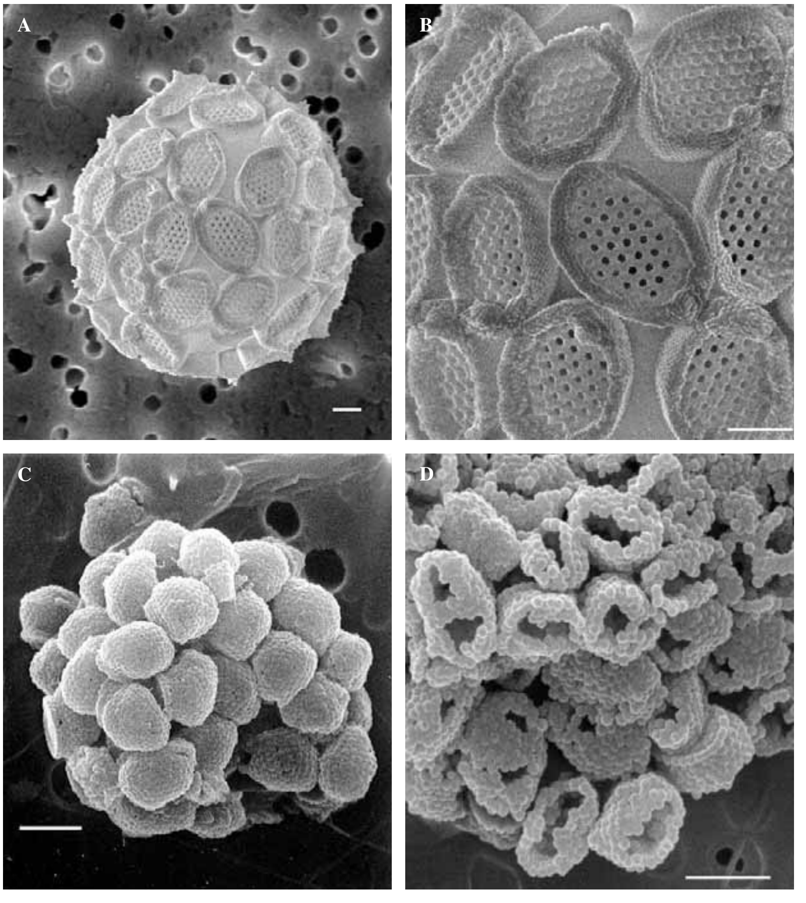

FIG. 94. – A-B, ***Calyptrosphaera dentata*** Kleijne: **A**, coccosphere with monomorphic coccoliths [Fans-3, K07, 25 m]; **B**, detail of Fig. A showing calyptroliths with a central area surface having six-sided regularly arranged perforations and a thick rim with a tooth-like protrusion. C-D, ***Calyptrosphaera 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.

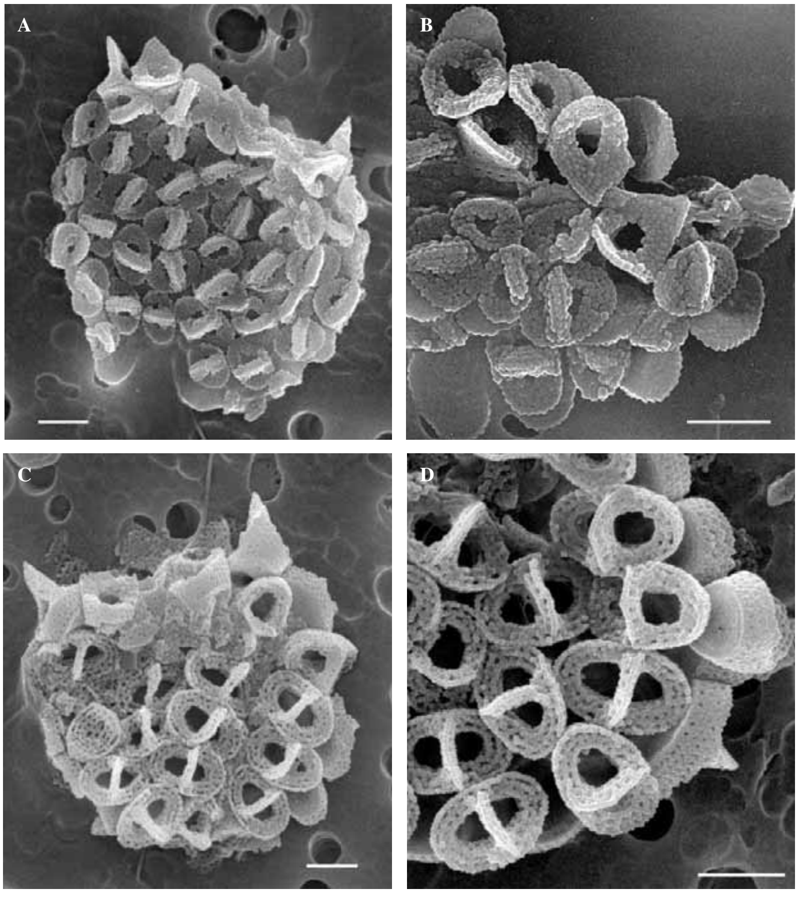

FIG. 95. – A-B, ***Corisphaera strigilis*** Gaarder: **A**, coccosphere with dimorphic coccoliths [Meso-96, G6, 5 m]; **B**, detail showing flat body coccoliths with thick bridge (lower) and circum-flagellar coccoliths with a leaf-like pointed extension (upper) [Fronts-95, 23D, 30 m]. C-D, ***Corisphaera tyrrheniensis*** Kleijne: **C**, coccosphere with several slightly disintegrated coccoliths; note the zygolith (centre left) which resembles the zygoliths of *Zygosphaera marsilii* (see *Z. marsilii* 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.

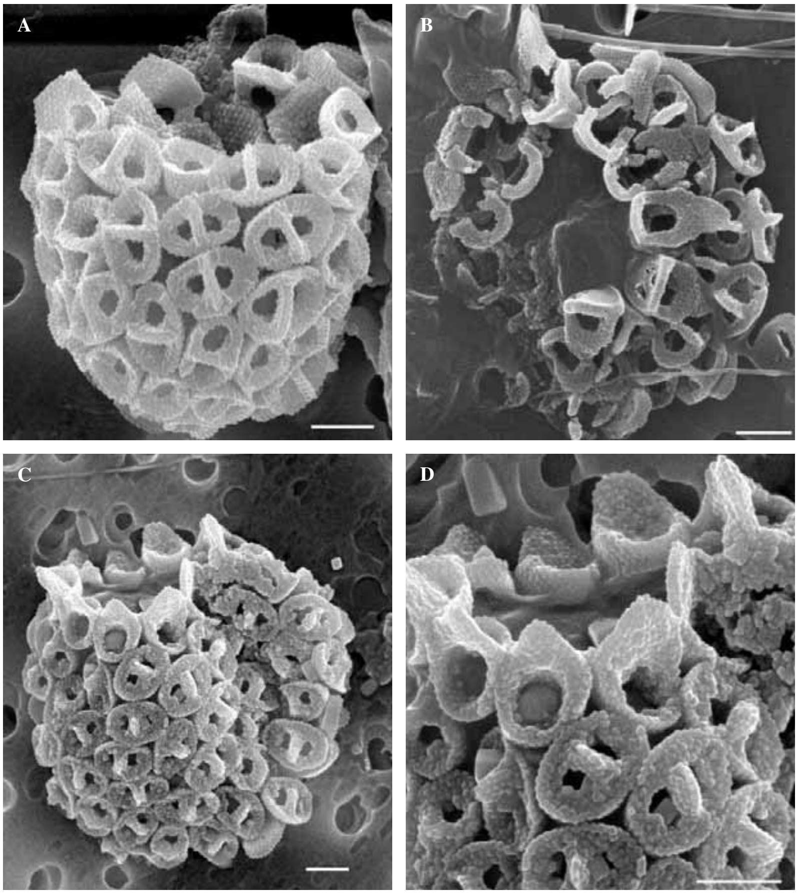

FIG. 96. – **A**, ***Corisphaera*** cf. ***gracilis***: coccosphere with dimorphic coccoliths [Fronts-96, 013, 30 m]. **B**, ***Corisphaera* sp.** (ornamented circum-flagellar coccoliths): collapsed coccosphere with dimorphic coccoliths; body zygoliths very low and flat, circum-flagellar coccoliths have 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 zygoliths 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.

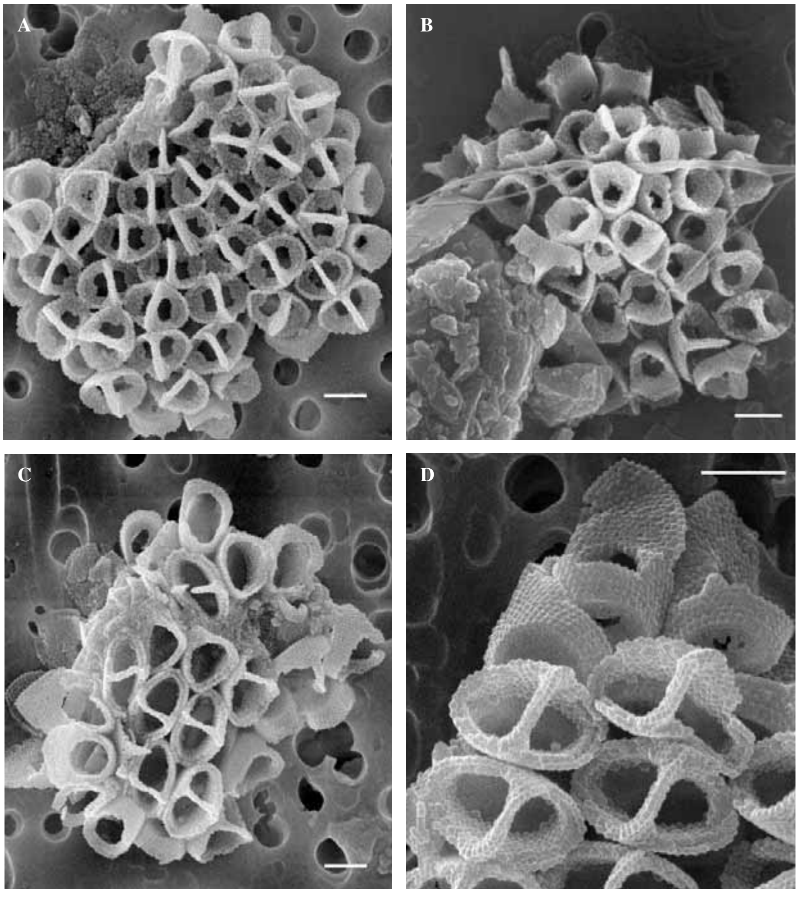

FIG. 97. – **A**, ***Corisphaera* sp.** (aff. type A of Kleijne, 1991, and *C. gracilis*): coccosphere with body zygoliths which have a well arranged distal rim of angular crystallites and a high and thin bridge spanning the wide central area [Meso-96, I4, 40 m]. **B**, ***Corisphaera* sp.** (body zygoliths 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, I4, 40 m]; **D**, detail showing the body zygoliths (bottom) and cicum-flagellar zygoliths (top) [Fans 1, 127, 25 m]. Scale bars = 1 µm.

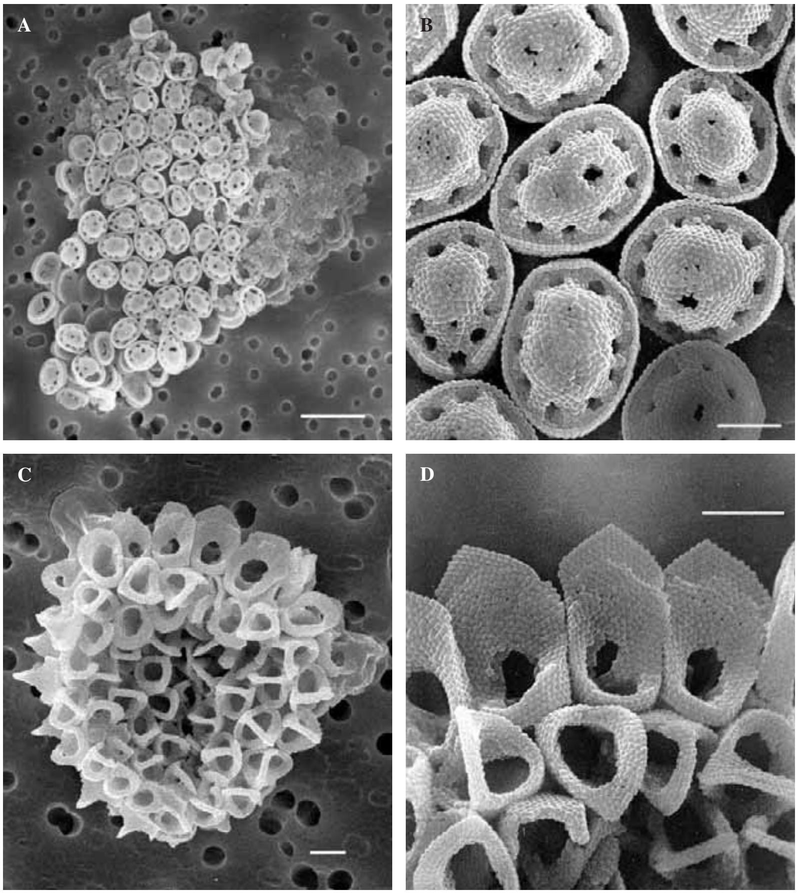

FIG. 98. – A-B, ***Daktylethra pirus*** (Kamptner) Norris: **A**, collapsed coccosphere showing calyptroliths with a vaulted distal protrusion and pores around the rim [Meso-95, 178, 40 m]; **B**, detail of Fig. A with calyptroliths in distal view showing a prominent rim, a vaulted central protrusion 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.

