

UNIVERSITAT DE BARCELONA

Planktonic coccolithophores of the NW Mediterranean

M. Lluïsa Cros i Miguel



UNIVERSITAT DE BARCELONA Departament d'Ecologia

PLANKTONIC COCCOLITHOPHORES OF THE NW MEDITERRANEAN



M. Lluïsa Cros i Miguel

UNIVERSITAT DE BARCELONA

Programa de Doctorat de Ciències del Mar

Bienni 1993-94

PLANKTONIC COCCOLITHOPHORES

OF THE NW MEDITERRANEAN

Memoria redactada per M. Lluïsa Cros i Miguel per a optar al grau de Doctor en Geologia

Vist-i-plau del Director de Tesi

RMargaly

Dr. Ramon Margalef i López

Barcelona, març de 2001

CONTENTS

RESUMEN	I – XVI
ACKNOWLEDGEMENTS / AGRAÏMENTS XV	'II – XVIII
CHAPTER I INTRODUCTION	1
CHAPTER II MATERIAL AND METHODS	12
CHAPTER III CLASSIFICATION OF LIVING SPECIES	22
CHAPTER IV COMBINATION COCCOSPHERES	99
CHAPTER V DISTRIBUTION OF IDENTIFIED SPECIES IN NW MEDITERRANEAN WATI	ers 107
CHAPTER VI CALCAREOUS NANNOPLANKTON IN SURFACE SEDIMENTS	150
CHAPTER VII COCCOLITH CHEMISTRY	157
Conclusions	163
References	165
PLATES	183 - 365

INTRODUCCION

INTRODUCCIÓN GENERAL

Este trabajo estudia las algas haptófitas que de una manera continuada, o en algún momento de su ciclo de vida, producen y llevan cocolitos. Los cocolitos son delicadas y muy bellas plaquitas de carbonato cálcico, que no se sabe bien para qué les sirven, pero que tienen un papel muy importante en la translocación del carbonato cálcico y otros elementos, desde la columna de agua hacia los sedimentos.

A estas algas se las ha llamado (y aún se las llama) cocolitoforales, coccolitofóridos y también cocolitóforos y aunque su clasificación está aún en continuo cambio, cada vez parece más claro que no se las puede agrupar en un solo orden taxonómico; así el nombre de cocolitoforales, con su terminación en '-ales' indicando el grado taxonómico de orden, parece cada vez más controvertido. Quizás el nombre de cocolitóforos con el sufijo -foros, que proviene del Griego '- *phoros*, *-phoron*, y significa 'llevar', sea el más adecuado, ya que simplemente indica 'portador de cocolitos'. O quizás fuera útil buscar un nombre en latín o griego para poder designarlos en todos los idiomas sin necesidad de más traducciones.

Los cocolitos, debido precisamente a la doble cualidad de estar formados biológicamente y a ser, ellos mismos formadores de sedimentos, son muy valiosos para la paleoceanografía y para la estratigrafía; ellos han sido, y son, muy útiles como fósiles con valor estratigráfico desde el Jurásico hasta nuestros días (Perch-Nielsen von Salis, 1985).

Estas algas, que pueden formar cocolitos, juegan un papel muy importante en el ciclo del carbono (Westbroek, 1991) pero además están relacionadas con el ciclo del azufre (Keller *et al.*, 1989; Charlson *et al.*, 1987; Simó & Pedrós-Alió, 1999), y son también, especialmente la *Emiliania huxleyi*, susceptibles de multiplicarse en grandes cantidades (Holligan *et al.*, 1983), formando las llamadas mareas blancas. Todas estas propiedades enunciadas ya y otras, como el ser productores de lípidos, hacen que los cocolitóforos puedan ser considerados como importantes agentes biogeoquímicos.

LOS COCOLITOFOROS Y LAS COCOSFERAS

Se considera que estos organismos pueden estar constituidos por la célula y por su envoltura de cocolitos. A la envoltura, formada por todos los cocolitos que envuelven la célula, se la llama cocosfera. Esta cocosfera suele estar constituida por una sola clase de cocolitos, aunque no son raras las especies y géneros que presentan diversos tipos de cocolitos en diferentes partes de la cocosfera. La forma de estos cocolitos es, aún actualmente, el más importante carácter para clasificar las especies.

Es necesario destacar que existen dos grandes grupos de cocolitos: los heterococolitos y los holococolitos. Los heterococolitos están formados por unidades cristalinas de forma y tamaño variable; su biomineralización es intracelular y se produce a partir del primer anillo formador del cocolito ('proto-coccolith ring') (Manton & Leedale, 1969; Inouye & Pienaar, 1988; Westbroek *et al.*, 1989; Young, 1989; Fresnel, 1989). Los holococolitos estan formados de numerosos cristalitos pequeños, y la calcificación parece ser extra-celular (Manton & Leedale, 1963; Klaveness, 1973; Rowson *et al.*,1986), y sucede dentro del periplasto (de Vrind-de Jong *et al.*, 1994). También existe un pequeño grupo de cocolitos que no parecen verdaderos heterococolitos ni holococolitos y que se distinguen fundamentalmente por poseer formas poco simétricas y no tener la característica cristalización de los otros grandes grupos (heterococolitos y holococolitos); a este tercer

grupo, actualmente, se le denomina nanolitos, por extensión del nombre que primeramente designaba estructuras calcáreas de origen incierto.

ESTRATEGIAS DE REPRODUCCIÓN Y FASES HETEROMÓRFICAS

Los cocolitóforos pueden multiplicarse vegetativamente por división binaria o por mitosis. Los ciclos de vida de diferentes taxones, especialmente de los géneros *Pleurochrysis* y *Emiliania*, han sido estudiados con detenimiento y ha quedado bien patente que estas haptófitas calcáreas pueden presentar ciclos de vida extraordinariamente complejos, incluyendo fases en las cuales estas algas no presentan coccolitos. Estas diferentes fases pueden presentar escamas orgánicas debajo de los coccolitos, sólo escamas orgánicas sin coccolitos o fases sin coccolitos ni escamas orgánicas (Fresnel, 1989; Billard, 1994).

Ha sido bien estudiado el ciclo de vida de especies costeras pertenecientes a las familias Pleurochrysidaceae y Hymenomonadaceae. Se ha podido conocer que estas especies presentan una fase diploide con heterococcolitos y una fase haploide, no calcificada, de aspecto pseudofilamentoso que es béntica; ambas fases parecen tener una capacidad ilimitada de reproducción vegetativa (von Stosch, 1967, Rayns, 1962; Leadbeater, 1970; Gayral & Fresnel, 1983; Fresnel, 1989, 1994; Fresnel & Billard, 1991).

Emiliania huxleyi Hay et Mohler presenta también una fase con cocolitos y otra sin cocolitos; pero en esta especie todas las fases son plantónicas (ver trabajos de Paasche & Klaveness, 1970; Klaveness & Paasche, 1971; Klaveness, 1972). Análisis con citometría de flujo han mostrado que las células con cocolitos tienen doble cantidad de DNA, por lo que se considera que son la fase diploide de esta especie (Green *et al.*, 1996).

Parke & Adams (1960) demostraron que en cultivos monoclonales del heterococolitóforo *Coccolithus pelagicus* (Wallich) Schiller podían aparecer células con holococolitos que anteriormente habían sido consideradas como petenecientes a una especie bien distinta, concretamente al holococolitóforo *Crystallolithus hyalinus* Gaarder et Markali; posteriormente, Rowson *et al.* (1986) mostraron que en esta fase de holococolitóforo se podían producir dos tipos de holococolitos: el tipo '*Crystallolithus hyalinus*' y un tipo de cocolito más agujereado, que había sido previamente descrito como *Crystallolithus braarudii* Gaarder 1962. Estudios del tipo de escamas en las especies mejor estudiadas y en estas fases del *C. pelagicus* han originado razonadamente la hipótesis de que en esta especie, la fase con heterococcolitos sería diploide y la fase con holococolitos sería haploide (Billard, 1994).

De una forma aislada, mientras se estudiaban muestras procedentes del plancton marino, se encontraron ejemplares "híbridos" de cocolitóforos, cocosferas combinadas que presentaban coccolitos previamente descritos como pertenecientes a especies diferentes. Incluso en estudios efectuados con microscopios ópticos se describieron explícitamente estas cocosferas (Kamptner, 1941; Lecal, 1961); a veces incluso con descripciones minuciosas y dibujos detallados como es el caso de las células combinadas de Syracosphaera tuberculata Kamptner (actualmente conocida como Coronosphaera mediterranea (Lohmann) Gaarder) y Zygosphaera wettsteinii Kamptner (actualmente Calyptrolithina wettsteinii (Kamptner) Kleijne) (Kamptner, 1941). Actualmente, con técnicas de microscopía electrónica se ha comprobado la existencia de tales especímenes y en la literatura hay registros fotográficos de gran detalle. Entre los ejemplares registrados hay que destacar los de Coccolithus pelagicus con Crystallolithus hyalinus (Samtleben & Schröder, 1992; Samtleben et al. 1995) cuyo ciclo de vida ha sido estudiado en cultivo. También se pueden destacar los ejemplares con Calcidiscus leptoporus (Murray et Blackman) Loeblich Jr. & Tappan y Crystallolithus rigidus Gaarder (Kleijne, 1991; Cortés, 2000) y la asociación de Syracosphaera sp. type A con un holococolitóforo no identificado

(Kleijne, 1991). Thomsen *et al.* (1991), reconocieron ejemplares combinados de heterococolitóforos de los géneros *Papposphaera* Tangen, *Pappomonas* Manton & Oates and *Wigwamma* Manton, Sutherland & Oates con holococolitos de los géneros *Turrisphaera* Manton, Sutherland & Oates, *Trigonaspis* Thomsen y *Calciarcus* Manton, Sutherland & Oates respectivamente. Actualmente a estas cocosferas combinadas con heterococolitos y holococolitóforo y holococolitóforo. También es de destacar la asociación encontrada por Alcober & Jordan (1997) con el heterococolitóforo *Neosphaera coccolithomorpha* Lecal-Schlauder y la especie *Ceratolithus cristatus* Kamptner; esta asociación ha sido ratificada posteriormente por otros autores (Young *et al.*, 1998; Sprengel & Young, 2000).

CLASIFICACIÓN

Actualmente, y a pesar de todos los inconvenientes hallados, la morfología de los cocolitos es aún el principal carácter para clasificar los cocolitóforos. Es necesario remarcar las muchas dificultades que presenta la clasificación de estas algas, como lo demuestran los numerosos cambios experimentados en su taxonomía y las diferentes clasificaciones en uso en la literatura. No obstante, el nivel de familia es un taxón robusto y ha sido universalmente aceptado como el principal nivel de clasificación (Jordan & Green, 1994; Young & Bown, 1997a), observándose pocos cambios en los últimos años dentro de este nivel taxonómico.

Para poder clasificar estas haptófitas podemos acudir a los trabajos de Cavalier-Smith (1998) y referencias citadas en él, para los más altos niveles taxonómicos; a Young and Bown (1997b) para las rangos taxonómicos a partir de orden; Jordan & Kleijne (1994) and Jordan & Green (1994) para rangos de familia y taxones de inferior nivel; Kleijne (1991) y Kleiine (1992)para las familias Calyptrosphaeraceae v Rhabdosphaeraceae respectivamente. Es necesario citar también los estudios de Perch-Nielsen (1985b). Chrétiennot-Dinet (1990), Heimdal (1993) y Kleijne (1993) como referencias de incalculable ayuda para la clasificación de estos organismos calcáreos.

EL NW DEL MEDITERRÁNEO.

Este mar relativamente pequeño, aunque profundo, que es el Mediterráneo, está conectado al Océano Atlántico, por el estrecho de Gibraltar. Es característico su clima con veranos calientes y secos e inviernos templados y medianamente húmedos. La evaporación es un factor de gran importancia en el Mediterráneo y es la causa de la relativamente alta salinidad de sus aguas (37-39 ‰ comparado con el 36.5 ‰ de las aguas atlánticas (Emelyanov & Shimkus, 1986)). También la temperatura de las aguas profundas es relativamente alta en este mar y es 8 o 10°C superior a la del Atlántico a igual profundidad, e incluso la supera en 13-14°C cerca del fondo.

El Mediterráneo occidental, limitado por los estrechos de Sicilia-Túnez y Gibraltar-Marruecos, tiene unos 860,000 Km² de superficie y una profundidad máxima de unos 3,700 m. La salinidad es de unos 38.5‰ en las aguas profundas y un poco menor cerca de la superficie. La temperatura del agua profunda es relativamente constante y es de unos 13°C, en cambio la de la superficie varía entre los 13° en invierno y cerca de los 26 °C en verano (Margalef, 1985a). La oxigenación es buena en toda la columna de agua. En esta área, la evaporación es superior a la entrada de aguas dulces (lluvia y aportes de ríos) por lo que el agua marina incrementa en salinidad y consecuentemente en densidad.

El estrecho de Gibraltar es el lugar donde se intercambian las aguas marinas el Mediterráneo con el Atlántico. Una corriente de agua profunda con alta salinidad atraviesa el estrecho hacia el Atlántico llevando aguas mediterráneas. Esta pérdida de agua es

compensada por otra corriente superficial que transporta hacia el Mediterráneo aguas atlánticas superficiales y, consecuentemente, pobres en nutrientes. Este balance negativo de nutrientes mantiene el Mediterráneo en un estado oligotrófico, donde el fósforo es el principal elemento limitante (Margalef, 1985a).

El presente estudio se sitúa en el NW del Mediterráneo, en el llamado mar Catalano-Balear, entre la Península Ibérica y las Islas Baleares. En esta área se pueden diferenciar tres masas de aguas superficiales: 1) agua costera de baja salinidad cercana a la Península Ibérica; 2) agua densa y fría, característicamente mediterránea, en la parte central; y 3) el agua más caliente y estratificada, de influencia atlántica, cercana a las Islas. Estas diferentes masas de agua están separadas entre si por dos frentes, el frente Catalán y el frente Balear, los cuales están asociados al talud Catalán y Balear respectivamente (Salat & Cruzado, 1981; Font *et al.*, 1986-1987; 1988; Tintore *et al.*, 1990; Pinot *et al.*, 1994). El agua costera fluye del NE al SW; el agua de influencia atlántica presenta sentido contrario en la parte de las Islas Baleares, esto es del SW hacia el NE; y en el centro existe una elevación persistente de isotermas e isohalinas, en forma de domo, que se puede interpretar como una verdadera divergencia. Tanto los frentes de talud como la divergencia dan fertilidad a la zona, como lo prueba el desarrollo de un fuerte máximo de clorofila profundo (DCM) durante el largo período de estratificación (Margalef & Estrada, 1987; Estrada & Margalef, 1988; Estrada & Salat, 1989; Salat, 1996, Estrada, 1996, 1999).

RESUMEN DEL TRABAJO REALIZADO

MUESTRAS RECOLECTADAS

Para el trabajo realizado se usaron muestras de agua marina recogidas de la columna de agua a diferentes profundidades, principalmente entre los 0 y 100 metros de profundidad y también se observaron muestras superficiales de sedimentos de esta área.

Las muestras de aguas fueron recolectadas principalmente a bordo de B/O 'Garcia del Cid' y durante las campañas MESO-95 (realizada entre el 30 Mayo y el 16 Junio de 1995), FRONTS-95 (realizada entre el 17 y el 23 de Junio de 1995), MESO-96 (entre el 18 de Junio y el 3 de Julio de 1996), FRONTS-96 (entre el 16 y el 21 de Septiembre de 1996), FANS-1 (entre el 1 y el 10 de Noviembre de 1996), FANS-2 (del 4 al 14 de Febrero de 1997) y FANS-3 (del 13 al 15 de Julio de 1997).

Los sedimentos procedían de 15 testigos recolectados a profundidades marinas entre 1000 y 2100 m durante la campaña VALSIS I (realizada desde el 1 y el 12 de Octubre de 1988) a bordo del B/O 'Suroit'.

METODOLOGÍA USADA

Las muestras de agua marina fueron normalmente recolectadas usando una 'rosette' equipada con botellas Niskin.

Las muestras procedentes de las campañas MESO-95 y FRONTS-95 fueron fijadas a bordo con formaldehído neutralizado y guardadas hasta su filtración en el laboratorio. Las muestras procedentes de las posteriores campañas (MESO-96, FRONTS-96, FANS-1, FANS-2 y FANS-3) y cuatro réplicas de muestras de la campaña MESO-95 fueron filtradas directamente a bordo. Los mejores resultados fueron obtenidos con las muestras filtradas directamente (ver en: Fijación *versus* no fijación), por lo cual las muestras de los años posteriores al 1995 fueron filtradas sin previa fijación.

Para filtrar el agua, generalmente unos 200 cc., se usó una bomba de vacío y filtros Nucleopore de 25 mm de diámetro y con un tamaño de poro de 0.8 μ m; debajo de este

filtro se usó un filtro de 3μ m de tamaño de poro para obtener una distribución homogénea de las partículas filtradas. La sales fueron eliminadas con unos 2cc. de agua comercial. Los filtros se secaron al aire, o bajo una luz, y luego se guardaron con vacio parcial en cajas herméticamente cerradas hasta la preparación para la observación en el Microscopio Electrónico de Barrido (MEB).

Tanto para los contajes como para la observación detallada y obtención de fotografías se usó un Microscopio Electrónico de Barrido Hitachi S-570 y la metodología usada para la preparación de la muestra ha sido la convencional para microscopía electrónica.

Sobre especímenes de la muestra de la estación 147 (MESO-95), filtrada sin previa fijación, se efectuaron análisis de rayos X con un Espectrómetro de Energia Dispersiva (EDS); la metodología usada fue la convencional para este tipo de análisis y el microscopio electrónico usado fue un STEREOSCAN Cambridge Instruments equipado con un detector de rayos X sensible a los elementos de número atómico mayor de 11.

Las muestras de sedimentos fueron preparadas, con ligeras modificaciones, según la técnica descrita en Perch-Nielsen (1985). Para la observación de las muestras y la toma de fotografías se usó un Microscopio Electrónico de Barrido Hitachi S-570.

FIJACIÓN VERSUS NO FIJACIÓN. COMPARACIÓN DE METODOLOGÍAS.

En la campaña MESO-95 se fijaron las muestras de agua con formaldehído neutralizado según la metodología clásica (Throndsen, 1978). Además, en cuatro estaciones se tomaron muestras paralelas que se filtraron directamente, sin previa fijación, a fin de comparar metodologías. Los procesos de preparación y observación posteriores fueron idénticos para todas las muestras estudiadas.

En las muestras tratadas previamente con fijador, se observó una peor conservación de los cocolitóforos así como una pérdida importante de especímenes, especialmente entre los holococolitóforos. A través de los cálculos efectuados con los resultados de estas 4 muestras con y sin fijador, se constataron pérdidas del 39 hasta el 69% en los cocolitóforos de las muestras previamente fijadas; estas pérdidas pueden llegar al 75, e incluso al 100%, en la comunidad de holococolitóforos.

LISTA TAXONÓMICA DE LAS ESPECIES OBSERVADAS

Durante el presente estudio se han encontrado, y se han representado con fotografías y descripciones, 166 diferentes cocolitóforos, de los cuales sólo 102 están bien descritos con nombres formales. Algunos de estos cocolitóforos no tienen aún nombre formal pero están descritos en la literatura, otros sólo están representados en la literatura con una figura y otros se presentan en este trabajo por primera vez para la ciencia. En este resumen se citan por orden alfabético las especies encontradas que estaban bien descritas en la literatura con nombre formal y, cuatro especies descritas sólo con nomenclatura abierta.

Acanthoica acanthifera Lohmann, 1912 ex Lohmann, 1913.

Acanthoica quattrospina Lohmann, 1903

Algirosphaera robusta (Lohmann, 1902) Norris, 1984

Alisphaera capulata Heimdal, in Heimdal et Gaarder, 1981.

Alisphaera unicornis Okada et McIntyre, 1977

Anacanthoica acanthos (Schiller, 1925) Deflandre, 1952

Anoplosolenia brasiliensis (Lohmann 1919) Deflandre, 1952

Anthosphaera cf. fragaria Kamptner, 1937 emend. Kleijne, 1991

Anthosphaera fragaria Kamptner, 1937 emend. Kleijne, 1991

Anthosphaera lafourcadii (Lecal 1967) Kleijne 1991

Anthosphaera periperforata Kleijne, 1991 Calcidiscus leptoporus (Murray et Blackman, 1898) Loeblich and Tappan, 1978. Calciopappus cf. rigidus Heimdal, 1981, in Heimdal & Gaarder, 1981 Calciosolenia murrayi Gran, 1912 Calicasphaera blokii Kleijne, 1991 Calicasphaera concava Kleijne, 1991 Calyptrolithina divergens (Halldal et Markali 1955) Heimdal 1982 var. divergens Calyptrolithina divergens var. tuberosa (Heimdal) Jordan et al., 1993 Calyptrolithina wettsteinii (Kamptner, 1937) Kleijne, 1991. (1) Calvptrolithophora gracillima (Kamptner, 1941) Heimdal 1980 Calyptrolithophora papillifera (Halldal) Heimdal in Heimdal et Gaarder, 1980 Calyptrosphaera cialdii Borsetti et Cati, 1976 Calyptrosphaera dentata Kleijne, 1991 Calyptrosphaera heimdaliae R.E. Norris, 1985, orth. emend. Jordan et Green, 1994 Calvptrosphaera oblonga Lohmann, 1902. (2) Calyptrosphaera sphaeroidea Schiller 1913 Ceratolithus cristatus Kamptner, 1950 Corisphaera cf. gracilis Kamptner 1937 Corisphaera sp. type A Kleijne, 1991. (3) Corisphaera strigilis Gaarder, 1962 Corisphaera tyrrheniensis Kleijne, 1991 Coronosphaera binodata (Kamptner, 1927) Gaarder, in Gaarder et Heimdal, 1977. Coronosphaera mediterranea (Lohmann) Gaarder in Gaarder et Heimdal, 1977. Cyrtosphaera aculeata (Kamptner, 1941) Kleijne, 1992 Cyrtosphaera cucullata (Lecal-Schlauder, 1951) Kleijne, 1992 Cyrtosphaera lecaliae Kleijne, 1992 Daktylethra pirus (Kamptner, 1937) Norris, 1985 Discosphaera tubifera (Murray et Blackman, 1898) Ostenfeld, 1900 Emiliania huxleyi (Lohmann, 1902) Hay and Mohler in Hay et al., 1967. Florisphaera profunda Okada and Honjo, 1973 Gaarderia corolla (Lecal 1965) Kleijne 1993 Gephyrocapsa ericsonii McIntyre et Bé, 1967 Gephyrocapsa muellerae Bréhéret 1978 Gephyrocapsa oceanica Kamptner, 1943 Gladiolithus flabellatus (Halldal and Markali, 1955) Jordan and Chamberlain 1993 Helicosphaera carteri (Wallich 1877) Kamptner, 1954 var. carteri Helicosphaera carteri var. hyalina (Gaarder) Jordan et Young, 1990 Helicosphaera carteri var. wallichii (Lohmann) Theodoridis, 1984 Helicosphaera pavimentum Okada et McIntyre, 1977 Helladosphaera cornifera (Schiller, 1913) Kamptner, 1937. Homozygosphaera arethusae (Kamptner) Kleijne 1991 Homozygosphaera triarcha Halldal and Markali, 1955. Michaelsarsia elegans Gran 1912, emend. Manton et al. 1984. Oolithotus antillarum (Cohen), Reinhardt, in Cohen and Reinhardt 1968 Oolithotus fragilis (Lohmann 1912) Martini et Müller, 1972 Ophiaster formosus Gran 1912, sensu Gaarder 1967, emend. Manton et Oates, 1983, var. formosus Ophiaster hydroideus (Lohmann) Lohmann emend. Manton et Oates, 1983 Palusphaera vandelii Lecal, 1965 emend. R.E. Norris, 1984

Papposphaera lepida Tangen, 1972 Periphyllophora mirabilis (Schiller) Kamptner, 1937. (4) Polycrater galapagensis Manton et Oates, 1980 Poricalyptra aurisinae (Kamptner 1941) Kleijne, 1991 Poricalyptra isselii (Borsetti and Cati, 1976) Kleijne, 1991 Poritectolithus poritectum (Heimdal 1980) Kleijne, 1991 Poritectolithus tyronus Kleijne, 1991 Reticulofenestra parvula (Okada et McIntyre, 1977) Biekart, 1989 var. parvula Rhabdosphaera clavigera Murray et Blackman, 1898. Rhabdosphaera xiphos (Deflandre and Fert, 1954) Norris, 1984 Scyphosphaera apsteinii f. dilatata Gaarder, 1970. Scyphosphaera apsteinii Lohmann, 1902 Sphaerocalyptra cf. adenensis Kleijne, 1991 Sphaerocalyptra quadridentata (Schiller, 1913) Deflandre, 1952 Svracolithus catilliferus (Kamptner, 1937) Deflandre, 1952. (5) Syracolithus confusus Kleijne, 1991. (6) Syracolithus dalmaticus (Kamptner) Loeblich et Tappan, 1966 Syracolithus quadriperforatus (Kamptner 1937) Gaarder 1980 Syracolithus schilleri (Kamptner) Kamptner, 1956 Syracosphaera cf. dilatata Jordan Kleijne and Heimdal, 1993 Syracosphaera ampliora Okada et McIntyre, 1977 Syracosphaera anthos (Lohmann 1912) Janin, 1987 Syracosphaera halldalii Gaarder ex Jordan et Green, 1994 Syracosphaera histrica Kamptner, 1941 Syracosphaera lamina Lecal-Schlauder, 1951 Syracosphaera marginaporata Knappertsbusch, 1993 (*) Syracosphaera molischii Schiller, 1925 Syracosphaera nana (Kamptner, 1941) Okada & McIntyre, 1977 Syracosphaera nodosa Kamptner, 1941 Syracosphaera noroitica Knappertsbusch, 1993, orthog. emend. Jordan et Green, 1994 (*) Svracosphaera ossa (Lecal) Loeblich Jr. et Tappan, 1968 Syracosphaera prolongata Gran ex Lohmann sensu Throndsen, 1972 Syracosphaera prolongata Gran ex Lohmann, 1913 sensu Heimdal & Gaarder, 1981 Syracosphaera pulchra Lohmann, 1902 Syracosphaera rotula Okada et McIntyre, 1977. Syracosphaera sp. type D Kleijne 1993. (*) Syracosphaera sp. type G Kleijne 1993. (*) Syracosphaera sp. type L Kleijne 1993. Syracosphaera tumularis Sánchez-Suárez, 1990. (*) Turrilithus latericioides Jordan et al. 1991 Umbellosphaera tenuis (Kamptner, 1937) Paasche in Markali et Paasche, 1955 Umbilicosphaera hulburtiana Gaarder, 1970 Umbilicosphaera sibogae (Weber-van Bosse 1901) Gaarder 1970 var. sibogae Umbilicosphaera sibogae var. foliosa (Kamptner, 1963) Okada et McIntyre 1977 ex Kleijne, 1993 Zygosphaera amoena Kamptner, 1937 Zvgosphaera bannockii (Borsetti and Cati, 1976) Heimdal, 1980. (7) Zygosphaera hellenica Kamptner, 1937 Zygosphaera marsilii (Borsetti and Cati 1976) Heimdal 1982

(*) Especies que a partir de este estudio se les reconoce que poseen cocolitos exotecales.

(1) Actualmente se considera como fase holococolitóforo de Coronosphaera mediterranea.

(2) Actualmente se considera como fase holococolitóforo de Syracosphaera pulchra.

(3) Actualmente se considera como fase holococolitóforo (tipo perforado) de *Syracosphaera bannockii*.

(4) Actualmente se considera como fase holococolitóforo de Syracosphaera anthos.

(5) Actualmente se considera como fase holococolitóforo de Helicosphaera carteri.

(6) Actualmente se considera como fase holococolitóforo (tipo perforado) de *Helicosphaera carteri*.

(7) Actualmente se considera como fase holococolitóforo de Syracosphaera bannockii.

COCOSFERAS COMBINADAS

En las muestras de aguas estudiadas se encontró un elevado número de cocosferas que eran combinación de dos especies previamente reconocidas. Algunas de estas combinaciones ya habían sido encontradas anteriormente; otras lo eran por primera vez; la mayoría estaban formadas por heterococolitos y holococolitos conjuntamente, pero otras tenían heterococolitos y nanolitos o incluso dos tipos diferentes de holococolitos.

Algunos tipos de combinaciones, que presentaban heterococolitos y holococolitos se encontraron repetidamente u otros autores habían encontrado el mismo tipo de combinación o el ejemplar hallado estaba tan bien formado que era difícil pensar en el azar como causa formadora de la combinación. En este grupo se pueden citar las combinaciones siguientes: *Helicosphaera carteri* con *Syracolithus catilliferus*; *Syracosphaera pulchra* con *Calyptrosphaera oblonga*; *Syracosphaera anthos* con *Periphyllophora mirabilis*;

Coronosphaera mediterranea con *Calyptrolithina wettsteinii*; *Syracosphaera nana* con un holococolitoforo sp; *Acanthoica quattrospina* con holococolitóforo sp.; *Syracosphaera* sp. aff. type K of Kleijne (1993) con *Corisphaera* sp. type A of Kleijne (1991). Así, estas parejas de cocolitóforos podrían ser en realidad una sola especie que puede presentar una o más fases diferentes.

También se encontraron otras asociaciones con heterococolitos y holococolitos que, aunque no se descarta la posibilidad de que sean verdaderos especímenes combinados, podrían muy bien ser sólo fruto del azar. De entre este grupo de posibles combinaciones podemos destacar: Syracosphaera molischii con Anthosphaera fragaria; Syracosphaera sp. type D de Kleijne (1993) con Homozygosphaera arethusae; Syracosphaera histrica con Calyptrolithophora papillifera; Syracosphaera nodosa con Helladosphaera cornifera; Syracosphaera sp. 4 (actualmente S. delicata sp. nov.) con Corisphaera sp. type B de Kleijne (1991); Rhabdosphaera clavigera con Sphaerocalyptra quadridentata; Acanthoica sp. con Sphaerocalyptra sp. 2.

Otro grupo diferente de cocosferas combinadas son las que presentan heterococolitos y nanolitos conjuntamente. Así, la combinación que se ha encontrado con *Neosphaera coccolithomorpha* var. *nishidae* y *Ceratolithus cristatus* ya ha sido citada anteriormente y es ya reconocida como una sola especie que puede presentar tres tipos diferentes de cocolitos: los llamados de '*Neosphaera coccolithomorpha*', los llamados 'hoop-like', que son cocolitos en forma de aro, y el característico nanolito *Ceratolithus*. Otro tipo de combinación, encontrada en el presente trabajo de forma repetida, pero que no había sido hallada anteriormente, es la combinación de diferentes *Polycrater* con *Alisphaera* y *Canistrolithus*. *Polycrater* es considerado como un cocolitóforo "*incertae sedis*" que tiene nanolitos, mientras que *Alisphaera* y *Canistrolithus* son considerados dos especies de heterococolitóforos con cocolitos de muy similar estructura (Jordan & Chamberlain, 1993).

Lo que tienen en común todas las 'especies' citadas en este grupo de combinaciones es la dificultad que presentan para clasificarlas; muchas de ellas estan consideradas especies '*incertae sedis*' y sobre otras se habían hecho intentos forzados de añadirlas en taxones bien organizados como es le caso de *Alisphaera* dentro de la familia Syracosphaeraceae.

Las combinaciones halladas que se presentan con dos tipos de holococolito son: Syracolithus catilliferus con Syracolithus confusus y Corisphaera sp. type A de Kleijne (1991) con Zygosphaera bannockii. En estas cocosferas combinadas se han podido distinguir cocolitos que parecen transición entre los dos principales formadores de la combinación.

Parece probable que las combinaciones entre heterococolitos y holococolitos representen la transición entre una fase de heterococolitóforo y otra fase de holococolitóforo análogas a las bien documentadas de la especie *Coccolithus pelagicus*; ya que la fase de transición parece ser un hecho esporádico y que ocurre en un tiempo breve, se puede comprender que las cocosferas combinadas sean encontradas en muy raras ocasiones.

La observación de los ejemplares de combinaciones de heterococolitos con nanolitos, tanto de la literatura como los encontrados en el presente trabajo, sugiere que los nanolitos podrían originarse dentro de las cocosferas de los heterococolitóforos. Una cocosfera de '*Neosphaera*' puede cobijar en su interior cocolitos de tipo aro, que son los que se encuentran envolviendo a los cocolitos grandes e irregulares tipo ceratolito. Algunos de los ejemplares hallados de *Polycrater* con *Alisphaera* y también los de *Polycrater* con *Canistrolithus* sugieren que *Polycrater* podría emerger del interior de *Alisphaera* o *Canistrolithus* o sea del considerado heterococolitóforo; el hecho de que sea relativamente usual ver cocosferas de *Alisphaera* con un gran agujero apical parece ser coherente con las anteriores observaciones. Así, los nanolitos podrían ser los más internos moradores de estas cocosferas mixtas.

Las cocosferas combinadas con dos tipos de holococolitos se diferencian de los anteriores grupos especialmente porque los cocolitos implicados en la combinación son muy parecidos, tanto en tamaño como en su forma e incluso en la cocosfera puede haber cocolitos que parecen formas transicionales. Tanto en las combinaciones de *Syracolithus catilliferus* y *Syracolithus confusus* como en la de *Zygosphaera bannockii* y *Corisphaera* sp type A los dos tipos de cocolitos se parecen mucho, pero uno es más perforado que el otro (tanto *Syracolithus confusus* como *Corisphaera* sp type A presentan agujeros) de la misma forma que los dos tipos de holococolitos de *Coccolithus pelagicus*. En este estudio han sido presentadas las asociaciones de *Helicosphaera carteri* con *Syracolithus catilliferus* y tambien *Syracosphaera* sp. *aff.* type K of Kleijne (1993) con *Corisphaera* sp. type A of Kleijne (1991) y por tanto estas asociaciones de un heterococolitóforo asociado con dos holococolitóforos muy parecidos entre si, pero uno más perforado que el otro, podrían ser análogas con el ciclo de vida de *Coccolithus pelagicus*.

Los dos tipos de cocolitóforo de la asociación *Helicosphaera carteri - Syracolithus catilliferus* parecen ocupar dos habitats diferentes. En las campañas realizadas, mientras *Syracolithus catilliferus* habitaba aguas superficiales, *Helicosphaera carteri* ocupaba, generalmente en las mismas estaciones, aguas más profundas y más ricas. Este comportamiento hace pensar en una estrategia ecológica de supervivencia.

Las cocosferas combinadas registradas proceden de muchas áreas diferentes, pero realmente se puede observar que una gran proporción procede del área Mediterránea y concretamente del Mediterráneo occidental. Este mar ha sido relativamente bien estudiado, pero también son muchos los estudios sobre cocolitóforos en comunidades naturales que se han efectuado en todo el mundo y en muy pocas ocasiones se han encontrado ejemplares híbridos. Parece pues probable que las condiciones del Mediterráneo occidental puedan de

alguna manera favorecer los cambios de fase frecuentes y, consecuentemente puedan incrementar la proporción de las posibilidades de encontrar cocosferas combinadas. El Mediterráneo es un mar pequeño con fuertes gradientes físico-químicos. Este mar presenta fuertes y bruscos cambios en las condiciones físicas y se puede pensar que estos cambios puedan inducir frecuentes cambios de fase, si éstos están realmente relacionados con las condiciones cambiantes. El Mediterráneo contiene una alta diversidad de especies (Margalef, 1997) y en términos generales es un mar oligotrófico y los holococolitóforos son más frecuentes en ambientes oligotróficos Kleijne (1991). Además, en este mar se forma un elevado máximo de clorofila profundo lo que puede favorecer los ciclos de vida adaptados a diferentes condiciones. O, ¿son sólo las facilidades para la mezcla de aguas y poblaciones lo que puede favorecer un mayor número de cambios de fase y, en último término, un aumento en las posibilidades de encontrar cocosferas combinadas?

DISTRIBUCIÓN DE ESPECIES IDENTIFICADAS EN LAS AGUAS DEL NW MEDITERRÁNEO

La campaña MESO-95 (del 30 Mayo al 16 Junio de 1995), en el mar Catalano-Balear, aportó una visión sinóptica espacial, en superficie y a 40m de profundidad, de la distribución de algunas especies. FRONTS-95 (del 17 al 23 de Junio de 1995), con el principal transecto delante de Barcelona y otro situado un poco más al Sur, aportó interesantes datos sobre la distribución vertical de las especies encontrándose una importante segregación respecto a la profundidad en un gran número de cocolitóforos. La campaña MESO-96 (del 18 Junio al 3 Julio de 1996), con varios transectos frente a la costa catalana, desde la desembocadura del Ter hasta la del Llobregat, confirmó la gran estratificación vertical observada en la anterior campaña y registró la distribución espacial de los cocolitóforos a principios del verano. FRONTS-96 (del 16 al 21 de Septiembre de 1996), con un transecto delante de Sant Feliu de Guíxols, registró la distribución vertical a finales de verano. Las campañas FANS-1 (del 1 al 10 Noviembre de 1996), FANS-2 (del 4 al 14 de Febrero de 1997) y FANS-3 (del 13 al 15 de Julio de 1997), en una área cercana y directamente influenciada por la desembocadura del Ebro, aportaron una visión espacial y también temporal de la distribución de los cocolitóforos en esta zona.

El presente estudio muestra claramente que algunas especies prefieren aguas de profundidades bien definidas, lo que confirman trabajos previos de otros autores (Okada & Honjo, 1973; Jordan & Winter, 2000). Los intentos para tipificar estos niveles se hicieron en base a criterios fóticos y generalmente, en la literatura, se describen tres zonas: zona fótica alta 'upper photic zone (UPZ)', zona fótica media 'middle photic zone (MPZ)' y zona fótica baja 'lower photic zone (LPZ)' aunque Okada & Honjo (1973) desdobló la zona fótica media diferenciando la parte superior de esta zona y la llamó la zona fótica mediaalta 'upper-middle photic zone'. En aguas sub-tropicales el límite entre la zona fótica alta y la media ha sido señalado a 80m de profundidad y el límite entre la media y la baja está señalado a 120m de profundidad (Winter et al., 1994; Jordan & Chamberlain, 1997). Las especies estudiadas en el NW del Mediterráneo presentaron distribuciones cuyas zonas preferenciales tenían una anchura menor que en otras áreas descritas en la literatura; también se ha observado que los límites de estas zonas, en el NW del Mediterráneo, están situados más arriba de la columna de agua, o sea en niveles menos profundos que los citados anteriormente en otras áreas; no obstante, está reconocido que estos limites dependen de la latitud (Okada & Honjo, 1973) y que condiciones locales pueden comportar importantes variaciones (Jordan & Winter, 2000). En el presente trabajo se han propuesto tentativamente cinco zonas: zona fótica alta, alta-media, media, parte alta de la zona fótica baja, y zona fótica baja. La zona fótica alta (≈ 0-30m) contiene las especies de holococolitóforos Syracolithus catilliferus, Calyptrosphaera heimdaliae, Calyptrosphaera

oblonga y, ademas, contiene también otros cocolitóforos como Calyptrolithina wettsteinii, Rhabdosphaera clavigera, Rhabdosphaera xiphos y Polycrater spp., que habitan esta zona o tambien la inmediata inferior, zona fótica alta-media. La zona fótica alta-media (≈ 30-40m) comparte con la anteriormente descrita los cocolitóforos C. wettsteinii, Rhabdosphaera clavigera, Rhabdosphaera xiphos and Polycrater spp. y contiene otras claramente prefieren esta zona: Calyptrolithophora papillifera, especies que Homozygosphaera arethusae and Umbellosphaera tenuis; además esta zona alta-media presenta las más altas densidades de Emiliania huxleyi y Syracosphaera pulchra. La zona fótica media (≈ 40-60m) contiene Syracosphaera molischii, Helicosphaera carteri, Gephyrocapsa ericsonii, Coronosphaera mediterranea y Alisphaera spp. La parte más alta de la zona fótica baja (≈ 60-80m) contiene Ophiaster hydroideus y Papposphaera spp.. La zona fótica baja (> 80m) contiene Florisphaera profunda.

Emiliana huxleyi ha sido considerada una especie con ausencia de preferencias respecto a las zonas fóticas; no obstante, tanto Okada & Honjo (1973) como Reid (1980) encontraron que esta especie tenía preferencia por la zona fótica media-alta; esta preferencia se ha corroborado en el presente trabajo. Además, en este estudio se ha observado que *E. huxleyi* tipo C y el tipo sobrecalcificado se encuentran preferencialmente en aguas de la zona fótica baja mientras que el tipo A aparece en la parte alta de la columna de agua; Hagino et al. (2000) observaron también la preferencia del tipo C para aguas profundas.

La preferencia de los holococolitóforos por las aguas superficiales ya ha sido observada anteriormente, pero la preferencia específica de algunas de estas especies por niveles concretos no había sido citada; en este estudio se ha observado que a algunos cocolitóforos como *Calyptrolithophora papillifera* les gusta habitar en una zona restringida, concretamente en la parte alta de la zona fótica media.

Es importante destacar el comportamiento de *Helicosphaera carteri*, cuyo heterococolitóforo se encontró preferencialmente en la zona fótica media; mientras que su holococolitóforo asociado, *Syracolithus catilliferus*, se encontró preferencialmente en las mismas estaciones, pero en la zona fótica alta. Debido a la presencia de un intenso máximo profundo de clorofila en esta área del Mediterráneo en el período de estratificación (Margalef & Estrada, 1987) y a la afinidad de los holococolitóforos para las aguas oligotróficas (Kleijne, 1993), se puede hipotetizar que esta diferente preferencia de hábitat de *H. carteri/ S. catilliferus* puede estar asociada a una estrategia ecológica del ciclo de vida, con la fase heterococolito habitando aguas relativamente ricas y profundas y la fase holococolito subsistiendo en aguas pobres pero mejor iluminadas.

Es bien conocido que las comunidades de cocolitóforos cambian con la latitud, incluso se han establecido diferentes zonas con grupos de cocólitoforos característicos de cada una de ellas, que están relacionadas con la latitud y con las más importantes corrientes superficiales (McIntyre and Bé, 1967; Okada and Honjo, 1973). Estudios detallados de áreas concretas también han mostrado la relación de diferentes comunidades de cocolitóforos con las diferentes masas de aguas (Samtleben & Schröder, 1992). En el presente trabajo, se han podido observar ciertas preferencias de algunas especies por una determinada masa de agua de este mar Catalano-Balear; *Emiliania huxleyi*, aunque está en todas partes, se le aprecia una mayor densidad en aguas con influencia costera cercanas a la Península Ibérica, mientras que *Gephyrocapsa ericsonii*, e incluso con mas claridad, *G. mullerae* y *G. oceanica* están más asociadas a aguas de origen atlántico, situadas cerca de las Islas Baleares. A través de todo el estudio se ha observado una preferencia de *Syracosphaera pulchra* por las aguas con influencia costera, mientras que *Syracosphaera molischi* tiende a estar situada mar adentro, asociada a las aguas que presentan más salinidad y son más característicamente mediterráneas.

Es interesante señalar los fuertes cambios en las comunidades de cocolitóforos asociados a la estacionalidad, que se han podido observar en el transcurso del presente estudio, especialmente a través de las campañas Fans-1, Fans-2, Fans-3 (realizadas en otoño, invierno y verano respectivamente) y Meso-96 y Fronts-96 (realizadas al principio y a finales de verano respectivamente). Los holococolitóforos fueron importantes componentes de la comunidad en verano, especialmente a principios de verano (29.6 y 17.5 % del total en Meso-96 y Fans-3, respectivamente); su abundancia decrecía durante el otoño y su representación fue casi nula en invierno (en la campaña Fans-2, en Febrero, ellos representaban solo el 0.1% del total de la abundancia de cocolitóforos). Emiliania huxleyi, la especie mayoritaria, presentó una tendencia de abundancias completamente opuesta a los holococolitóforos. En las campañas Fans, E. huxleyi mostró una abundancia relativa del 61.2% en Noviembre y alcanzó el 78.6 % en Febrero; en verano su abundancia relativa fue del 46.8 %. E. huxleyi mostró incluso más bajas abundancias relativas en las campañas Meso-96 (31.8%) y Fronts-96 (45.45%) realizadas a principios y a finales de verano respectivamente; estas abundancias más bajas de las campañas Meso-96 y Fronts-96 pueden ser explicadas por las condiciones más oligotróficas del área donde se realizaron, lejos de la influencia de las aguas del rio Ebro, respecto al área donde se muestrearon las campañas Fans, directamente influenciada por los aportes fluviales del Ebro. En la literatura existen abundantes datos sobre la época en que Emiliania huxleyi presenta mayores abundancias: en el Pacifico central, a 28°N, Reid (1980) encontró las más altas abundancias en invierno; en el Atlántico, a 29°N y 34°N, con muestras de trampas de sedimentos, Sprengel et al., (2000) y Broerse et al., (2000) encontraron los máximos de Emiliania entre enero y marzo mientras que a 48°N estos máximos ocurrían en abril (Broerse et al., 2000; Ziveri et al., 2000) y en las latitudes altas, al sur de Islándia, se observan las importantes proliferaciones de Emiliania (Holligan et al 1983, 1993) a principios de verano. Si observamos todos los datos citados anteriormente, vemos que los máximos de abundancia de Emiliania huxleyi retrasan su aparición a medida que la latitud aumenta, observación que ya es bien conocida en las proliferaciones de fitoplancton (Margalef, 1945).

NANOPLANCTON CALCÁREO EN LOS SEDIMENTOS SUPERFICIALES

Los sedimentos superficiales del NW del Mediterráneo estudiados eran ricos en remanentes biológicos, mayoritariamente de carbonato cálcico. El nanoplancton calcáreo fue el resto inorgánico biológico más común en todos los sedimentos estudiados, principalmente como cocolitos aislados, aunque, excepcionalmente, se observaron algunas cocosferas enteras. Se encontraron también otros tipos de restos de fitoplancton, como tecas de dinoflageladas calcáreas. Es interesante señalar que los restos de diatomeas eran muy escasos y aparecían corroídos. También se observaron foraminíferos calcáreos, pero los restos silíceos de radiolarios fueron escasos y corroídos, con signos obvios de disolución.

Emiliania huxleyi fue el cocolito más abundante con un 68.2 a 80.7% de los cocolitos observados. La contribución de *Gephyrocapsa* era de 8.2 a 20.4 %. En general, los valores de *Gephyrocapsa* se incrementaban cuando decrecían los de *Emiliania*, excepto en algunas muestras como en una estación situada al sur del delta del Ebro, en donde ambos taxones estaban poco representados. Esta estación se mostró sorprendentemente pobre en cocolitos, pero en cambio presentaba abundante proporción de elementos terrígenos.

La distribución de las abundancias del nanoplancton calcáreo en los sedimentos del mar Catalano-Balear presenta una disposición regional en franjas más o menos paralelas a la costa. Las abundancias relativas de *Emiliania huxleyi* decrecen cerca del 10% desde la Peninsula Ibérica hacia las Islas Baleares, mientras que *Gephyrocapsa* tiene la tendencia opuesta, esto es, incrementa cerca del 10% desde el oeste hacia el Este. Las abundancias de

Gephyrocapsa parecen estar relacionadas a las masas de agua caliente y estratificada de origen atlántico. En este sentido Knappertsbusch (1993) describía a G. oceanica como un trazador para las aguas de superficie de origen atlántico en el Mediterráneo. Es interesante la distribución de Umbilicosphaera, con valores bajos cerca de los márgenes de la Península Ibérica y las Islas Baleares y un claro incremento hacia el centro y el noreste de la cuenca; este tipo de distribución coincide con la estructura domal, de divergencia, en el centro de la cuenca (Margalef 1985, Estrada 1985, y Estrada & Margalef 1988) y está en concordancia con las preferencias de Umbilicosphaera para las aguas salinas y relativamente ricas en nutrientes (Roth, 1994). La distribución de Helicosphaera tiende a incrementarse hacia el centro y hacia el Norte de la cuenca con bajos valores cerca los márgenes; la muestra situada al Sur del delta del Ebro es una excepción ya que presenta valores más altos encontrados de Helicosphaera. Esta muestra también presenta las más altas abundancias de Calcidiscus. Tanto los cocolitos de Helicosphaera como los de Calcidiscus están considerados como cocolitos altamente resistentes a la disolución (Shneidermann, 1977) y están incluidos en el grupo de especies robustas que más se conservan en condiciones de disolución y retrabajamiento (Findlay, 1998). Trabajos geológicos en esta área (Alonso et al. 1991) revelaban un talud con inestabilidad sedimentaria donde se producía importante retrabajamiento y transporte de sedimentos desde la plataforma hacia esta área. Estas circunstancias ambientales pueden favorecer, y pueden explicar, la gran proporción de estos cocolitos altamente resistentes en esta zona.

Los sedimentos del mar Catalano-Balear presentan una muy alta proporción de restos carbonatados y una gran pobreza de restos silícicos. La mayoría de los escasos restos de esqueletos de sílice encontrados estaban corroídos, sugiriendo que el ópalo biogénico es fácilmente disuelto en esta área. Según Emelianov & Shimkus (1986), en sedimentos mediterráneos, las tasas de acumulación de la sílice amorfa son de 50 a 100 veces menores que las de carbonato cálcico. Según estos autores las altas temperaturas del agua profunda del Mediterráneo, así como el relativamente alto pH, facilitarían esta disolución.

En estas muestras de sedimentos se encontraron muy pocos holococolitos, en claro contraste con la abundancia de los heterococolitos. El hecho de que los holococolitos estén presentes y sean comunes en la columna de agua indica que la escasez hallada en los sedimentos puede ser el resultado de su reconocido bajo potencial de preservación. Estas diferencias, en las características de preservación, pueden ser observadas también a nivel de especies tanto de los holococolitos como de los heterococolitos. Así, mientras el género *Gephyrocapsa* está representado en los sedimentos, principalmente por *G. muellerae* y *G. oceanica*, que son escasos en la columna de agua, en cambio en ésta se encuentra mayoritariamente *G. ericsonii*, que a su vez es una especie escasa en los sedimentos.

El nanoplancton contenido en los sedimentos refleja la comunidad de cocolitóforos de la columna de agua, pero de una forma sesgada, con sobrerepresentación de las especies resistentes y baja representación de las poco resistentes. Queda bien patente que las diferencias que presentan las especies a la disolución juegan un importantísimo papel en la estructura de la comunidad de nanoplancton en los sedimentos. No obstante, rasgos característicos de las comunidades que habitan las diferentes masas de agua se mantienen en los sedimentos subyacentes como ya habían observado otros autores (Samtleben and Schröder, 1992). Además, los sedimentos pueden integrar los restos producidos a través de todas las estaciones del año, lo que les confiere una cualidad de síntesis muy importante para el conocimiento de las masas de agua y su comportamiento.

COMPOSICIÓN ELEMENTAL DEL NANOPLANCTON CALCÁREO

Debido a que los sedimentos del mar Catalano-Balear son ricos en nanoplacton calcáreo

y que el Mar Mediterráneo conserva bien los restos carbonatados, es importante conocer los elementos que contienen los cocolitóforos, ya que éstos tendrán en el Mediterráneo un importante papel como translocadores de los elementos que contienen, desde la columna de agua hasta el sedimento. Estos elementos, al quedar atrapados en el registro sedimentario, no podrán tener un papel activo en su ciclo biogeoquímico. Por tanto el estudio del contenido elemental de los cocolitóforos es muy importante para evaluar las pérdidas debidas a estas algas en los ciclos biogeoquímicos de tales elementos.

En el presente estudio se intenta hacer una primera aproximación al conocimiento de la composición elemental de diferentes grupos de cocolitóforos con la técnica de 'X-ray' microanálisis. Para poder comparar la composicion de estas algas con otros grupos de fitoplancton con partes esqueléticas y para controlar técnicas, también fueron analizados ejemplares de diatomea y de dinoflagelado.

Los filtros en blanco daban respuestas tan pequeñas en el microanálisis que se hizo dificil ver señales de elementos en ellos. La diatomea presentó altas señales de Si y pequeños picos de S, Ca y Fe. La dinoflagelada mostró claras señales de Cl, Si y Ca y tambien trazas de Al, Mg, K y Cu.

El análisis de cocolitóforos indicó una alta proporción de calcio y señales que corresponden principalmente a Si, S, y Cl. La mayoría de los cocolitóforos dieron trazas de Al y varios presentaron tambien señales de Ag. Repetidas señales de P y Mg han sido observadas tambien.

La comparación de la composición elemental de los diferentes grupos de fitoplancton estudiados muestra, obviamente, la presencia de grandes señales de Ca en cocolitóforos y de grandes señales de Si en diatomeas. Además, se ha citado la clara presencia de S en los cocolitóforos, especialmente en los holococolitóforos; esta presencia es menos notoria en la diatomea y en el dinoflagelado. La presencia de S puede relacionarse con la produccion de DMSP y DMS.

La presencia de los elementos Al y Ag ha de considerarse con cautela, ya que el 'stub' del microscopio fue de Al, y se usó Ag coloidal para fijar los trozos de filtro en el 'stub'. Las señales de P han sido observadas especialmente en los especímenes de *Emiliania huxleyi* y *Calyptrosphaera heimdaliae*; pero, debido a los problemas técnicos con estas señales en presencia de cantidades importantes de calcio (se sabe que el microanalizador empleado puede dar señales secundarias de calcio que se pueden confundir con picos de P), y aunque se usó un programa de ordenador para corregir estos problemas, se considera que tales picos deben ser también considerados cautelosamente. No obstante Siesser (1977) encontró P en los cocolitos y sus analisis le ofrecían confianza.

Se observó que la señal de Mg es imperceptible en los heterococolitóforos de *Emiliania huxleyi* y falta en *Syracosphaera pulchra* y *Rhabdosphaera clavigera*, pero está obviamente presente en los especímenes de holococolitóforos tanto de *Calyptrolithina wettsteinii*, *Calyptrosphaera heimdaliae* y *Helladosphaera cornifera*. Estos resultados sugieren la presencia de cationes de Mg en los retículos de carbonato de los holococolitóforos.

Siesser (1977) no detectó Mg en la calcita de los cocolitóforos. Pero el trabajo cita que los cocolitos estudiados por Siesser fueron principalmente *Coccolithus pelagicus* y también *Reticulofenestra*. Se puede especular que, en los sedimentos fósiles en los que trabajó este autor, los demás cocolitos estudiados fuesen también heterococolitos. En el presente estudio los heterococolitos no dieron señales perceptibles de Mg con lo que los presentes resultados, en principio, no se contradicen con los de Siesser, sino que podrían corroborarlos. Estudios sobre la composición química de *Emiliania huxleyi* enfocados en la relación Ca:C (Fagerbakke et al. 1994), mostraron señales de Na, Mg, S y Cl; pero un análisis de correlaciones entre elementos sugirió a los autores que la presencia de estas señales podría

explicarse por contaminación a causa del agua marina.

No es posible descartar que el alto Mg contenido en los holococolitóforos observados en nuestro estudio sea producido por contaminación del agua marina, especialmente por la mayor relación superficie/volumen que la estructura del holococolito sugiere. Pero si la presencia de Mg se corrobora, este resultado puede ayudar a explicar el bajo potencial de preservación de los holococolitóforos, ya que es sabido que la presencia de Mg aumenta la solubilidad del carbonato cálcico (Margalef, 1974) y que los organismos con calcita de alto contenido en Mg están considerados altamente frágiles (Siesser, 1971).

En este trabajo de la composición elemental de los cocolitos se han obtenido resultados que aunque preliminares y mirados con cautela, se piensa que pueden ser muy importantes. La confirmación de la presencia de Mg en los holococolitóforos puede ser realmente importante tanto para entender mejor las diferencias entre heterococolitos y holococolitos como para poder profundizar un poco mas en los ciclos de vida de estos organismos. Se sabe que el fósforo es un elemento limitante en el Mediterráneo (Margalef 1985); por tanto, el conocimiento de su presencia, y cuantificación clara, en los cocolitóforos es de maxima importancia, tanto para profundizar en el ciclo geobioquímico de este elemento, como para comprender las relaciones del fósforo y el Mediterráneo y sus consecuencias en la vida de los organismos en este mar.

CONCLUSIONES

1.- Para estudiar los cocolitóforos es necesario que durante todo el tratamiento de la muestra no se disuelvan los cocolitos. El usar una metodología con fijación de la muestra antes del filtrado puede disolver arbitrariamente los cocolitos y este hecho puede causar una gran variación en los resultados. La comparación de muestras filtradas sin ningún tipo de fijación previa, con réplicas que fueron anteriormente fijadas (con formaldehído neutralizado) presentaron diferente comunidad de cocolitóforos; en las muestras previamente fijadas se observaron pérdidas del 39 al 69 % del total de cocolitóforos, y estos porcentajes alcanzaban el 75 e incluso el 100% en la comunidad de holococolitóforos.

2.- En el presente estudio se presentan 166 cocolitóforos, de los cuales sólo 102 especies y subespecies tienen nombre formal; otros están bien descritos en la literatura pero aún tienen un nombre informal; otros están sólo citados o representados con una imagen, y otros se presentan aquí por primera vez para la ciencia.

3.- Se ha trabajado en profundidad en el complejo género *Syracosphaera*. Este género posee especies que ahora quedan bien clarificadas, como es el caso de *S. nana* o *S. tumularis* e incluso se ha descrito una especie nueva, *S. delicata* sp. nov., anteriormente no reconocida ni presentada en la literatura. También se han descritos por primera vez 11 tipos de cocolitos exotecales que no habían sido previamente reconocidos; las especies a las que pertenecen son: *Syracosphaera* sp. I cf. *S. epigrosa* de Kleijne (1993), *S. marginaporata*, *S.* sp. II cf. *S. epigrosa* de Kleijne (1993), *S. tumularis*, S. sp. (aff. *S. orbiculus*, ovoide), S. sp. (aff. *S. orbiculus*, esferica), S. sp. (aff. *S. nana*), *S. cf. dilatata*, *S.* sp. type D de Kleijne 1993, *S. noroitica* y *S.* sp. type G de Kleijne (1993).

4.- La familia *Papposphaeraceae*, que se asocia en la literatura a aguas frías, presenta en el Mediterráneo un alto número de posibles nuevas especies e incluso un posible nuevo género.

5.- Se han reconocido siete combinaciones de heterococolitóforos con holococolitóforos con un alto grado de confianza y se han observado también otras siete posibles, aunque con un menor grado de confianza. Las asociaciones bien establecidas son: *Helicosphaera carteri* con *Syracolithus catilliferus*, *Syracosphaera pulchra* con *Calyptrosphaera oblonga*, *Syracosphaera anthos* con *Periphyllophora mirabilis*, *Coronosphaera mediterranea* con *Calyptrolithina wettsteinii*, *Syracosphaera nana* con holococolitos, *Acanthoica quattrospina* con holococolitoforo sp. y *Syracosphaera* sp. *aff*. tipo K de Kleijne con *Corisphaera* sp. tipo A de Kleijne (actualmente *Syracosphaera bannockii* comb. nov.).

Dos holococolitóforos que forman parte de las combinaciones anteriormente mencionadas, también se han encontrado formando asociaciones con otras especies de holococolitoforos (*Syracolithus catilliferus* con *Syracolithus confusus* y *Corisphaera* sp. tipo A de Kleijne with *Zygosphaera bannockii*). En ambos casos, los dos tipos de holococolito difieren esencialmente en la presencia o ausencia de perforaciones.

Se han encontrado por primera vez asociaciones de *Polycrater*, coccolitos considerados de tipo nanolito, con heterococolitóforos: *Polycrater* spp. con *Alisphaera* spp., y *Polycrater* galapagensis var A (moteado) con *Canistrolithus* sp. 1.

6.- En la combinación de *Helicosphaera carteri* con *Syracolithus catilliferus* (hetero- con holococolitóforo) se ha observado que, en aguas oligotróficas estivales del NW del Mediterráneo, el heterococolitóforo *Helicosphaera carteri* habita la zona fótica media mientras que la fase holococolitoforo, *S. catilliferus*, vive en las aguas superficiales mas pobres; tal comportamiento puede ser una estrategia ecológica para su ciclo de vida.

7.- La estructura de la comunidad de cocolitóforos presenta importantes variaciones verticales, horizontales y estacionales. Es notorio la fuerte estratificación vertical que presentan algunas especies y la importancia que tienen los cambios estacionales en los cocolitóforos de esta área.

8.- Los microanálisis de rayos X practicados en cocolitóforos detectan un mayor contenido en magnesio en los holococolitóforos que en los heterococolitóforos.

9.- Los sedimentos superficiales del mar Catalano-Balear contienen una alta proporción de restos carbonatados y escasez de restos silícicos. La mayor parte de estos restos silícicos se encontraron corroidos, sugiriendo que el ópalo es fácilmente disuelto en esta área.

10.- Los restos de cocolitóforos encontrados en los sedimentos presentaban una distribución de especies con bandas mas o menos paralelas a la costa lo cual refleja el modelo de distribución de las diferentes masas de agua en esta área.

11.- El nanoplancton calcáreo contenido en los sedimentos refleja la comunidad de cocolitóforos de la columna de agua, pero con una sobrerepresentación de las especies altamente resistentes y subrepresentación de las especies con bajo potencial de preservación. La disolución aparece como un factor de control importantísismo para los restos de nanoplancton en los sedimentos.

ACKNOWLEDGMENTS / AGRAÏMENTS

The first motor of this study was Dr. Ramon Margalef, who highlighted the importance of a thorough examination of coccolithophores in the NW Mediterranean with Scanning Electronic Microscopy and encouraged this work. Dra. Marta Estrada promoted the collection of samples and provided the necessary support to implement the research.

I had the pleasure to have Dr. Margalef as advisor of this thesis. He directed it with a delicate personal attitude, with few words and a lot of ideas, trying to make it a rigorous work.