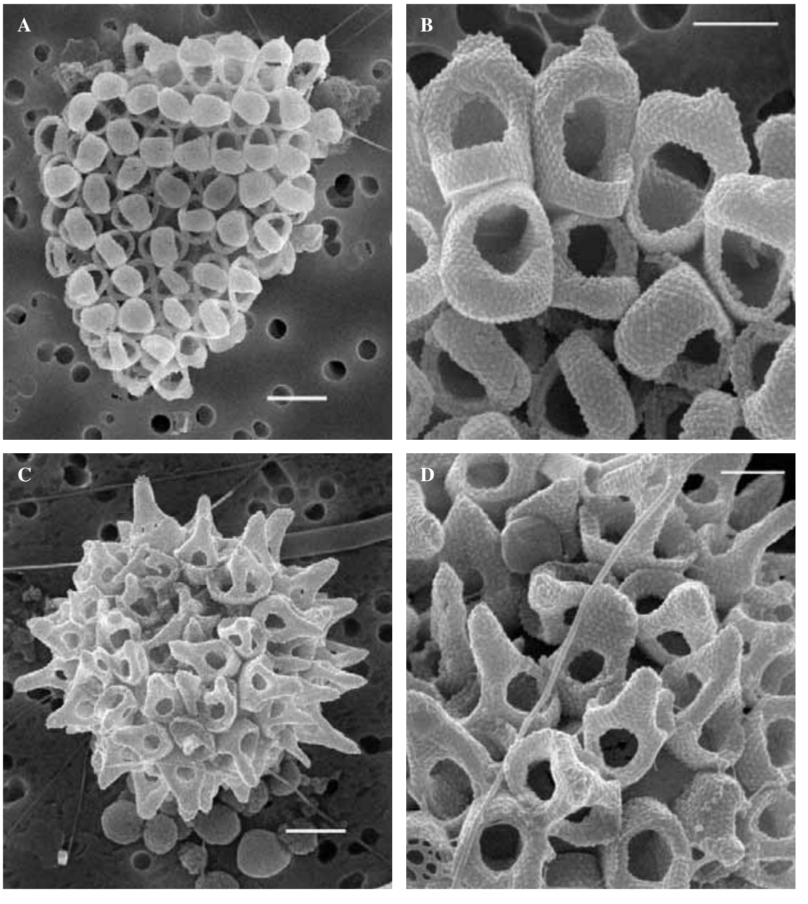

FIG. 99. – A-B, ***Homozygosphaera arethusae*** (Kamptner) Kleijne: **A**, complete coccosphere showing body zygoliths with broad bridges and apical circum-flagellar zygoliths with higher bridges adorned with a distal protrusion (upper middle) [Fans-1, 123, 5 m]; **B**, detail of body zygoliths (bottom) 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.

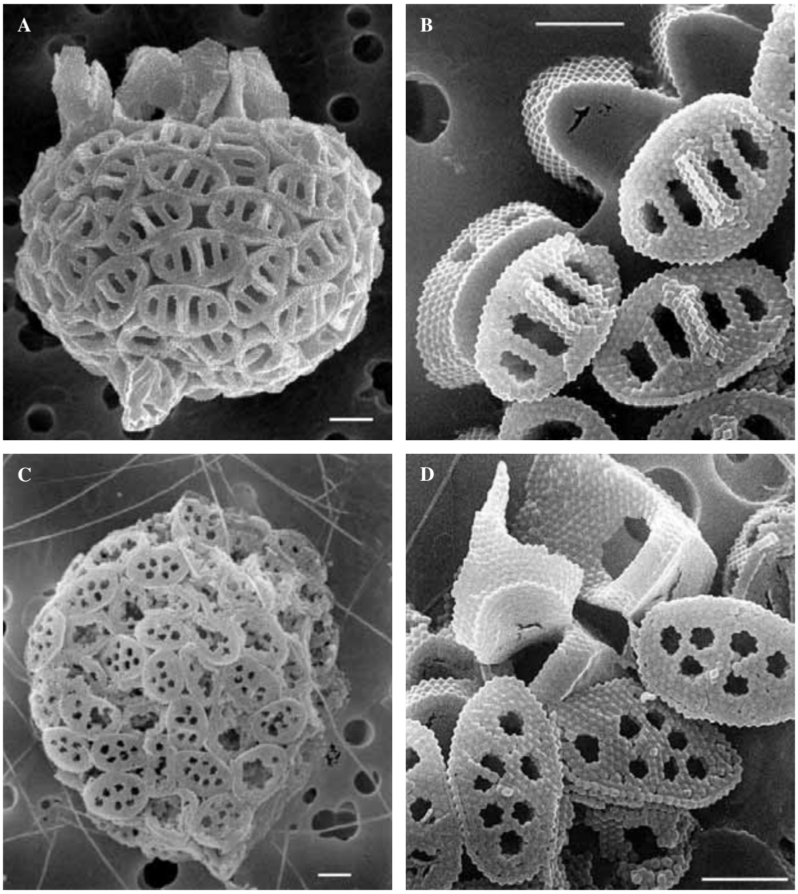

FIG. 100. – A-B, ***Poricalyptra aurisinae*** (Kamptner) Kleijne: **A**, complete coccosphere showing body calyptroliths with transverse slits and circum-flagellar helladoliths [Fans-3, K12, 60 m]; **B**, detail with body calyptroliths in latero-proximal view (left) showing the perforated wall, and in distal view showing the transverse slits and a central transverse protrusion with crystallites [Meso-95, 163, 40 m]. C-D, ***Poricalyptra isselii*** (Borsetti *et* 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.

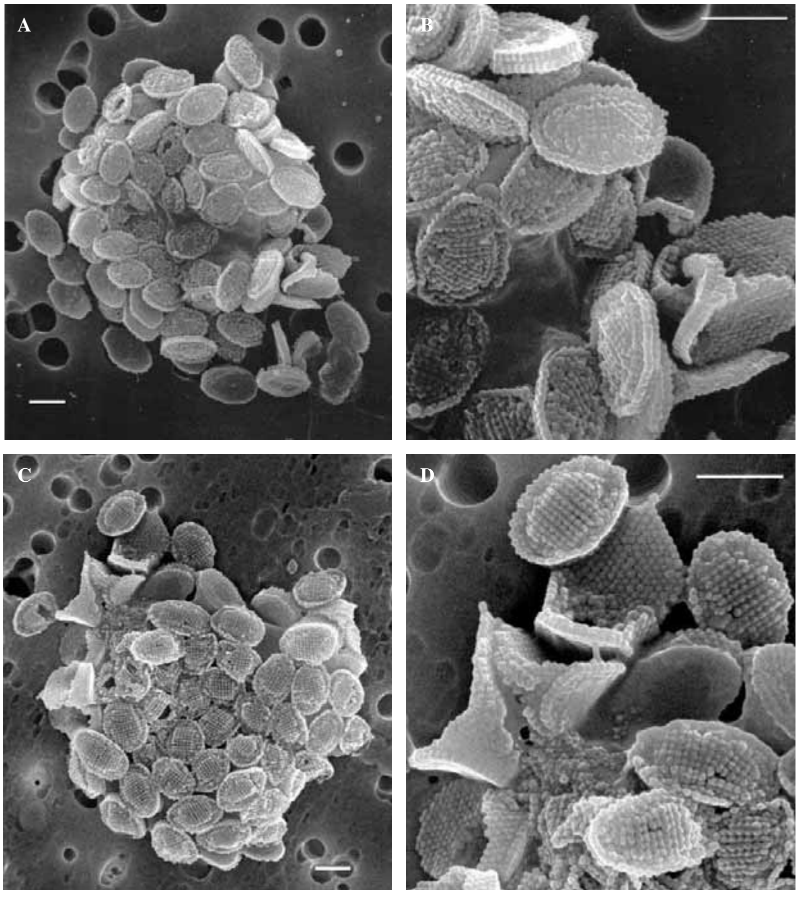

FIG. 101. – A-B, ***Poritectolithus* sp. 1**: **A**, coccosphere having flat and thin calyptroliths and helladoliths without tube [Fronts-95, 24W, 30 m]; **B**, detail of Fig. A with body coccoliths distally covered by rows of crystallites and circum-flagellar coccoliths resembling helladoliths but lacking 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.

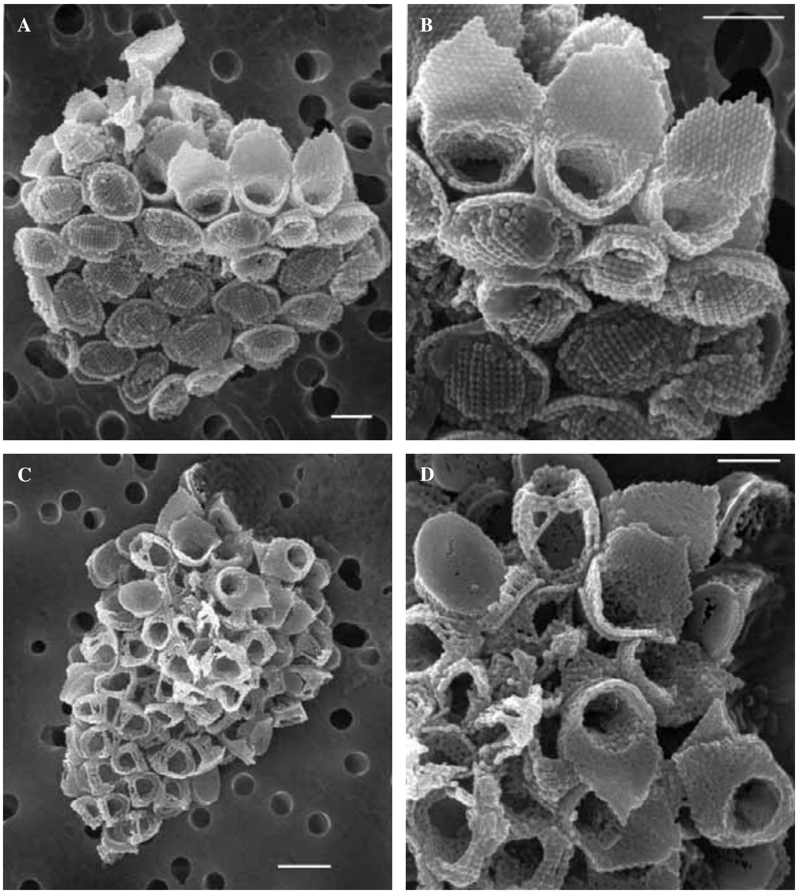

FIG. 102. – A-B, ***Poritectolithus poritectus*** (Heimdal) Kleijne, orthog. emend. Jordan *et* Green: **A**, coccosphere with helladoliths and varimorphic calyptroliths, higher and more vaulted near the apical area [Meso-96, E2, 70 m]; **B**, detail of Fig. A showing helladoliths and calyptroliths with 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.

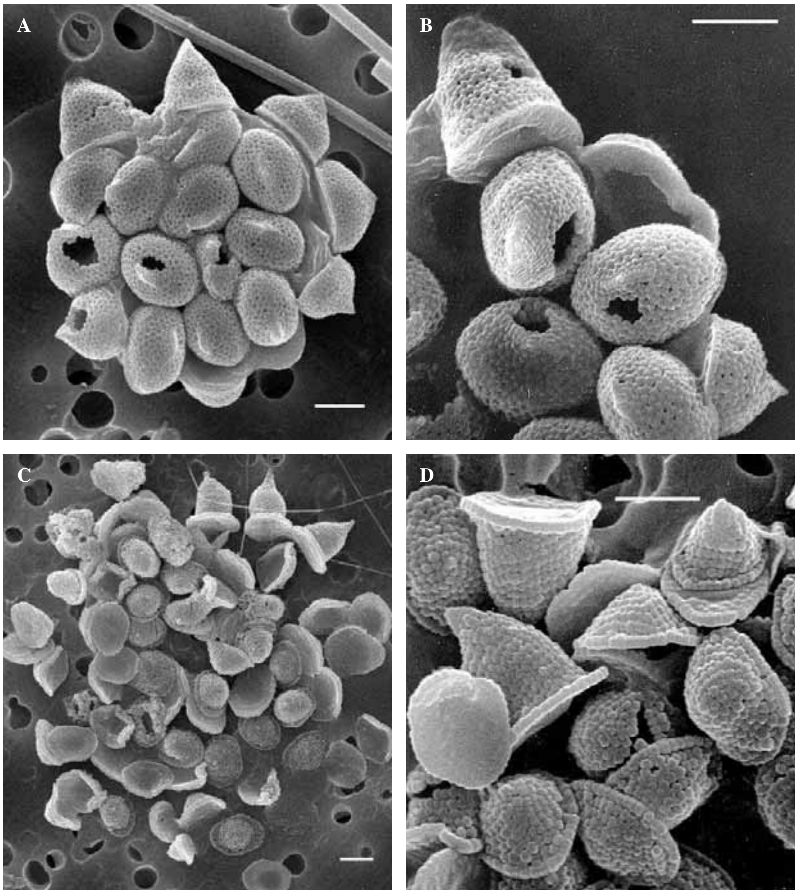

FIG. 103. – A-B, ***Sphaerocalyptra quadridentata*** (Schiller) Deflandre: **A**, coccosphere with some body calyptroliths slightly broken [Fronts-96, 013, 10 m]; **B**, detail with body calyptroliths and one high circum-flagellar calyptrolith (upper left); the coccoliths are constructed of irregularly 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.

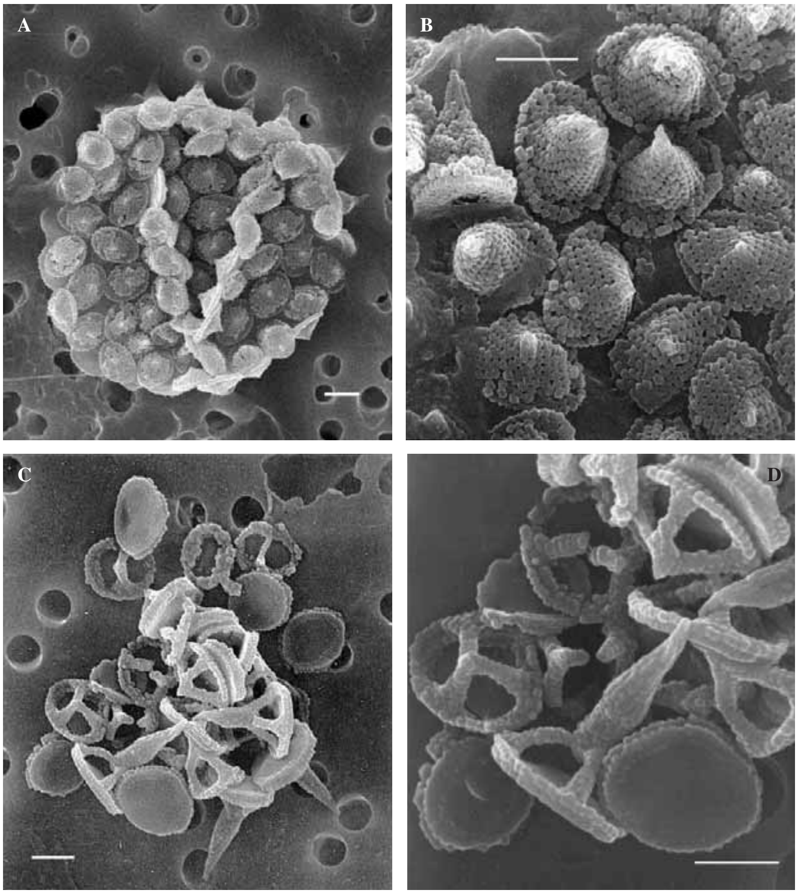

FIG. 104. – A-B, ***Sphaerocalyptra* sp. 1**: **A**, coccosphere showing body and circum-flagellar calyptroliths [Fans-3, K03, 10 m]; **B**, detail showing the angular crystallites of the calyptroliths which are distally pointed and constructed on a basal ring; circum-flagellar calyptroliths (upper left) 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.

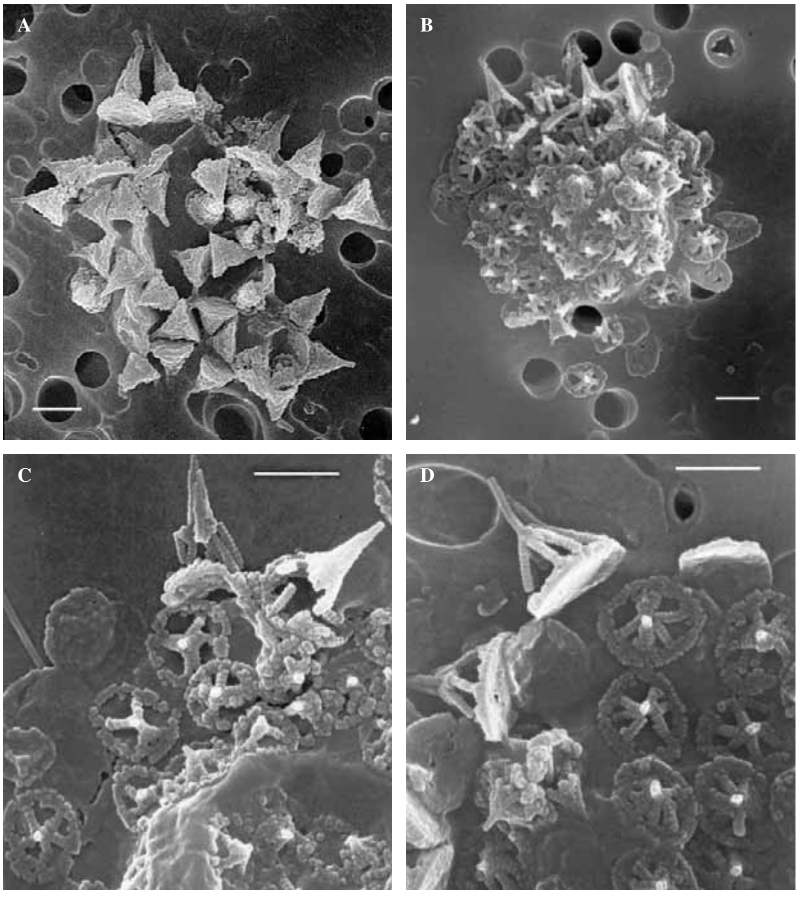

FIG. 105. – **A**, ***Sphaerocalyptra* sp. 2**: disintegrated coccosphere showing cone-shaped body calyptroliths with very thin pointed endings; circum-flagellar coccoliths are higher and more robust (top) [Meso-96, D6, 5 m]. B-D, ***Sphaerocalyptra* sp. 3**: **B**, coccosphere with very perforated and 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.

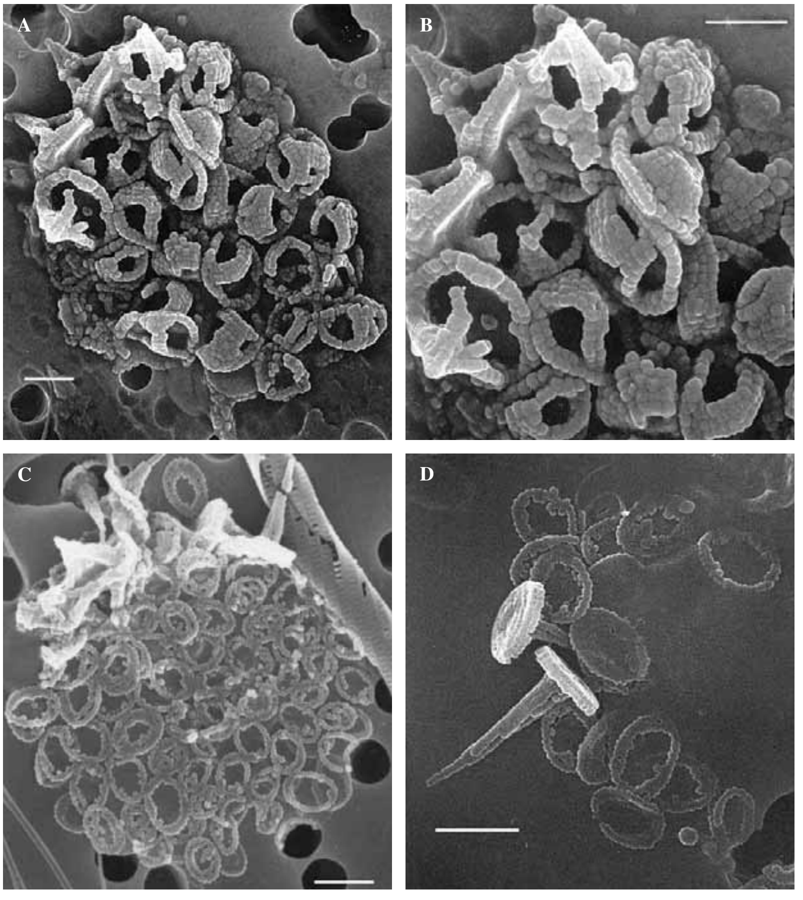

FIG. 106. – A-B, ***Sphaerocalyptra* sp. 5**: **A**, coccosphere with perforated, highly diverse-shaped calyptroliths [Meso-96, I8, 40 m]; **B**, detail of Fig. A showing the pointed circum-flagellar coccoliths and the rounded body calyptroliths which are constructed of large crystallites. C-D, ***Sphaerocalyptra* 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.

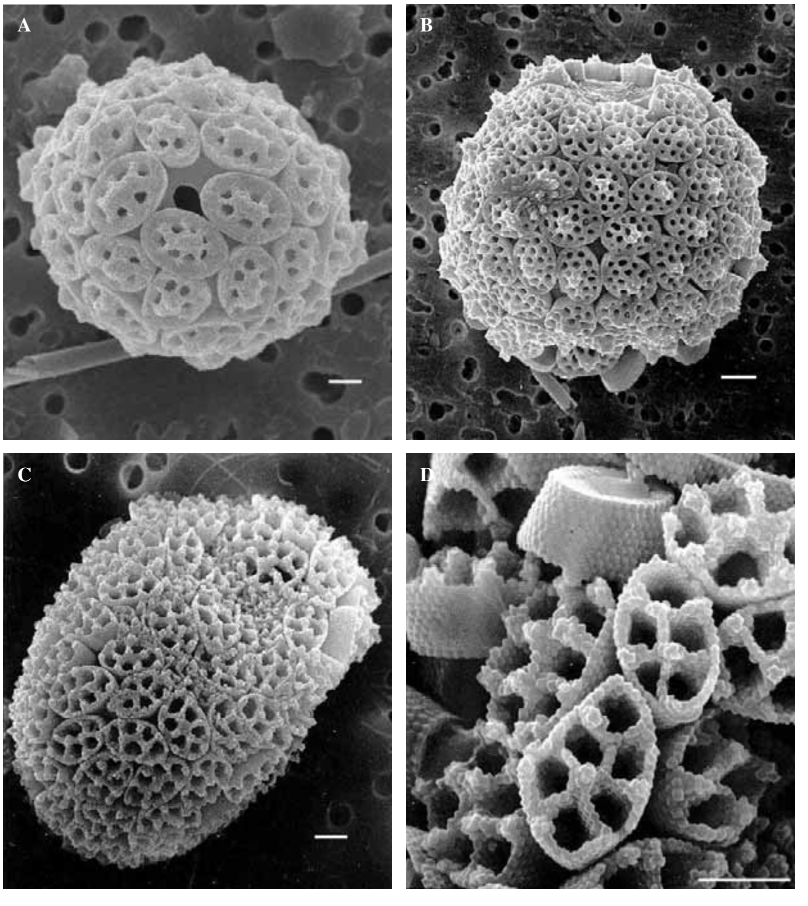

FIG. 107. – **A**, ***Syracolithus dalmaticus*** (Kamptner) Loeblich *et* Tappan: coccosphere with coccoliths which show a thick cover and a hollow central part [Hivern-99, 69, 40 m]. **B**, ***Syracolithus schilleri*** (Kamptner) Kamptner: coccosphere with a flagellar opening (centre); the coccoliths 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.

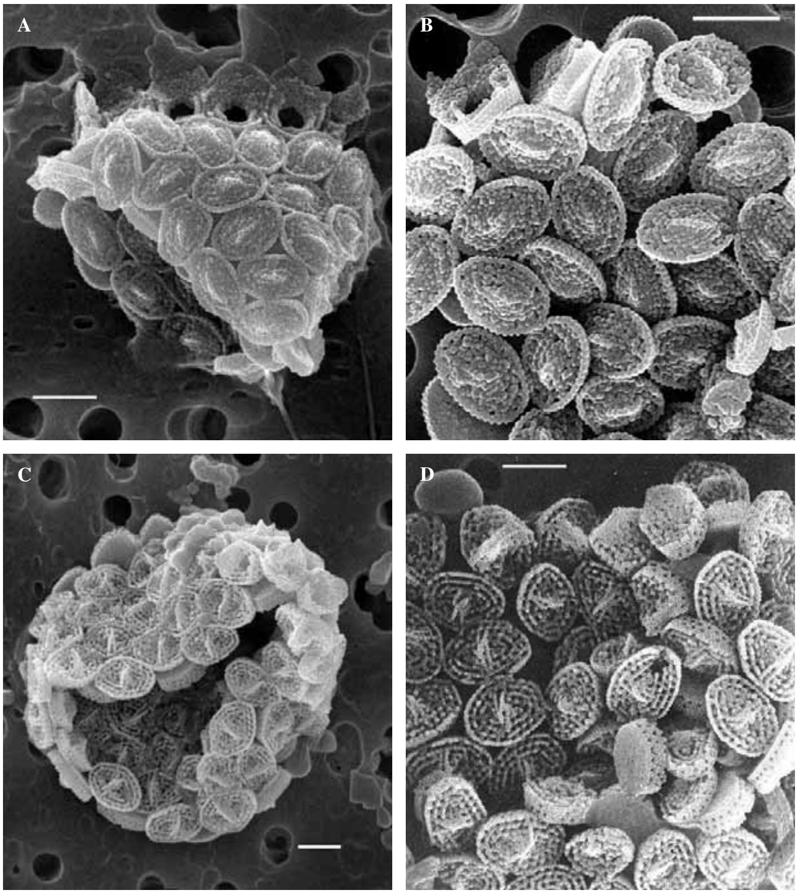

FIG. 108. – A-B, ***Zygosphaera amoena*** Kamptner: **A**, complete coccosphere showing circum-flagellar zygoliths (top) with double-layered wall and body laminoliths [Fans-3, K12, 60 m]; **B**, detail with zygoliths in lateral view (upper left) and laminoliths showing the longitudinal mound and the regularly arranged angular crystallites at the border [Meso-96, E3-4, 40 m]. C-D, ***Zygosphaera marsilii*** (Borsetti *et* 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.