Both Drs. R. Margalef and M. Estrada made this study possible and I am pleased to thank them, now that the thesis preparation has come to an end.

Written discussions and also personal communications with Drs. Annelies Kleijne and Jeremy R. Young were very valuable. I greatly appreciated the always quick replies and concise e-mails from Dr. J.R. Young.

Some parts of the present thesis reflect comments and corrections made by coauthors and reviewers of already published papers and here I would like to give my aknowledgement to all of them.

The International Nannoplankton Association, INA, (5 th, 6 th, and 7 th conferences) and the Coccolithophorid Evolutionary Biodiversity and Ecology Network, CODENET, (workshops in Blagnac, Caen and Barcelona) gave me the opportunity to meet coccolith workers and to improve my knowledge of calcareous nannoplankton. Thanks to all who made possible such meetings and to everyone who made suggestions and gave me advice to improve this work. Thanks to all.

I would like to thank Belén Alonso and Albert Palanques who kindly provided the sediment samples studied in Chapter VI. The water samples were collected mainly by Laura Arin, and also by Dolors Blasco, Marta Estrada, Gloria Medina, Xelu A. G. Morán, Beatriz Diez, Dolors Vaqué and Magda Vila. The hydrographic data were provided by Jordi Salat. I would like to thank these colleagues and all the others who helped in the cruises.

The SEM counts and micrographs were undertaken at the Institut de Ciències del Mar (ICM). I would like to express my sincere acknowledgements to José Manuel Fortuño who took direct care of the micrographs; these images have been essential for the development of the present study. Thanks also to Joan Biosca who made high quality technical photographic work, before the SEM images were computer-digitalized.

Laura Arin kindly provided the *Syracosphaera pulchra* combination coccosphere figured in Plate 78 figs. 3 a-b. The techniques learned from Ian Probert to isolate cells and the sticky filter prepared by José Manuel Fortuño made it possible to observe the same specimen also in the SEM (Pl. 78 fig. 4).

The X-ray microanalyses (Chap. VII) were performed at the Servei d'Espectroscopia de la Universitat de Barcelona and I would like to thank Ramon Fontarnau and Antonia Santiago for their direct assistance and help in the work.

A very special acknowledgement to Ian Probert, who had the patience to correct the English language of this thesis. The valuable help of Eva Sastre Mulet in classical languages is gratefully recognized; translations from German language of bits of literature were provided especially by Montse Sala and also by Renate Sharek, Anngret Lieb and Lluís Vena.

The staff of the library service of the ICM, Marta Ezpeleta, Gloria Medina and Carmen Losada, helped in the literature search and specially in finding old bibliography. The maps of Chapters 1 and 2, several graphics of Chapter 5 (specifically figs. 5.1, 5.2, 5.3, 5.9, 5.10, 5.35, 5.37 and 5.39) and the graphics of Chapters 6 and 7 were improved by José M. Anguita. The figures of vertical distributions in Chapter 5 were prepared by Laura Arin. Plates 78, 79, 80, 81, 82, 84 and 86 were composed by Jordi Corbera. Ramón A. Vena helped with the bibliography. Enric Saiz, and Roberto Fernández helped in finishing the last version of the thesis. Thanks to all of them.

Vull agraïr a totes les persones del ICM i del Departament d'Ecologia de la Universitat de Barcelona l'ajut que m'han proporcionat en tot moment. Gràcies a tots!

I també vull expresar aquí el meu agraïment a tota la meva familia, amics i persones que m'estimen; sobretot per compendre tantes ausencies i per totes les ajudes aportades. I de manera molt especial vull donar les gràcies als meus pares per tot el soport i l'estímul rebuts. I també a en Ramón i a en Lluís, per l'ajuda i comprensió durant aquest treball.

A tots: Moltes Gràcies!

This research was supported by the C.S.I.C. and projects MAR91-0359, GRQ93-8041, AMB94-0853; MAS2-CT93-0063, MAS3-CT96-0051, FRMX-ET97-0113 and MAR98-0932. Samples were provided from cruise Valsis I, projects MAS2-CT930063, MAS3-CT95-0037, MAS3-CT95-0016 and Programme PICASSO (MEC-HF98-207).

The EC TMR project Coccolithophorid Evolutionary Biodiversity and Ecology Network (FRMX-ET97-0113) gave me the possibility to meet the CODENET people, to learn and to talk about coccolithophores, and to discuss in a very friendly atmosphere, especially in Blagnac, where most of the CODENET meetings were held.

I. INTRODUCTION

I.1 THE COCCOLITHOPHORIDS OR COCCOLITHOPHORES

COCCOLITHOPHORAL, COCCOLITHOPHORID OR COCCOLITHOPHORE, WHICH IS THE CORRECT NAME?

During recent years, several different names have been used to designate the group of calcareous Haptophyta which present the singular characteristic of bearing (having the cell surrounded by) coccoliths. Since the present study deals with this specific haptophyte group, some discussion about the issue of nomenclature employed in the literature is appropriate. All three names above mentioned express the main morphological characteristic of the group, but when analysed in detail, some differences are observed:

COCCOLITHO+PHOR+AL; (PHOR, from Greek *-phoros*, *-phoron*, bearing) and (-AL, taxonomic suffix which indicates the ORDER status).

COCCOLITHO+PHOR+ID; (PHOR, from Greek *-phoros*, *-phoron*, bearing) and (-ID, from Latin *-is*, *-ides*; from the Greek *-is*, *ides*; is a patronymic suffix which means: 'belonging to' or 'connected with').

COCCOLITHO+PHORE; (-PHORE, from Modern Latin *-phorus*, *-phorum*, from Greek *-phoros*, *-phoron*, bearing). The suffix -phore is an english combining form which constitute nouns: 'bearer', 'producer'.

This group of haptophytes was previously considered with a taxonomic rank of order, but nowadays this status is repeatedly questioned (see below). For this reason the suffix –al (or -ales) is ill-advised at the moment. The suffix –id, on the other hand, is not an accurate description of the real characteristic of the group, i.e. that all of them 'bear coccoliths' and not that they are 'related with the coccolith bearers'. This characteristic of 'bearing' coccoliths is correctly described by the suffix –phore, and for this reason the word coccolithophore (coccolith bearer) is here considered the appropriate name.

OUTLINE

These pages consider coccolithophores, a group without rigorous taxonomic meaning, as embracing all (golden-brown) microalgae which in a continuous way, or 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 translocation 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 from the Jurassic until present (Perch-Nielsen von Salis, 1985 a,b) and detailed chronostratigraphic and paleoecological reconstructions have been successfully established (e.g. the studies of NW Mediterranean Pliocene sediments by Matias, 1982, 1990 and of W Mediterranean Pleistocene-Holocene sediments by Flores *et al.* 1997).

The coccolithophores play key roles in global biogeochemical cycles, particularly in the carbon-carbonate cycle (Honjo, 1976; Westbroek, 1991; Westbroek *et al.*, 1994), but also in the sulphur cycle since they produce dimethylsulphoniopropionate (DMSP), the precursor of dimethyl sulphide (DMS) (Keller *et al.*, 1989; Malin & Kirst, 1997) which may influence climate through stimulating cloud formation and influencing the Earth's radiative balance (Charlson *et al.*, 1987; Simó & 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.*, 1983), 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. From a study of English chalk, H. C. Sorby (1860, 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. In 1860, G. C. Wallich, aboard a transatlantic cruise, studied mud samples and found ball-shaped bodies having coccoliths at regular intervals; he called them 'coccospheres'. Like Sorby, Wallich 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 electronic microscopy (TEM) and scanning electronic 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 μ m 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 (see Heimdal, 1993; Young *et al.*, 1997). Detailed cytological investigations have been undertaken, including studies of the formation of coccoliths and scales (Klaveness & Paasche, 1971; Inouye & Pienaar, 1984; Inouye & Pienaar, 1988; Fresnel, 1989; Fresnel & Billard, 1991) and detailed descriptions of complex organelles such as the haptonema (Inouye & 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 & Leedale, 1969; Inouye & Pienaar,

INTRODUCTION

1988; Westbroek *et al.*, 1989; Young, 1989; Fresnel, 1989, Fresnel & Billard, 1991; Pienaar, 1994). The holococcoliths are formed of numerous minute ($<0.1 \mu$ m) crystallites; their calcification appears to occur extra-cellularly (Manton & 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 & Pienaar, 1980; Hori & Inouye, 1981; Hori & Green, 1985).

The studies of von Stosch (1955, 1967), Parke & Adams (1960), Klaveness & Paasche (1971) and Fresnel (1989) have shown that coccolithophores of very different types can be involved in highly complex life cycles (Billard, 1994). Parke & 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 & 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 (see 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 coastal genera Pleurochrysidaceae in the 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 nonmotile 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 & 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 & 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 & 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 & 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) Kleijne). 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. & Tappan and the holococcolithophore *Crystallolithus rigidus* Gaarder. 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.* (1991a), examining natural Arctic samples with TEM techniques, recognized cells of the heterococcolithophore genera *Papposphaera* Tangen, *Pappomonas* Manton & Oates and *Wigwamma* Manton, Sutherland & Oates that included or combined elements typical of the holococcolithophore genera *Turrisphaera* Manton, Sutherland & Oates, *Trigonaspis* Thomsen and *Calciarcus* Manton, Sutherland & 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 & Schröder (1992); another specimen with *C. pelagicus* heterococcoliths covered by holococcoliths of *Crystallolithus hyalinus* is figured by Samtleben in Winter & Siesser (1994) and in Samtleben et al. (1995).

Alcober & 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, further evidence of several of these previously recorded combinations (Cortés, 2000; Sprengel & Young, 2000; Cros *et al.*, 2000) as well as new combination coccospheres (Cros *et al.*, 2000) has been reported.

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.* (2000), are presented in Chapter IV.

It has seemed advisable to deal with the frequent observation of such "hybrid" forms, as the source of some difficulties in the taxonomic evaluation of the observed cells.

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 (see below and Chapter III).

Braarud *et al.* (1955) classified the coccoliths into three groups: heterococcoliths, holococcoliths and pentaliths. The latter group is now designated, in a more general sense, as nannoliths (see Young & 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 consequently grouped into a single family, the Calyptrosphaeraceae (Kleijne 1991, Jordan & Green, 1994; Young & Bown, 1997b).

HISTORY OF CHANGES IN HIGHER CLASSIFICATION

To evaluate the formal higher classifications now adopted and to understand their complexity, it is necessary to review recent taxonomic changes (see below, where the taxa are reviewed in descending order of rank, using bold type for the taxa-names where coccolithophores have been included). The families as accepted here behave as robust taxa (Jordan & Green, 1994) and they have been universally accepted as the main level of classification (Young & Bown, 1997a), to which relatively few changes have been introduced in recent years. For more clarity the taxonomic changes proposed below the family level will be reviewed inside each respective taxonomic group.

Kingdom

From Aristotle's time to the middle of the twentieth century, most biologists were content to distribute the living world into two kingdoms: **Plants** and Animals. Since the middle of the nineteenth century, however, many systematists have been convinced that

certain organisms, such as bacteria and fungi, differ from plants and animals more than plants and animals differ from each other.

Ernst Haeckel (1834 -1919) proposed a third kingdom of organisms, the Protista (Haeckel, 1866), that included the most primitive organisms of uncertain affinity, separate from the plants and animals. However, most biologists ignored such proposals or considered them without importance.

The climate of opinion began to change in the 1960s, largely as a result of the knowledge gained by the new biochemical and electron microscopy techniques and the kingdom Protoctista was proposed by Copeland (1956) to contain the microalgae as well as the macroalgae. A system of five kingdoms was proposed for the first time by R. W. Whittaker in 1959 (Whittaker & Margulis, 1978) and used, with few modifications, by Margulis & Schwartz (1982) in the guide "Five Kingdoms", where the new kingdom **Protoctista** included organisms that are neither animals, plants, fungi, nor prokaryotes; these authors recognized that this kingdom is defined by exclusion from the other well defined kingdoms: *Monera*, *Fungi*, *Animalia* and *Plantae*.

Cavalier-Smith (1981, 1986, 1989) established the kingdom **Chromista** and grouped in it all the organisms with chromoplasts located inside the rough endoplasmic reticulum (RER) and /or with tubular hairs (mastigonemes) on the surface of one or of both cilia, and he hypothesized that all the chromists descended from ancestors that had both characters. He based the differences to be retained between the members of that kingdom on their flagellar structure, pigments and chloroplasts. Most chromists are 'algae' with chloroplasts containing chlorophylls a and c, which are located not in the cytosol but within the lumen of the RER. In addition to their double chloroplast envelopes, chromistan plastids are surrounded by an additional smooth membrane, the periplastid membrane (Cavalier-Smith, 1989). Cavalier-Smith (1998) stated his confidence that all chromistan algae are evolutionary chimeras in which an eukaryotic host and, probably, a red algal symbiont are involved; the periplastid membrane would be a relict of the red algal plasma membrane.

Subkingdom

Cavalier-Smith (1986, 1989) elevated **Chromophyta** to subkingdom to be placed in the divisions Heterokonta and Haptophyta, segregating the Cryptophyta into another subkingdom, and he argued that these two subkingdoms differ with respect to the structure of their cilia, mitochrondria, plastids and periplast.

Infrakingdom

The infrakingdom **Haptophyta** Cavalier-Smith 1995 was proposed to raise the level of the separation between Heterokonta and Haptophyta from the division status to the rank of infrakingdom, recognizing the phenotypic diversity of the Heterokonta and the convenience of dividing this infrakingdom into distinct divisions. Though most heterokonts are algae grouped in the division Ochrophyta, a significant minority of genera are exclusively heterotrophic and have no plastids; nevertheless, molecular phylogeny using ribosomal RNA sequences supports the monophyly of heterokonts. Nowadays, with the incorporation of the new heterotrophic heterokont phylum (division) Bygira, this classification becomes even more justified (see Cavalier-Smith, 1998 and references therein). The infrakingdom Haptophyta contains only one division with the same name.

Division

The division **Haptophyta** (Hibberd, 1972; Cavalier-Smith, 1986) has its origins in the class erected by Christensen in 1962 to group all the organisms with an haptonema and to keep them apart from the class Chrysophyceae Pascher 1914. An alternative name for the group, Prymnesiophyceae (based on the genus *Prymnesium*), was proposed (and validated for class level) by Hibberd in 1976, following changes in the rules of botanical nomenclature, and in 1980 Hibberd elevated this group to the division level, but it was Cavalier-Smith who validated the name Haptophyta, as a *divisio nova*, using the published latin description of Hibberd 1976 for the Prymnesiophyceae. The Haptophyta thus conceived groups biciliate cells lacking tubular mastigonemes, but possessing chloroplast endoplasmic reticulum and usually one haptonema (Cavalier-Smith, 1986). It is now accepted that the division Haptophyta includes all those algae which at some stage in their life cycle possess a complete or vestigial haptonema, and only very rarely has this organelle completely disappeared (Jordan *et al.*, 1995). The division Haptophyta contains the single class Prymnesiophyceae.

N.B. In their revision of systematic history and taxonomy, Green & Jordan (1994) point out that, at the division level, the name Chromophyta (Christensen, 1962, 1990) represents conceptually a division wider than either the Haptophyta (Hibberd, 1972; Cavalier-Smith, 1986) or the Prymnesiophyta (Hibberd, 1976). These last two names, one descriptive and the other typified, have been used alternatively as synonyms in recent years. Nevertheless the name Prymnesiophyta, although in common use, has never been validated.

Class

In the scheme used by Jordan & Green (1994) there is only one class within the Haptophyta for which the typified name **Prymnesiophyceae** Hibberd 1976 (see the above explanation for the division level) is used. However, Cavalier-Smith (1993, 1994) recognizes two classes, the **Patelliferea** including those species with two equal or subequal smooth flagella and plate-scales and / or coccoliths, and the Pavlovea for *Pavlova* and related genera, whose members lack plate-scales or coccoliths and have anisokont flagella.

Subclass

There are important differences between *Pavlova* and related genera that set them apart from other haptophytes. For this reason and following morphological criteria, the relatives of *Pavlova* were grouped in one order, the Pavlovales (see Chrétiennot-Dinet, 1990), but Cavalier-Smith (1993), on the basis of 18s rRNA sequence data, separated the Pavlovea at the class level. Jordan & Green (1994) prefer to separate *Pavlova* and related genera from the rest of the haptophytes at the level of subclass, following Cavalier-Smith (1986). So, according to Jordan & Green (1994) and Jordan *et al.* (1995), the class Prymnesiophyceae would contain the subclasses Pavlovophycidae and **Prymnesiophycidae** (typified names based on the genera *Pavlova* and *Prymnesium* respectively, with the conventional botanical endings).

Order

Recent taxonomic schemes (e.g. Parke & Green in Parke & Dixon, 1976; Hibberd 1980; Green *et al.*, 1989; Chrétiennot-Dinet, 1990; Chrétiennot-Dinet *et al.*, 1993) have divided the Prymnesiophyceae into four orders, based on morphological characters:

INTRODUCTION

Coccosphaerales, Isochrysidales, Prymnesiales and Pavlovales. Each of these orders includes one or more families whose genera share common characteristics. Of these orders, only the Pavlovales appears to be a natural group (Hibberd 1980, Green et al., 1989, Cavalier-Smith 1993, see the above reference to the division level). If this classification is maintained, some coccolithophores should be placed in orders other than the Coccosphaerales. Emiliania huxleyi, for example, should join the Isochrysidales on the basis of the microanatomy of the living cells and their production of long chain alkenones (Parke & Dixon, 1976; Tappan, 1980; Green et al., 1989; Marlowe et al., 1990, Kleijne, 1993). The criteria used for separation within the class have proved to be inconsistent, and Jordan & Green (1994) have retained only two orders, the Pavlovales in the subclass Pavlovophycidae and the Prymnesiales (Papenfuss, 1955) in the subclass Prymnesiophycidae (see above).

Nowadays, with the Pavlovales separated as a discrete subclass, Pavlovophycidae, and all the other Prymnesiophyceae grouped in the subclass Prymnesiophycidae, the classification schemes for all coccolithophores, fossil and extant, proposed first by Perch-Nielsen (1985a,b) and improved by Bown & Young (1997) and Young & Bown (1997a,b) seem acceptable. Moreover, to underline important relationships between accepted families and the structure of their respective coccoliths, Young & Bown (1997a) proposed the reintroduction of orders, which are of current use in studies of fossil nannoplankton, to reorganize the structural relationships between different families of Mesozoic and Cenozoic ages (including the extant coccolithophores). Nevertheless some families and genera remain in a suspended position without clear location, and remain as *incertae sedis*.

Accepting the above arrangement, it should be necessary to create new orders or to restore former ones in order to locate those members of the Prymnesiophycidae which at no point in their life cycle bear coccoliths (i.e. the former order Prymnesiales and those Isochrysidales which do not bear coccoliths). This task is beyond the scope of the present study which deals only with the coccolith-bearing Prymnesiophycidae.

The orders which have representatives in the studied NW Mediterranean samples will be considered in the taxonomic section below (III.2).

Family

Lohmann (1902) placed the coccolithophores in one family, the **Coccolithophoridae**, with two subfamilies depending on the presence or absence of a flagellar opening. As the number of species increased, so did the complexity and number of families and higher level taxa, but nowadays family level coccolithophore classification is considered robust (Jordan *et al.*, 1995; Young & Bown, 1997a). At present, coccolithophore families are distinguished by the coccolith types (for example, caneoliths are characteristic of the Syracosphaeraceae, while pappoliths are only found in the Papposphaeraceae) and in comparison with higher levels, few family level changes have been made in recent years. Changes proposed in the course of this study, as well as the characteristics of the families (and lower taxa), will be presented and discussed in the taxonomy section of the NW Mediterranean coccolithophores.

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 & 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.

I.2 THE NW MEDITERRANEAN

The Mediterranean is a relatively small and deep sea situated between Europe, Asia and Africa. The Black Sea, the Eastern Mediterranean and the Western Mediterranean form a string of basins which finally open into the Atlantic. The characteristic Mediterranean climate with hot dry summers and mild humid winters induces a negative water balance. Evaporation is of great importance in this area and is the cause of the relatively high salinity of the water: 37-39 ‰ compared with 36.5 ‰ in Atlantic waters (Emelyanov & Shimkus, 1986). The water temperature remains relatively high near the bottom in all the deep water areas of the Mediterranean and exceeds those of the Atlantic Ocean at the same depth by 8 - 10°C and even by 13 - 14°C near the bottom.

The Western Mediterranean covers 860,000 Km² and has a maximal depth of 3,700 m. It is effectively limited by the sills of Sicily – Tunis (close to 400 m depth) and of Gibraltar – Morocco (extending down to 320 m). The salinity is close to 38.5 ‰ in deep water and a little less closer to the surface. The deep water temperature is near 13°C and is relatively constant; the temperature of surface waters varies between approximately 13°C in winter, and about 26°C in summer (Margalef, 1985a). The water is well oxygenated throughout. In this area, evaporation exceeds the input of rainfall waters (direct or carried by rivers) and the sea waters increase in salinity and consequently in density. Sea water exchange occurs across the Gibraltar sill with two overlaying currents flowing in opposite directions: the relatively high salinity deep Mediterranean water flows into the Atlantic through a deep current, compensated by a surface current of Atlantic water which spreads nutrient poor water over the Mediterranean. This negative nutrient balance maintains the Mediterranean in an oligotrophic state, where phosphorus is the main limiting element (Margalef, 1985a).

Calcium carbonate biogenic remains are abundant in Mediterranean sediments (Emelyanov & Shimkus, 1986). The continental slope of the Southwestern Balearic Margin has shown a calcium carbonate content between 40 and 60 % contributed mainly by planktonic foraminifers and coccoliths (Vázquez & Zamarreño, 1993). The recent sediments of the Western Mediterranean present a nannoplankton assemblage typical of a temperate zone (Müller, 1985) and *Emiliania huxleyi* is the most frequent species found in those sediments (Bartolini, 1970; Mateu, 1985; Vázquez, 1988; Vázquez et al., 1991; Flores et al., 1993, 1997; Knappertsbusch, 1993b).

The extant coccolithophores in the Mediterranean Sea waters present a high number of living species, both heterococcolithophores and holococcolithophores (Lecal-Schlauder,

INTRODUCTION

1954, Lecal, 1965a,; Borsetti and Cati, 1972, 1976, 1979; Kleijne, 1991, 1993) with a strong seasonal variability and regional patchiness (Knappertsbusch, 1993b).

The present study concerns the NW Mediterranean and more precisely the so-called Catalano-Balearic Sea between the Iberian Peninsula and the Balearic Islands (see Figs. 1.1 and 1.2). Studies on phytoplankton distribution and their relationship with the hydrographic heterogeneity in this area revealed different ecological zones between the Iberian Peninsula and the Balearic Islands (Margalef, 1978, 1985b; Estrada, 1985, 1991, 1999; Margalef & Estrada, 1987; Estrada & Margalef, 1988). In this area three well differentiated surface waters have been recognized; they are separated by two fronts, associated respectively with the Catalan and Balearic slopes (Salat & Cruzado, 1981; Font et al., 1986-1987; Font et al., 1988). The Catalan Front is the boundary between the low salinity coastal water masses influenced by continental discharges, flowing southwestward, and the central area with dense and cooler Mediterranean sea waters (Font et al., 1988). The Balearic Front separates the Mediterranean sea water, without a definite circulation, from the warmer and well-stratified water mass of Atlantic influence which flows from the southwest to the northeast (Font et al., 1988; Pinot et al., 1994). The central area shows high vertical mesoscale instability (Font et al., 1988; Pinot et al., 1994) with cyclonic eddies and filaments which interchange waters with the neighbouring masses (Tintore et al., 1990; Pinot et al., 1994). In this area, mid-way between the Iberian Peninsula and the Balearic Islands, a well developed ridge shaped structure of isopycnals is recognized (Margalef 1989, Margalef & Estrada, 1987; Estrada & Margalef, 1988; Estrada & Salat, 1989; Salat, 1996). This structure implies upward movement of water and enhances productivity as proved by the persistence of a well developed deep chlorophyll maximum in the stratification period (Margalef, 1985b, 1989; Estrada, 1985, 1996, 1999), approximately from April to November (Margalef & Ballester, 1967). This ridge-shaped physical structure is recognized from the north of Corsica (Prieur, 1979; Prieur & Tiberti, 1985) to Ibiza. It is considered a real divergency (Margalef, 1989) product of the cyclonic movement impelled by the two main currents with opposite directions: the coastal water flowing southwestwards and the atlantic-influencied waters flowing northeastwards. This divergency, a real fertile front, contributes too, to maintain the central waters saltier and cooler than the surrounding water masses.

Thus, due to the existence of these strong gradients in a relatively reduced spatial dimension, the Catalano-Balearic Sea, an area of relatively high primary production as seen in remote sensing images, is an ideal location to study nannoplankton and particularly the relations between different water masses and coccolithophore distribution.

1.3 OBJECTIVES OF THE PRESENT STUDY

The coccolithophores of this area were poorly known, also due to unsuitable fixation (with iodide) and thus low preservation in the plankton samples obtained previously. The main objective of the present study is to identify the coccolithophore species present in NW Mediterranean waters using EM techniques in order to evaluate the diversity of this important phytoplankton group in this area (Chapter III). The mesoscale distribution of these organisms is outlined in Chapter V and the distribution of coccoliths in seafloor sediments in Chapter VI. A preliminary attempt of coccolithophore elemental composition is given in Chapter VII. The combination coccospheres found during the present study, which contribute greatly to our understanding of the life cycles and ecology of the involved 'species', are presented in Chapter IV.



Fig. 1.1.- General map of the western Mediterranean.



Fig. 1.2.- Sketch of circulation (modified from Font, 1986, Salat, 1996 and Estrada, 1999). The dotted line represents the divergency (after Estrada & Margalef, 1988). The rectangle encloses the studied area.
II. MATERIAL AND METHODS

II.1 WATER SAMPLES

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. Fig. 2.1 and Fig. 2.2 show the positions of the stations sampled in the 1995 and 1996 cruises respectively, and Table 1 and Table 2 detail the geographic positions of the 1995-96 stations as well as the date and time (in GMT) that they were visited. In addition a programme of three cruises held in different seasons of the year was conducted offshore of the Ebro Delta (see Fig. 2.3): 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). Fig. 2.3 illustrates the position of the stations sampled in the Fans



Fig. 2.1. Position of the sampled stations during the year 1995 (Cruises Meso-95 and Fronts-95)



Fig. 2.2. Position of the sampled stations during the cruises Meso-96 and Fronts-96.

cruises and Table 3 gives the geographic positions of stations as well as the date and time (in GMT) 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.

Surface samples collected off-shore of Masnou (MEDEA sampling, March 1998), offshore and in the harbour of Barcelona (PICASSO workshop, July 1998) and also four sampled stations (Est. 25 at 40.82°N, 2.75°E; Est. 64 at 40.68°N, 2.87°E; Est. 69 at 41.17°N, 2.50°E; Est.76 at 41.23°N, 3.60°E) collected during HIVERN-99 cruise (20th February to 14th March 1999) aboard the R/V "García del Cid" were considered only for taxonomic purposes.



Fig. 2.3. Position of the sampled stations during the cruises Fans 1, Fans 2 and Fans 3.

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 (see the fixation method, below, in "Comparison of methodologies"), except in four stations where parallel samples were filtered on board without fixation in order to compare the results (see below in "Fixation versus non-fixation"). In the 1996 cruises, knowing the results of the comparison of fixation versus non-fixation, all the samples were directly filtered on board following the general filtration technique, without any previous fixation.

Stations	Date	Time	Latitude	Longitude	Sampled depths,
	day - month	(on GMT)	(North)	(East)	meters
Series	Meso-95				
005	31-5	21h 31'	41 13.8	2 20.5	0,40
007	01-6	00h 54'	41 01.5	2 32.2	0,40
011	01-6	15h 26'	40 49.3	2 44.1	0,40
015	02-6	01h 25'	40 36.8	2 55.2	0,40
021	02-6	14h 15'	40 24.9	3 06.8	0,40
023	02-6	18h 41'	40 12.6	3 18.4	0,40
112	11-6	19h 42'	40 09.4	1 34.6	0,40
114	12-6	01h 44'	39 51.9	1 15.0	0,40
115	12-6	03h 16'	39 47.5	1 22.9	0,40
117	12-6	06h 38'	39 35.4	1 38.2	0,40
118	12-6	08h 47'	39 29.2	1 44.1	0,40
119	12-6	10h 50'	39 22.9	1 50.0	0,40
132	13-6	06h 38'	39 33.7	0 54.5	0,40
136	13-6	13h 22'	39 36.3	0 22.1	0,40
138	13-6	16h 43'	39 27.6	0 38.5	0,40
139	13-6	18h 29'	39 23.3	0 46.3	0,40
140	13-6	20h 26'	39 19.0	0 54.7	0,40
142	14-6	00h 13'	39 09.4	1 09.9	0,40
147	14-6	08h 05'	39 13.1	0 42.7	0,40
151	14-6	15h 02'	39 29.7	0 10.6	0,40
155	14-6	20h 19'	39 23.4	0 01.4	0,40
156	14-6	21h 36'	39 16.3	0 01.0	0,40
157	14-6	23h 00'	39 08.2	0 00.4	0,40
161	15-6	05h 14'	38 59.6	0 16.5	0,40
163	15-6	08h 27'	38 59.0	0 33.4	0,40
169	15-6	14h 24'	38 49.8	0 37.3	0,40
178	16-6	05h 42'	39 06.4	0 34.6	0,40
Series	Fronts-95				
18P	21-6	14h 20'	41 21.2	2 17.8	5,10,20,30,40,50,60,65
19T	21-6	18h 37'	41 08.8	2 28.0	5,10,20,30,40,50,60,70.85
201	21-6	23h 08'	41 01.5	2 40.6	5,10,20,30,40,50,60,70,80
23D	22-6	07h 30'	40 40.3	2 52.0	5,10,20,30,40,50,60,70,80
24W	22-6	13h 05'	40 33.9	2 38.7	5,10,20,30,40,50,60,70,80
25W	22-6	19h 00'	41 02.3	2 14.7	5,10,20,30,40,50,60,70,80
26W	22-6	22h 00'	41 11.9	2 06.5	5,10,20,30,40,50,60,70,80
28C	23-6	03h 02'	41 29.1	2 29.0	5,10,20,30,35

Table 1. Local and temporal position of samples collected during the 1995 cruises (see Fig. 2.1).