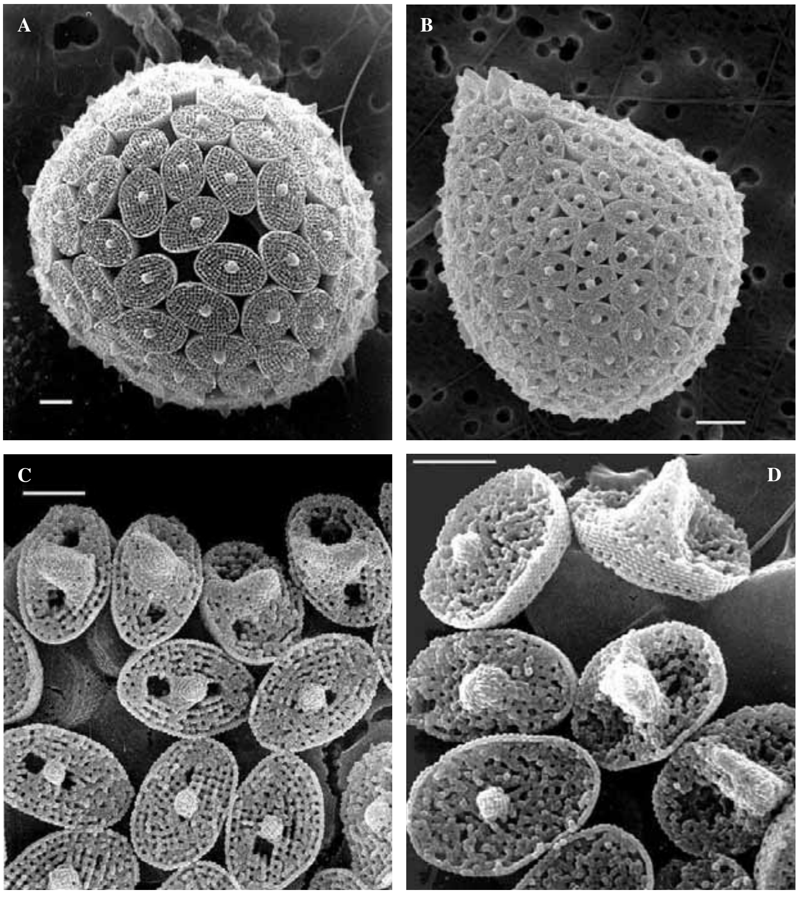

FIG. 109. – ***Zygosphaera hellenica*** Kamptner: **A**, complete coccosphere showing body laminoliths only [Meso-95, 023, surface]; **B**, complete coccosphere showing body laminoliths, several with pores, and two circum-flagellar zygoform coccoliths (upper left) [Workshop Picasso, T4, surface]; **C**, 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.

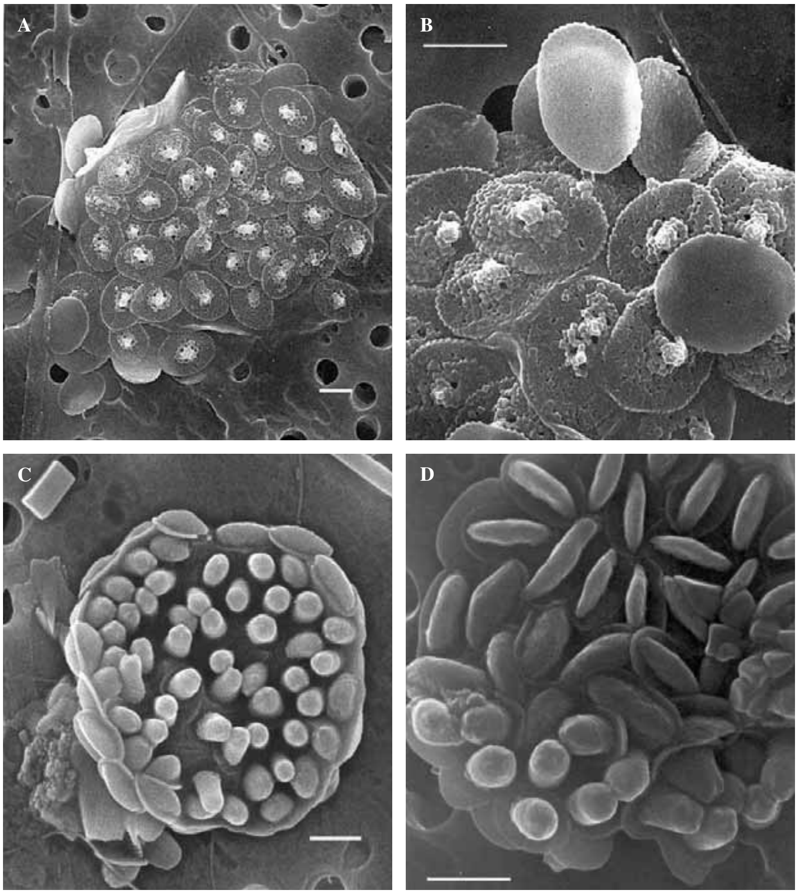

FIG. 110. – A-B, **Holococcolithophore sp. 1** (coccoliths have two small pores in proximal side): **A**, holococcolithophore showing monomorphic coccoliths [Meso-96, D4, 5 m]; **B**, detail with holococcoliths in distal and proximal view; the proximal side of the coccoliths has two diagonally arranged pores. [Fronts-95, 23D, 5 m]. C-D, **Coccolithophore sp. 1** (affinity to Rhabdosphaeraceae?): **C**, coccosphere 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.

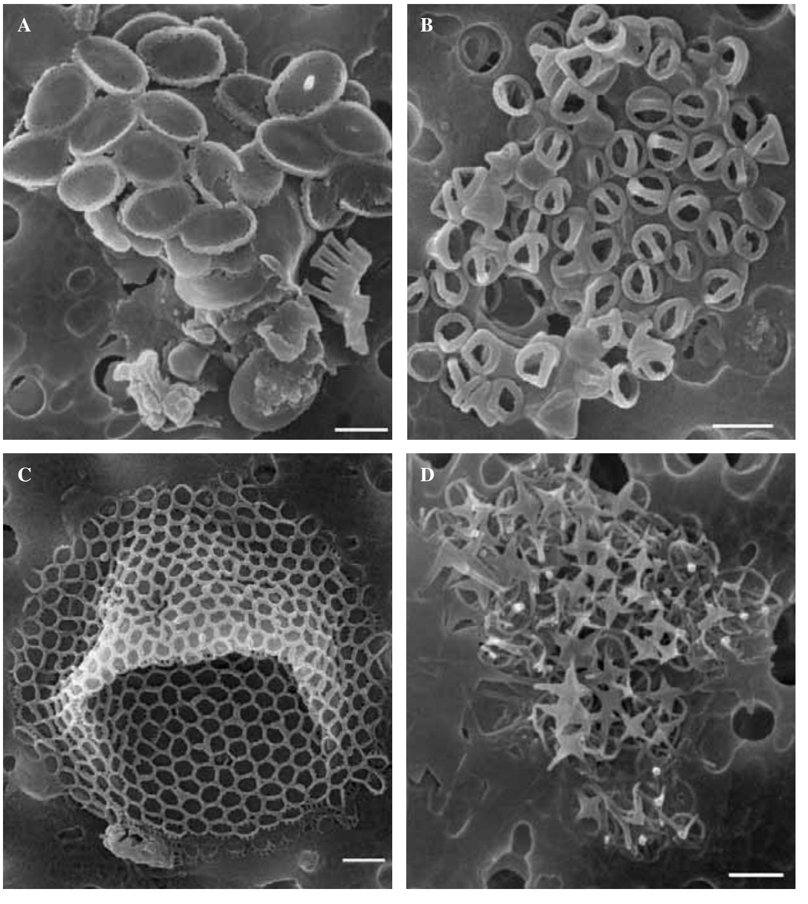

FIG. 111. – **A**, **Coccolithophore sp. 2** (affinity to *Syracosphaera*?): collapsed coccosphere; coccoliths resemble muroliths with a very low wall; central area might be constructed of wide laths joined together; the coccolith near the upper-right corner appears to have a central spine [Meso-96, 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.

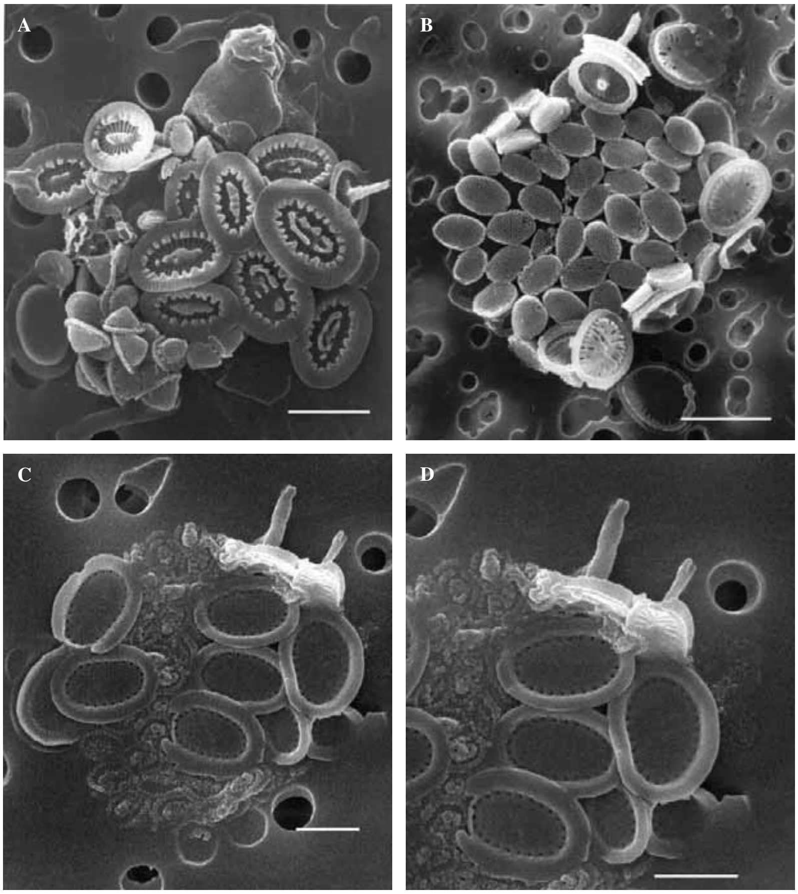

FIG. 112. – **Other possible heterococcolith - holococcolith combinations**: **A**, a collapsed mixed coccosphere with a circum-flagellar caneolith with spine and several body caneoliths of *Syracosphaera molischii* surrounding the body and circum-flagellar holococcoliths of *Anthosphaera fragaria* [Fronts-95, 20I, 20 m]; **B**, a collapsed coccosphere of *Calyptrolithophora papillifera* surrounded by heterococcoliths of *Syracosphaera histrica* [Meso-96, I4, 40 m]; **C**, coccosphere with heterococcoliths of *Syracosphaera marginaporata* (body coccoliths and circum-flagellar coccoliths in apical position) and holococcoliths 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.

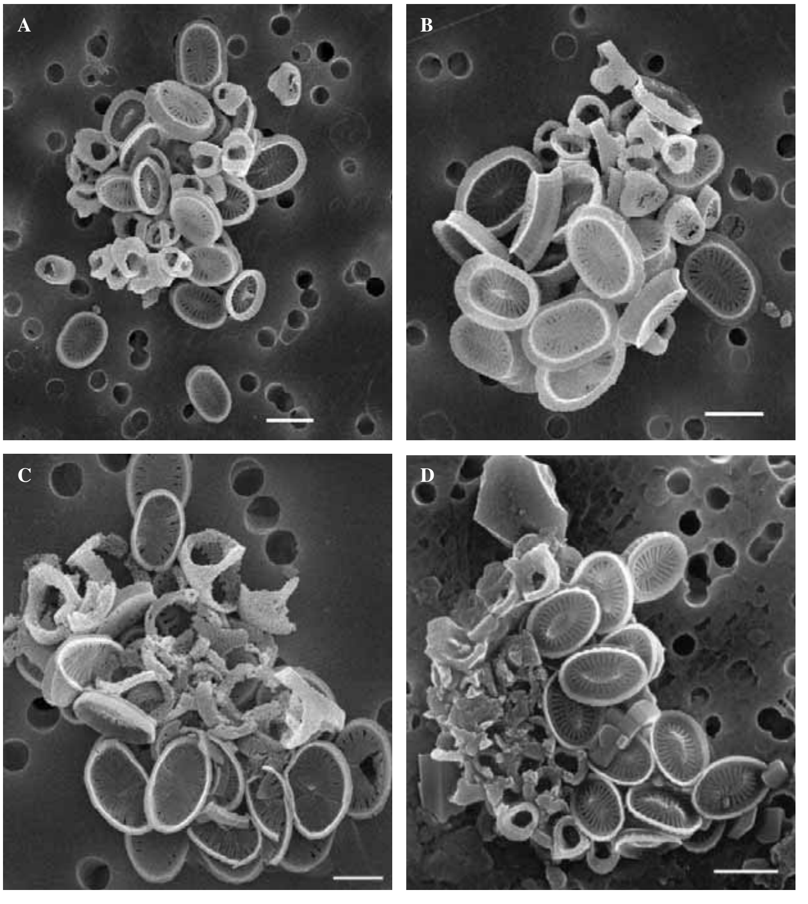

FIG. 113. – **Other possible heterococcolith - holococcolith combinations**: **A**, heterococcoliths of *Syracosphaera* sp. type D (see Kleijne, 1993) mixed with holococcoliths of *Homozygosphaera arethusae* [Fronts-96, 013, 66 m]; **B**, another mixed group of the same combination of coccoliths as Fig. A [Fronts-96, 013, 66 m]; **C**, mixed collapsed coccosphere 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 coccosphere consisting half of body caneoliths of the heterococcolithophore *Syracosphaera nodosa* (right) and half of holococcoliths of *Helladosphaera cornifera* (left); some circum-flagellar helladoliths are clearly visible in the upper-left corner [Meso-96, I8, 40 m]. Scale bars: A, B, D = 2 µm; C = 1 µm.

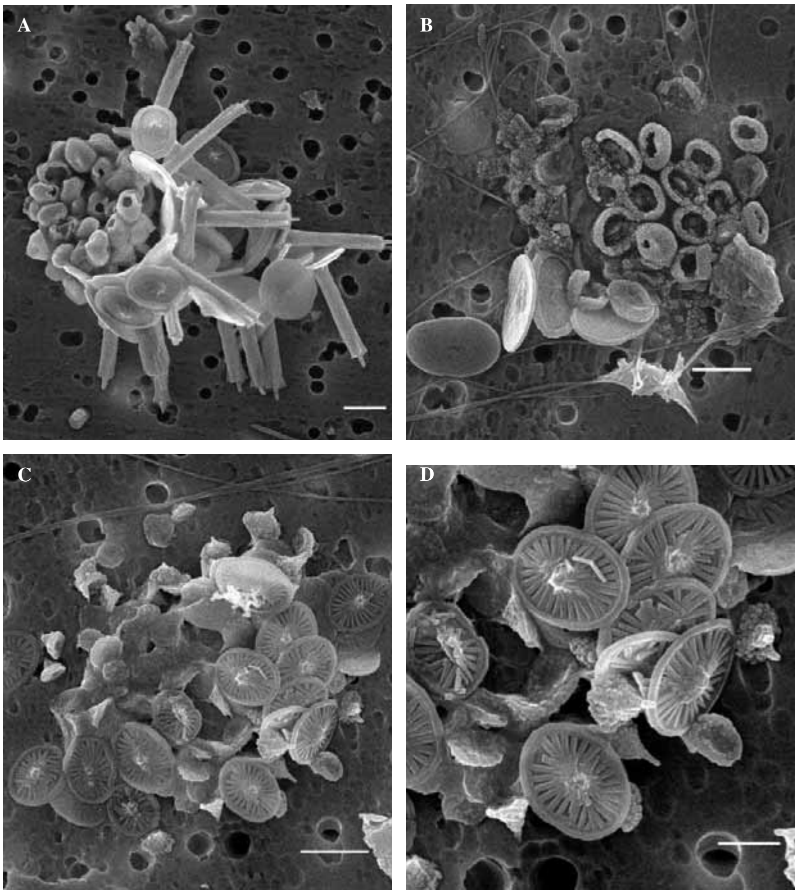

FIG. 114. – **Other possible heterococcolith - holococcolith combinations**: **A**, collapsed *Rhabdosphaera clavigera* coccosphere partially covering a coccosphere of *Sphaerocalyptra quadridentata* [Picasso workshop, T1 (off. Barcelona), surface]; **B**, disintegrated coccosphere of *Sphaerocalyptra 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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REFERENCES

Alcober, J. and R.W. Jordan. – 1997. An interesting association between *Neosphaera coccolithomorpha* and *Ceratolithus cristatus* (Haptophyta). *Eur. J. Phycol*., 32: 91-93.

Aubry, M.-P. – 1989. Phylogenetically based calcareous nannofossil taxonomy: implications for the interpretation of geological events. In: J.A. Crux and S.E. van Heck (eds.), *Nannofossils and their aplications*: *Proceedings INA Conference*, *London 1987*, pp. 21-40. Ellis Horwood, Chichester.

Biekart, J.W. – 1989. The distribution of calcareous nannoplankton in late Quaternary sediments collected by the Snellius II Expedition in some southeast Indonesian basins. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, B, 92: 77-141.

Billard, C. – 1994. Lyfe cycles. In: J.C. Green and B.S.C. Leadbeater (eds.), *The Haptophyte Algae*, pp. 167-186, Systematics Association Special Volume 51. Clarendon Press, Oxford.

Black, M. – 1968. Taxonomic problems in the study of coccoliths. *Palaeontology*, 11: 793-813.

Black, M. – 1971. The systematics of coccoliths in relation to the paleontological record. In: B.M. Funnel and W.R. Riedel (eds.), *The Micropaleontology of the Oceans*, pp. 611-624. Cambridge University Press, Cambridge.

Bollmann, J. – 1997. Morphology and biogeography of *Gephyrocapsa* coccoliths in Holocene sediments. *Mar. Micropaleontol.*, 29: 319-350.

Borsetti, A.M. and F. Cati. – 1972. Il nannoplancton calcareo vivente nel Tirreno centro-meridionale. *Giornale Geol.* (2), 38: 395-452.

Borsetti, A.M. and F. Cati. – 1976. Il nannoplancton calcareo vivente nel Tirreno centro-meridionale. Parte II. *Giornale Geol.* (2), 40: 209-240.

Borsetti, A.M. and F. Cati. – 1979. Il nannoplancton calcareo vivente nel Tirreno centro-meridional. Parte III. *Giornale Geol.* (2), 43: 157-174.

Boudreaux, J.E. and W.W. Hay. – 1969. Calcareous nannoplankton and biostratigraphy of the late Pliocene-Pleistocene-Recent sediments in the Submarex cores. *Rev. esp. Micropaleontol.,* 1: 249-292.

Bown, P.R. – 1998. *Calcareous nannofossil biostratigraphy*. Chapman and Hall, Cambridge.

Bown, P.R. and J.R. Young. – 1997. Mesozoic calcareous nannoplankton classification. *J. Nannoplankton Res.,* 19: 21-36.

Bown, P.R. and J.R. Young. – 1998. Introduction. In: P.R. Bown (ed.), *Calcareous nannofossil biostratigraphy*, pp. 1-15. Chapman and Hall. London.

Braarud, T., G. Deflandre, P. Halldal and E. Kamptner. – 1955. Terminology, nomenclature, and systematics of the Coccolithophoridae. *Micropaleontology*, 1: 157-159.

Bramlette, M.N. and E. Martini. – 1964. The great change in calcareous nannoplankton fossils between the Maestrichtian and Danian. *Micropaleontology*, 10: 291-322.

Brassell, S.C., G. Eglinton, I.T. Marlowe, U. Pflaumann and M. Sarnthein. – 1986. Molecular stratigraphy: a new tool for climatic assessment. *Nature*, 320: 129-133.

Bréhéret, J.G. – 1978. Formes nouvelles quaternaries et actualles de la famille des Gephyrocapsaceae (Cocolithophorides). *C. R. Acad. Sc. Paris. Série D*, 287: 447-449.

Cavalier-Smith, T. – 1981. Eucaryote kingdoms, seven or nine?. *BioSystems*, 14: 461-481.

Cavalier-Smith, T. – 1986. The Kingdom Chromista: Origin and Systematics. In: F.E. Round and D.J. Chapman (eds.), *Progress in Phycological Research*, vol. 4, pp. 309-347. Biopress Ltd., Bristol.

Cavalier-Smith, T. – 1998. A revised six-kingdom system of life. *Biol. Rev. Camb. Philos. Soc*., 73: 203-266.

Cavalier-Smith, T., M.T.E.P. Allsopp, M.M. Häuber, G. Gothe, E.E. Chao, J.A. Couch, and U.G. Maier. – 1996. Chromobiote phylogeny: the enigmatic alga *Reticulosphaera japonensis* is an aberrant haptophyte, not a heterocont. *Eur. J. Phycol*., 31: 255-263.

Charlson, R.J., J.E. Lovelock, M.O. Andreae and S.G. Warren. – 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature*, 326: 655-661.

Chrétiennot-Dinet, M.-J. – 1990. *Atlas du phytoplancton marin*, 3. Editions du C.N.R.S., Paris.

Cohen, C.L.D. – 1964. Coccolithophorids from two Caribbean deep-sea cores. *Micropaleontology* , 10: 231-250.

Cohen, C.L.D. and P. Reinhardt. – 1968. Coccolithophorids from the Pleistocene Caribbean deep-sea core CP-28. *Neues Jahrb. Geol. Pal.; Abh.*, 131: 289-304.

Cortés, M.Y. – 2000. Further evidence for the heterococcolith-holococcolith combination *Calcidiscus leptoporus - Crystallolithus rigidus*. *Mar. Micropaleontol*., 39: 35-37.

Cros, L. – 2000. Variety of exothecal coccoliths of *Syracosphaera*. *J. Nannoplankton Res*., 22: 41-51.

Cros, L. – 2001. *Planktonic coccolithophores of the NW Mediterranean*. Ph. D. thesis, Univ. Barcelona.

Cros, L. – 2002. *Planktonic coccolithophores of the NW Mediterranean*. Published Ph. D. thesis. Publlicacions de la Universitat de Barcelona, Barcelona.