Stations	Date	Time	Latitude	Longitude	Sampled depths,
	day - month	(on GMT)	(North)	(East)	meters
Series	Meso-96				
A1	18-6	22h 39'	42 00.0	3 17.3	5,40,70,100
A3	19-6	1h 38'	41 54.0	3 37.1	5,40,70,100
A5	19-6	11h 57'	41 48.0	3 56.9	5,40,70,100
D2	21-6	6h 36'	41 38.9	3 15.0	5,40,70,100
D4	21-6	3h 31'	41 26.6	3 26.5	5,40,70,100
D6	20-6	23h 55'	41 14.3	3 38.0	5,40,70,100
D8	20-6	20h 34'	41 02.0	3 49.5	5,40,70,100
E2	30-6		41 33.0	3 03.0	5,40,70,100
E3-4	1-7		41 23.0	3 10.2	5,40,70,100
E8	2-7	8h 30'	40 55.1	3 36.6	5,70,100
F2	23-6	23h 58'	41 27.2	2 52.0	5,40,70,100
F4	24-6	4h 12'	41 13.7	2 59.7	5,40,70,100
G2	24-6	9h 15'	41 20.9	2 33.7	5,20,40,50,70,100
G4	24-6	17h 27'	41 08.6	2 45.2	5,40,70,100
G6	25-6?	9h 53'	40 56.3	2 56.7	5,40,70,100
I1-2	29-6		41 17.0	2 17.8	5,40,70,100
12	24-6	23h 00'	41 13.9	2 20.7	5,40,70,100
13	28-6		41 07.7	2 26.5	5,40,70,100
I4	25-6	2h 09'	41 01.6	2 32.2	5,40,70,100
16	25-6	5h 27'	40 49.3	2 43.7	5,40,70,100
18	27-6		40 37.0	2 55.2	5,40,70,100
Series	Fronts-96				
013	16-9	03h 12'	41 17.8	3 51.2	10,30,60,66,75,90
019	17-9	bef. 10h 55'	41 19.3	3 33.5	5,30,57,100
021	17-9	11h 55'	41 11.7	3 41.6	20,30,50,68,90
027	18-9	10h 39'	41 46.7	3 03.9	5,10,20,30,45
038	20-9	15h 23'	41 51.0	3 12.0	15,35,45,60
039	21-9	08h 51'	41 35.3	3 15.8	10,30,40,50,70,160

Table 2. Local and temporal position of samples collected during the 1996 cruises (see Fig. 2.2).

			-	-	
Stations	Date	Time	Latitude	Longitude	Sampled depths,
	Day-month-year	(on GMT)	(North)	(East)	meters
Series	Fans-1				
64	04-11-96	19h 49'	40 35.7	1 07.6	5,25,40,60,75,81
78b	06-11-96	01h 40'	40 35.7	0 48.0	5,12
100	07-11-96	00h 02'	40 17.0	0 55.2	5,25,40,60,75,85
123	07-11-96	23h 11'	39 59.6	0 44.4	5,25,40,60,75,88
127	08-11-96	01h 42'	39 52.8	0 54.0	5,25,40,60,75,100
Series	Fans-2				
J03	10-02-97	22h 36'	40 24.7	0 44.5	5,10,25,40,58
J07	11-02-97	06h 07'	40 09.6	1 05.9	5,25,40,60,75,100
J13	11-02-97	12h 43'	40 01.3	1 17.4	5,25,40,60,75,100
M01	12-02-97	20h 12'	40 17.9	0 26.8	5,10,25,30
M03	12-02-97	22h 10'	40 11.3	0 36.8	5,10,25,40,66
M07	13-02-97	02h 37'	39 57.1	0 56.9	5,25,40,60,75,150
N07	13-02-97	12h 29'	39 54.6	0 51.7	5,10,25,40,60,75
Series	Fans-3				
K03	13-07-97	19h 43'	40 19.4	0 40.4	5,10,25,40, 60 ,66
K05	13-07-97	22h 03'	40 12.4	0 53.2	5,10,25,41, 64 ,84
K07	14-07-97	00h 52'	40 04.8	1 03.1	5,25,40,60, 75 ,100
K12	14-07-97	06h 04'	40 00.3	1 10.4	6,24,40,60,75,150
M11	15-07-97	10h 40'	39 53.9	1 01,0	5,25,40,60,75,100

Table 3. Local and temporal position of samples collected during FANS 1-2-3 (see Fig. 2.3).

COMPARISON OF METHODOLOGIES. FIXATION VERSUS NON-FIXATION

The **fixation methodology**, initially employed with the aim of saving working time on board the ship, was based on the techniques of Throndsen (1978) and Gaarder & Hasle (1971). The sample was fixed with formaldehyde neutralized with hexamethylenetetramine until subsequent filtration in the laboratory. The fixing solution was prepared by diluting grade formalin (of 40%) to 20% with distilled water and adding 100 g. of hexamethylenetetramine to 1 litre of the 20% solution to neutralize the aqueous solution. A final concentration of 0.4% HCHO was achieved in the samples by adding 2 ml. of the fixing solution to each 100 ml. of sea water. In the laboratory, filtration was conducted following the technique described below.

The **methodology without fixation** was based on Okada and Honjo (1973); Winter *et al.* (1979); Nishida (1986); and Kleijne (1991); and involved direct filtration of the samples without adding chemicals. The technique of filtration was the same as the method with fixation.

The results of the four parallel samples collected in the MESO-95 cruise from surface water of the stations 005, 015, 023 and 147, which were treated with and without fixation before the filtering process, are given in Table 4. Lower abundances of coccospheres, particularly of holococcolithophores, were recorded in the samples treated with fixation.

Table 4.- Comparison of counts obtained from four surface samples (Cruise Meso-95) that were differently treated, with and without fixation (counts refer to a volume of 1 litre).

	not fix.	fixed						
	S.005	S.005	S.015	S.015	S.023	S.023	S.147	S.147
Emiliania huxleyi	6162	4160	5464	5547	5732	4457	9032	4216
Gephyrocapsa ericsonii	770	0	994	1040	1528	1485	1178	351
G. muellerae	0	0	0	0	382	297	0	0
Syracosphaera pulchra	6162	4853	497	0	0	297	1571	1054
S. cf. epigrosa	0	0	0	0	382	0	0	0
S. molischii	770	693	497	347	382	297	0	0
S. halldalii (protr. type)	3081	0	497	0	764	0	1963	351
S. marginaporata	0	0	0	0	382	0	0	0
S. sp. type L (Kleijne)	0	0	0	0	382	0	393	0
S. histrica	0	0	0	0	0	0	393	0
Gaarderia corolla	770	693	0	0	0	0	0	351
Coronosphaera binodata	0	0	0	0	0	0	393	0
Rhabdosphaera clavigera	0	0	1490	0	6879	0	9425	4919
R. xiphos	0	0	0	0	5350	0	5105	4568
Cyrtosphaera cucullata	0	0	497	0	0	0	0	0
Acanthoica acanthifera	0	0	497	0	0	0	0	351
Umbellosphaera tenuis	0	0	497	0	382	297	393	351
Polycrater galapagensis	0	0	497	0	382	0	4320	1405
Calcidiscus lept. f.rigidus	0	0	0	0	764	0	0	0
Calyptrosphaera oblonga	770	0	0	0	1529	0	0	0
C. dentata	0	0	0	0	382	0	0	0
C. sphaeroidea	0	0	0	0	1529	0	0	0
C. heimdalae	0	0	0	0	1529	0	5105	0
Periphyllophora mirabilis	0	0	0	0	764	0	0	0
Syracolithus quadriperforatus	0	0	0	0	1146	0	2356	351
S. catilliferus	0	0	0	0	0	0	4713	1054
S. dalmat.+conf.+schilleri	0	0	0	0	0	0	5891	3162
Anthosphaera fragaria	0	0	0	0	382	0	393	0
Homozygosphaera arethusae	0	0	0	0	0	0	1571	351
Calyptrolithina wettsteinii	3081	0	497	0	2293	0	3927	703
C. divergens f. tuberosa	0	0	0	0	0	0	785	0
Sphaerocalyptra cf. adenensis	0	0	0	0	3439	0	8247	2811
S. quadridentata	0	0	0	0	1529	0	3142	1405
Zygosphaera hellenica	0	0	0	0	764	0	0	0
Z. marsilii	0	0	0	0	764	0	0	0
Helladosphaera cornifera	0	0	0	0	764	0	6283	1054
Corisphaera sp.	0	0	0	0	1529	0	0	0

The loss of holococcolithophore species, as well as the bad preservation of some heterococcolithophores, were greater in the fixed before filtration methodology, in comparison with direct filtration onboard the ship. The samples of MESO-95 were systematically stored on the main deck, suffering high temperatures and vibrations. Despite not having parallel samples with and without fixation for comparison, it is believed that the samples from the FRONTS-95 cruise were better preserved than those of the cruise MESO-95; due probably to the former samples having stayed a comparatively shorter time aboard the ship (Bé & Anderson, 1976, discuss the adverse effects of shaking and high temperatures during storage of samples fixed with formaldehyde on the preservation of calcareous organisms).

The best results were obtained without fixation of the material. The loss of holococcolithophore species as well as the bad preservation of some heterococcolithophores were clearly observed in the prefixed before filtration methodology. Losses of 39 to 69 % can occur in the coccolithophores from the fixed samples and these percentages may reach 75 and even 100 % in the holococcolithophore community (calculations from Table 4). The damage to calcareous specimens as a consequence of use of chemicals has been discussed by Hodgkinson (1991). In view of these results indicating the greater efficacy of the methodology without fixation, the samples of the 1996 cruises were filtered on board without adding chemicals.

FILTRATION TECHNIQUE

About 200 ml of sea water were filtered, using a vacuum pump, onto polycarbonate Nuclepore filters of 0.8 μ m 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). Another filter with pore size of 3 μ m (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. The filters were air dried and stored under partial vacuum in hermetically closed boxes until preparation for the Scanning Electron Microscope (SEM).

COCCOLITHOPHORE DETERMINATION AND COUNTING

A part of the filter was placed on a SEM stub and coated with a film (of about 150 Å) 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 as well as the counts were conducted in a Hitachi S-570 Scanning Electron Microscope. For every SEM stub, the coccospheres were identified and counted in one hundred random fields under 600x magnification (each field measured 189.5 μ m x 158.9 μ m; i.e. 0.03011 mm²). The number of cells l⁻¹ was estimated by converting the number of counted coccospheres in the investigation area to the total filled area of the filter and dividing by the quantity of water filtered:

cells
$$l^{-1} = N \cdot S/s \cdot V^{-1} \cdot 1000$$

where N= number of coccolithophores, S/s= ratio between the total covered surface of the filter and the scanned surface (S= total covered surface of the filter, s= scanned surface of the filter) and V= volume, in ml., of filtered sea water.

MEASUREMENTS ON COCCOSPHERES AND COCCOLITHS

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 μ m). All these measurements were made by the author from the Mediterranean area and they are recorded in chapter III, without any specification of provenance. Where measures are reported from other authors or from other areas, the reference is given next to the number.

X-RAY MICROANALYSIS

X-ray measurements were conducted with an Energy Dispersive Spectrometer (EDS) on specimens from the stations 005, 015, 023 and 147 of the cruise MESO-95, exclusively with the samples filtered without previous fixation. A small part of the filters was placed on aluminium stubs and coated with mineral carbon in order to prevent "charging" and to avoid interference from the gold or palladium-gold usually used to coat SEM samples. The SEM used was a Cambridge Instruments STEREOSCAN equipped with an X-ray detector capable of responding to elements of atomic weight higher than 23. The detector chamber was of silica lined with lithium, both not perceptible for the detector. The capture analysis time was of 100 s.

II. 2 SURFACE SEDIMENTS

SAMPLES

The study was conducted on 15 core tops (0-3 cm), collected from depths between 1000 m and 2100 m during the VALSIS I cruise, aboard the SUROIT between 1-12 October 1988. The geographic locations of the stations where the cores were extracted are illustrated in figure 2.4.

TECHNIQUES TO STUDY THE NANNOPLANKTON

The samples were prepared according to the technique outlined in Perch-Nielsen (1985) with slight modifications. A small amount of the surficial sediment was treated ultrasonically for a few seconds with distilled water, to which a few drops of NaOH solution was added to achieve pH 7. The samples were then centrifuged at 2000 rpm for 30 seconds, and the process repeated three times. Two drops of the water containing the cleaned coccoliths were then left to dry on a scanning electron microscope stub and the preparation was coated with gold-palladium in a vacuum in order to prevent charging. Micrographs were taken at a scanning magnification of x2000 in order to count the nannoplankton in a portion of the sample. At least 500 coccoliths were scarce and only 124 could be counted. The results are expressed as relative frequencies of the different taxa.



Fig. 2.4 Geographic location of the sediment stations.

III. CLASSIFICATION OF LIVING SPECIES

III.1 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, Chapter I.1).

COCCOLITHOPHORES AND COCCOSPHERES

In a motile coccolithophore cell (Fig. 3.1), 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**.



Fig. 3.1. Coccolithophore cell

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. 3.2), 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 defined 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 differences 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 be a constant and conclusive character.



Fig. 3.3. 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.

COCCOLITHS

The most common form of coccoliths (specially of those found in sediments and fossil deposits) are the **heterococcoliths**, formed of complex arrays of crystal units typically arranged in cycles (rings) (see Fig. 3.3, A). Heterococcoliths have two morphologically differentiated parts, the **central-area** and the **rim** (see Figs. 3.4 and 3.5). 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). Detailed studies of the structure of the heterococcolith rim have resulted in the classification of three 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 a well developed part, the **shield**, parallel to the central area (placoliths) (see Fig. 3.4). 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 can form the most stable 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 (see: 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. 3.3, B), constructed of numerous minute euhedral crystallites, show a high degree of morphological diversity (see: Heimdal & Gaarder, 1980; Norris, 1985; Kleijne, 1991; Young et al, 1997).



Fig. 3.4. Heterococcolith types according the rim morphology. Outlined cross-sections of a planolith, a murolith without and with flanges, and a placolith.



Fig. 3.5. 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).

In addition to heterococcoliths and holococcoliths, a third type of calcified structure are the **nannoliths** (Fig. 3.3, C), which were originally defined, by exclusion, as calcareous nannofossils lacking the typical features of calcareous dinophytes, heterococcoliths or holococcoliths and so of uncertain affinity (see Perch-Nielsen 1985). Nowadays the same name, by extension, can be applied to a few living taxa where the calcareous structures are not definitely homologous (even architecturally) with heterococcoliths or holococcoliths e.g. *Braarudosphaera* (pentaliths), *Florisphaera* (plates), *Ceratolithus* (ceratoliths) (Young, 1992; Young and Bown, 1997; Bown & Young, 1998).

III.2. GENERAL TAXONOMIC LIST AND ABRIDGED DESCRIPTIONS OF THE OBSERVED SPECIES

The present classification scheme follows essentially Cavalier-Smith (1998) and Young and Bown (1997 a,b) for the higher classification; Jordan & Kleijne (1994) and Jordan & Green (1994) for family rang and below taxa and Kleijne (1991) and Kleijne (1992) for the families Calyptrosphaeraceae and Rhabdosphaeraceae respectively. The published PhD of Kleijne (1993) and the publications of Perch-Nielsen (1985 a,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, shapes, etc. refer to the specimens actually observed in the Mediterranean by the author. Since it is generally not possible to count all coccoliths on a given coccosphere, estimations 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 μ m, 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. Notes on previous findings give reports from the literature but are not exhaustive.

The taxa referred to with the epithet "sp." means that they 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 SUBKINGDOM CHROMOPHYTA Cavalier-Smith 1986 INFRAKINGDOM HAPTOPHYTA Cavalier-Smith 1995 DIVISION HAPTOPHYTA Hibberd ex Cavalier-Smith 1986 CLASS PRYMNESIOPHYCEAE Hibberd 1976 SUBCLASS PRYMNESIOPHYCIDAE Cavalier-Smith, Jordan *et* Green 1994.

III.2.1 ORDER ZYGODISCALES Young and Bown 1997

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 & Green, 1994). A member of this family, *Helicosphaera carteri*, has been shown to form combination coccospheres with holococcoliths (see Chapter IV in the present study).

Extant species are motile, forming ellipsoidal coccospheres with a prominent flagellar opening (Young & Bown 1997). 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 coccoliths, 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 or flange shape (Young & Bown 1997).

Within this genus, Jordan & Kleijne (1994) and Jordan & 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

Plate 1, figs. 1, 2, 3 and 4.

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, 1985, 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 & 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 & Friedinger in Winter & Siesser 1994, p. 121 fig. 23A-B.

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

Two combination coccospheres of *Helicosphaera carteri* with *Syracolithus catilliferus* (Kamptner) Deflandre have been found in the course of the present study (Chapter IV, Pl. 77 figs. 3-5). These findings favour the opinion that these two species are related in the same way as *Coccolithus pelagicus*, which has both a heterococcolith phase (*C. pelagicus*) and a holococcolith phase (formerly known as *Crystallolithus hyalinus*).

Coccolith numbers: (16-) 18-22 (-30) helicoliths.

Dimensions: coccosphere long axis (15-) 17-23 (-26) μ m, short axis (12-) 13-15 (-17) μ m; coccoliths long axis (8-) 8.8-9.7 (-11) μ m.

Previous findings: Atlantic, Pacific, Mediterranean Sea, Indian Ocean, Indo-Malayan region, Red Sea, Arabian Sea, Caribbean Sea, Okhotsk.

Helicosphaera carteri var. hyalina (Gaarder) Jordan et Young, 1990

Plate 2, fig. 3.

Helicosphaera hyalina Gaarder 1970, pp. 113-119, figs. 1a-g, 2a-d, 3a.; Borsetti & 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 coccoliths of var. *hyalina* were smaller than these of var. *carteri* (ca. 6.5 μ m compared to ca 9.2 μ m), did not have pores, and showed a well differentiated central area filled with large sized needle-shaped elements.

Coccolith numbers: 12-22 helicoliths.

Dimensions: coccosphere long axis (11-) 13-14 (-16) μ m, short axis (10-) 11.5-12.5 (-13) μ m; coccolith long axis (5.5-) 6.2-6.8 (-7.5) μ m.

Previous findings: Atlantic, Pacific, Mediterranean Sea, Indian Ocean, Red Sea, Caribbean Sea, Okhotsk Sea.

Helicosphaera carteri var. wallichii (Lohmann) Theodoridis, 1984

Plate 2, fig. 1.

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 & Hay 1969, pp. 272-273, pl. 6, fig. 9. *Helicosphaera wallichii* (Lohmann) Okada et McIntyre, 1977, p. 14, pl. 4. fig. 8; Delgado & 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*.

Remarks: Transitional shapes between *H. carteri* v. *carteri* and *H. carteri* v. *wallichii* exist, even on the same coccosphere, as reported by Jordan & Young (1990) and Kleijne (1993) and illustrated by Nishida 1979, pl. 9 Fig. 4a,b,c. Even Okada & 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 μ m, short axis 13.4 μ m; coccolith long axis ca. 9 μ m.

Previous findings: Atlantic, Pacific, Mediterranean Sea, Indian Ocean, Red Sea, Caribbean Sea.

Helicosphaera pavimentum Okada et McIntyre, 1977

Pl. 2, figs. 3 and 4.

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

Helicosphaera pavimentum Okada et McIntyre 1977, Borsetti & 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 & Siesser, 1994, p. 122 (micrograph from Winter & 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.

Coccolith numbers: 17-30 helicoliths.

Dimensions: coccosphere long axis (9-) 12.5-13.5 (-15) μ m, short axis (8-) 11.5-12.5 (-13) μ m; coccolith long axis (3.5-) 4.4-5.2 (-6) μ m.

Previous reports: Atlantic, Pacific, Mediterranean Sea, Indian Ocean, Caribbean Sea, Okhotsk Sea.

FAMILY PONTOSPHAERACEAE Lemmermann, 1908

Cells normally bearing heterococcoliths in at least one stage of their life-cycle (Jordan & 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*.

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

Plate 3, figs. 1, 2, 3, 4 and 5.

Scyphosphaera apsteini Lohmann, 1902, p. 132, pl. 4, figs. 26-30; Boudreaux *et* Hay, 1969, pp. 274-275, pl. 4, figs 16-18; Borsetti & Cati, 1972, p. 399, pl. 41, fig. 3, pl. 42, figs. 1-2; Delgado & 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; Winter & 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) μ m, short axis (21-) 25-30 (-33) μ m; discoliths long axis (7-) 8.5-9.1 (-10) μ m, short axis (4-) 5.9-6.6 (-7.5) μ m; discoliths with rim long axis (6-) 6.5-7 (-8) μ m, short axis (4-) 4.5-5 (-6) μ m; lopadoliths length (11-) 11.5-13 (-13.5) μ m, width (11-) 12.5-14 (-15) μ m.

Previous reports: Atlantic, Pacific, Mediterranean Sea, Caribbean Sea.

Scyphosphaera apsteinii f. dilatata Gaarder, 1970.

Plate 3, fig. 6.

Scyphosphaera apsteinii f. dilatata Gaarder, 1970, p. 119, figs. 4-6.

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.

Remarks: 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. 4 e), 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 specimen presented here as *Scyphosphaera apsteinii* f. *dilatata*, the only one found in the present study, has only one lopadolith. Since the lopadolith is inside the coccosphere (Pl. 3 Figs 3, 4) the specimen is presented as *S. apsteinii* f. *dilatata*. The lopadolith is, however, partially covered by cribriliths and it is hence not possible to definitively establish that it is a real *S. apsteinii* f. *dilatata* lopadolith. Further work might prove that *S. apsteinii* f. *dilatata* is merely an early developmental form of *S. apsteinii* f. *apsteinii*.

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

Dimensions: discoliths (six specimens) long axis (6.5-) 8-10.5 (-9) μ m, short axis (5-) 6-8 (-7) μ m; lopadolith (one specimen) length 6 μ m, width 9.2 μ m.

Previous reports: Gulf of Mexico.

III.2.2 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.

FAMILY CALCIOSOLENIACEAE Kamptner, 1927

Extant species have elongate fusiform coccospheres which may possess spine-bearing polar coccoliths. Coccoliths are rhomboidal muroliths (named rhomboliths and 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 rhomboliths 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 & 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.

Biostratigraphic remarks: 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 (in Grassé, 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

Plate 4, figs 1-4.

Cylindrotheca brasiliensis Lohmann, 1920, p. 187, Bild 56.

Anoplosolenia brasiliensis (Lohmann) Deflandre, 1952, p. 458, Fig. 356 D-E; Halldal & Markali, 1955, pp. 14-15, Pl. 16; Gaarder & Hasle, 1971, p. 523, Fig. 3 a-c; Manton & 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 & Gaarder (1981) "all spindleshaped 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 rhombolith 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.

Remarks: 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 & Markali (1955) described the coccoliths, using TEM techniques, they remarked that the rhomboliths shown by Deflandre & 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 & Markali (1955) and Gaarder & Hasle (1971).

Coccolith numbers: 160-190 rhomboliths.

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

Previous reports: Atlantic, Pacific, Mediterranean Sea, Red Sea, Indian Ocean, Arabian Sea.

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

Plate 5, figs. 1-5.

Calciosolenia sinuosa Schlauder in Halldal & 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 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 rhomboliths are larger than those of *Anoplosolenia* brasiliensis, and long spines are present on apical and antapical poles.

Coccolith numbers: 110-160 rhomboliths; 3-16 polar spines.

Dimensions: coccosphere (2 specimens measured) long axis without spines 28.5-29.0 μ m, short axis 5.3-7.7 μ m; length/width ratio ca. 4.5; spines 16-25 μ m; coccoliths (6 measured) major diagonal 3.4 - 3.7 μ m, minor diagonal 1.6-1.8 μ m, long side ca. 2.3 μ m, short side ca. 1.8 μ m, ratio long/short diagonals ca. 2.1, ratio long/short sides ca. 1.3.

Previous reports: Atlantic, Pacific, Mediterranean Sea, Red Sea, Indian Ocean, Arabian Sea.

III.2.3 ORDER RHABDOSPHAERALES Ostenfeld, 1899

The coccospheres may consist of one, two or even more kinds of coccoliths which are planoliths or modified forms thereof.

FAMILY RHABDOSPHAERACEAE (Haeckel, 1894) Ostenfeld, 1899.

The coccoliths have a 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.

The coccoliths of this family are named rhabdoliths, a name first employed to designate coccoliths with a central styliform process.

N.B. Some representatives of this family, in the genera *Acanthoica* and *Rhabdosphaera*, form combination coccospheres with holococcoliths (see Chapter IV in the present study).

Taxonomic remarks: in the recent literature, three different authors are reported as authorities for the family name in different taxonomic revisions. Kleijne (1992) points out that: "Haeckel (1894) introduced the invalid family name Rhabdosphaeralen (not in latinized form). The name was validated by Ostenfeld (1899), who introduced the name Rhabdospherales, corrected to Rhabdosphaerales (Ostenfeld, 1900). According to the ICBN, Art. 32.5 this family name with an improper Latin termination must be changed conserving the author's name and date of publication. Because Lemmermann (1908) was the first to use the name Rhabdosphaeraceae, the family has been often unjustly attributed to him."

Biostratigraphic remarks: In the Eocene, the Rhabdosphaeraceae formed a diverse and abundant group (Perch-Nielsen, 1985) but the modern form *Rhabdosphaera clavigera* appears in the Plocene and its variety *stylifera* is only recorded from the Pleistocene. *Discosphaera tubifer* has been reported only from Pleistocene and Holocene sediments.

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.

Plate 6, figs. 1, 2 and 3.

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 & 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.

Remarks: In the course of the present study some specimens have been found with the characteristics of this species (Pl. 6, figs. 1 and 2) but other specimens have less tilted radial laths and a less sacculiform and flattened protrusion (see Pl. 6, fig. 3). This observation suggests that some transitional forms between this species and *A. quattrospina* may occur. I think that more work is necessary to clarify this point.

Coccolith numbers: ca. 50 coccoliths...

Dimensions: coccospheres 6-7 μ m; longest spines ca. 6 μ m; intermediate spines ca. 3 μ m; shortest spines 1.2-2.2 μ m.; body coccoliths long axis (1.5-) 1.8-1.9 (-2.2) μ m.

Previous reports: Atlantic, Mediterranean Sea, Caribbean Sea, Indian Ocean, Pacific.

Acanthoica quattrospina Lohmann, 1903

Plate 6, figs. 4, 5 and 6.

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 & Siesser, 1994, p. 128, fig. 72 (phot. from Nishida).

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 Remarks in A. acanthifera description) leads me 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 (see Kleijne, 1992) and the specimen figured in Plate 6 (4) 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 Pl. 6 (5) 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).

Combination coccospheres of *Acanthoica quattrospina* with an undescribed holococcolithophore have been found in the course of the present study (Chapter IV, Pl. 82, Figs. 2-6.). Again, these findings favour the opinion that these two species are related in the same way as *Coccolithus pelagicus* heterococcolith and holococcolith phases.

Dimensions: Coccospheres (6-) 7-8 (-12) μ m; longer spines ca. 9 μ m; intermediate spines ca. 7 μ m; shortest spines 1.5-3.0 μ m.; body coccoliths (flat rhabdoliths) long axis (1.6-) 1.9-2.2 (-2.6) μ m.

Previous reports: Atlantic, Mediterranean Sea, Pacific, Indian Ocean, Caribbean Sea, Arabian Sea, Okhotsk Sea.

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

Plate 7, figs. 1, 2, 3 and 4.

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

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

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

Dimensions: Coccospheres (7-) 8.5-10.0 (-12) μ m; body rhabdoliths long axis (1.2-) 1.8-2.2 (-2.8) μ m, short axis (0.7) 0.9-1.1 (-1.3) μ m; height (with central protrusion) 1.4-1.6 μ m; circum-flagellar rhabdoliths long axis ca. 3μ m.

Previous reports: Atlantic, Mediterranean Sea, Red Sea, Indian Ocean, Pacific, Arabian Sea.

Genus Anacanthoica Deflandre, 1952

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

Anacanthoica acanthos (Schiller, 1925) Deflandre, 1952

Plate 7, figs. 5 and 6.

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 & 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. Coccolith numbers: around 78 coccoliths

Dimensions: coccosphere long axis (only one specimen) 8.5μ m; rhabdoliths long axis 2.1-2.6 μ m, short axis 1.7 - 2.1 μ m.

Previous reports: Mediterranean Sea, North Atlantic, Pacific, Indian Ocean, Caribbean Sea.

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

Plate 8, figs. 1, 2.

Acanthoica aculeata, Kamptner, 1941, pp. 76, 133, pl. 1, figs 1, 3; Samtleben & 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 (see 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 μ m; coccolith long axis (2.1-) 2.5-2.8 (-3.1) μ m, short axis of (1.4-) 1.7-2.0 (-2.3) μ m.

Previous reports: North Atlantic, Mediterranean Sea, Red Sea, Arabian Sea, Indian Ocean, Pacific, Caribbean Sea.

Cyrtosphaera cucullata (Lecal-Schlauder, 1951) Kleijne, 1992

Plate 8, figs. 5, 6.

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.

Remarks: 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 μ m; coccolith long axis (2.1-) 2.5-2.7 (-3.0) μ m, short axis 1.9-2.2 μ m, height 1.2-2.3 μ m.

Previous reports: Mediterranean Sea, North Atlantic.

Cyrtosphaera lecaliae Kleijne, 1992

Plate 8, figs. 3,4.

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 μ m; coccolith long axis (2.4-) 2.9-3.2 (-3.7) μ m, short axis 1.9-2.2 μ m.

Previous reports: North Atlantic, Mediterranean Sea, Indian Ocean, Pacific, Caribbean Sea.

Genus Discosphaera Haeckel, 1894

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

Discosphaera tubifera (Murray et Blackman, 1898) Ostenfeld, 1900

Plate 9, figs. 1, 2.

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 spine-like small structure (pl. 9, fig. 2) which may be organic (see Kleijne, 1992); the trumpet-like distal structure, which is loosely attached, is formed by needle-shaped elements which become tile-shaped in the flaring distal part.

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

Previous reports: Atlantic, Indian Ocean, Mediterranean Sea, Red Sea, Pacific, Caribbean Sea, Okhotsk Sea.

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

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

Palusphaera vandelii Lecal, 1965 emend. R.E. Norris, 1984

Plate 9, figs. 3, 5.

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 & Bailey, 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 by 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 μ m; coccosphere diameter including processes 10-14 μ m; coccolith proximal disc width (1.2-) 1.5-1.9 (-2.1) μ m; spine length 3.5-9 μ m, spine thickness ca. 0.1 μ m (maximum ca. 0.3 μ m in the thicker proximal part).

Previous reports: Atlantic, Mediterranean Sea, Indian Ocean, Pacific, Arabian Sea, Red Sea, Caribbean Sea.

Palusphaera sp. 1 (type robusta)

Plate 9, figs. 4, 6.

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

? Specimen shown by Knapertsbusch, 1990, pl. 7 fig. 3.

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

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

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

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

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.

Plate 10, figs. 1, 2 and 3.

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, has 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*). The latter shape has small "wings" of laterally extending elements instead of a straight end (see Pl. 10, fig. 2) and 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 (see 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.

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) μ m; coccosphere diameter including spines (14-) 17-20 (-21) μ m; endothecal coccolith base plate long axis (3.1-) 3.3-3.7 (-3.9) μ m, short axis 2.5-2.8 μ m, rim width 0.4-0.5 μ m; spine length (3.7-) 5.0-5.3 (-5.8) μ m; exothecal coccolith long axis (2.7-) 3.4-3.7 (-3.9) μ m, short axis 1.7-2.5 μ m, rim width 0.2-0.3 μ m.