Cros, L., A. Kleijne and J.R. Young. – 2000a. Coccolithophorid diversity in the genus *Polycrater* and possible relationships with other genera. *J. Nannoplankton Res*., 22: 92.
Cros, L., A. Kleijne, A. Zeltner, C. Billar and J.R. Young. – 2000b. New examples of holococcolith-heterococcolith combination coccospheres and their implications for coccolithophorid biology. *Mar. Micropaleontol*., 39: 1-34.
Deflandre, G. – 1952. Classe des Coccolithophoridés. (Coccolithophoridae Lohmann, 1902). In: P.-P. Grassé (ed.), *Traité de Zoologie,* 1, pp. 439-470. Masson, Paris.
Deflandre, G. and C. Fert. – 1953. Aplication du microscope electronique a l'étude des coccolithophoridés. *Bull. Soc. Hist. Nat. Toulouse*, T. 88: 301-313.
Deflandre, G. and C. Fert. – 1954. Observations sur les coccolithophoridés actuels et fossiles en microscopie ordinaire et électronique. *Ann. Paléontol*., 40: 115-176.
Delgado, M. and J.M. Fortuño. – 1991. Atlas de Fitoplanton del Mar Mediterráneo. *Sci. Mar*., 55(Supl. 1).
Edvardsen, B., W. Eikrem, J.C. Green, R.A. Andersen, S.Y.M. Staay van der and L.K. Medlin. – 2000. Phylogenetic reconstructions of the Haptophyta inferred from 18S ribosomal DNA sequences and available morphological data. *Phycology,* 39: 19-35.
Ehrenberg, C.G. – 1836. Bemerkugen uber feste mikroscopische anorganische Formen in den erdigen und derben Mineralien. *Bericht. Verh. K. Preuss. Akad. Wiss. Berlin*: 84-85.
Farinacci, A. – 1971. Round Table on calcareous Nannoplankton. In: A. Farinacci (ed.), *Procedings of the II Planktonic Conference*, pp. 1343-1369. Tecnoscienza, Roma.
Findlay, C.S. – 1998. *Living and Fossil Calcareous Nannoplankton from the Australian Sector of the Southern Ocean: Implications for Paleoceanography*. Ph. D. thesis, Univ. Tasmania.
Flores, J.A., F.J. Sierro, G. Francés, A. Vázquez and I. Zamarreño. – 1997. The last 100.000 years in the western Mediterranean: sea surface water and frontal dynamics as revealed by coccolithophores. *Mar. Micropaleontol*., 29: 351-366.
Fresnel, J. – 1989. *Les Coccolithophorides (Prymnesiophyceae) du littoral: Genres:* Cricosphaera, Pleurochrysis, Cruciplacolithus, Hymenomonas *et* Ochrosphaera. *Ultrastructure, cycle biologique, systématique.* Ph. D. thesis, Univ. Caen.
Fresnel, J. – 1994. A heteromorphic life cycle in two coastal coccolithophorids, *Hymenomonas lacuna* and *Hymenomonas coronata* (Prymnesiophyceae). *Can. J. Bot*., 72: 1455-1462.
Fresnel, J. and C. Billard. – 1991. *Pleurochrysis placolithoides* sp. nov. (Prymnesiophyceae), a new marine coccolithophorid with remarks on the status of cricolith-bearing species. *Br. Phycol. J*., 26: 67-80.
Fujiwara, S., M. Tsuzuki, M. Kawachi, N. Minaka and I. Inouye. – 2001. Molecular phylogeny of the haptophyta based on the rbcL gene and sequence variation in the spacer region of the rubisco operon. *J. Phycol*., 37: 121-129.
Gaarder, K.R. – 1962. Electron microscope studies on holococcolithophorids. *Nytt Mag. Bot.*, 10: 35-51.
Gaarder, K.R. – 1967. Observations on the genus *Ophiaster* Gran (Coccolithineae). *Sarsia*, 29: 183-192.
Gaarder, K.R. – 1970. Three New Taxa of Coccolithineae. *Nytt Mag. Bot*., 17: 113-126.
Gaarder, K.R. and G.R. Hasle. – 1971. Coccolithophorids of the Gulf of Mexico. *Bull. Mar. Sci*., 21: 519-544.
Gaarder, K.R. and B.R. Heimdal. – 1977. A revision of the genus *Syracosphaera* Lohmann (Coccolithineae). "*Meteor" Forschungs-Ergeb., Reihe* D, 24: 54-71.
Gaarder, K.R. and E. Ramsfjell. – 1954. A new coccolithophorid from northern waters. *Calciopappus caudatus* n. gen., n. sp. *Nytt Mag. Bot*., 2: 155-156.
Gallagher, L.T. – 1989. *Reticulofenestra*: A critical review of taxonomy, structure and evolution. In: J.A. Crux and S.E. van Heck (eds.), *Nannofosils and their aplications*, pp. 41-75. Ellis Horwood, Chichester.
Gartner, S. and D. Bukry. – 1969. Tertiary holococcoliths. *J. Paleontol*., 43: 1213-1221.
Gayral, P. and J. Fresnel. – 1983. Description, sexualité et cycle de développement d'une nouvelle Coccolithophoracée (Prymnesiophyceae): *Pleurochrysis pseudoroscoffensis* sp. nov. *Protistologica*, 19: 245-261.
Geisen, M., L. Cros, I. Probert and J.R. Young. – 2000. Life-cycle associations involving pairs of holococcolithophorid species: complex life cycles or cryptic speciation? *J. Nannoplankton Res*., 22: 99.
Giraudeau, J. and G.W. Bailey. – 1995. Spatial dynamics of coccolithophore communities during an upwelling event in the Southern Benguela system. *Cont. Shelf Res*., 15: 1825-1852.
Gran, H.H. – 1912. Pelagic plant life. In: J. Murray and J. Hjort (eds.), *The Depths of the Ocean*, pp. 307-386. Macmillan, London..
Green, J.C., P.A. Course and G.A. Tarran. – 1996. The life-cycle *Emiliania huxleyi*: A brief review and a study of relative ploidy levels analysed by flow cytometry. *J. Mar. Systems*, 9: 33-44.
Haeckel, E. – 1894. *Sistematische Phylogenie der Protisten und Pflanzen*. Reimer, Berlin.
Hagino, K. and H. Okada. – 1998. *Gladiolithus striatus* sp. nov. (Prymnesiophyceae), a living coccolithophore from the lower photic zone of the Pacific Ocean. *Phycologia*, 37: 246-250.
Halldal, P. – 1953. Phytoplankton investigations from weather ship M in Norwegian Sea, 1948-49. *Hvalräd. Skr*., 38: 1-91.
Halldal, P. and J. Markali. – 1954a. Morphology and microstructure of coccoliths studied in the electron microscope. Observations on *Anthosphaera robusta* and *Calyptrosphaera papillifera*. *Nytt Mag. Bot*., 2: 117-121.
Halldal, P. and J. Markali. – 1954b. Observations on coccoliths of *Syracosphaera mediterranea* Lohm., *S. pulchra* Lohm., and *S. molischi* Schill. in the electron microscope**.** *J. Cons. Int. Exp. Mer*, 19: 329-336.
Halldal, P. and J. Markali. – 1955. Electron microscope studies on coccolithophorids from the Norwegian Sea, the Gulf Stream and the Mediterranean. *Nor. Vidensk.-Akad. Oslo, Avh. Mat.-Nat. Kl*., 1: 1-30.
Hallegraeff, G.M. – 1984. Coccolithophorids (calcareous nanoplankton) from Australian waters. *Bot. Mar*., 27: 229-247.
Hay, W.W., H.P. Mohler, P.H. Roth, R.R. Schmidt and J.E. Bourdeaux. – 1967. Calcareous nannoplankton zonation of the Cenozoic of the Gulf Coast and Caribbean-Antillean area, and transoceanic correlation. *Trans. Gulf Coast Assoc. Geol. Soc*., 17: 428-480.
Hay, W.W., H.P. Mohler and M.E. Wade. – 1966. Calcareous nannofossils from Nal'chik (northwets Caucasus). *Ecologae Geol. Helv*., 59: 379-399.
Heimdal, B.R. – 1973. Two new taxa of recent coccolithophorids. *"Meteor" Forsch.-Ergebn., Reihe* D, 13: 70-75.
Heimdal, B.R. – 1982. Validation of the names of some species of *Zygosphaera* Kamptner. *Int. Nannoplankton Assoc. Newslett.*, 4: 52-56.
Heimdal, B.R. – 1993. Modern Coccolithophorids. A Guide to Naked Flagellates and Coccolithophorids. In: C.R. Tomas (ed.), *Marine Phytoplankton*, pp. 147-243. Academic Press, London.
Heimdal, B.R. and K.R. Gaarder. – 1980. Coccolithophorids from the northern part of the eastern central Atlantic. I. Holococcolithophorids. *"Meteor" Forsch.-Ergebn., Reihe* D, 32: 1-14.
Heimdal, B.R. and K.R. Gaarder. – 1981. Coccolithophorids from the northern part of the eastern central Atlantic. II. Heterococcolithophorids. *"Meteor" Forsch.-Ergebn., Reihe* D, 33: 37-69.
Hibberd, D.J. – 1972. Chrysophyta: definition and interpretation. *Br. Phycol. J*., 7: 281.
Hibberd, D.J. – 1976. The ultrastructure and taxonomy of the Chrysophyceae and Prymnesiophyceae (Haptophyceae): A survey with some new observations on the ultrastructure on the Chrysophyceae. *Bot. J. Linn. Soc*., 72: 55-80.
Holligan, P.M., E. Fernandez, J. Aiken, W.M. Balch, P. Boyd, P.H. Burkill, M. Finch, S.B. Groom, G. Malin, K. Muller, D.A. Purdie, C. Robinson, C.C. Trees, S.M. Turner and P. van der Wal. – 1993. A biogeochemical study of the coccolithophore *Emiliania huxleyi* in the North Atlantic. *Global Biogeochem. Cycles*, 7: 879-900.
Honjo, S. – 1976. Coccoliths: production, transportation and sedimentation. *Mar. Micropaleontol*., 1: 65-79.
Hori, T. and T.C. Green. – 1985. An ultrastructural study of mitosis in non-motile coccolith-bearing cells of *Emiliania huxleyi* (Lohm) Hay and Mohler (Prymnesiophyceae). *Protistologica*, 21: 107-120.
Hori, T. and I. Inouye. – 1981. The ultrastructure of mitosis in *Cricosphaera roscoffensis* var. *haptonemifera* (Prymnesiophyceae). *Protoplasma*, 106: 121-135.
Inouye, A. and M. Kawachi. – 1994. The haptonema. In: J.C. Green and B.S.C. Leadbeater (eds.), *The Haptophyte Algae*, *Systematics Association Special Volume 51,* pp. 73-89. Clarendon Press, Oxford.

Inouye, I. and R.N. Pienaar. – 1984. New observations on the coccolithophorid *Umbilicosphaera sibogae* var. *foliosa* (Prymnesiophyceae) with reference to cell covering, cell structure and flagellar apparatus. *Br. Phycol. J*., 19: 357-369.
Inouye, I. and R.N. Piennar. – 1988. Light and electron microscope observations of the type species of *Syracosphaera, S. pulchra* (Prymnesiophyceae). *Br. Phycol. J*., 23: 205-217.
Jafar, S.A. and E. Martini. – 1975. On the validity of the calcareous nannoplankton genus *Helicosphaera*. *Senckenbergiana Lethaea*, 56: 381-397.
Janin, M.-C. – 1987. Micropaléontologie de concrétions polymétalliques du Pacifique central: zone Clarion-Clipperton, chaine Centre-Pacifique, Iles de la Ligne et archipel des Tuoamotou (Eocène-Actuel). *Mém. Soc. Géol. Fr.*, 152: 1-317.
Jerkovic, L. – 1970. *Noëlaerhabdus* nov. gen. type d'une nouvelle famille de Coccolithophoridés fossiles: Noëlaerhabdaceae du Miocène supérieur de Yougoslavie. *C. R. Acad. Sci., Paris, Ser. D*, 270: 468-470.
Jordan, R.W. – 1991. Problems in the taxonomy and terminology of living coccolithophorids. *Int. Nannoplankton Assoc. Newslett*., 13: 52-53.
Jordan, R.W. and A.H.L. Chamberlain. – 1993a. *Canistrolithus valliformis* gen. *et* sp. nov. (Syracosphaeraceae, Prymnesiophyta) a comparison with the genus *Alisphaera*. *Phycologia*, 32: 373-378.
Jordan, R.W. and A.H.L. Chamberlain. – 1993b. *Vexillarius cancellifer* gen. *et* sp. nov. and its possible affinities with other living coccolithophorids. In: B. Hamrsmíd and J.R. Young (eds.), *Nannoplankton Research, vol. II: Tertiary biostratigraphy and paleoecology; quaternary coccoliths*. *Knihovnička ZPN*, 14: 305-325. MND Hodonín, Prague.
Jordan, R.W. and J.C. Green. – 1994. A check-list of the extant Haptophyta of the world. *J. mar. biol. Ass. U. K*., 74: 149-174.
Jordan, R.W. and A. Kleijne. – 1994. A classification system for living coccolithophores. In: A. Winter and W.G. Siesser (eds.), *Coccolithophores*, pp. 83-105. Cambridge University Press, Cambridge.
Jordan, R.W., A. Kleijne and B.R. Heimdal. – 1993. Proposed changes to the classification system of living coccolithophorids III. *Int. Nannoplankton Assoc. Newslett*., 15: 18-21.
Jordan, R.W., A. Kleijne, B.R. Heimdal and J.C. Green. – 1995. A Glossary of the extant Haptophyta of the world. *J. mar. biol. Ass. U.K*., 75: 769-814.
Jordan, R.W., M. Knappertsbusch, W.R. Simpson and A.H.L. Chamberlain. – 1991. *Turrilithus latericioides* gen. *et* sp. nov., a new coccolithophorid from the deep photic zone. *Br. Phycol. J*., 26: 175-183.
Jordan, R.W. and J.R. Young. – 1990. Proposed changes to the classification system of living coccolithophorids. *Int. Nannoplankton Assoc. Newslett*., 12: 15-18.
Kamptner, E. – 1927. Beitrag zur Kenntnis adriatischer Coccolithophoriden. *Arch. Protistenk.*, 58: 173-184.
Kamptner, E. – 1937. Neue und bemerkenswerte Coccolithineen aus dem Mittelmeer. *Arch. Protistenk.*, 89: 279-316.
Kamptner, E. – 1941. Die Coccolithineen der Südwestküste von Istrien. *Ann. Naturh. Mus. Wien*, 51: 54-149.
Kamptner, E. – 1943. Zur Revision der Coccolithineen-Spezies *Pontosphaera huxleyi* Lohm. *Akad. Wiss. Wien, Math.-Naturw. Kl.*, 80: 43-49.
Kamptner, E. – 1950. Über den submikroskopischen Aufbau der Coccolithen. *Akad. Wiss. Wien, Math.-Naturw. Kl.*, 87: 152-158.
Kamptner, E. – 1954. Untersuchungen über den Feinbau der Coccolithen. *Arch. Protistenk*., 100:1-90.
Kamptner, E. – 1956. Morphologische Betrachtungen uber Skelettelemente der Coccolithineen. *Österr. Bot. Z.*, 103: 142-163.
Kamptner, E. – 1963. Coccolithineen-Skelettreste aus Tiefseeablagerungen des Pazifischen Ozeans. *Naturh. Mus. Wien, Ann*., 66: 139-204.
Kamptner, E. – 1967. Kalkflagellaten - Skelettreste aus Tiefseeschlam des Sudatlantisken Ozeans. *Naturh. Mus. Wien, Ann*., 71: 117-198.
Kawachi, M. and I. Inouye. – 1999. Phylogenetic analysis of the 18 srrna gene sequence from members of the haptophyceae. *Report CODENET 2nd annual workshop, Carbara, France*. pp. 90-91.
Keller, M.D., W.K. Bellows and R.R.L. Guillard. – 1989. Dimethyl sulfide production in marine phytoplankton. In: E.S. Saltzman and W.J. Cooper (eds.), *Biogenic sulfur in the environment*, pp. 183-200. American Chemical Society, Washington.
Klaveness, D. – 1972a. *Coccolithus huxleyi* (Lohmann) Kamptner. I.- Morphological investigations on the vegetative cell and the process of coccolith formation. *Protistologica*, 8: 335-346.
Klaveness, D. – 1972b. *Coccolithus huxleyi* (Lohmann) Kamptner. II.- The flagellate cell, aberrant cell types, vegetative propagation and life cycles. *Br. Phycol. J*., 7: 309-318.
Klaveness, D. – 1973. The microanatomy of *Calyptrosphaera sphaeroidea*, with some supplementary observations in the motile stage of *Coccolithus pelagicus*. *Nor. J. Bot*., 20: 151-162.
Klaveness, D. and E. Paasche. – 1971. Two different *Coccolithus huxleyi* cell types incapable of coccolith formation. *Arch. Mikrobiol*., 75: 382-385.
Kleijne, A. – 1991. Holococcolithophorids from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Mar. Micropaleontol*., 17: 1-76.
Kleijne, A. – 1992. Extant Rhabdosphaeraceae (coccolithophorids, class Prymnesiophyceae) from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Scripta Geol.*, 100: 1-63.
Kleijne, A. – 1993. *Morphology, taxonomy and distribution of extant coccolithophorids (Calcareous nannoplankton)*. FEBO, Enschede.
Kleijne, A., R.W. Jordan, B.R. Heimdal, C. Samtleben, A.H.L. Chamberlain and L. Cros. – 2001. Five new species of the coccolithophorid genus *Alisphaera* (Haptophyta), with notes on their distribution, cocolith structure and taxonomy. *Phycologia*, 40: 583-601.
Knappertsbusch, M. – 1993. *Syracosphaera noroiticus* sp. nov., and *S. marginaporata* sp. nov., (Syracosphaeraceae, Prymnesiophyta), new coccolithophorids from the Mediterranean Sea and North Atlantic Ocean. *J. Micropalaeontol*., 12: 71-76.
Knappertsbusch, M., M.Y. Cortés and H.R. Thierstein. – 1997. Morphologic variability of the coccolithophorid *Calcidiscus leptoporus* in the plankton , surface sediments and from the early Pleistocene. *Mar. Micropaleontol*., 30: 293-317.
Leadbeater, B.S.C. – 1970. Preliminary observations on differences of scale morphology at various stages in the life cycle of "*Apistonema-Syracosphaera*" sensu von Stosch. *Br. Phycol. J*., 5: 57-69.
Lecal-Schlauder, J. – 1951. Recherches morphologiques et biologiques sur les Coccolithophorides Nord-Africains. *Ann. Inst. Océanogr*., 26: 255-362.
Lecal-Schlauder, J. – 1961. Anomalies dans la composition des coques de flagelles calcaires. *Bull. Soc. Hist. Nat. Afr. Nord*, 52: 63-66.
Lecal, J. – 1965a. Coccolithophorides littoraux de Banyuls. *Vie et Milieu*, 16: 251-270.
Lecal, J. – 1965b. A propos des modalités d'élaboration des formations épineuses des Coccolithophoridés. *Protistologica*, 1: 63-70.
Lecal, J. – 1967. Le nannoplancton des côtes d'Israel. *Hydrobiologia*, 29: 305-387.
Lemmermann, E. – 1903. Das Phytoplankton des Meeres. II. Beitrag. *Abh. hrsg. Nat.wiss. Ver. Brem.*, 17, 341-418.
Lemmermann, E. – 1908. Flagellatae, Chlorophyceae, Coccosphaerales und Silicoflagellatae. In: K. Brandt and C. Apstein (eds*.), Nordisches Plankton. Botanischer Teil*, pp. 1-40. Lipsius and Tischer, Kiel.
Loeblich, A.R., Jr. and H. Tappan. – 1963. Type fixation and validation of certain calcareous nannoplankton genera*. Proc. Biol. Soc. Wash*., 76: 191-196.
Loeblich, A.R., Jr. and H. Tappan. – 1966. Annotated index and bibliography of the calcareous nannoplankton. *Phycologia*, 5: 81-216.
Loeblich, A.R., Jr. and H. Tappan. – 1968. Annotated index and bibliography of the calcareous nannoplankton. 2. *J. Paleontol*., 42: 584-598.
Loeblich, A.R., Jr. and H. Tappan. – 1978. The coccolithophorid genus *Calcidiscus* Kamptner and its synonyms. *J. Paleontol*., 52: 1390-1392.
Lohmann, H. – 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, Zugleich ein Beitrag zur Kenntnis des Mittelmeerauftriebs. *Arch. Protistenk*., 1: 89-165.
Lohmann, H. – 1903. Neue Untersuchungen über den Reichthum des Meeres an Plankton und über die Brauchbartkeit der verschiedenen Fangmethoden. Zugleich auch ein Beitrag zur Ken-

ntnis des Mittelmeerauftriebs. *Wiss. Meeresunters. Abt. Kiel*, 7: 1-87.
Lohmann, H. – 1912. Untersuchungen über das Pflanzen- und Tierleben der Hochsee. Zugleich ein Bericht über die biologischen Arbeiten auf der Fahrt der "Deutschland" von Bremerhaven nach Buenos-Aires in der Zeit vom 7 Mai bis 7 September 1911. *Univ. Berlin, Veröff. Inst. Meereschundund, Geogr.-Nat.wiss*., 1: 1-92.
Lohmann, H. – 1913. Beiträge zur Charakterisierung des Tier- und Pflanzenlebens in den von der "Deutschland" wahrend ihrer Fahrt nach Buenos Aires Durchfahrenen Gebieten des Atlantischen Ozeans. II. Teil. *Internat. Revue Hydrobiol. Hydrogr*., 5: 343-372.
Lohmann, H. – 1919. Die Bevölkerung des Ozeans mit Plankton nach den Ergebnissen der Zentrifugenfänge während der Ausreise der "Deutschland" 1911. *Arch. Biontol*., 4: 1-617.
Lohmann, H. – 1920. Die Bevölkerung des Ozeans mit plankton. Nach den Ergebnissen der Zentrifugenfängen während der Ausreise der Deutschland 1911. *Arch. Biontol*., 4: 1-617.
Malin, G. and G.O. Kirst. – 1997. Algal production of dimethyl sulfide and its atmospheric role. *J. Phycol*., 33: 889-896.
Manton, I., G. Bremer and K. Oates. – 1984. Nanoplankton from the Galapagos Islands: *Michaelsarsia elegans* Gran and *Holopappus adriaticus* Schiller (coccolithophorids) with special reference to coccoliths and their unmineralized components. *Phil. Trans. R. Soc. Lond. B*, 305: 183-199.
Manton, I. and G.F. Leedale. – 1963. Observations on the microanatomy of *Crystallolithus hyalinus* Gaarder and Markali. *Arch. Mikrobiol*., 47: 115-136.
Manton, I. and G.F. Leedale. – 1969. Observations on the microanatomy of *Coccolithus pelagicus* and *Cricosphaera carterae*, with special reference to the origin and nature of coccoliths and scales. *J. mar. biol. Ass . U. K*., 49: 1-16.
Manton, I. and K. Oates. – 1975. Fine-structural observations on *Papposphaera* Tangen from the southern hemisphere and on *Pappomonas* gen. nov. from South Africa and Greenland. *Br. Phycol. J*., 10: 93-109.
Manton, I. and K. Oates. – 1980. *Polycrater galapagensis* gen. et sp. nov., a putative coccolithophorid from the Galapagos Islands with an unusual aragonitic periplast. *Br. Phycol. J*., 15: 95-103.
Manton, I. and K. Oates. – 1983. Nanoplankton from the Galapagos Islands: Two genera of spectacular coccolithophorids (*Ophiaster* and *Calciopappus*) with special emphasis on unmineralized periplast components. *Phil. Trans. R. Soc, London B*, 300: 435-462.
Manton, I. and K. Oates. – 1985. Calciosoleniaceae (coccolithophorids) from the Galapagos Island: unmineralized components and coccolith morphology in *Anoplosolenia* and *Calciosolenia,* with comparative analysis of equivalents in the unmineralized genus *Navisolenia* (Haptophyceae = Prymnesiophyceae). *Phil. Trans. R. Soc. Lond. B*, 309: 461-477.
Manton, I., J. Sutherland and M. McCully. – 1976a. Fine structural observations on coccolithophorids from South Alaska in the genera *Papposphaera* Tangen and *Pappomonas* Manton and Oates. *Br. Phycol. J*., 11: 225-234.
Manton, I., J. Sutherland and K. Oates. – 1976b. Arctic coccolithophorids: two species of *Turrisphaera* gen. nov. from West Greeland, Alaska, and the Northwest Passage. *Proc. R. Soc. Lond. B*, 194: 179-194.
Markali, J. and E. Paasche. – 1955. On two species of *Umbellosphaera*, a new marine coccolithophorid genus. *Nytt Mag. Bot*., 4: 95-100.
Marlowe, I.T., J.C Green, A.C. Neal, S.C. Brassell, G. Eglinton and P.A. Course. – 1984. Long chain (n-C_{37}-C_{39}) alkenones in the Prymnesiophyceae. Distribution of alkenones and other lipids and their taxonomic significance. *Br. Phycol. J*., 19: 203-216.
Martini, E. and C. Müller. – 1972. Nannoplankton aus dem nordlichen Arabischen Meer. *"Meteor" Forsch.-Ergeb., Reihe C*, 10: 63-74.
Matias i Sendra, M.I. – 1990. *Els nanofossils calcaris del Pliocé de la Mediterrània Nord-Occidental*. Ph. D. thesis. Univ. Barcelona.
McIntyre, A. and A.W.H. Bé. – 1967. Modern coccolithophoridae of the Atlantic Ocean - I. Placoliths and cyrtholiths. *Deep-Sea Res*., 14: 561-597.
Medlin, L.K., G.L.A. Barker, J.C. Green, P.K. Hayes, D. Marie, S. Wrieden and D. Vaulot. - 1996. Genetic characterization of *Emiliania huxleyi* (Haptophyta). *J. Mar. Systems*, 9: 13-32.
Mostajo, E.L. – 1985. Nanoplancton calcáreo del océano Atlántico sur. *Rev. Española Microp.*, 17: 261-280.
Murray, G. and V.H. Blackman. – 1898. On the nature of the coccospheres and rhabdospheres. *Phil. Trans. R. Soc. London (B),* 190: 427-441.
Nishida, S. – 1979. Atlas of Pacific Nannoplanktons. *News Osaka Micropaleontol. Spec. Pap*., 3: 1-31.
Norris, R.E. – 1965. Living cells of *Ceratolithus cristatus* (Coccolithophorineae). *Arch. Protistenk.*, 108: 19-24.
Norris, R.E. – 1983. The family position of *Papposphaera* Tangen and *Pappomonas* Manton and Oates (Prymnesiophyceae) with records from the Indian Ocean. *Phycologia*, 22: 161-169.
Norris, R.E. – 1984. Indian Ocean nannoplankton. I. *Rhabdosphaeraceae* (Prymnesiophyceae) with a review of extant taxa. *J. Phycol*., 20: 27-41.
Norris, R.E. – 1985. Indian Ocean nannoplancton. II. Holococcolithophorids (Calyptrosphaeraceae, Prymnesiophyceae) with a review of extant genera. *J. Phycol*., 21: 619-641.
Okada, H. and S. Honjo. – 1973. The distribution of oceanic coccolithophorids in the Pacific. *Deep-Sea Res*., 20: 355-374.
Okada, H. and A. McIntyre. – 1977. Modern coccolithophores of the Pacific and North Atlantic Oceans. *Micropaleontology*, 23: 1-55.
Okada, H. and A. McIntyre. – 1979. Seasonal Distribution of Modern Coccolithophores in the Western North Atlantic Ocean. *Mar. Biol*., 54: 319-328.
Okada, H. and A. McIntyre. – 1980. Validation of *Florisphaera profunda* var. *elongata* (2). *Int. Nannoplankton Assoc. Newslett.,* 2: 81.
Ostenfeld, C.H. – 1899. Über Coccosphaera und einige neue Tintinniden im Plankton des nördlichen Atlantische Oceans. *Zool. Anz*., 22: 433-439.
Ostenfeld, C.H. – 1900. Über Coccosphaera. *Zool. Anz*., 23: 198-200.
Paasche, E. and D. Klaveness. – 1970. A Physiological Comparison of Coccolith-Forming and Naked Cells of *Coccolithus huxleyi*. *Arch. Mikrobiol*., 73 : 143-152.
Parke, M. and I. Adams. – 1960. The motile (*Crystallolithus hyalinus* Gaarder and Markali) and non-motile phases in the life history of *Coccolithus pelagicus* (Wallich) Schiller. *J. mar. biol. Ass. U.K*., 39: 263-274.
Parke, M. and P.S. Dixon. – 1976. Check-list of British marine algae - third revision. *J. mar. biol. Ass. U.K*, 56: 527-94.
Perch-Nielsen, K. – 1985a. Mesozoic calcareous nannofossils. In: H.M. Bolli, J.B. Saunders and K. Perch-Nielsen (eds.), *Plankton Stratigraphy*, pp. 329-426. Cambridge University Press, Cambridge.
Perch-Nielsen, K. – 1985b. Cenozoic calcareous nannofossils In: H.M. Bolli, J.B. Saunders and K. Perch-Nielsen (eds.), *Plankton Stratigraphy*, pp. 427-555. Cambridge University Press. Cambridge.
Piennar, R.N. – 1994. Ultrastructure and calcification of coccolithophores. In: A. Winter and W. G. Siesser (eds.) *Coccolithophores*, pp. 13-37. Cambridge University Press. Cambridge.
Probert, I., M. Geissen, H. Kinkel and J.R. Young. – 2000. Culture studies of *Algirosphaera robusta. J. Nannoplankton Res.*, 22: 132-133.
Rayns, D.G. – 1962. Alternation of generations in a coccolithophorid, *Cricosphaera carterae* (Braarud and Fragerl.) Braarud. *J. mar. biol. Ass. U.K*., 42: 481-484.
Reid, F.M.H. – 1980. Coccolithophorids of the North Pacific Central Gyre with notes on their vertical and seasonal distribution. *Micropaleontology*, 26: 151-176.
Renaud, S. and C. Klaas. – 2001. Seasonal variations in the morphology of the coccolithophore *Calcidiscus leptoporus* off Bermuda (N. Atlantic). *J. Plank. Res*., 23: 779-795.
Riaux-Gobin, C., M.J. Chrétiennot-Dinet and C. Descolas-Gros. – 1995. Undamaged sedimented coccolithophorids in a deep environment (continental slope of the Gulf of Lions). *Mar. Geol*., 123: 239-252.
Rowson, J.D., B.S.C. Leadbeater and J.C. Green. – 1986. Calcium carbonate deposition in the motile (*Crystallolithus*) phase of *Coccolithus pelagicus* (Prymnesiophyceae). *Br. Phycol. J.*, 21: 359-370.
Samtleben, C. – 1980. Die Evolution der Coccolithophoriden-Gattung *Gephyrocapsa* nach Befunden im Atlantik. *Päleontologis-*