Previous reports: Atlantic, Mediterranean Sea, Red Sea, Indo-Malayan region, Indian Ocean, Pacific, Caribbean Sea, Okhotsk Sea.

Rhabdosphaera xiphos (Deflandre et Fert, 1954) Norris, 1984

Plate 10, figs. 4-6.

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 μ m; coccosphere diameter including spines 15-20 μ m; endothecal coccolith diameter 1.1-1.3 μ m, spine length 5-7 μ m; exothecal coccolith long axis (1.4-) 1.7-1.8 (-1.9) μ m, short axis 1.1-1.4 μ m.

Previous reports: North Atlantic, Mediterranean Sea, Red Sea, Indian Ocean, Pacific.

III.2.4 ORDER SYRACOSPHAERALES Ostenfeld, 1899.

This order groups families which bear muroliths, but they can possess planoliths and/or modified derivatives on the same coccosphere.

FAMILY SYRACOSPHAERACEAE (Lohmann) Lemmermann, 1903

The characteristic coccolith of this family is the caneolith, a murolith with laths in the central area. 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 (see Chapter IV in the present study).

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

A. 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 electronic microscopy 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 & Honjo, 1973; Okada & McIntyre, 1979) found particularly in shallow waters (Samtleben & Schröder, 1992; Samtleben et al., 1995) whilst *C. rigidus* is a species described from the subtropical North Atlantic (Heimdal & Gaarder, 1981), possibly related to subtropical to tropical waters and particularly to nutrient-enriched environments (Kleijne, 1993).

Calciopappus cf. rigidus Heimdal, 1981, in Heimdal & Gaarder, 1981

Plate 11, figs. 1, 2 and 3.

C. rigidus Heimdal, in Heimdal & 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 & Oates 1983, pp. 452-455, pl. 7-8.

Coccosphere stiff, slender, cone-shaped; this species is described as having tetramorphic coccoliths (see Heimdal & 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 surrounds the whorl planoliths.

Coccolith numbers: 60-85 body caneoliths, 7-12 subcircular planoliths; 4-9 spine-like appendages.

Dimensions: coccosphere (7 specimens measured) long axis (8-) 9-11 (-15) μ m, short axis (4-) 6-7 (-8) μ m; body caneoliths major axis (1-) 1.3-1.6 (-2) μ m, minor axis (0.5-) 0.75-0.9 (-1.1) μ m; whorl planoliths major axis (0.95-) 1.5-1.7 (-1.75) μ m; minor axis ca. 1.2 μ m; spine length (13-) 15-18 (-21) μ m.

N.B. Since in at least 10 specimens studied, the apical caneolith with spine was not observed, these specimens are classified as C. cf. *rigidus* rather than C. *rigidus*.

Calciopappus sp. (very small)

Plate 11, figs. 5 and 6.

Small and weekly calcified *Calciopappus*. Small coccosphere (5 to 6.5 μ m long axis) with delicate caneoliths (from 60 to 70) which have only the rim well calcified; the whorl planoliths (around 10) have two finger like spines, one directed towards the coccosphere and the other, approximately at 90° forming a tangential anticlockwise pattern on the coccosphere in distal view; the appendages (around 10 to 12) are short and thin.

Dimensions: coccosphere (2 specimens) long axis 5-6.5 μ m, short axis ca. 3.4 μ m; body caneoliths major axis (0.7-) 0.8-0.9 (-1.2) μ m; spine length (3-) 6.5-7.5 (-8) μ m.

Genus Michaelsarsia Gran emend. Manton et al., 1984

Coccospheres with four kinds of coccoliths: flangeless body caneoliths, rhomboid circumflagellar 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.

Plate 12, figs. 1- 6.

Michaelsarsia elegans Gran, 1912, in Murray & Hjort, 1912, p. 332; Heimdal & 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 by 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.

Remarks: *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) μ m, short axis (8-) 9-11 (-13) μ m; body caneolith major axis (1.8-) 2.2-2.5 (-2.7) μ m, minor axis (1.1-) 1.2-1.5 (-1.7) μ m; small apical caneoliths with occluded tube ca. 1.5 μ m; ring-shaped coccoliths major axis ca. 3.5 μ m; appendage (composed of three link coccoliths) length ca. 22 μ m

Previous reports: Atlantic, Mediterranean Sea, Indian Ocean, Pacific, Caribbean Sea.

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

Plate 13, figs. 1, 2, 3 and 4.

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 & 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 spine 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 μ m; body caneoliths major axis (0.7-) 1.1-1.3 (-1.45) μ m, minor axis 0.7-0.8 μ m; apical caneolith spine length ca. 1.3 μ m; osteolith length (1.9-) 2.6-2.8 (3.2-) μ m, width (0.7-) 0.9-1.1 (-1.2) μ m.

Ophiaster hydroideus (Lohmann) Lohmann emend. Manton et Oates, 1983

Plate 13, figs. 5 and 6.

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 & Oates 1983, pp. 441-443, 460, pls. 1-2; Kleijne, 1993, p. 236, pl. 3, fig. 8.

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

Remarks: 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 μ m; body caneoliths major axis (0.6-) 1.1-1.3 (-1.4) μ m, minor axis 0.7-0.9 μ m; apical caneolith spines 1.1-1.4 μ m; osteolith length (2.1-) 2.6-2.8 (-3.1) μ m, width 0.4-0.5 μ m.

Previous reports: Atlantic, Mediterranean Sea, Indian Ocean, Pacific, Caribbean Sea.

B. 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.

N.B. Young & 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.

Plate 14 figs. 1, 2 and 3.

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

Coronosphaera binodata (Kamptner) Gaarder, in: Gaarder & 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 two 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 spine.

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

Previous reports: Pacific, Atlantic, Caribbean Sea.

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

Plate 14, figs. 4, 5 and 6.

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

Coronosphaera mediterranea (Lohmann) Gaarder in Gaarder & 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*.

This species can form combination coccospheres with *Calyptrolithina wettsteinii* (see Kamptner, 1941, and present study, in Chap. IV). These observations favour the opinion that these two species can be related in the same way as the *Coccolithus pelagicus* heterococcolith and holococcolith phases.

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 μ m, short axis 13- 14.5 μ m; body caneoliths major axis (3-) 3.3-3.7 (-4) μ m, minor axis (2.3-) 2.4-2.6 (-2.7) μ m; apical caneolith spine (1.2-) 1.3-1.7 (-2.1) μ m.

Previous reports: Mediterranean, Pacific, Atlantic, Caribbean Sea, Indian Ocean, Okhotsk Sea.

Genus Gaarderia Kleijne, 1993

The coccosphere is dithecate. Both endothecal and exothecal coccoliths are caneoliths with an anticlockwise 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

Plate 15 figs. 1-6.

Syracosphaera corolla Lecal, 1965a, pp. 252-253, pl. 1, fig. 1-4; Okada & McIntyre, 1977, p. 20, p. 20, pl. 8, figs 1-2.

Umbellosphaera corolla (Lecal) Gaarder, in: Heimdal & 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.

Taxonomic remarks: This species was erected as *Syracolithus corolla*, with *Syracolithus* being a subgenus of *Syracosphaera* by Lecal (1965). Later, Gaarder, in Heimdal & 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. I am confident that 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 this species could, in my opinion, be placed back in the genus *Syracosphaera*. Nevertheless, I think it is wise 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) μ m; body coccolith length (2-) 2.2-2.6 (-3.1) μ m, width (1.1-) 1.3-1.8 (-2.3) μ m; exothecal coccolith length (4-) 4.5-5.1 (-5.5) μ m, width (2.8-) 3.0-3.5 (-4.1) μ m.

Previous reports: Mediterranean, Pacific, Atlantic, Caribbean Sea, Indian Ocean.

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 (see also Annex 3); 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.

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 murolith, is constituted by the rim and the central area. The rim consists of the wall and flanges (proximal, mid-wall and distal) (see Fig. 3.4). The central area contains laths, a connecting external ring and a connecting central structure (see Fig. 3.5).

N.B. 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.

Taxonomic notes: This group was divided into three genera (*Syracosphaera "sensu stricto*", *Caneosphaera* and *Coronosphaera*) by Gaarder & 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 (having three flanges) *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 & McIntyre, 1977) and considered the proposed classification of Gaarder & 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 & Young, 1990). In recent taxonomical work (Jordan, 1991; Kleijne 1993, Jordan & Kleijne 1994, Jordan & Green, 1994, Young & 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.

Syracosphaera ampliora Okada et McIntyre, 1977

Plate 16, figs. 1-2

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

Syracosphaera ampliora Okada et McIntyre, 1977, p. 19-20, pl. 7, figs. 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 of 18 to 30 centrally widened laths.

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

Dimensions: coccosphere long axis 6.5-8.5 μ m; caneolith long axis (1.8-) 2.4-2.7 (-3) μ m, width (1.5-) 1.8-2.0 (-2.2) μ m.

Remarks: 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 and in not having a smooth distal flange as in *S. ossa*. Previous reports: Tyrrhenian Sea, North Atlantic Ocean, Pacific.

Syracosphaera anthos (Lohmann 1912) Janin, 1987

Plate 16, figs. 3-6

Deutschlandia anthos Lohmann, Reid, 1980, p. 156, pl. 2 figs. 5-6; Heimdal & 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.

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. This species can form hetero-holococcolithophore combination coccospheres with *Periphyllophora mirabilis* (see Chap. IV). The body caneoliths have neither distal nor midwall 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 posses 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.

Dimensions: coccosphere diameter (7-) 9.0-11.0 (-13) μ m; caneolith major axis (2-) 2.2-2.5 (-2.8) μ m, minor axis 1.4-1.9 μ m; circum-flagellar caneolith central spine length ca. 1 μ m; exothecal coccolith diameter 3.0-5.5 μ m.

Taxonomic notes: Heimdal & Gaarder (1981) demonstrated that Deutschlandia anthos Lohmann, 1912 was the correct name of the species reported as Syracosphaera variabilis (Halldal & Markali, 1955) by various authors (Okada & McIntyre 1977; Nishida, 1979; Winter et al., 1979), but not the species reported by Halldal & 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 & McIntyre, 1977; Janin, 1987) do not agree completely and assume a morphological variation inside the genus Syracosphaera wider than that accepted by Gaarder & Heimdal (1977) (see the former description of Syracosphaera genus). Hence, the genus Deutschlandia has been transferred to the genus Syracosphaera (Janin, 1987; Jordan & Young, 1990) and in later taxonomical works (Kleijne, 1993; Jordan & Kleijne, 1994, Jordan & 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.

Previous reports: Atlantic, Mediterranean Sea, Red Sea (Gulf of Elat), Indian Ocean, Indo-Malayan Region, Pacific Ocean, Caribbean Sea, Okhotsk.

Syracosphaera cf. dilatata Jordan Kleijne et Heimdal, 1993

Plate 17, figs. 1-6

Caneosphaera halldalii f. dilatata Heimdal, in Heimdal & Gaarder, 1981, p. 44, pl. 2, figs. 9 a-b.

Syracosphaera halldalii f. dilatata (Heimdal, in Heimdal & 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 & Green, 1994, pp. 156, 160, 161.

Coccosphere considered dithecate (see Plate 17) 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 & Gaarder, 1981; Hallegraef, 1984), and a robust process that ends in four small peaks. The probable 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 & Gaarder (1981) pl. 2 fig. 9 as *Caneosphaera halldalii* f. *dilatata*.

Remarks: 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.

Notes: 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 circumflagelar caneoliths have the same dimensions and show similar nodules on the external side of the wall as the specimens recorded by Heimdal & Gaarder (1981) and Hallegraef (1984). The similarity between the exothecal caneoliths of this *Syracosphaera* and the caneoliths illustrated in Heimdal & Gaarder (1981) pl. 2 fig. 9 as *Caneosphaera halldalii* f. *dilatata*, suggests that the coccoliths shown in Heimdal & 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 & Gaarder (1981).

Taxonomic notes: Heimdal & Gaarder (1981) described this species as a variety of *Caneosphaera halldalii* f. *halldalii* Heimdal; Jordan & 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 & Gaarder (1981).

Dimensions: coccosphere long axis (9-) (10-12) (-14) μ m; body caneoliths major axis (2-) 2.3-2.5 (-2.7) μ m, minor axis 1.3-1.8 μ m; circum-flagellar caneoliths diameter 1.5-2 μ m, spine length 1.5-2 μ m; exothecal caneoliths major axis (2.3-) 2.7-2.9 (-3.1) μ m, minor axis 1.7-1.8 μ m.

Previous reports of S. dilatata: North Atlantic, Pacific Ocean, Indian Ocean Caribbean Sea and Red Sea.

Syracosphaera halldalii Gaarder ex Jordan et Green, 1994

Plate 18, figs. 1-6

Syracosphaera mediterranea Lohmann sensu Halldal & Markali 1954b, p. 330, figs 2 a-d.

Syracosphaera halldalii Gaarder in Gaarder & Hasle 1971, p. 536; Borsetti & Cati, 1976, p.215 plate 14 fig. 11-12; Okada & McIntyre, 1977, p. 23, 26 Plate 10, figs. 1-2.

Syracosphaera halldalii Gaarder f. halldalii in Kleijne 1993 p. plate 4 figs. 4-6; Winter & Siesser, 1994, p. 136 fig. 111 (phot. A. Winter/P. Friedinger)

Caneosphaera halldalii (Gaarder) Gaarder in Gaarder & 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 line. Circum-flagellar caneoliths very few in number, with a central spine, square in section.

Remarks: 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" (plate 18, figs. 1, 2 and 3) with a very wide and smooth distal flange that has tooth-like protrusions, and c) the "finger-like form" (plate 18, figs. 4, 5 and 6) 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 my opinion the "ordinary form" and the "tooth-like form" may be the same species (see in Plate 18, fig. 1 a "tooth-like form" specimen having some coccoliths resembling those of the "ordinary form" figured in Gaarder & 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.

Taxonomic notes: The classical description of a complete caneolith, given by Halldal & Markali (1954), 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 & Hasle (1971) proposed the new name of *S. halldalii* Gaarder for Halldal & Markali's specimen. Further studies on this species were carried out by Gaarder & Heimdal (1977) leading to a re-identification of Halldal & Markali's coccoliths with the new generic name of *Caneosphaera*. Jordan & 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 (1954) and Gaarder and Heimdal (1977) which included the *S. protudens* described by Okada & McIntyre (1977).

Dimensions: "tooth-like form" coccosphere 45 to 75 body caneoliths, around 6 apical spine-bearing caneoliths, coccosphere diameter 9-12 μ m, body caneolith major axis (2-) 2.5-3.0 (3.2) μ m.; "finger-like form" coccosphere 50 to 120 body caneoliths, around 6 apical spine-bearing caneoliths, coccosphere diameter 7-12 μ m, body caneolith major axis (1.6-) 2-2.5 (-3) μ m.

Previous records: Atlantic, Mediterranean Sea, Red Sea, Arabian Sea, Indian Ocean, Pacific, Caribbean Sea.

Syracosphaera histrica Kamptner, 1941

Plate 19, figs. 1 and 2

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

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 and anastomosing root system.

Coccolith numbers: (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) μ m; body caneolith major axis (1.9-) 2.3-2.7 (-3.3) μ m; circum-flagellar caneolith spine length ca. 1.4 μ m; exothecal coccolith long axis (2.1-) 3.0-3.2 (-3.6) μ m.

Previous reports: Mediterranean Sea, Atlantic, Indian Ocean, Pacific, Caribbean Sea.

Syracosphaera lamina Lecal-Schlauder, 1951

Plate 19, figs. 3-6.

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

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 shapes; may possess exothecal coccoliths but no differentiated circum-flagellar endothecal coccoliths. Endothecal caneoliths have a high and slenderly undulated wall 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 (see Pl. 19, fig. 6) 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.

Remarks: 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 μ m; body caneolith major axis (3.1-) 3.4-3.8 (-4.0) μ m; exothecal coccolith diameter ca. 3.5 μ m.

Previous reports: Mediterranean Sea, Atlantic Indian Ocean, Caribbean Sea and Pacific.

Syracosphaera marginaporata Knappertsbusch, 1993

Plate 20, figs. 1-4.

Syracosphaera marginaporata Knappertsbusch, 1993a, p. 72-74, pl. 2 figs. 1-4; Samtleben et al., 1995, plate 2 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 in the present study, 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 porelike gaps occurs between the elements, next to the smooth distal flange; the number of the 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 μ m length) tipped by four endings; usually they lack the distal flange (Plate 20, fig. 2 and fig. 3 from Knappertsbusch, 1993a) possibly because it is easily broken (see Plate 20, fig. 4). 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.

Remarks: The smooth appearance of the caneoliths and the row of gaps between the central area and the distal flange is characteristic of this species. I 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*.

The coccospheres (13 specimens) have (16-) 28-36 (-42) body caneoliths ; 2 to 6 spines; when present (2-) 5-6 (-8) exothecal coccoliths.

Dimensions: coccosphere long axis 3-6 μ m; body caneolith major axis (1.0-) 1.4-1.7 (-1.9) μ m; circum-flagellar caneolith spine length ca. 1 μ m; exothecal complex undulating coccolith diameter 1.3-1.9 μ m.

Previous reports: North Atlantic, Northeastern Indian Ocean, Mediterranean Sea.

Syracosphaera molischii Schiller, 1925

Plate 20, figs. 5-8.

Syracosphaera molischii Schiller, Halldal *et* Markali, 1954b, p. 332-333, fig. 5; Borsetti & Cati 1972, p.401, pl. 45, fig. 2 a-b; Okada & McIntyre, 1977, pp. 24, pl. 8, fig. 4-5; Samtleben & Schröder, 1992, p. 345 pl. 1 fig. 2; Kleijne 1993 p. 238 pl. 3 fig. 10-11; Winter & Siesser 1994 p. 137 figs. 115 A, B; Samtleben *et al.* 1995 p. 235, pl. 2, fig. 5.

Caneosphaera molischii (Shiller) Gaarder, in Gaarder & Heimdal 1977, pp. 66-68, pl. 7, pl. 8 fig.49; Heimdal & Gaarder 1981, pp. 44-46, pl. 3; Hallegraeff 1984, p. 242 fig. 47 a-b.

Syracosphaera corrugis Okada et McIntyre 1977 p. 21 pl. 8 figs. 3, 6.

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 & Gaarder, 1981); the distal side is highly ornamented and 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 (see Plate 20, fig. 5).

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 μ m; body caneoliths length (1.7-) 2.3-2.7 (-3.4) μ m; circum-flagellar caneolith spine length ca. 1.5 μ m; complex undulated exothecal coccolith diameter ca. 2.5 μ m.

Previous reports: Atlantic, Pacific, Mediterranean Sea, Red Sea, Arabian Sea, Indian Ocean and Caribbean Sea.

Syracosphaera nana Kamptner, 1941

Plate 21, figures 1-6 Syracosphaera 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.

Coccosphere dithecate with dimorphic endothecal caneoliths. Hetero-holococcolithophore combination coccospheres involving this species have been observed (Kleijne, 1991; present study, Chapter IV) and hence *S. nana* is considered to have an holococcolithophore life-cycle phase (Kleijne, 1991).

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 three-cornered at the extremes of the coccolith ellipse and otherwise four-cornered (plate 21, fig. 4 and Kleijne, 1991, pl. 20 fig. 6); this solid central part is slightly convex in distal view. Coccospheres of the holococcolithophore phase possess dimorphic coccoliths; body laminoliths and zygolith-like circum-flagellar holococcoliths (see pl. 21, fig. 6).

Remarks: The ovoid shape of the coccosphere is characteristic (pl. 20, fig. 1), 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.

N.B. The coccospheres figured as *S. nana* by Halldal & Markali (1955), by Okada & McIntyre (1977), by Nishida (1979) and in Winter & 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). The holococcolith coccosphere consists of 94 to 112 body holococcoliths; sometimes with circum-flagellar holococcoliths (from 10 to 12).

Dimensions: heterococcolith coccosphere long axis 5-7 μ m; body caneoliths long axis (0.9-) 1.4-1.6 (-1.9) μ m; circum-flagellar caneolith spine height 0.1- 0.2 μ m; exothecal coccolith long axis (1.8-2.2) μ m.; holococcolith coccosphere diameter 5.5-7.5 μ m; body holococcoliths major axis (0.9-) 1.1-1.3 (-1.5) μ m.

Previous reports: Mediterranean Sea, Atlantic.

Syracosphaera nodosa Kamptner, 1941

Plate 22, figs. 1-4.

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

Coccosphere dithecate with dimorphic endothecal caneoliths. Body caneoliths, without neither distal nor 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 by 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.

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) μ m; body caneoliths long axis (1.7-) 2.3-2.5 (-2.6) μ m; circum-flagellar caneolith spine height 1.3 μ m; exothecal coccolith diameter 2.5 μ m.

Previous reports: Mediterranean Sea, Atlantic, Pacific, Indian Ocean, Caribbean Sea.

Syracosphaera noroitica Knappertsbusch, 1993, orthog. emend. Jordan et Green, 1994.

Plate 23, figs 1-6.

Syracosphaera sp. type E, Kleijne (1993), p. 242, pl. 6, fig. 4.

Syracosphaera noroiticus Knappertsbusch, 1993a, p. 71-72, pl. 1 fig. 1-3

The coccosphere is recognizably dithecate in our material and the endotheca consists of 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 extensions of the laths of the smallest caneoliths, at the antapical pole, are marked, some protruding as thorns above the rim of the wall (see Plate 24, fig. 5 and 6). 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 apical circum-flagellar caneoliths possess a long central spine, forked at the end. The exothecal coccoliths are true elliptical caneoliths 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.

Coccolith numbers: 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) μ m; varimorphic body caneolith major axis (1.3-) 1.8-2.2 (-2.5) μ m, with 20-29 laths; circum-flagellar caneolith spine length ca. 2 μ m; exothecal caneolith major axis 2.0-2.5 μ m, with 27-29 laths.

Previous reports: Atlantic, Red Sea, Mediterranean Sea, Pacific, Indian Ocean.

Syracosphaera ossa (Lecal) Loeblich Jr. et Tappan, 1968

Plate 24, figs. 1-6.

Syracorhabdus ossa Lecal, 1965a, p. 253-254 pl. 2 figs 5-8.

Syracosphaera ossa (Lecal) Loeblich & Tappan, Okada & McIntyre 1977, pp. 25-26, pl.10, figs 9-10; Kleijne, 1993 p. 240 pl. 5, figs 4-5; Winter & 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 (see Pl. 24, figs. 1, 4, 5 and 6; 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.

Remarks: *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*.

Coccolith numbers: 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) μ m; body caneolith major axis (1.4-) 1.9-2.1 (-2.6) μ m; circum-flagellar caneolith spine length (1.3-) 1.4-1.6 (-1.8) μ m; exothecal coccolith long axis 2.0-2.4 μ m.

Previous reports: Atlantic, Pacific, Mediterranean Sea, Red Sea, Arabian Sea, Indian Ocean, Caribbean Sea.

Syracosphaera prolongata Gran ex Lohmann sensu Throndsen, 1972

Plate 25, figs. 1-4.

Syracosphaera prolongata Gran ex Lohmann, 1913, in Throndsen, 1972, pp. 57-59, figs. 22-28; Okada & 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 & Heimdal 1977, pp. 56-58, pl.3; in Winter & Siesser 1994 p. 139, fig. 120 (Phot. from Winter).

The coccosphere is dithecate with dimorphic endothecal caneoliths; it can be elongated (see Throndsen, 1972, figs. 22-25) or can be from spherical to obpyriform (plate 25, fig. 1). 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 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 appear to protrude out of the wall forming a beaded proximal flange; the low wall has a very narrow distal flange. Both endothecal and exothecal caneoliths show a characteristic thread-like pattern across the laths around the coccolith (see plate 25, figs. 3-4).

Remarks: 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.

Coccolith numbers: The studied coccospheres consisted of (42-) 50-66 (-94) body caneoliths (7 specimens); 3 to 8 circum-flagellar caneoliths with spine; and from 14 to 24 exothecal caneoliths (N.B. the exothecal coccoliths are very loosely attached to the coccosphere and so may easily be lost).

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

Previous reports: Atlantic, Mediterranean Sea, Pacific, Indian Ocean and Arabian Sea.

Syracosphaera prolongata Gran ex Lohmann, 1913 sensu Heimdal & Gaarder, 1981

Plate 25, figs. 5-8.

Syracosphaera prolongata Gran ex Lohmann, Heimdal & Gaarder, 1981, p. 60-62, pl. 10 figs. 48-50; in Winter & Siesser, 1994, p. 139 fig. 121 (Phot. from Knappertsbusch).

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.

Remarks: 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 bigger caneoliths with this characteristic twisted mound central structure as opposed to a small rounded nodule.

Coccolith numbers: 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) μ m; body caneolith long axis (1.9-) 2.4-2.7 (-3.3) μ m; circum-flagellar caneolith spine length ca. 2μ m; exothecal caneolith diameter (2.3-) 2.7-3.0 (-3.8) μ m.

Previous reports: Atlantic, Mediterranean Sea.

Syracosphaera pulchra Lohmann, 1902

Plate 26, figs. 1-5

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 & Tappan, 1963, p. 193; Okada & McIntyre, 1977, p. 27, pl. 10 figs. 11-12; Gaarder & Heimdal, 1977, p. 55 pl. 1 figs. 1-8; Borsetti & 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 & Pienaar, 1988, pp. 207-216, figs. 1-15; Delgado & 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 & 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.

Remarks: *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 & 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.

Two combination coccospheres of *Syracosphaera pulchra* with *Calyptrosphaera oblonga* Lohmann have been found in the course of the present study (Chapter IV, Pl. 78, figs. 2-4). These findings together with previous notes in the literature favour the opinion that these two species can be related in the same way as the *Coccolithus pelagicus* heterococcolith and holococcolith phases.

Notes: In sediments as well as in two samples of Mediterranean water I have observed 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 (pl. 26, fig. 4).

Coccolith numbers: 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) μ m; body caneolith long axis (5.1-) 5.2-5.6 (-6.1) μ m; circum-flagellar caneolith spine length 2.5-3.5 μ m; exothecal caneolith long axis (4.7-) 5.2-5.8 (-6.7) μ m.

Previous reports: Mediterranean Sea, Red Sea, Indian Ocean, Atlantic, Pacific, Caribbean Sea and Okhotsk Sea.

Syracosphaera rotula Okada et McIntyre, 1977.

Plate 26, figs. 6-7

Syracosphaera rotula Okada *et* McIntyre, 1977, p. 27, Plate 9 fig. 12; Borsetti & Cati, 1979, p. 161, pl. 17, figs. 1-2; Kleijne, 1993, p. 241, pl. 5 fig. 9; Winter & 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 laths and a central part composed of two plates.

Only one specimen recorded from winter samples (Hivern-99 cruise)

Remarks: The exothecal coccoliths of *Syracosphaera rotula* strongly resemble those of *S*. *nodosa*, differing mainly in having longer laths and a narrower and bent rim.

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

Dimensions: coccosphere diameter (one collapsed specimen) ca. 5-6 μ m; body caneolith long axis 1.2 -2.3 μ m; exothecal caneolith diameter ca. 2.5 μ m.

Previous reports: Indian Ocean, Arabian Sea Red Sea, Mediterranean Sea, Atlantic, Pacific.

Syracosphaera tumularis Sánchez-Suárez, 1990.

Plate 27, figs. 1-7

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 & 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 & Siesser 1994, p. 137, fig. 114 (phot. S. Nishida).

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

In the present study, this coccosphere is considered dithecate 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 and thin sub-circular 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.

Notes: 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, I conclude that this species is recognizably dithecate, with only one kind of endothecal coccolith.

Coccolith numbers: 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 μ m; body caneoliths long axis (3.3-) 3.5-3.8 (-4.2) μ m; exothecal coccolith diameter (3.8-) 4.0-4.4 (-4.6) μ m.

Previous reports: Mediterranean Sea, Caribbean Sea, Atlantic, Pacific, Indo-Malayan Region (North Australian Sea Waters).

*Syracosphaera species which have not received formal names, but that can be recognized in the literature

Syracosphaera sp. type D Kleijne 1993.

Plate 28, figs. 1-7

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 & Gaarder 1981, p. 60. pl. 8 figs. 40-41; Sánchez-Suárez 1992, p. 115-117, figs. A-C.

Coccosphere with dimorphic endothecal caneoliths and recognizably dithecate in our material. The body caneoliths have a proximal, a folded 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, according to my interpretation, are caneoliths very similar to the ordinary ones (see Pl. 28, fig. 4); 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.

Remarks: This species closely resembles *S*. cf. *dilatata* (see above) in general shape, in the morphology of circum-flagellar caneoliths and in the presumed similarity in the structure of exothecal caneoliths. The body caneoliths have a folded 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*.

Coccolith numbers: 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) μ m; body caneolith long axis (2.1-) 2.3-2.6 (-3.1) μ m; circum-flagellar caneolith spine length 1.5-1.9 μ m; exothecal caneolith long axis (3.1-) 3.4-3.6 (-3.8) μ m.

Previous reports: North Atlantic, Caribbean Sea, Mediterranean Sea.

Syracosphaera sp. type G Kleijne 1993.

Plate 29, figs. 1-4

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

Coccosphere dithecate in our material; 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.

Remarks: S. 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 S. sp. type G is very low and distally is characteristically different from that of the other related species.

Coccolith numbers: 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 long axis (1.1-) 1.6-1.8 (-2.1) μ m; circum-flagellar caneolith spine length 1.2-1.4 μ m; exothecal caneolith long axis ca. 1.8 μ m. Previous reports: Indian Ocean, Arabian Sea, Red Sea.

Syracosphaera sp. type L Kleijne 1993.

Plate 29, figs. 5-6

Syracosphaera sp. type L, Kleijne 1993, p. 245 pl. 5 fig. 1-2.

Dithecate coccosphere with monomorphic endothecal caneoliths; these coccospheres are usually spherical in shape. 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.

Remarks: The caneoliths of *Syracosphaera* sp. type L 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.

Coccolith numbers: 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 μ m; body caneolith long axis (2.0-) 2.1-2.2 (-2.4) μ m; exothecal coccolith diameter (1.7-) 1.8-1.9 (-2) μ m.

Previous reports: Indian Ocean, Arabian Sea, Atlantic, Mediterranean Sea.

*Syracosphaera species which have not received formal names, and are not clearly recognizable in the literature

Syracosphaera sp. 1 (affinis to S. nodosa)

Plate 22, figs. 5-7.

Syracosphaera cf. nodosa, Heimdal & Gaarder 1981, pl. 9, fig. 45.

Syracosphaera nodosa Kamptner in Sánchez-Suárez, 1992, p. 117, fig. 3D-E.

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*.

Remarks: Syracosphaera sp. 1 strongly resembles S. nodosa: caneoliths of Syracosphaera sp. 1 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 μ m high compared to 0.3 μ m 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 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.

Coccolith numbers: 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 μ m; body caneolith major axis (2.4-) 2.7-2.9 (-3.2) μ m, rim height ca. 0.6 μ m; circum-flagellar caneolith spine height ca. 1 μ m; exothecal coccolith diameter (3.0-) 3.2-3.3 (-3.5) μ m.