che Zeitschrift, 54: 91-127.
Samtleben, C., K.-H. Baumann and A. Schröder-Ritzrau. – 1995. Distribution, composition and seasonal variation of coccolithophore comunities in the northern North Atlantic. In: J. A. Flores and F. J. Sierro (eds.), *Proceedings of the 5th INA Conference.*, pp. 219-235. Universidad de Salamanca, Salamanca.
Samtleben, C. and A. Schöder. – 1990. Coccolithophoriden-Gemeinschaften und Coccolithen-Sedimentation im Europäischen Nordmeer: Zur Abbildung von planktischer Zönosen im Sediment. *Ber. Sonderforschungsbereich. Kiel*., 25: 1-52.
Samtleben, C. and A. Schröder. – 1992. Living coccolithophore communities in the Norwegian-Greenland Sea and their record in sediments. *Mar. Micropaleontol*., 19: 333-354.
Sánchez-Suárez, I.G. – 1990. Three new Coccolithophorids (Haptophyta) from the South-Eastern Caribbean Sea: *Cyclolithella ferrazae* sp. nov. *Syracosphaera florida* sp. nov. *Syracosphaera tumularis* sp. nov. *Biol. Mar. Acta Científica Venezolana*, 41: 152-158.
Sánchez-Suárez, I.G. – 1992. Coccolithophorids (Haptophyta) from the South-Eastern Caribbean Sea: II Order Syracosphaerales. *Biol. Mar. Acta Científica Venezolana*, 43: 109-124.
Saugestad, A.H. and B.R. Heimdal. – 2002. Light microscope studies on coccolithophorids from the western Mediterranean Sea, with notes on combination cells of *Daktylethra pirus* and *Syracosphaera pulchra. Plant Ecosyst.*, 136: 3-28.
Schiller, J. – 1913. Vorläufige Ergebnisse der Phytoplankton-Untersuchungen auf den Fahrten S.M.S. "Najade" der Adria 1911-1912. I. Die Coccolitophoriden- K. *Akad. Wiss, Wien, Sitzber., Math. Natyrw. K.l.*, 122: 597-617.
Schiller, J - 1925. Die planktonischen Vegetationen des adriatischen Meeres. A. Die Coccolithophoriden-Vegetation in den Jahren 1911-14. *Arch. Potistenkd*., 51: 1-130.
Schiller, J. – 1930. Coccolithineae. In: L. Rabenhorst (ed.), *Kryptogamen-Flora von Deutschland, Österreich und der Schweiz* , 10, pp. 89-267. Akademische Verlagsgesellschaft, Leipzig.
Schlauder, J. – 1945. *Reserches sur les flagellés calcaires de la baie d'Alger*. Dipl. Fac. Sci., Université d'Alger.
Siesser, W.G. – 1994. Historical background of coccolithophore studies. In: A. Winter and W.G. Siesser (eds.) *Coccolithophores*, pp. 1–11. Cambridge University Press, Cambridge.
Siesser, W.G. – 1998. Calcareous nannofosil Genus *Scyphosphaera*: structure, taxonomy, biostratigraphy, and phylogeny. *Micropaleontology*, 44: 351-384.
Siesser, W.G. and A. Winter. – 1994. Composition and morphology of coccolithophore skeletons. In: A. Winter and W.G. Siesser (eds.) *Coccolithophores*, pp. 51-62. Cambridge University Press, Cambridge.
Simó, R. and C. Pedrós-Alió. – 1999. Role of vertical mixing in controlling the oceanic production of dimethyl sulphide. *Nature*, 402: 396-399.
Sorby, H.C. – 1861. On the organic origin of the so-called "crystalloids" of the chalk. *Ann. Mag. Nat. Hist., Ser. 3*, 8: 193-200.
Sprengel, C. and J.R. Young. – 2000. First direct documentation of associations of *Ceratolithus cristatus* ceratoliths, hoop-coccoliths and *Neosphaera coccolithomorpha* planoliths. Mar. Micropaleontol., 39: 39-41.
Stacey, V. J. and R.N. Pienaar. – 1980. Cell division in *Hymenomonas carterae* (Braarud et Fagerland) Braarud (Prymnesiophyceae). *Br. Phycol. J*., 15: 365-376.
Steinmetz, J. C. – 1991. Calcareous nannoplankton biocoenosis: sediment trap studies in the Equatorial Atlantic, Central Pacific, and Panama Basin. *Ocean Biocoenosis Ser.*, 1: 1-85.
Stosch, H.A. von. – 1967. Chrysophyta. In: H. Ettl, D.G. Muller, K. Neumann, H.A. von Stosch and W. Weber (eds.), *Vegetative Florpflaunzung, Parthenogenese und Apogamie bei Algen*, pp. 637-656. Springer-Verlag, Berlin.
Tangen, K. – 1972. *Papposphaera lepida*, gen. nov., sp. nov, a new marine coccolithophorid from Norwegian coastal waters. *Nor. J. Bot*., 19: 171-178.
Tappan, H. – 1980. Haptophyta, coccolithophores, and other calcareous nannoplankton. In: H. Tappan (ed.), *The Paleobiology of plant protists*, pp. 678-803. Freeman, California.
Theodoridis, S. – 1984. Calcareous nannofossil biostratigraphy of the Miocene and revision of the helicoliths and discoasters. *Utrecht Micropaleont. Bull*., 32; 1-271.
Thomsen, H.A. – 1980. Two species of *Trigonaspis* gen. nov. (Prymnesiophyceae) from West Greenland. *Phycologia*, 19: 218-229.
Thomsen, H.A., P.D.P. Bjørn, L. Højlund, J. Olensen and J.B. Pedersen. – 1995. *Ericiolus* gen. nov. (Prymnesiophyceae), a new coccolithophorid genus from polar and temperate regions. *Eur. J. Phycol*., 30: 29-34.
Thomsen, H.A. and K.R. Buck. – 1998. Nanoflagellates of East Pacific coastal Waters: Morphology, taxonomy, and biogeography of weakly calcified coccolithophorids (Prymnesiophyceae). *Cryptogamie Algol*., 19: 29-48.
Thomsen, H.A., K.R. Buck and F.P. Chavez. – 1994. Haptophytes as components of marine phytoplankton. In: J.C. Green and B.S.C. Leadbeater (eds.), *The Haptophyte Algae*, *Systematics Association Special Volume 51,* pp. 187-208. Clarendon Press, Oxford.
Thomsen, H.A., K.R. Buck, S.L. Coale, D.L. Garrison and M.M. Gowing. – 1988. Nanoplanktonic coccolithophorids (Prymnesiophyceae, Haptophyceae) from the Weddell Sea, Antarctica. *Nord. J. Bot*., 8: 419-436.
Thomsen, H.A. and K. Oates. – 1978. *Balaniger balticus* gen et sp. nov. (Prymnesiophyceae) from Danish Coastal Waters. *J. mar. biol. Ass. U.K*., 58: 773-779.
Thomsen, H.A., J.B. Østergaard and L.E. Hansen. – 1991. Heteromorphic life histories in Arctic coccolithophorids (Prymnesiophyceae). *J. Phycol*., 27: 634-642.
Throndsen, J. – 1972. Coccolithophorids from the Caribbean Sea. *Nor. J. Bot*., 19: 51-60.
Verbeek, J.W. – 1989. Recent Calcareous Nannoplankton in the Southernmost Atlantic. *Polarforschung*, 59: 45-60.
Volkmen, J.K., G. Eglinton, E.D.S. Corner and T.E.V. Forsberg. – 1980. Long-chain alkenes and alkenones in the marine coccolithophorid *Emiliania huxleyi*. *Phytochemistry*, 19: 2619-2622.
Vrind-de Jong, E.W. de, P.R.V. Emburg and J.P.M. de Vrind. – 1994. Mechanisms of calcification: *Emiliania huxleyi* as model system. In: J.C. Green and B.S.C. Leadbeater (eds.), *The Haptophyte Algae*, *Systematics Association Special Volume 51,* pp. 149-166. Clarendon Press, Oxford.
Wallich, G.C. – 1877. Observations on the coccosphere. *Ann. Mag. Nat. Hist., (Ser. 4)*, 19: 342-350.
Weber-van Bosse, A. – 1901. Etudes sur les algues de l'Archipel Malaisien 3. Note préliminaire sur les résultats algologiques de l'éxpedition du Siboga. *Ann. Jard. Bot. Buitenzorg. (ser. 2)*, 17: 126-141.
Westbroek, P. – 1991. *Life as a geological force. Dynamics of the Earth*. Norton, New York.
Westbroek, P., J.E. van Hinte, G.-J. Brummer, M. Veldhuis, C. Brownlee, J.C. Green, R. Harris and B.R. Heimdal. – 1994. *Emiliania huxleyi* as a key to biosphere-geosphere interactions. In: J.C. Green and B.S.C. Leadbeater (eds.), *The Haptophyte Algae*, *Systematics Association Special Volume 51,* pp. 321-334. Clarendon Press, Oxford.
Westbroek, P., J.R. Young and K. Linschooten. – 1989. Coccolith production (Biomineralization) in the marine alga *Emiliania huxleyi*. *J. Protozool*., 36: 368-373.
Winter, A., Z. Reiss and B. Luz. – 1978. Living *Gephyrocapsa protohuxleyi* in the Gulf of Elat. *Mar. Micropaleontol*., 3: 295-298.
Winter, A., Z. Reiss and B. Luz. – 1979. Distribution of living coccolithophore assemblages in the Gulf of Elat ('Aqaba). *Mar. Micropaleontol.*, 4: 197-223.
Winter, A. and W.G. Siesser. – 1994. Atlas of living coccolithophores. In: A. Winter and W.G. Siesser (eds.), *Coccolithophores*, pp. 107-159. Cambridge University Press, Cambridge.
Young, J.R. – 1989. Observations on heterococcolith rim structure and its relationship to developmental processes. In: J. A. Crux and S. E. van Heck (eds.), *Nannofossils and their aplications*, pp. 1-20. Ellis Horwood, Chichester.
Young, J.R. – 1992a. The description and analysis of coccolith structure. In: B. Hamrsmíd and J.R. Young (eds.), *Nannoplankton Research, vol. II: Tertiary biostratigraphy and paleoecology; quaternary coccoliths*, pp. 35-71. MND Hodonín, Prague.
Young, J.R. – 1992b. Report - Terminology working group meeting, London April 1992. *Int. Nannoplankton Assoc. Newslett*., 14: 6-8.
Young, J.R. – 1998. Neogene. In: P.R. Bown (ed.), *Calcareous Nannofossil Biostratigraphy*, pp. 225-265. Chapman and Hall, London.
Young, J.R., J.A. Bergen, P.R. Bown, J.A. Burnett, A. Fiorentino, R.W. Jordan, A. Kleijne, B. van Niel, A.J.T. Romein and K.

von Salis. – 1997. Guidelines for coccolith and calcareous nannofossil terminology. *Palaeontology*, 40: 875-912.
Young, J.R. and P.R. Bown. – 1997a. Higher classification of calcareous nannofossils. *J. Nannoplankton Res*., 19: 15-20.
Young, J.R. and P.R. Bown. – 1997b. Cenozoic calcareous nannoplankton classification. *J. Nannoplankton Res*., 19: 36-47.
Young, J.R., R.W. Jordan and L. Cros. – 1998. Notes of nannoplankton systematics and life-cycles *Ceratolithus cristatus*, *Neosphaera coccolithomorpha* and *Umbilicosphaera sibogae*. *J. Nannoplankton Res*., 20: 89-99.
Young, J.R. and P. Westbroek. – 1991. Genotypic variation in the coccolithophorid species *Emiliania huxleyi*. *Mar. Micropaleontol*., 18: 5-23.

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Taxonomic Index

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