Previous reports: Caribbean Sea, Atlantic (off NW-Africa).

Syracosphaera sp. 2 (slender, with recognizable exothecal coccoliths)

Plate 30, figs. 1-2.

Syracosphaera sp. II cf. S. epigrosa Kleijne 1993

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*.

Coccolith numbers: 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 caneoliths.

Dimensions: coccosphere long axis 6-10 μ m; body caneolith long axis (1.3-) 1.7-1.9 (-2.2) μ m; circum-flagellar caneolith spine length 1.8-2.3 μ m; antapical caneolith spine length 2-3 μ m; exothecal caneolith length (2.3-) 2.5-2.7 (-3.1) μ m.

Previous reports: Indian Ocean, Red Sea, Mediterranean Sea, Atlantic.

Syracosphaera sp. 3 caneoliths with laths having perpendicular rod protrusions.

Plate 30, figs. 3-6.

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

Syracosphaera sp. I cf. epigrosa Kleijne 1993, p. 237, pl. 4 fig. 1.

Dithecate coccosphere 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 (figs. 3, 5), but in others the nodules/rods are arranged very regularly (figs 4 and 6); 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, not previously reported, are simple undulating coccoliths (see figs. 3, 4 and 6) with the ends bent upwards, giving a distally concave aspect.

Remarks: 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.

Taxonomic notes: 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 S. 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 S. sp. II cf. *epigrosa*, with a narrow distal flange and no nodules. I suspect that the presence or absence of dimorphic endothecal coccoliths between S. *epigrosa* and S. sp. I cf. *epigrosa* and the very different aspect of the central processes in the circum-flagellar caneoliths between S. *epigrosa* and S. sp. II cf. *epigrosa* indicates very important reasons to consider these three taxa as essentially different. As a result, the three taxa could legitamately be considered as different species.

Coccolith numbers: 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) μ m; body caneolith long axis (1.4-) 1.7-1.9 (-2.5) μ m; exothecal coccoliths long axis (1.7-) 1.9-2.1 (-2.4) μ m.

Previous reports: Mediterranean Sea, North Atlantic.

Syracosphaera sp. 4 (now, S. delicata sp. nov., see Cros et al. 2000)

Plate 31, figs. 1-3.

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.

Remarks: 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.

Taxonomic notes: The coccosphere resembles the images and description of *Pontosphaera* nana by Halldal & Markali (1977), particularly with respect to the endothecal caneoliths; both have no distal flange, a wide and flat central area and a fragile appearance, but *Syracosphaera* sp. 4 (*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* sp. 4). *Syracosphaera* sp. 4 (*delicata*) also resembles *S orbiculus* Okada & 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 μ m compared to 1 μ m described by Okada & McIntyre, 1977) and smaller exothecal coccoliths with a narrower rim.

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

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

Syracosphaera sp. 5 (aff. S. sp. type K of Kleijne, 1993), now S. bannockii comb. nov. (see Cros et al. 2000).

Plate 31, figs. 4-7.

Syracosphaera nana Kamptner in Nishida, 1979, Plate 7, Fig. 4

Syracosphaera orbiculus in Samtleben et al., 1995, Plate II, fig. 4.

?Syracosphaera sp. type K Kleijne, 1993, p. 244, pl. 6 fig. 11

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.

Syracosphaera sp. 5 strongly resembles *Syracosphaera* sp. type K Kleijne, 1993, p. 244, pl. 6 fig. 11, but differs mainly in having exothecal coccoliths without thickened or stratified parts as shown in the coccoliths of *Syracosphaera* sp. type K.

This *Syracosphaera* can form combination coccospheres with holococcoliths (see chapter IV).

Coccolith numbers: 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 μ m; body caneoliths long axis (1.3-) 1.5-1.7 (-2.0) μ m; circum-flagellar caneolith spine length ca. 0.5 μ m; exothecal coccoliths long axis (2.0-) 2.4-2.8 (-2.9) μ m.

Previous reports: Pacific and North Atlantic.

Syracosphaera sp. 6 (with stratified/thickened exothecal coccoliths)

Plate 32, figs. 1-4.

Syracosphaera nana auct. non (Kamptner) in Okada & 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 structure).

Remarks: The caneoliths of *Syracosphaera* sp. 6 have double layered ordinary caneoliths resembling the caneoliths of *S*. sp. 5 (aff. type K of Kleijne) 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 *Syracosphaera* sp. 6.

Taxonomic notes: The specimens figured by Okada & McIntyre (1977) pp. 24-25, pl. 8 figs. 7-8 as *Syracosphaera nana* (Kamptner), by Heimdal & Gaarder (1981) p. 60, pl. 8, figs. 42a-b as *S*. cf. *nana* (Kamptner) Okada & McIntyre and *Syracosphaera* sp. type J Kleijne, 1993, p. 244, pl. 5 fig. 3 all resemble *Syracosphaera* sp. 6, 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 & McIntyre (1977) pl. 8 fig. 9 and *S*. sp. 6. I consider that two different, but very close taxa may exist: *S*. sp. 6 and *S*. sp. type J Kleijne.

Coccolith numbers: 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 μ m; body caneoliths long axis (1.5-) 1.6-1.8 (-2) μ m; circum-flagellar caneolith spine length ca. 0.5 μ m; exothecal coccoliths diameter 2.5-2.9 μ m.

Syracosphaera sp. 7 (aff. S. nana; small coccoliths and laths with sinistral obliquity)

Plate 32, figs. 5-7.

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 (some opposite laths have extensions, giving the appearance of parallel lines in the middle of the caneolith). Circumflagellar caneoliths have laths oriented anticlockwise and a blunt low spine as a central structure. Exothecal coccoliths are small, oval, disc-like coccoliths.

Taxonomic notes: 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 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 bigger than *S*. sp.7.

Coccolith numbers: Three coccospheres studied: 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 μ m; body caneolith long axis (1.1-) 1.4-1.5 (-1.7) μ m; circum-flagellar caneolith spine length ca. 0.3 μ m; exothecal coccoliths long axis 1.6-1.9 μ m.

Syracosphaera sp. 8 (aff. to S. orbiculus (ovoid shape))

Plate 33, figs. 1-2.

Coccosphere subcircular 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.

Remarks: 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 & McIntyre (1977) pl. 9 fig. 6, and in possessing smaller and more elliptical exothecal coccoliths.

N.B. The body caneoliths of specimen 2, on which exothecal coccoliths were not seen, appear to have slightly thinner wall and narrower central structure than those of specimen 1; the circumflagellar caneoliths have spines which are slightly different in these specimens, those of specimen 1 having pointed endings. These slight differences may either merely reflect intraspecific variability, or may represent two taxa within this S. sp. 8. More specimens are needed to clarify if there are one or two taxa.

Coccolith numbers: Three studied coccospheres, estimated body caneoliths 64, 64 and 70; 4 circum-flagellar caneoliths with spine; only two exothecal caneoliths.

Dimensions: coccosphere long axis 8-9 μ m; body caneolith long axis (1.8-) 1.9-2.1 (-2.3) μ m; circum-flagellar caneolith spine length ca. 0.8 μ m; exothecal coccolith long axis ca. 2.7 μ m.

Syracosphaera sp. 9 (aff. to S. orbiculus (spherical shaped))

Plate 33, figs. 3-5.

? 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.

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

Coccolith numbers: Four studied coccospheres; 26, 42, 42 and 60 body caneoliths; 4 circum-flagellar caneoliths with spine; many detached exothecal caneoliths.

Dimensions: coccosphere long axis 6-9 μ m; body caneolith long axis (1.4-) 2.0-2.2 (-2.4) μ m; circum-flagellar caneolith spine length ca. 1 μ m; exothecal caneolith length 2.5-3.0 μ m.

Previous observations: ?Southern Ocean (Australian sector), North Atlantic (M. Cachao and A. Oliveira, personal communication, 1999).

C <u>Genera pending a taxonomic change</u> (inside a group that includes nannolithheterococcolith forms)

Genus Alisphaera Heimdal, 1973, emend. Jordan et Chamberlain, 1993

Alisphaera is accepted as a monothecate genus with monomorphic elliptical coccoliths which have no biaxial symmetry; the 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.

This genus can form combination coccospheres with *Polycrater* (see Chapter IV).

Taxonomic remarks: Until now, the genus *Alisphaera* has been included in the family *Syracosphaeraceae*, but in the literature the fact that their coccoliths are not real caneoliths is recognized, some authors referring to them as placolith-like coccoliths (Young & Bown, 1997b) or as modified caneoliths (Chrétiennot-Dinet, 1990; Jordan and Chamberlain, 1993a). Following the discovery of coccospheres combining *Alisphaera* with the nannolith-bearing genus *Polycrater* (see Chap. IV), it seems advisable to group these genera as a new taxon associated with all the former genera which are related to the nannolith-bearing coccolithophores.

Alisphaera capulata Heimdal, in Heimdal et Gaarder, 1981.

Plate 34, figs. 1-2.

Alisphaera capulata Heimdal, in Heimdal & Gaarder, 1981, p. 39-40, pl. 1 Fig. 3 -4 ; Kleijne, 1993, p. 233, pl. 2, fig. 7.

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 clear slit.

Coccolith numbers: between 68 and 90.

Dimensions: coccospheres long axis 4.5-7.0 μ m; coccolith long axis 1.4-1.6 μ m. Previous reports: Atlantic, Mediterranean Sea, Caribbean Sea.

Alisphaera unicornis Okada et McIntyre, 1977

Plate 35, figs. 5-6

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. 41 a-b; Winter & Siesser, 1994, p. 132, fig. 90A (phot. from Winter and Friedinger).

Alisphaera spatula Steinmetz, 1991, pp. 29-30, pl. 15, figs. 6-8; Jordan et Chamberlain, 1993a, p. 378, figs. 9, 10 e-f; Kleijne, 1993, p. 234, pl. 2, fig. 11.

The coccoliths have a pointed protrusion like a horn on the wider distal flange and a longitudinal irregularly shaped opening in the central area.

Taxonomic notes: It is very difficult to distinguish between *Alisphaera unicornis* and *A*. *spatula* Steinmetz, 1991, the blade-like protrusion, characteristic of the latter species, is not always obvious, and specimens must be examined carefully under very high magnification to distinguish it; even the *A. unicornis* holotype figured in Okada & McIntyre (1977) is not distinguishable since the magnification of the figure is not sufficient to determine whether the

blade-like element is present or absent below the thorn. I am not able, at present, to distinguish properly these two species until more information is available. Since *A. unicornis* was described first, I include under this name the specimens either with or without the blade-like element. I am confident that the coccosphere figured in the present study, in plate 35, fig. 5 belongs to the same species as the holotype from Okada & McIntyre (1977) Plate, 6, fig. 7.

Coccolith numbers: around 140 coccoliths.

Dimensions: coccosphere diameter ca. 11 μ m; coccolith long axis 2.4-2.7 μ m.

Previous reports: Atlantic, Mediterranean Sea, Pacific.

Alisphaera sp. cf. A. unicornis (of Kleijne, 1993)

Plate 34, figs. 5-6.

Alisphaera sp. *cf. A. unicornis* Okada & McIntyre 1977, Kleijne, 1993, p. 233, pl. 2, fig. 10. Plate 34, figs. 5-6.

The coccoliths have a longitudinal slit 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.

Coccolith numbers: 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 μ m; coccolith long axis (1.3-) 1.5-1.6 (-1.8) μ m.

Previous reports: Indian Ocean.

Alisphaera sp. aff. A. unicornis (with extended wider flange)

Plate 34, figs. 3-4. sp.

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, pointed extension on the outside part of the wider distal flange.

Coccolith numbers: (one coccosphere) around 88 coccoliths.

Dimensions: coccosphere long axis ca. 8 μ m; coccolith long axis 1.6-1.9 μ m. Previous reports: Mediterranean Sea, Atlantic.

Alisphaera sp. aff. A. unicornis (with a beak-like protrusion)

Plate 35, figs. 3-4.

Alisphaera unicornis Okada et McIntyre, 1977 p. 18, pl. 6, fig 8 (not fig. 7); Kleijne, 1993, p. 233, pl. 2, fig. 9; Winter & Siesser, 1994, p. 132, fig. 90B (phot. from Samtleben).

The coccoliths have on the wider distal flange a pointed projection like a beak or asymmetrical spine and a longitudinal irregularly shaped opening in the central area.

Combination coccospheres of this species with *Polycrater* have been observed (see Chap. IV).

Coccolith numbers: (one coccosphere) around 158 coccoliths.

Dimensions: coccosphere diameter ca. 10 μ m; coccolith long axis 1.6-2 μ m. Previous reports: Mediterranean Sea, Atlantic.

Alisphaera sp. aff. A. ordinata (with a five sided extension)

Plate 35, figs. 1-2

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 raised protrusion which is more or less five-sided, situated in the centre of the wide distal flange, covering a slit present in the outer part of the same flange.

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

Coccolith numbers: 60, 62, 80 and 112 coccoliths.

Dimensions: coccosphere long axis 6.5-8 μ m; coccolith long axis (1.3-) 1.4-1.7 (-2.1) μ m.

Remarks: The coccospheres belonging to this taxon were formerly grouped inside *A*. *ordinata* (Kamptner) Heimdal, 1973, but differ from this latter species mainly in possessing a five-sided protrusion instead of the rather broad protrusion extended over nearly all of the distal flange.

Previous reports: Mediterranean Sea, Atlantic.

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 usually has nodules along the inner periphery of the flange; an organic membrane appears to cover the proximal central area of the coccolith.

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

Taxonomic remarks: This genus is classified inside the family Syracosphaeraceae because the authors who described recognized the resemblance with the genus *Alisphaera* (Jordan & Chamberlain, 1993). 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* (see Pl. 36, fig. 1 and below in Chapter IV), it seems necessary to group *Polycrater* with *Alisphaera*, and to define this newly emerging genus perhaps within a new higher taxon which would contain all the genera that have relationships with nannolith-bearing coccolithophores.

Canistrolithus sp. 1

Plate 36, figs. 1-4.

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 (see Chap. IV).

Remarks: *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.

Coccolith numbers: In the more complete coccosphere, around 212 coccoliths.

Dimensions: coccosphere diameter (one specimen) ca. 19 μ m; coccolith long axis (2.3-) 2.6-2.9 (-3.1) μ m.

III.2.5 ORDER PRINSIALES Young et Bown, 1997

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

FAMILY NOËLAERHABDACEAE Jerkovic, 1970 emend. Young et Bown, 1997b.

Placoliths of the *Reticulofenestra*-type: 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 & Green, 1994), and in recent phylogenetic studies (Kawachi & Inouye, 1999) they appear to be related to *Isochrysis galbana* Parke emend. Green et Pienaar. Even authors who follow the classification of Parke & Green, in Parke & 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 & Green, 1994).

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

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

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

Plates 37 and 38.

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 & 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 considered 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 and 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 & Westbroek, 1991) and *E. huxleyi* var. *corona* Okada & 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 (Plate 37, figs. 1-2; Plate 38, figs. 1-4). Type C coccospheres (Plate 37, figs. 3-4; Plate 38, fig. 5) 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 (Plate 37, figs. 4-5), a morphology related to type C (see Young & Westbroek, 1991), and an overcalcified type with the inner tube elements growing into the central area (Plate 37, fig. 6; Plate 38 figs. 4 and 6), which was frequently observed in waters deeper than 40m. At present, I consider it prudent 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.

Coccolith numbers: (9-) 14-20 (-50) coccoliths.

Dimensions: coccosphere diameter (4.4-) 5-6 (9.5) μ m; coccolith long axis (2.7-) 3.2-3.6 (-4.2) μ m.

Previous reports: Worldwide.

Genus Gephyrocapsa Kamptner, 1943

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

Gephyrocapsa is a complex genus with considerable interspecific variability. Some authors (see 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).

Gephyrocapsa ericsonii McIntyre et Bé, 1967

Plate 39, figs. 3-6.

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 μ m long axis) and have the bar at a low angle (around 15°) with the long axis (see 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, Plate 39, fig. 3), *protohuxleyi* (with slits between distal shield elements, Plate 39, fig. 4), and *protohuxleyi-"with thorn"* (with well developed slits and also a slender thorn that grows from the placolith inner tube, Plate 39, fig. 5-6). These groups may be considered as different species, or as morphological variants along a continuous gradient.

The type *protohuxleyi-"with thorn"* was figured by Borsetti & 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.

In this study, three groups are considered as morphological or ecomorphological types and will be designated as *G. ericsonii* type *ericsonii* (fig. 3), *G. ericsonii* type *protohuxleyi* (fig. 4) and *G. ericsonii* type *protohuxleyi-with thorn* (figs. 5-6).

Coccolith numbers: between 12 and 18 (-26).

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

Previous reports: Atlantic, Mediterranean Sea, Red Sea, Indian Ocean, Pacific, Arabian Sea. But *G. ericsonii* type *protohuxleyi-with thorn* has only been recorded in Mediterranean waters.

Gephyrocapsa muellerae Bréhéret, 1978

Plate 39, fig. 2

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 (around 3 μ m along the long axis) and have the bar forming a higher angle with the long axis than in G. ericsonii (see Samtleben, 1980).

Coccolith numbers: between 14 and 24 coccoliths (5 coccospheres).

Dimensions: coccosphere diameter (5.3-) 7-8 (8.8) μ m; coccolith long axis (3.1-) 3.5-3.7 (-3.9) μ m.

Previous reports: Atlantic, Mediterranean Sea, Pacific, Caribbean Sea.

Gephyrocapsa oceanica Kamptner, 1943

Plate 39, fig. 1

Gephyrocapsa oceanica Kamptner, 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.

Coccolith numbers: 9 to 14 coccoliths (5 coccospheres).

Dimensions: coccosphere diameter (5.8-) 6-7 (-10) μ m; coccolith long axis (3.4-) 4.2-5.0 (6.0) μ m.

Previous reports: Worldwide in warm waters (Kleijne, 1993).

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

Placoliths without slits between the distal shield elements and no structures in the distal central area; proximal side of the central area can be filled by either a reticulate grid or by a more or less solid plate, or may appear open.

Reticulofenestra parvula (Okada et McIntyre, 1977) Biekart, 1989 var. parvula

Plate 40, fig. 1

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 $(1.5 - 2 \ \mu m \text{ along the long axis})$ 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.

Notes: Some specimens of *Gephyrocapsa ericsonii* from the NW Mediterranean have placoliths without a bridge which closely resemble the placoliths of *R. parvula* var. *parvula* (Plate 40, figs. 2 and 3). Similar specimens were figured by Heimdal & Gaarder (1981) pl. 4, figs. 20 a-b; Moreover, Okada & McIntyre (1977) point out the similarity between placoliths of *G. ericsonii* and *R. parvula* var. *parvula*; *Reticulofenestra* lacks the bridge that characterizes *Gephyrocapsa* specimens. A specimen of *G. ericsonii* type *protohuxleyi-with thorn* lacking the bridge in one placolith is also figured in Plate 40, fig. 4. Considering this

observation, 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.

Coccolith numbers: 20 coccoliths (1 coccosphere).

Dimensions: coccosphere diameter ca. 3.7 μ m; coccolith long axis 1.4-1.9 μ m.

Previous reports: Atlantic and Pacific, Indian Ocean.

III.2.6 ORDER COCCOSPHAERALES Haeckel, 1894 emend. Young & Bown, 1997

Monomorphic coccospheres with placoliths, usually without structures in the central area and with curved and overlapped shield elements. Alternation 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 (see Kleijne, 1991, and Cortes, 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 spherical to subspherical coccosphere which is robust.

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

Plate 41, figs. 1-6.

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.

The cell is either non-motile with the coccosphere consisting of placoliths (heterococcoliths) or motile with the coccosphere consisting of holococcoliths (Kleijne, 1991, 1993; Cortes, 2000). The holococcolith-bearing phase was previously described as *Crystallolithus rigidus* Gaarder, 1980 in Heimdal & Gaarder (1980)

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

Dimensions: heterococcolith coccospheres diameter (14.5-) 18.5-19.0 (-19.5) μ m; placolith diameter (8.4-) 9-10 (11.7) μ m; holococcolith coccospheres (collapsed) approximate diameter 8-15 μ m; holococcolith long axis (1.6-) 1.9-2.3 (-2.4) μ m.

Previous reports: Caribbean Sea, Atlantic, Mediterranean Sea, Indian Ocean, Pacific, Okhotsk Sea.

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

Plate 42, fig. 1

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

Oolithotus antillarum (Cohen), Reinhardt, in Cohen and Reinhardt, Kleijne, 1993, pp. 195-196, pl. 2, figs. 4-7

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

Remarks: 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 & McIntyre (1977), Hallegraeff (1984), and Kleijne (1993).

Coccolith numbers: Four coccospheres, 21, 24, 34 and 38 coccoliths.

Dimensions: coccosphere diameter 10-13 μ m; coccolith long axis 4.5-6.5 μ m.

Previous reports: Atlantic, Caribbean Sea, Red Sea, Indian Ocean, Pacific.

Oolithotus fragilis (Lohmann 1912) Martini et Müller, 1972

Plate 42, fig. 2.

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 sized coccospheres and placoliths which have a higher proximal/distal shield relationship and a less asymmetrically placed tube.

Coccolith numbers: around 30 coccoliths.

Dimensions: coccosphere diameter ca. 20 μ m; coccolith long axis 6.7-8.7 μ m.

Previous reports: Atlantic, Mediterranean Sea, Indian Ocean, Pacific, Red Sea, Arabian Sea, Caribbean Sea, Okhotsk Sea.

Genus Umbilicosphaera Lohmann, 1902

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

Umbilicosphaera hulburtiana Gaarder, 1970

Plate 42, fig. 3

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: coccolith diameter impossible to measure in single collapsed coccosphere; coccolith long axis 4 μ m.

Previous reports: Atlantic, Caribbean Sea, Mediterranean Sea, Indian Ocean, Pacific, Arabian Sea.

Umbilicosphaera sibogae var. *foliosa* (Kamptner, 1963) Okada et McIntyre 1977 ex Kleijne Plate 42, figs. 4

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.

Coccolith numbers: around 25 coccoliths.

Dimensions: Coccosphere diameter 12-13 μ m; coccolith diameter (4.7-) 5.0-5.5 (-6.3) μ m.

Previous reports: Atlantic, Mediterranean Sea, Indian Ocean, Pacific, Caribbean Sea, Okhotsk Sea.

Umbilicosphaera sibogae (Weber-van Bosse 1901) Gaarder 1970 var. sibogae

Plate 42, figs. 5-6

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.

Coccolith numbers: 84, 94 and 124 coccoliths on three collapsed coccospheres.

Dimensions: (collapsed) coccosphere diameter 20-30 μ m; coccolith diameter (3-) 4.5-5.5 (-7) μ m.

Previous reports: Atlantic, Mediterranean Sea, Indian Ocean, Pacific, Arabian Sea, Red Sea, Caribbean Sea, Okhotsk Sea.

III.2.7 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 & 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 & 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.*, 1976). 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, 1982; 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 species without an official name observed in this NW Mediterranean study, and for the absence of most of the known species. Of the described species, only *Papposphaera lepida* Tangen, 1972, was found 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

Plate 43, figs 1-6.

Papposphaera lepida Tangen, 1972, pp. 172, 175, 176, 177, Figs. 1-13.

Papposphaera lepida Tangen, 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 by 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 & Buck (1998) from Mexico (bahia de los Angeles, Sea of Cortez).

The distal structures of this species are highly variable, being from rounded to squared and even flower-shaped. In addition to the rim and the central area, the length and width of the spine can also be very variable. Moreover, this species can have polymorphic coccoliths even on one coccosphere, with differences in shape and size of the different parts of the pappolith (see the squared specimen figured in Thomsen & Buck, 1998, which also has a discoid calyx structure).

Coccolith numbers: 45-90 coccoliths (coccospheres usually collapsed, making estimations difficult).

Dimensions: coccosphere diameter 4.5-8 μ m; coccolith base long axis (0.5-) 0.7-1.0 (-1.5) μ m, spine length (0.5-) 0.7-1.7 (-2.7) μ m; distal structure (0.4-) 0.8-1 (-1.6) μ m.

Previous reports: Norwegian coastal waters, Caribbean Sea, Atlantic, Pacific.

Papposphaera sp. type 1

Plate 44, figs 1 and 2.

A single coccolith described and figured as *Deflandrius* cf. *intercisus* (Deflandre) Bramlette & Martini, 1964 by Norris (1983), p. 165, fig. 5 (the coccolith was found in the gut of a salp collected in the Indian Ocean, 31°08'S, 78°23'E, July 4 1963).

Papposphaera sp. 1 Thomsen & 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 wristlets and the calyx structure is formed by "four quasi-rectangular, diverging plates".

Remarks: The pappolith of this new species has an axial cross in the base plate instead of the diagonal cross that is present in the specimens figured as *Deflandrius* cf. *intercisus* (Deflandre) by Bramlette & Martini (1964). Moreover, the coccoliths are much larger in the latter species.

The number of specimens studied from NW Mediterranean waters was 8.

Coccolith numbers: 60-110 coccoliths.

Dimensions: coccosphere diameter 4.1-5.6 μ m; coccolith base long axis 0.5-0.8 μ m; coccolith height (0.4-) 0.7-1.0 (-1.6) μ m.

Papposphaera sp. type 2

Plate 44, figs. 3 and 4.

Dimorphic coccosphere, 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.

Coccolith numbers: (one specimen) 8 coccoliths with long spines; about 34 coccoliths with small central process.

Dimensions: coccosphere diameter ca. 5 μ m; coccolith base long axis 0.5-1.0 μ m; spine height 0.5-1.5 μ m.

Papposphaera sp. type 3

Plate 44, figs 5 and 6.

Varimorphic coccosphere, 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 real 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.

Coccolith numbers: around 50-60 coccoliths.

Dimensions: coccosphere diameter ca. 10 μ m; coccolith base long axis 0.6-0.8 μ m, height of long spines ca. 3μ m; distal structure 0.6 to 1.2 μ m.

Papposphaera sp. type 4

Plate 45, figs 1 and 2.

Varimorphic coccosphere, the proximal side of 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.

Coccolith numbers: (one specimen) ca. 50 coccoliths.

Dimensions: coccosphere diameter ca. 6 μ m; coccolith base long axis 0.7-0.8 μ m; stem height 0.7-2.0 μ m.

?Papposphaera sp. type 5 (only three elements compose the distal structure)

Plate 45, figs 3 and 4.

Varimorphic coccosphere, having coccoliths with 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.

Coccolith numbers: (two coccospheres) ca. 90 to 120 coccoliths.

Dimensions: coccosphere diameter 6-7 μ m; coccolith base long axis ca. 0.7 μ m; coccolith height (including stem) 0.6-1.5 μ m.

?Papposphaera sp. type 6 (only three elements compose the distal structure)

Plate 45, figs. 5 and 6.

Varimorphic coccosphere, coccoliths with distal structure larger than *Papposphaera* sp. type 5; 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.

Coccolith numbers: (one coccosphere) ca. 62 coccoliths.

Dimensions: coccosphere diameter 5-6 μ m; coccolith base long axis 0.7-1.1 μ m; coccolith height 1.0-2.5 μ m.

Papposphaera as "Turrisphaera" phase (Thomsen et al., 1991; Thomsen & Buck, 1998)

(Formerly genus Turrisphaera Manton, Sutherland et Oates, 1976)

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

Papposphaera as "Turrisphaera" phase sp. type A

Plate 46, figs 1 and 2.

The holococcoliths are "apple-core" shaped structures like the coccoliths of *Turrisphaera* borealis, but shorter and wider.

Coccolith numbers: (one coccosphere) ca. 60 coccoliths.

Dimensions: coccosphere diameter ca. 5 μ m; coccolith base diameter ca. 0.8 μ m; coccolith height 0.8-1.6 μ m.

Papposphaera as "Turrisphaera" phase sp type B

Plate 46, figs 3 and 4.

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.

Coccolith numbers: (one coccosphere) ca. 45 coccoliths.

Dimensions: coccosphere diameter ca. 8 μ m; coccolith base diameter ca. 0.7 μ m; coccolith height 1-2 μ m.

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 *Trigonaspis* Thomsen (Thomsen, 1980a) 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 & Oates (results referred from Ostergaard in Thomsen & Oates, 1978).

Pappomonas sp. type 1

Plate 47, fig. 1

Body coccoliths having elements that form two concentric rows 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 long axis ca. 1.2 μ m; coccoliths with spines long axis 0.6-1.2 μ m, stem height ca. 2.5 μ m.

Pappomonas sp. type 2

Plate 47, fig. 2.

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.

Coccolith numbers: ca. 16 coccoliths with calicate spines (spines with calyx); 32-42 coccoliths without central process.

Dimensions: coccosphere diameter 6-8 μ m; coccoliths without spines long axis 0.5-1.5 μ m; coccoliths with spines long axis 0.6-0.8 μ m, distal structure ca. 1.5 μ m wide, coccolith height (including stem) ca. 2.3 μ m.

Pappomonas sp. type 3

Plate 47, fig. 3 and 4.

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.

Coccolith numbers: (3 coccospheres) 23, 30 and 37 coccoliths with calicate spines; 52, 58 and 80 coccoliths without spines.

Dimensions: coccosphere diameter 12-15 μ m; coccoliths without spines long axis ca. 1 μ m; coccoliths with spines long axis base 0.5-1.0 μ m, height 3.5-5.0 μ m.

?Pappomonas sp. type 4

Plate 47, fig. 5

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.

Remarks: 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.

Coccolith numbers: (one coccosphere) ca. 112 coccoliths.

Dimensions: coccosphere diameter ca. 6μ m; coccoliths long axis ca. 1 μ m; spine height 0.5-2.5 μ m.

?Pappomonas sp. type 5

Plate 47, fig. 6

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. See also the Remarks in *Pappomonas* sp. type 4.

Coccolith numbers: (one coccosphere) ca. 105 coccoliths; 4 with short spine, about 21 with long bent spine, and 80 without spine.

Dimensions: coccosphere diameter ca. 7 μ m; coccoliths without spine long axis 0.5-0.8 μ m; coccoliths with short spine long axis ca. 1 μ m, spine length 1 μ m; apical coccoliths with long, bent spines base diameter ca. 0.5 μ m, spine length 2.5-3 μ m.

Genus Type A

Coccoliths with a long central structure and a rim formed by rectangular plates. Qualitative X-ray analysis of several specimens of this genus have proved the calcium content of the coccoliths.

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

Genus Type A, species type 1

Plate 48, fig. 1.

Coccosphere monomorphic; coccoliths having long and sharp spines without distal structure.

Coccolith numbers: (one coccosphere) ca. 50 coccoliths.

Dimensions: coccosphere diameter ca. 15 μ m; coccolith base long axis 1 μ m; spine length 5-6 μ m.

Genus Type A, species type 2

Plate 48, fig. 2.

Coccosphere apparently with monomorphic coccoliths. The coccoliths with a long, square central process that flaress and bends distally, resulting in a very characteristic feather-like structure.

Dimensions: coccosphere diameter ca. 10 μ m; coccolith base long axis ca. 0.7 μ m; spine length 2-5 μ m (highly variable).

Genus Type A, species type 3

Plate 48, figs. 3 and 4.

Coccosphere with varimorphic coccoliths. Coccoliths with a curved central process that gradually flares distally, resulting in a characteristically hollow distal structure. 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 μ m; coccolith base long axis ca. 0.8 μ m; spine length 1.5-5 μ m (highly variable).

Genus Type A, species type 4

Plate 48, figs. 5 and 6.

Coccosphere with varimorphic coccoliths. Coccoliths with a curved square central process. The longest spines increase gradually in thickness from base to apex, finishing abruptly in a blunt end.

Dimensions: coccosphere diameter 6-10 μ m; coccolith base long axis ca. 0.8 μ m; central process length 1-3 μ m.

FAMILY CERATOLITHACEAE Norris, 1965

Cells with two extremely different types of coccoliths: a single horseshoe-shaped coccolith 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 cell can bear 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 side being slightly shorter than the other. The coccosphere also bears ring-shaped coccoliths, named hoop-like coccoliths, which are numerous but seem not to preserve well. Several cells, each with a ceratolith, may be present within a single sphere constructed by hoop-like coccoliths. It is now known that these cells can generate another kind of coccolith, the formerly *Neosphaera* coccoliths (Alcober & Jordan, 1997; Young *et al.*, 1998, Cros *et al.*, 2000; Sprengel & Young, 2000; this work).

Ceratolithus cristatus Kamptner, 1950

Plate 49, figs. 1-6.

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 and 3.

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 & 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.

c) "*Neosphaera*" coccoliths. They vary considerably in size and diameter of the centralopening; 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 even to the suspicion that the three coccolith types belong to the same coccolithophore taxon.

Coccolith numbers: 1-2 ceratoliths; a very variable number of hoop-like coccoliths; around 21 coccoliths of the type "*Neosphaera*".

Dimensions: "*Neosphaera*" type coccosphere diameter 7-10 μ m; ceratoliths length (14-) 17-19 (-21) μ m, width (8.9-) 9-10 (-13) μ m; "*simplex forma*" length 7.4 μ m, width 6.3 μ m; hoop-like coccoliths very thin (ca. 0.1 μ m), ring diameter (4.5-) 5-6 (-7.5) μ m; "*Neosphaera*" type coccoliths diameter (3.2-) 4.5-5.0 (-6.0) μ m.

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; usually only the small umbelloliths are preserved in the sediments (Perch-Nielsen 1985).

Umbellosphaera tenuis (Kamptner, 1937) Paasche in Markali et Paasche, 1955

Plate 50, figs. 1 and 2.

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; 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 inexistent 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).

Coccolith numbers: coccospheres consist of between 14 and 30 coccoliths.

Dimensions: coccospheres long axis (8-) 10-11 (-12) μ m; micrococcolith long axis 2.5-3.0 μ m; macrococcolith long axis 2.6-6.8 μ m.

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

Plate 50, figs. 3 and 4.

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 with fine spine-like projections on the distal side; the lepidoliths are elliptical disc-like planoliths consisting of two elements (platelets) separated by a suture line which is perpendicular to the long axis of the coccolith.

Dimensions: coccosphere long axis ca. 12 μ m; tubular coccoliths long axis 5-8 μ m, short axis ca. 2 μ m; lepidolith major axis 1.5-2.0 μ m.

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 Plate 50, figs. 5 and 6. *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.

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

Plate 51, figs. 1-6

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 & 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 & McIntyre, 1977; 1980), var. *profunda* being smaller, more quadrangular and in a zigzag pattern of lines at the base and top (see Pl. 51, fig. 4), while var. *elongata* is larger in size, with side profiles tapered towards the bottom, and the top profile straight with an outstanding peak (see Pl. 51, fig. 3). 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 plate 51, fig. 6, 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 pointed out by Young (1998).

Dimensions: coccosphere diameter (5.4-) 7.5-8.5 (-11) μ m; coccoliths length (1.7-) 2.2-2.6 (-3.0) μ m, coccolith width (1.0-) 1.5-1.8 (-3.0) μ m.

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 now with many different and new specimens found in the course of the present work and figured below, the genus description must be emended in order to embrace all of the possible new species.

Emended description: The coccosphere has numerous and very small coccoliths of angular architecture wedged together in approximately regular meridial rows with the short coccolith axis presumably in a polar direction. The coccoliths are asymmetrical in relation to the major axis, having one half bigger than the other; they can present or not a bowl-like distal side, but all of them present a cross-like proximal side.

Notes on coccolith structure: The special coccoliths have two well differentiated parts comparable to a flower, as clearly represented in fig. 5 of Manton & 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

Plate 52, figs. 1 and 2.

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.

Previous record: (there are only three records) in tropical Pacific waters (Galapagos), Atlantic (by Chrétiennot-Dinet, 1990) and Pacific, from a California transect, where the observed cells had flagella and a coiling haptonema (Thomsen *et al.*, 1994).

Coccolith numbers: 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) μ m; coccolith major axis (0.55-) 0.6-0.7 (-0.75) μ m.

Polycrater galapagensis var. A (with dots)

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

Plate 52, figs. 3 and 4.

This coccosphere closely resembles *P. galapagensis*, but the distal part of the smaller half of coccoliths has dots (little nodes) and usually a v-shaped incision in the higher corner.

Coccolith numbers: coccosphere possesses between 1000 and 1300 coccoliths (estimated numbers 1088 and 1286).

Dimensions: coccosphere diameter 13.8-15.8 μ m; coccolith major axis (0.7-) 0.80-0.85 (-0.95) μ m.

Polycrater sp. 1 (with slit)

Plate 52, figs. 5 and 6.

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

Dimensions: coccosphere diameter ca. 9 μ m; coccolith major axis (0.61-) 0.65-0.75 (-0.91) μ m.

Polycrater sp. 2 (with holes, reminiscent of Gaudí's architecture)

Plate 53, figs. 1 and 2.

Polycrater galapagensis auct. non Manton et Oates, Giraudeau & 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.

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

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

Dimensions: coccosphere diameter (5.6-) 7-9 (-10.6) μ m; coccolith major axis (0.63-) 0.72-0.82 (-0.86) μ m.

Polycrater sp. 3 (with lip-like borders)

Plate 53, figs. 3 and 4.

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

This coccosphere resemble *P. galapagensis*, but coccoliths are smaller (0.3 to 0.5 μ m 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) μ m; coccolith major axis (0.35-) 0.44-0.48 (-0.55) μ m, with very simple sepal-like part ca. 0.4 μ m.

Polycrater sp. 4 (minimum, the smallest coccoliths)

Plate 53, figs. 5 and 6.

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

Coccolith numbers: (one coccosphere) estimated 1870 coccoliths.

Dimensions: coccosphere diameter ca. 6 μ m; coccolith major axis (0.25-) 0.3-0.4 (-0.5) μ m.

Polycrater sp. 5 (two petal-like structures very modified; ladle-like coccoliths)

Plate 54, figs. 1 and 2.

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 μ m; coccolith width 0.4-0.5 μ m, height of the spiny part 0.5-0.6 μ m.

Polycrater sp. 6 (two petal-like structures very modified, two others absent).

Plate 54, figs. 3, 4, 5 and 6

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.

Dimensions: coccosphere diameter 4-6 μ m; coccolith length 0.4-0.7 μ m, width in distal part variable (up to 0.3 μ m).

Family CALYPTROSPHAERACEAE Boudreaux et Hay, 1969

This family embrace all the holococcolithophores which have only holococcoliths in their known life cycle. Holococcoliths are composed of microcrystals arranged in an ordered manner. In 1960, Parke & Adams realized 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 & Markali, emend. Gaarder 1980 (in Heimdal & Gaarder, 1980); *Turrisphaera* Manton, Sutherland and Oates, 1976) have been taken out of this family in recent revisions and check

lists (Kleijne, 1991; Jordan & Kleijne, 1994; Jordan & Green, 1994; Young & 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 & Green (1994) and not separated by their monomorphism or dimorphism, since in some genera it is difficult to identify if they have mono- or dimorphic coccospheres.

Genus Anthosphaera Kamptner emend. Kleijne, 1991

Coccosphere with clear dimorphic coccoliths. The calyptrolith-like body coccoliths have characteristic proximal rims of one crystal thickness; the circum-flagellar coccoliths are fragarioliths with 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

Plate 55, figs. 1, 2 and 3.

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.

Coccolith numbers: (4 coccospheres) 8, 7, 8 and 10 fragarioliths, 54, 44, 60 and 66 body coccoliths.

Dimensions: coccosphere diameter (5-) 6.5-7.0 (-8) μ m; fragariolith height (2.1-) 2.2-2.6 (-2.9) μ m; body coccolith major axis (1.0-) 1.15-1.30 (-1.8) μ m.

Previous reports: Mediterranean Sea, Atlantic.

Anthosphaera cf. fragaria Kamptner, 1937 emend. Kleijne, 1991

Plate 55, fig. 4.

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.

Coccolith numbers: between 6 and 8 fragarioliths and 50 to 80 body coccoliths.

Dimensions: coccosphere diameter ca. 5.5 μ m; fragariolith height 1.7-2.0 μ m; body coccolith major axis (0.75-) 0.85-0.95 (-1.1) μ m.

Anthosphaera lafourcadii (Lecal 1967) Kleijne 1991

Plate 55, figs. 5 and 6.

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.

Coccolith numbers: ca. 10 fragarioliths; 72, 62 and 48 body coccoliths.

Dimensions: coccosphere diameter 4.1-5.1 μ m; fragariolith height (0.77-) 0.85-0.95 (-1.1) μ m; body coccolith major axis (0.76-) 0.8-1.0 (-1.1) μ m.

Previous reports: Mediterranean Sea, Atlantic.

Anthosphaera periperforata Kleijne, 1991

Plate 56, figs 1-6.

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.

Previous reports: Mediterranean Sea, Arabian Sea, Atlantic.

- A. periperforata type 1.

Plate 56, figs. 1-2.

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.

Coccolith numbers: 10 to 14 fragarioliths; 64 to 80 body coccoliths.

Dimensions: coccosphere diameter ca. 6-7 μ m; fragariolith height (1.2-) 1.3-1.4 (-1.6) μ m; body coccolith major axis (1.0-) 1.15-1.30 (-1.4) μ m.

- A. periperforata type 2.

Plate 56, figs. 3-4.

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.

Coccolith numbers: 5 to 8 fragarioliths; 52 to 96 body coccoliths.

Dimensions: coccosphere diameter 4.8 - 6.5 μ m; fragariolith height (1.25-) 1.35-1.65 (-1.75) μ m; body coccolith major axis (0.95-) 1.10-1.35 (-1.40) μ m.

- A. periperforata type 3.

Plate 56, figs. 5-6.

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.

Coccolith numbers: 54 to 100 coccoliths.

Dimensions: coccosphere diameter 4.5 - 6.5 μ m; fragariolith height ca. 1.5 μ m; body coccolith major axis (0.95-) 1.10-1.20 (-1.25) μ m.

Anthosphaera sp. type A (very ornamented; sp. nov. ¿ origami ?)

Plate 57, figs 1 and 2.

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.

Coccolith numbers: 6 to 8 fragarioliths; 42 to 60 body coccoliths.

Dimensions: coccosphere diameter ca. 5 μ m; fragariolith height ca. 1.2 μ m; body coccolith major axis (1.0-) 1.10-1.20 (-1.35) μ m.

Genus Calicasphaera Kleijne, 1991

Monomorphic coccospheres without 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

Plate 57, figs 3 and 5.

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.

Coccolith numbers: around 32 coccoliths.

Dimensions: coccosphere diameter ca. 6 μ m; coccolith height ca. 1.3 μ m, proximal diameter ca. 0.9 μ m, distal major axis ca. 1.6 μ m.

Previous reports: North Atlantic.

Calicasphaera blokii Kleijne, 1991

Plate 57, figs 4 and 6.

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.

Remarks: 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.

Coccolith numbers: around 62 coccoliths.

Dimensions: coccosphere diameter ca. 6 μ m; coccolith proximal major axis ca. 1.1 μ m; distal major axis 1.0-1.3 μ m.

Previous reports: Mediterranean Sea.

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

Plate 58, figs. 1 and 2.

Zygosphaera divergens Halldal and Markali 1955 p. 8 pl. 2.

Zygosphaera divergens Halldal and Markali 1955 emend. Heimdal, in: Heimdal and Gaarder (1980), p. 12, pl. 3, fig. 24 a, b.

Calyptrolithina divergens (Halldal and 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.

Coccolith numbers: around 60 body coccoliths.

Dimensions: body coccolith major axis (1.4-) 1.6-1.7 (-1.9) μ m.

Previous reports: Indian Ocean, Arabian Sea, North Atlantic, Red Sea, Pacific.

Calyptrolithina divergens var. tuberosa (Heimdal) Jordan et al., 1993

Plate 58, figs. 3 and 4.

Zygosphaera divergens Halldal and Markali, Borsetti and Cati, 1976, p. 223, pl. 18, fig. 1.

Zygosphaera divergens Halldal and Markali, f. tuberosa Heimdal, in: Heimdal and Gaarder, 1980, pp. 12, 13. pl. 3, fig. 25 a,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 (see fig. 3) areas with and without clear perforations are present. The coccoliths figured in Heimdal & Gaarder (1980) have masked perforations whilst the coccoliths figured in Borsetti & Cati (1976) and Kleijne (1991) are clearly perforated with large pores, like those in fig. 4.

Coccolith numbers: 62, 100 and 122 body coccoliths in three specimens.

Dimensions: body coccolith major axis (1.5-) 1.8-2.1 (-2.4) μ m.

Previous reports: North Atlantic, Mediterranean Sea.

Calyptrolithina wettsteinii (Kamptner, 1937) Kleijne, 1991. N.B. C. wettsteinii is now considered to be the holococcolith phase of Coronosphaera mediterranea (see Chap. IV).

Plate 58, figs. 5 and 6.

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 (see fig. 5).

Combination coccospheres of this species with *Coronosphaera mediterranea* have been observed (see Kamptner, 1941; this work, Chap. IV), the two species therefore seemingly joined in the same life-cycle (Cros *et al.* 2000).

Coccolith numbers: around 6 to 12 circum-flagellar zygoliths; 60 to 116 body coccoliths.

Dimensions: coccosphere major axis (9.5-) 12-14 (-14.5) μ m; zygolith major axis ca. 2.2 μ m; body coccolith major axis (1.9-) 2.1-2.3 (-2.6) μ m.

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

Plate 59, figs. 1 and 2.

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 circumflagellar calyptroliths is larger, sometimes forming a bridge crossing the short axis of the coccolith.

Coccolith numbers: 6 to 8 circumflagellar coccoliths; 64 to 120 body coccoliths.

Dimensions: coccosphere major axis 10-14 μ m; coccolith major axis (2.1-) 2.2-2.3 (-2.5) μ m.

Previous reports: Mediterranean Sea, Caribbean Sea, Pacific, from the Atlantic, I have found it in samples from off Lisboa (cruise Codenet II).
Calyptrolithophora papillifera (Halldal) Heimdal in Heimdal et Gaarder, 1980

Plate 59, figs. 3, 4, 5 and 6.

Calyptrosphaera papillifera Halldal, 1953, p. 48, fig. 14; Halldal and Markali, 1954, 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 the usual hexagonal pattern. The circumflagellar calyptroliths have a convex distal side with characteristic parallel rows of crystallites.

Coccolith numbers: 118 to 152 coccoliths.

Dimensions: coccosphere major axis ca. 12–14 μ m; coccolith major axis (1.5-) 1.7-1.9 (-2.0) μ m.

Previous reports: Mediterranean Sea, Atlantic, Pacific, Indian Ocean, Red Sea.

Genus Calyptrosphaera Lohmann, 1902.

This genus bears dome-shaped calyptroliths, and is 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

Plate 60, figs. 1 and 2.

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 (see fig. 2). 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.

Coccolith numbers: 64, 116 and 130 coccoliths in three specimens.

Dimensions: coccosphere major axis 15-17 μ m; coccolith major axis (2.3-) 2.5-2.7 (-2.9) μ m.

Previous reports: Mediterranean Sea.

Calyptrosphaera dentata Kleijne, 1991

Plate 61, figs. 1 and 2.

Sphaerocalyptra cf. papillifera Halldal, Borsetti & Cati (1976), p. 213, pl. 14, fig. 1.

Sphaerocalyptra aff. S. papillifera (Halldal) Halldal, Okada & 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, having 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.

Coccolith numbers: between 46 and 70 coccoliths.

Dimensions: coccosphere major axis 11-15 μ m; coccolith major axis (2.5-) 2.9-3.0 (-3.3) μ m.

Previous reports: Mediterranean Sea, Pacific.

Calyptrosphaera heimdaliae R.E. Norris, 1985, orth. emend. Jordan et Green, 1994

Plate 60, figs. 3 and 4

Homozygosphaera tholifera (Kamptner) Halldal & 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.

Coccolith numbers: 30 to 44 coccoliths.

Dimensions: coccosphere major axis 10-11 μ m; coccolith major axis (2.0-) 2.5-2.9 (-3.2) μ m.

Calyptrosphaera oblonga Lohmann, 1902. Now C. oblonga is considered as the holococcolith phase of Syracosphaera pulchra (see Chap. IV)

Plate 61, figs. 3 and 4.

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 capshaped 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.

This species can form combination coccospheres with *Syracosphaera pulchra* (see Chapter IV, and also Lohmann, 1902; Kamptner 1941; and Lecal-Schlauder 1961); this *Calyptrosphaera* could thus be the holococcolith phase of the latter species (see Chapter IV and Cros *et al.*, 2000).

Coccolith numbers: 60 to 178 coccoliths (6 specimens).

Dimensions: coccosphere major axis 10-20 μ m; coccolith major axis (1.8-) 2.2-2.5 (-2.8) μ m.

Calyptrosphaera sphaeroidea Schiller 1913

Plate 61, figs. 5 and 6.

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, Borsetti and Cati, 1976, p. 211, pl. 12, fig. 6,7.

Spherical coccosphere built up of spherical 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 sometimes is incompletely constructed (see fig. 6).

Coccolith numbers: 48 to 182 coccoliths (7 specimens).

Dimensions: coccosphere major axis (5.5-) 6-7 (-12) μ m; coccolith major axis (0.9-) 1.1-1.3 (-1.5) μ m.

Calyptrosphaera sp. type 1 (smaller heimdaliae)

Plate 60, figs. 5 and 6

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.

Coccolith numbers: 54 to 78 coccoliths.

Dimensions: coccosphere major axis 7-12 μ m; coccolith major axis (1.9-) 2.2-2.5 (-2.7) μ m.

Genus Corisphaera Kamptner 1937

Coccospheres with dimorphic coccoliths. Body coccoliths are zygoliths. The circumflagellar 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 & Kleijne, 1994; Jordan & 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. I believe a more profound study of this genus in the Mediterranean, including a review of the old literature of LM studies and further detailed observation of LM and parallel SEM samples, is necessary. Only after such a study, which surpasses the scope and the limited time of the present work, could a clear idea of the *Corisphaera* to be found in NW Mediterranean waters be formed. For this reason, I include only the clearly classified *Corisphaera* species in Plate 62, and I represent the high diversity of *Corisphaera* morphologies in Plate 63 without going deeper for the moment.

Corisphaera strigilis Gaarder, 1962

Plate 62, figs. 1 and 2.

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 (see 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 (see 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.

Coccolith numbers: 62 to 90 coccoliths.

Dimensions: coccosphere long axis 5-7 μ m; coccolith long axis (0.9-) 1.15-1.25 (-1.33) μ m

Previous records: Mediterranean Sea, Atlantic, Indian Ocean, Red Sea.

Corisphaera tyrrheniensis Kleijne, 1991

Plate 62, figs. 3 and 4.

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.

Coccolith numbers: 28 to 60 coccoliths.

Dimensions: coccosphere long axis 4.5-7.5 μ m; coccolith long axis (1.25-) 1.50-1.60 (-1.75) μ m.

Previous records: Mediterranean Sea , Atlantic.

Corisphaera sp. type A Kleijne, 1991. N.B. This species is now considered as the holococcolith (perforated) phase of *Syracosphaera bannockii* (see Chap. IV) Plate 62, figs. 5 and 6.

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.

Coccolith numbers: 70 to 88 coccoliths.

Dimensions: coccosphere long axis 5-7 μ m; coccolith long axis (1.0-) 1.3-1.4 (-1.5) μ m.

Corisphaera cf. gracilis Kamptner 1937

Plate 63, fig. 1

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.

Coccolith numbers: ca. 60 coccoliths (1 specimen).

Dimensions: coccosphere long axis ca. 6 μ m; coccolith long axis 1.4-1.6 μ m.

Corisphaera sp. 1 (resembling type A of Kleijne, 1991)

Plate 63, fig. 2

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 C. sp. type A. Some specimens appear more fragile, possibly representing a variety of the species.

Coccolith numbers: 70 to 140 coccoliths.

Dimensions: coccosphere long axis 5.5-9.2 μ m; coccolith long axis (1.2-) 1.4-1.5 (-1.7) μ m

Corisphaera sp. 2 (aff. type A of Kleijne (1991) and *C. gracilis*, but having a high bridge) Plate 63, fig. 3.

? 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.

Coccolith numbers: ca. 80 coccoliths (1 collapsed specimen).

Dimensions: coccolith long axis 1.5-1.8 μ m.

Corisphaera sp. 3 (double-layered zygoliths with S-shaped bridge)

Plate 63, fig. 4.

? 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.

Coccolith numbers: 38 to 48 coccoliths.

Dimensions: coccosphere long axis 7-8 μ m; coccolith long axis (1.8-) 1.9-2.0 (-2.2) μ m.

Corisphaera sp. 4 (with a high and pointed bridge)

Plate 63, fig. 5.

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.

Coccolith numbers: 60 to 80 coccoliths.

Dimensions: coccosphere long axis 7-9 μ m; coccolith long axis 1.3-1.6 μ m.

Corisphaera sp. 5 (low body zygoliths and high leaf-like circum-flagellar bridge)

Plate 63, fig. 6.

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

Dimensions: coccosphere diameter ca. 6μ m (1 collapsed specimen); body coccolith long axis 1.3-1.4 μ m.

Genus Daktylethra Gartner (in: Gartner and Bukry, 1969)

This genus is considered monomorphic, with characteristic 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

Plate 64, figs. 1, 2 and 3.

Calyptrosphaera pirus Kamptner, Throndsen, 1972, pp. 53-56, figs. 2-9; Reid, 1980, p. 164, pl. 7, figs. 2,3.

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 by characteristic calyptrolith-like holococcoliths (figs. 2 and 3 show such coccoliths in distal and side view respectively). The internal thickened ridges distinctive of this species (see Norris, 1985) were not visible in these studied specimens.

Although this species is considered to have monomorphic coccoliths, presumed circumflagellar coccoliths with a short conical extension protruding from the central area are observed (Throndsen, 1972; Heimdal, 1993; see fig. 3).

Coccolith numbers: ca. 180 coccoliths (1 specimen).

Dimensions: coccospheres major axis 6-18 μ m; coccolith major axis (2.2-) 2.4-2.7 (-3.2) μ m.

Previous reports: Mediterranean Sea, Atlantic, Indian Ocean, Indo-Malayan region, Pacific.

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.

Plate 64, figs. 4, 5, 6 and 7.

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.

Coccolith numbers: 10-12 circum-flagellar coccoliths; (40-) 54-84 (-106) body zygoliths.

Dimensions: coccosphere major axis (6-) 7-8 (-11.5) μ m; body coccolith major axis (1.1-) 1.4-1.5 (-1.6) μ m.

Previous reports: Mediterranean Sea, Atlantic, Indian Ocean.

Genus Homozygosphaera Deflandre, 1952

This genus bears zygoliths, and is considered to contain monomorphic species; nevertheless, some coccoliths near the flagellar area may be higher than the others and may even possess a papilla.

Homozygosphaera arethusae (Kamptner) Kleijne 1991

Plate 65, figs. 1 and 2.

Corisphaera arethusae Kamptner, 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.

Coccolith numbers: 54 to 96 coccoliths.

Dimensions: coccospheres major axis (6-) 9-10 (-15) μ m; coccolith major axis (1.2-) 1.6-

1.8 (-2.0) μ m, coccolith height ca. 0.8 μ m increasing near apical pole up to 1.8 μ m. Previous reports: Mediterranean Sea, Red Sea, Atlantic, Indian Ocean.

Homozygosphaera triarcha Halldal and Markali, 1955.

Plate 65, figs. 3 and 4.

Homozygosphaera triarcha Halldal and Markali, 1955, p. 9, pl. 4, figs. 1-4.

Homozygosphaera triarcha Halldal and Markali, 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.

Coccolith numbers: 86 to 88 coccoliths.

Dimensions: coccosphere major axis 10-13 μ m; coccolith major axis (1.7-) 1.9-2.2 (-2.4) μ m.

Previous reports: Mediterranean Sea, Red Sea, Atlantic, Indian Ocean, Indo-Malayan region, Pacific.

Genus Periphyllophora Kamptner, 1937

At present *Periphyllophora* is a monospecific genus; the association of the only species in this genus with a *Syracosphaera* species is demonstrated in this study. Coccosphere monomorphic consisting of helladoliths.

Periphyllophora mirabilis (Schiller) Kamptner, 1937. *P. mirabilis* is now considered as the holococcolith phase of *Syracosphaera anthos* (see Chap. IV)

Plate 65, figs. 5 and 6.

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 helladoliths which possess clear double-layered protrusions. Two combination specimens of this species with *Syracosphaera anthos* were found during this study (see chapter IV), suggesting that *Periphyllophora* might be the holococcolith-bearing phase of this *Syracosphaera* species.

Coccolith numbers: ca. 100 coccoliths.

Dimensions: coccosphere diameter 11-13 μ m; coccolith major axis (1.5-) 1.9-2.2 (-2.5) μ m.

Previous reports: Mediterranean Sea, Atlantic, Indian Ocean, Pacific.

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

Plate 66, figs. 1, 2 and 3.

Helladosphaera aurisinae, Kamptner, 1941, p. 91, pl. 11, figs. 121-124.

Helladosphaera aurisinae Kamptner, Borsetti and Cati, 1972, p. 403, pl. 49, fig. 1 a,b; Nishida, 1979, pl. 20, fig. 2 a,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, 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.

Coccolith numbers: 60 to 64 coccoliths.

Dimensions: coccosphere major axis 7-12 μ m; coccolith major axis (2.1-) 2.3-2.4 (-2.6) μ m.

Previous reports: Mediterranean Sea, Atlantic, Indian Ocean, Pacific.

Poricalyptra isselii (Borsetti and Cati, 1976) Kleijne, 1991

Plate 66, figs. 4, 5 and 6.

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.

Coccolith numbers: 68 to 92 coccoliths.

Dimensions: coccosphere major axis 9.5-11.5 μ m; coccolith major axis (1.7-) 1.9-2.1 (-2.4) μ m.

Previous reports: Mediterranean Sea, Atlantic.

Genus Poritectolithus Kleijne, 1991

Coccosphere with dimorphic coccoliths. Body holococcoliths with characteristic strings of crystallites on the distal face. Circum-flagellar coccoliths are helladoliths. Within *Poritectolithus* there are two clearly distinguishable groups; one with body coccoliths like calyptroliths and the other with body coccoliths like zygoliths. N.B. Kleijne (1991) described this genus as possessing zygolith-like body coccoliths.

Poritectolithus taxa bearing calyptrolith-like body coccoliths

This group contains the *Poritectolithus* species with calyptrolith-like body coccoliths which have a closed roof. These calyptroliths can be flat like laminoliths, e.g. *Poritectolithus* sp. 1, or with the central area of the distal side slightly convex, e.g. *Poritectolithus tyronus*, or like real calyptroliths with a distally widening wall, e. g. *Poritectolithus poritectus*.

Poritectolithus sp. 1

Plate 67, figs. 1-2 and Plate 68, fig. 3

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.

Coccolith numbers: ca. 100 coccoliths.

Dimensions: body coccolith major axis 1.5-1.6 μ m, width 0.95-1.05 μ m, height 0.16-0.22 μ m; circum-flagellar coccolith height 1.4-1.7 μ m.

Poritectolithus tyronus Kleijne, 1991

Plate 67, figs. 3 and 4 and Plate 68, fig. 4.

Body calyptroliths with a slightly convex central distal part which has crystals arranged in rows, leaving narrow, elongate openings (Kleijne, 1991). Circum-flagellar helladoliths with a basal part similarly constructed and a straight and flat leaf-like protrusion. The circum-flagellar coccoliths have a very sharply pointed protrusion which ends in a peak of one crystal width (see upper right corner of Plate 67, fig. 4).

Coccolith numbers: ca. 92 coccoliths.

Dimensions: (collapsed) coccosphere diameter ca. 9 μ m; body coccolith major axis 1.25-1.75 μ m, width 0.9-1.0 μ m, height ca. 0.3 μ m; circum-flagellar coccolith height 1.5-2.0 μ m.

Previous report: North Atlantic.

Poritectolithus poritectum (Heimdal 1980) Kleijne, 1991

Plate 67, figs. 5 and 6 and Plate 68, fig. 5.

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, p. 153, fig. 184.

The body holococcoliths are more calyptrolith-like than zygolith-like; they are constructed of relatively big 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 (see arrows) which is also clearly shown in the micrographs of Heimdal & Gaarder (1980); the wall slightly widens distally and protrudes the neighbouring distal roof. Circum-flagellar helladoliths with a flared wall and a large protrusion.

Coccolith numbers: ca. 66 coccoliths.

Dimensions: coccosphere diameter ca. 9 μ m; body coccolith major axis 1.3-1.8 μ m, width 1.1-1.3 μ m, height 0.2-0.5 μ m; circum-flagellar coccolith height ca. 2 μ m.

Previous report: Atlantic.

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 vallted bridge, e.g. *Poritectolithus* sp. 2, or possess a very high and vallted bridge, e.g. *Poritectolithus maximus* Kleijne, 1991.

Poritectolithus sp 2.

Plate 68, figs. 1, 2 and 6.

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.

Coccolith numbers: ca. 80 coccoliths.

Dimensions: coccosphere long axis ca. 14 μ m; body coccolith major axis 1.7-1.9 μ m, width ca. 1.3 μ m; circum-flagellar coccolith height ca. 1.8 μ m.

N.B. The studied specimen closely resembles the specimen figured in Kleijne (1991) as *Poritectolithus poritectum* and that figured, with the same name, in Winter & Siesser (1994), fig. 185.

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.

Two species of this genus appear to have relationships with species of the family Rhabdosphaeraceae (see Chap. IV).

Sphaerocalyptra quadridentata (Schiller, 1913) Deflandre, 1952

Plate 69, figs. 1 and 2.

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*.

Coccolith numbers: 30 to 56 coccoliths (6 specimens).

Dimensions: coccosphere diameter 5-8.5 μ m; body coccolith major axis (1.3-) 1.6-1.8 (-2.3) μ m.

Previous reports: Atlantic, Mediterranean Sea, Red Sea.

Sphaerocalyptra cf. adenensis Kleijne, 1991

Plate 69, figs. 3 and 4.

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.

Coccolith numbers: 58 to 74 coccoliths (3 specimens).

Dimensions: coccosphere diameter 5.5-8.5 μ m; body coccolith major axis (1.2-) 1.55-1.75 (-2.0) μ m.

Previous reports: Indian Ocean, Gulf of Aden, Red Sea.

Sphaerocalyptra sp. 1 (coccoliths with a very pointed protrusion, tipped by a few crystallites). This taxa is now considered as the holococcolith phase of *Acanthoica quattrospina* (see Chap. IV).

Plate 69, figs. 5, 6 and Plate 70, figs. 1, 2.

Body coccoliths are of small size and steeply tapered, with a thin central protrusion tipped by one crystallite; some specimens have a few crystallites on the distal side (Plate, 70, figs. 1 and 2) and it is possible to see clearly the well packed crystals of the basal ring (plate 70, fig. 2, lower right corner). Circum-flagellar calyptroliths are notably higher than body calyptroliths and are tipped by a thin and acute protrusion.

Three combination coccospheres of this species (specimens with a few crystallites forming the distal tip) with *Acanthoica quattrospina* have been found (see Chap. IV). It therefore seems likely that this *Sphaerocalyptra* is the holococcolith phase of *A. quattrospina*.

Coccolith numbers: 62 to 134 coccoliths.

Dimensions: coccosphere diameter 6-10 μ m; body coccolith major axis (1.2-) 1.35-1.55 (-1.9) μ m.

Sphaerocalyptra sp. 2 (cone-shaped body coccoliths)

Plate 70, fig. 3

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.

Coccolith numbers: ca. 44 coccoliths.

Dimensions: coccosphere collapsed; body coccolith major axis 0.7-0.9 μ m, height (0.65-) 0.8-0.9 (-1.05) μ m; circum-flagellar coccolith proximal diameter ca. 1 μ m, height ca. 1.7 μ m.

Sphaerocalyptra sp. 3 (string-formed calyptroliths)

Plate 70, figs. 4, 5 and 6

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).

Coccolith numbers: ca. 84 coccoliths (1 specimen).

Dimensions: coccosphere diameter ca. 5 μ m; body coccolith major axis (0.7-) 1.0-1.2 (-1.3) μ m, height ca. 0.5 μ m; circum-flagellar coccolith height 1.2-1.7 μ m.

Sphaerocalyptra sp. 4 (circum-flagellar coccoliths having a stick- like protrusion)

Plate 71, figs. 1 and 2.

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.

Coccolith numbers: ca. 30 coccoliths (1 collapsed specimen).

Dimensions: body coccolith diameter (1.4-) 1.6-1.8 (-1.9) μ m, height ca. 1.2 μ m; circum-flagellar coccolith diameter 1.8-1.9 μ m, height 2.4-2.7 μ m.

Sphaerocalyptra sp. 5 (arch-shaped calyptroliths with irregularly filled distal side) Plate 71, figs. 3 and 4

The body calyptroliths appear to have a basal rim two crystals thick and the calyptroform side is formed by rounded irregularly widened arches. Circum-flagellar calyptroliths tipped by a long spine-like protrusion composed of three rows of crystallites.

Coccolith numbers: 34 to 60 coccoliths (2 specimens).

Dimensions: coccosphere long axis 6-7 μ m; body coccolith major axis (1.1-) 1.4-1.7 (-2.1) μ m; circum-flagellar coccolith diameter 1.3-1.9 μ m, height ca. 1.5 μ m.

Sphaerocalyptra sp. 6 (rings-shaped residual calyptroliths)

Plate 71, figs. 5 and 6.

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.

Coccolith numbers: ca. 8 circum-flagellar coccoliths; ca. 100 body coccoliths.

Dimensions: coccosphere long axis 5-6 μ m; body ring coccoliths major axis (0.5-) 0.7-0.9 (-1.1) μ m; circum-flagellar coccolith diameter 0.8-1.1 μ m, spine height (1.5-) 1.8-2.2 (-2.5) μ m.

Genus Syracolithus (Kamptner, 1941) Deflandre, 1952.

Monomorphic coccosphere consisting of laminoliths. Certain representatives of this genus form associations with *Helicosphaera*.

Syracolithus catilliferus (Kamptner, 1937) Deflandre, 1952. S. catilliferus is now considered as the holococcolith phase of *Helicosphaera carteri* (see Chap. IV).

Plate 72, figs. 1 and 2.

Syracosphaera (Syracolithus) catillifera Kamptner, Kamptner, 1941, pp. 81, 103, pl. 4, figs. 43-45.

Syracolithus catillifera Kamptner, Deflandre, 1952, p. 453, fig. 351cd.

Calyptrosphaera catillifera (Kamptner) Gaarder, Nishida, 1979, pl. 17, fig. 3ab.

Calyptrolithophora catillifera (Kamptner), Norris, 1985, p. 626, fig. 33.

Syracolithus catilliferus (Kamptner) Deflandre, Kleijne, 1991, p. 34, pl. 6, fig. 1,2.

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

Two combination coccospheres with coccoliths of *S. catilliferus* and *Helicosphaera carteri* have been found (see Chap. IV); this species can thus be considered as the holococcolithbearing phase of the latter species. Moreover, coccoliths of this species have been found associated with *Syracolithus confusus* coccoliths on single coccospheres (see Chapter IV). As a result, *Helicosphaera carteri, Syracolithus catilliferus* and *Syracolithus confusus* should be considered the same species, analogous with the *Coccolithus pelagicus* case (see Cros *et al.*, 2000).

Coccolith numbers: 60 to 100 coccoliths (5 specimens).

Dimensions: coccosphere long axis 12-15.5 μ m; coccolith long axis (1.8-) 2.7-3.0 (-3.5) μ m, protrusion height 0.8-1.0 μ m.

Previous reports: Atlantic, Mediterranean Sea, Red Sea, Indian Ocean, Indo-Malayan region, Pacific.

Syracolithus confusus Kleijne, 1991. S. confusus is now considered as the perforated holococcolith phase of *Helicosphaera carteri* (see Chap. IV).

Plate 72, fig. 3.

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

Laminoliths with a pointed protrusion surrounded by 5-8 surface pits.

Several coccospheres were found bearing laminoliths of both *S. catilliferus* and *S. confusus* (see Chap. IV). As noted above, these two taxa together with *Helicosphaera carteri* should all be considered the same species.

Coccolith numbers: 44 to 124 coccoliths (5 specimens).

Dimensions: coccosphere long axis (9-) 10-11.5 (-14) μ m; coccolith long axis (2.1-) 2.6-2.8 (-3.1) μ m.

Previous reports: Mediterranean Sea, Red Sea, Pacific.

Syracolithus dalmaticus (Kamptner) Loeblich et Tappan, 1966

Plate 72, fig. 4

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.

Coccolith numbers: In the studied coccospheres were counted around of 45 coccoliths.

Dimensions: coccosphere long axis 10-11 μ m; coccolith long axis 2.7-2.9 μ m.

Previous reports: Mediterranean Sea, Atlantic, Red Sea, Indian Ocean, Pacific.

Syracolithus schilleri (Kamptner) Kamptner, 1956

Plate 72, fig. 5.

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.

Coccolith numbers: 60 to 98 coccoliths.

Dimensions: coccosphere long axis 10.5-14.0 μ m; coccolith long axis 2.7-3.7 μ m. Previous reports: Mediterranean Sea, Pacific.

Syracolithus quadriperforatus (Kamptner 1937) Gaarder 1980

Plate 72, fig. 6.

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.

Coccolith numbers: 78 to 108 coccoliths (3 specimens).

Dimensions: coccosphere long axis 10.5-12.5 μ m; coccolith long axis (1.6-) 1.9-2.2 (-2.4) μ m.

Previous reports: Atlantic, Mediterranean Sea, Red Sea, Indian Ocean, Pacific.

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 *Z bannockii*) have, in my opinion, real zygoliths as circum-flagellar coccoliths.

Zygosphaera amoena Kamptner, 1937

Plate 73, figs. 1 and 2.

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.

Coccolith numbers: 64 to 86 body coccoliths; ca. 6 circum-flagellar coccoliths.

Dimensions: coccosphere long axis 5-7 μ m; coccolith long axis (0.9-) 1.15-1.25 (-1.4) μ m.

Previous reports: Atlantic, Mediterranean Sea, Indian Ocean.

Zygosphaera bannockii (Borsetti and Cati, 1976) Heimdal, 1980. N.B. Z. bannockii is now considered as the holococcolith phase of Syracosphaera bannockii (see Chap. IV).

Plate 73, figs. 3 and 4.

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.

Several coccospheres bearing laminoliths of *Z. bannockii* with coccoliths of *Corisphaera* type A Kleijne, 1991 have now been found (Heimdal & Gaarder, 1980, pl. 2, fig. 18 a,b; Winter *et al.*, 1979, pl. 5, fig. 7; Cros et al. 2000; Zeltner, personal communication; this study Chap. IV). These taxa are thus apparently joined in only one species. Since *C.* type A has been found combined with *Syracosphaera* cf. type K (see Chap. IV), these two holococcolith forms should be regarded as the holococcolith phase of *Syracosphaera* sp. cf. type K, in the same way that *Crystallolithus hyalinus* and *C. braarudii* are the well known holococcolith phases of the *Coccolithus pelagicus* (see Cros *et al.*, 2000).

Coccolith numbers: 48 to 76 coccoliths (3 specimens).

Dimensions: coccospheres long axis 4.5-6.5 μ m; coccolith long axis (1.1-) 1.15-1.25 (-1.4) μ m.

Previous reports: Atlantic, Mediterranean Sea, Red Sea, Indian Ocean.

Zygosphaera hellenica Kamptner

Plate 74, figs. 1-6.

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 rows, but this arrangement is not observed in some specimens (Pl. 74, figs. 5-6.).

Coccolith numbers: 88 to 140 coccoliths (5 specimens).

Dimensions: coccosphere long axis 8-11 μ m; coccolith long axis (1.9-) 2.0-2.2 (-2.5) μ m. Previous reports: Atlantic, Mediterranean Sea, Indian Ocean, Pacific.

Zygosphaera marsilii (Borsetti and Cati 1976) Heimdal 1982

Plate 73, figs. 5 and 6.

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.

A coccolith of this species has been found on a *Corisphaera tyrrheniensis* coccosphere (see Pl. 62, fig. 3 in this study); it is notable that both species, C. *tyrrheniensis* and Z. *marsilii*, have coccoliths of similar size and with a similar crystallite pattern.

Coccolith numbers: 76 to 102 coccoliths (3 specimens).

Dimensions: coccosphere long axis 6.5-8.5 μ m; coccolith long axis (1.2-) 1.30-1.45 (-1.6) μ m.

Previous reports: Atlantic, Mediterranean Sea, Red Sea, Indian Ocean.

Holococcolithophore sp. 1 (coccoliths have two small pores in the proximal side)

Plate 75, figs. 1 and 2.

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 structure and crystallite arrangement of these holococcoliths, especially on the distal side, resembles that of the genus *Sphaerocalyptra*. The calyptroliths of this species are, however, smaller than those of the genus *Sphaerocalyptra*.

Coccolith numbers: 80 to 98 coccoliths (4 specimens).

Dimensions: coccosphere long axis 6.5-8.5 μ m; coccolith long axis (1.3-) 1.5-1.7 (-2.0) μ m.

Holococcolithophore sp. 2 (Anthosphaera affinity?)

Plate 75, figs. 3 and 4.

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*.

Coccolith numbers: 10 to 12 circum-flagellar coccoliths; 170 to 268 body coccoliths.

Dimensions: coccosphere long axis 5-8 μ m; body coccolith long axis (0.4-) 0.6-0.7 (-0.8) μ m; circum-flagellar coccolith height 1.3-1.5 μ m.

SPECIES INCERTAE SEDIS

Coccolithophore sp. A (affinity to *Rhabdosphaeraceae* family?)

Plate 75, figs. 5 and 6.

The coccosphere appears to have three types of coccoliths, each of which seem to be sacculiform and flattened (some in height, others laterally) rhabdoliths; 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).

Coccolith numbers: 102 to 140 coccoliths (4 specimens).

Dimensions: coccosphere long axis 4.5-6.5 μ m; coccolith long axis 0.9-1.5 μ m.

Coccolithophore sp. B (affinity to Syracosphaera genus?)

Plate 76, fig. 1

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.

Coccolith numbers: ca. 36 coccoliths.

Dimensions: (collapsed) coccosphere diameter ca. 5 μ m; coccolith long axis 1.4-1.65 μ m.

Coccolithophore sp. C (affinity to Sphaerocalyptra genus?)

Plate 76, fig. 2

Very small calyptrolith-like coccoliths consisting of a ring with a bridge forming the cover of the calyptrolith; certain coccoliths are bigger and appear to be the circum-flagellar calyptroliths. These forms, I suspect, are 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.

Coccolith numbers: 72 and 77 coccoliths (2 specimens).

Dimensions: coccolith diameter (0.55-) 0.61-0.66 (-0.75) µm, height 0.3-0.6 µm.

Unidentified sp. no. 1

Plate 76, figs. 3 and 4.

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.

Component numbers: 456 to 896 small pieces or coccoliths? (3 specimens).

Dimensions: (collapsed) sphere diameter 5-8 μ m; component (coccolith?) diameter (0.15-) 0.45-0.65 μ m.

Unidentified sp no. 2

Plate 76, figs. 5 and 6.

This specimen covered by star-like shapes, 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.

IV. COMBINATION COCCOSPHERES

The water samples studied contained a relatively large number of combination coccospheres, which show together coccoliths that would be recognized as were considered previously as different species. While several of these combinations have been already signalled previously, others are described here for the first time.

Most of the combination coccospheres found had heterococcoliths and holococcoliths together; others combined either heterococcoliths with nannolith type coccoliths or coccoliths of two considered different holococcolithophores.

Here there are documented these observed combination coccospheres with notes on the distribution, particularly the vertical distribution, of the 'normal' coccospheres that enter in the combinations.

IV. 1 HETEROCOCCOLITH-HOLOCOCCOLITH COMBINATION COCCOSPHERES THAT HAD BEEN ALREADY RECORDED

The combination coccospheres presented here have been found at least twice in our samples, or have been reported by other authors previously, or have the different coccoliths so well combined that they really appear to belong to one composed coccolithophore.

Helicosphaera carteri and Syracolithus catilliferus

Helicosphaera carteri (Plate 77, 1) was generally found in samples deeper than 20 meters; only occasionally was it present in the subsurface water. *Syracolithus catilliferus* (Plate 77, 2) was very abundant in the upper 30 meters of the water column. Usually, these monomorphic coccospheres co-occurred at the same stations, with *Syracolithus catilliferus* in the surface (0 - 20 m) and *Helicosphaera carteri* below 30 m depth (see Chapter V).

A collapsed coccosphere of *Syracolithus catilliferus*, partially covered by some overlapping heterococcoliths of *Helicosphaera carteri* was found at 20 m depth at station 24W (Plate 77, 3). Another *H. carteri* - *S. catilliferus* combination coccosphere found at station G4 at a depth of 70 m, shows a well formed coccosphere with overlapping helicoidal heterococcoliths covering the juxtaposed holococcoliths (Plate 77, 4).

Syracosphaera pulchra and Calyptrosphaera oblonga

The dithecate Syracosphaera pulchra (Plate 78, 1) was common in the NW Mediterranean with a widely distributed in depth (see Chapter V). Calyptrosphaera oblonga, was found occasionally in the subsurface waters. A single large coccosphere of Calyptrosphaera oblonga including some caneoliths of Syracosphaera pulchra (Plate 78, 2) was found at station 021, 20 m (FRONTS-96). Moreover, another S. pulchra - C. oblonga combination coccosphere was recognized under optical microscope (Plate 78, 3) from Masnou coastal waters (MEDEA-98); half of this specimen consisted of C. oblonga, the other half of S. pulchra coccoliths. It was successful transferred on a SEM-stub, but it was found collapsed in the SEM (Plate 78, 4).

Syracosphaera anthos and Periphyllophora mirabilis

Syracosphaera anthos (Plate 79, 1) was not abundant in our samples and was found at depths of more than 30 m (see Chapter V). The species *Periphyllophora mirabilis* (Plate 79, 2) was found occasionally in the upper 0-30 m.

A single combination coccosphere showing holococcoliths of *Periphyllophora mirabilis* covering the juxtaposed endothecal caneoliths of *Syracosphaera anthos* (Plate 79, 3,4) was found in the 40 m sample of station 178 from MESO-95; this coccosphere contained both

the exothecal coccoliths and endothecal caneoliths of *S. anthos*. The same association was found again in MESO-96, station G4 at 40 meters depth; this specimen is a well formed coccosphere of *P. mirabilis* with one clearly visible caneolith of *S. anthos* near the surface and two others just visible between the helladoliths (Plate 79, 5,6).

Coronosphaera mediterranea and Calyptrolithina wettsteinii

The heterococcolithophore *Coronosphaera mediterranea* (Plate 80, 1) was found between 30 and 80 m depth and especially at 50 meters depth. *Calyptrolithina wettsteinii* (Plate 80, 2), was found mostly in the upper 0 - 40 m.

In MESO-96, Station I₂ at 40 m depth, a single combination coccosphere consisting half of *C. mediterranea* and half of *C. wettsteinii* (Plate 80, 3) was found. This specimen strongly resembles the specimen figured by Kamptner (1941) as fig. 152 in plate XV (see Plate 80, 4).

Syracosphaera nana with holococcoliths

The small egg-shaped coccospheres of *Syracosphaera nana* were observed in several samples. This species (Plate 81, 1) was found especially in samples from more than 30 m depth. The holococcolith phase (Plate 81, 2) is a coccosphere with dimorphic coccoliths and was found occasionally in the upper 50 m of the water column.

In a sample of station 013 - 75 m. (FRONTS-96), a coccosphere of *Syracosphaera nana* holococcolith phase showed caneoliths and exothecal coccoliths of the heterococcolith phase (Plate 81, 3,4). (The same combination was figured as *Syracosphaera* sp. type A in Kleijne, 1991, p. 21, pl. 20, figs. 5-6).

Acanthoica quattrospina and Holococcolithophore sp.

In some NW Mediterranean samples *Acanthoica quattrospina* (Plate 82, 1) was abundant and in some of these samples an undescribed holococcolithophore that appears related to the genus *Sphaerocalyptra* (Plate 82, 2) was also present.

In station N7, 5m (FANS-2) the holococcolithophore sp. was found with heterococcoliths of *Acanthoica quattrospina* (Plate 82, 3,5). In station J3, 10m (FANS-2) a collapsed coccosphere of *Acanthoica quattrospina* presenting the same holococcoliths (Plate 82, 4,6) was observed.

Syracosphaera sp. aff. type K of Kleijne (1993) (S. bannockii comb. nov, see Cros et al. 2000) and Corisphaera sp. type A of Kleijne (1991)

Both, the *Syracosphaera* sp. 5 (*aff. S.* sp. type K of Kleijne, 1993) (Plate 83, 1) and the *Corisphaera* sp. type A of Kleijne (1991, p. 54, pl. 13, figs. 1-2) (Plate 83, 2) were observed occasionally in the studied samples.

A single coccosphere consisting of half of *Syracosphaera* sp. *aff.* type K of Kleijne and half of *Corisphaera* sp. type A (Plate 83, 3-4) was found at station G_{6} , at 40 m depth, (MESO-96). The right hand half of the coccosphere consists of endothecal heterococcoliths and adjacent to it two exothecal coccoliths are visible (see arrows).

IV.2 OTHER OBSERVED HETEROCOCCOLITH-HOLOCOCCOLITH COMBINATIONS

Seven additional rarely observed combinations of heterococcoliths with holococcoliths are presented here. In each case only one or even two specimens were found, but the coccospheres were not preserved as well as in the combinations described above.

Syracosphaera molischii and Anthosphaera fragaria

Both Syracosphaera molischii and Anthosphaera fragaria were found in the samples from the NW Mediterranean. A single "hybrid" collapsed cell showing dimorphic endothecal coccoliths of Syracosphaera molischii with both body and circumflagellar coccoliths of Anthosphaera fragaria (Plate 84, 1) was found at station 20 I, 20 m depth (FRONTS-95).

Syracosphaera sp. type D of Kleijne (1993) and Homozygosphaera arethusae

Syracosphaera sp. type D of Kleijne (1993) and *Homozygosphaera arethusae* are present in the NW Mediterranean waters. Two groups with heterococcoliths of *Syracosphaera* sp. type D and holococcoliths of *Homozygosphaera arethusae* were found (Plate 84, 3 and 4) at station 013, 66 m depth (FRONTS-96).

Syracosphaera histrica and Calyptrolithophora papillifera

Syracosphaera histrica and Calyptrolithophora papillifera were found in the NW Mediterranean sea waters. One collapsed coccosphere of dimorphic Calyptrolithophora papillifera surrounded by coccoliths of Syracosphaera histrica (Plate 84, 2) was found at station I4, 40 m depth (MESO-96).

Syracosphaera nodosa and Helladosphaera cornifera

Syracosphaera nodosa and *Helladosphaera cornifera* are present in the NW Mediterranean waters. A group of coccoliths which appeared to be a mixed collapsed coccosphere of *Syracosphaera nodosa* with *Helladosphaera cornifera* was found at station I8 - 40 m (Plate 84, 6).

Syracosphaera sp. 4 (now, S. delicata sp. nov. see Cros et al. 2000) and Corisphaera sp. type B of Kleijne (1991)

This *Syracosphaera* (see cap. III and Cros et al. 2000) has a delicate appearance showing weak body caneoliths; it is dithecate with dimorphic coccoliths in the endotheca, but their circumflagellar caneoliths are difficult to distinguish. Both species, *S. delicata* sp. nov. and *Corisphaera* sp. type B, were scarce in NW Mediterranean waters. In the 100 m sample of station 127 (FANS-1), a mixed and disintegrated combination coccosphere of this *S. delicata* sp. nov. with *Corisphaera* sp. type B was found (Plate 84, 5).

Rhabdosphaera clavigera and Sphaerocalyptra quadridentata

Rhabdosphaera clavigera is common in superficial and sub-superficial waters of the NW Mediterranean (see Chapter V) and *Sphaerocalyptra quadridentata* (Plate 85, 4) was repeatedly found in superficial waters of the several stations. A coccosphere belonging to *S. quadridentata* half surrounded by part of a collapsed coccosphere of *R. clavigera* (Plate 85, 1, 2) was found in the Barcelona offshore station T1, from the workshop named "Picasso" (July, 1998). In the station T5 of the same Picasso workshop, it was found a disintegrated coccosphere of *S. quadridentata* next to several exothecal coccoliths of *R. clavigera* (Plate 85, 3).

Acanthoica sp. and Sphaerocalyptra sp. 2

One collapsed coccosphere (Plate 85, 5, 6) with heterococcoliths of *Acanthoica* genus, showed by Chretienot-Dinet (1990) in fig. 469, and holococcoliths classified as

Sphaerocalyptra sp. 2 in the present study, was found at 25 m depth of station M11 from Fans-3.

IV.3 HETEROCOCCOLITH-NANNOLITH COMBINATION COCCOSPHERES

In these associations at least one of the species involved in each combination has been considered in the literature as a nannolith bearing species and most of the involved species have been repeatedly considered as belonging to *"incertae sedis"* genera.

Neosphaera coccolithomorpha var. nishidae and Ceratolithus cristatus

Both, Neosphaera coccolithomorpha var nishidae (Plate 86, 1) and Ceratolithus cristatus (Plate 86, 2) were found occasionally in the studied samples, always from surface waters (less than 10 meters depth). The presence of N. coccolithomorpha tended to coincide with that of C. cristatus, but as only a few specimens were found, the significance of this co-occurrence could not be established. Several examples of the well documented association of ceratoliths and hoop-shaped heterococcoliths of C. cristatus were found.

In the 10 m depth sample of station 013 (FRONTS-96), which contained N. *coccolithomorpha* as well as *C. cristatus*, a combined coccosphere was observed with heterococcoliths of *N. coccolithomorpha* var. *nishidae* enclosing a large number of the hoop-like coccoliths of *C. cristatus* (Plate 86, 3,4).

Alisphaera sp. and Polycrater sp.

The genera *Polycrater* and *Alisphaera* have been found repeatedly in NW Mediterranean waters, *Polycrater* was common in superficial waters and *Alisphaera* in deeper waters (usually from 40 to 60 m depth).

One coccosphere that appear to be composed by two different thecas, one of *Polycrater* inside the other of *Alisphaera* (Plate 87, 1), has been found at 5 m depth of the station M11 of the Fans-3 cruise; the *Polycrater* involved is classified in the present study as sp. "resembling Gaudí architecture" and the *Alisphaera* sp. is *aff.* to *A. unicornis* (with a beak-like protrusion). Details of the same specimen are figured in Plate 87, 2-4.

In the station 25 of cruise Hivern99, at 40 m depth was found an *Alisphaera* specimen associated with the remains of a *Polycrater* coccosphere (Plate 87, 5-6); the *Alisphaera* specimen appear close to the defined above, but possessing notable tooth-like protrusions inwards from the distal flange; *Polycrater* remains have very small and no identifiable coccoliths.

Canistrolithus sp. 1 and Polycrater sp. (with dots)

The genus *Canistrolithus*, in contrast to *Polycrater*, was very scarcely in the studied samples; it was found twice in the cruise Fans-3, station K05, at 84 m, associated with specimens of *Polycrater* (Plate 88, 1-6); *Canistrolithus* coccoliths appear to cover the *Polycrater* sp. 1 (with dots) coccoliths. *Canistrolithus* coccoliths are identified as *C*. sp. 1 in the present study.

IV.4 COMBINATION COCCOSPHERES WITH HOLOCOCCOLITHS THAT WOULD BE RECOGNIZED PREVIOUSLY AS TWO DIFFERENT SPECIES

Two associations consisting of holococcoliths usually considered to be characteristic of discrete species were encountered. The species involved in such associations have coccoliths very close one to each other and even is possible to see coccoliths, as transitional forms, with characteristics of the both involved species.

Syracolithus catilliferus and Syracolithus confusus

Syracolithus catilliferus (see chapter III) and *S. confusus* (see also chapter III) usually cooccurred at stations in the NW Mediterranean Sea in the surface and subsurface waters.

Two coccospheres having both, coccoliths of *Syracolithus catilliferus* and of *S. confusus* were found in Meso-96, at the station F2, at 5m (Plate 89, figs. 1-2).

In this study the combination of *Helicosphaera carteri* and *Syracolithus catilliferus* is presented. The life-cycle transition of *Helicosphaera carteri* to *Syracolithus catilliferus* and the association of *Syracolithus catilliferus* with *Syracolithus confusus* could form an analogy to the life-cycle of *Coccolithus pelagicus*.

Corisphaera sp. type A (see Kleijne, 1991) and Zygosphaera bannockii

Corisphaera sp. type A (see chapter III) was common in Mediterranean waters; *Zygosphaera bannockii* (see chapter III), in contrast, was found very rarely.

Three specimens having coccoliths of *Corisphaera* sp. type A, *Zygosphaera bannockii* and transitional forms between them were found in the cruise Fans-1 (Plate 89, figs. 3-6).

IV.5 DISCUSSION

RELIABILITY AND SIGNIFICANCE OF THE HETEROCCOLITH-HOLOCOCCOLITH COMBINATIONS

Two of the hetero-holococolith combinations documented here have been illustrated previously: Coronosphaera mediterranea with Calyptrolithina wettsteinii, by Kamptner (1941); Syracosphaera nana with holococcoliths, by Kleijne (1991) as Syracosphaera sp. type A with holococcoliths. The combination Helicosphaera carteri with Syracolithus catilliferus was found twice and there are homologous descriptions in the literature (see Lecal-Schlauder, 1961). Syracosphaera pulchra with Calyptrosphaera oblonga was found twice and there are previous descriptions in the literature that might be the same kind of combination (see Lohmann 1902; Kamptner, 1941; Lecal-Schlauder, 1961). Syracosphaera anthos with Periphyllophora mirabilis was found twice in a non collapsed and well combined specimens. Acanthoica quattrospina with the holococcolithophore sp. was found twice and moreover another specimen of Acanthoica was found combined with a holococcolithophore Sphaerocalyptra. The combination coccosphere of Syracosphaera sp. aff. type K and Corisphaera sp. type A was found once but the specimen is particularly well organized and convincing of to be a combination and not a chimerical random product.

It seems that all these examples almost certainly represent life-cycle transitions between hetero- and holococcolithophore phases, analogous to those well documented in *Coccolithus pelagicus*. Since the transition between one and another phase is sporadic and is supposed to be a relatively fast process, it can be anticipated that these combination coccospheres should be only occasionally found.

The combination of *Rhabdosphaera clavigera* with *Sphaerocalyptra quadridentata* appears as possible if we look at the specimen figured in Plate 85, 1-2 but the coccoliths figured in Plate 85, 3 have a less convincing appearance. The specimens of *Syracosphaera molischii* with *Anthosphaera fragaria* is collapsed but the coccoliths of both species appear combined in a stable way. *Syracosphaera* sp. type D with *Homozygosphaera arethusae* was found twice but kind of collapsed. The other three collapsed specimens having heterococcoliths and holococcoliths (*Syracosphaera histrica* coccoliths surrounding a collapsed *Calyptrolithophora papillifera* coccosphere, *S. delicata* sp. nov. with *Corisphaera* sp. type B and *Syracosphaera nodosa* with *Helladosphaera cornifera*) might

be conceivably chance associations or less stable combination coccospheres, but they are suggestive of further and might be verified by future observations.

RELIABILITY AND SIGNIFICANCE OF THE HETEROCOCCOLITH-NANNOLITH COMBINATIONS

In some cases the nannoliths may be modified holococcoliths, in others modified heterococcoliths and, even in others they can be independently evolved structures (Young et al. 1999). Consequently we cannot relate them to life-cycle stages.

Associations consisting of large coccospheres of hoop-like *Ceratolithus* heterococcoliths with internal ceratoliths are well documented (Norris 1965, Winter & Siesser 1994, Alcober & Jordan 1997). More recently the hoop-shaped *Ceratolithus* heterococcoliths have also been found associated with *Neosphaera* heterococcoliths (Alcober & Jordan, 1997, Young et al. 1998, Cros *et al.* 2000 and Sprengel and Young 2000). These observations suggest a life-cycle with three different types of cell covering: hoop-shaped heterococcoliths; planolith heterococcoliths ("*Neosphaera*"); and ceratoliths. The simplest plausible life-cycle would appear to be for a "*Neosphaera coccolithomorpha*" heterococcolithophore to develop hoop-like coccoliths inside, followed by increase in coccosphere size with only the hoop-like coccoliths present; finally one or more ceratoliths can grow inside the coccosphere of hoop-shaped coccoliths.

The observation of both kinds of coccoliths and the nannoliths in the same waters implies that these morphologies are able to coexist in similar conditions, in surficial waters. The observations from this study and those of Kleijne (1993) on the distribution of these forms suggest that *Neosphaera coccolithomorpha* var. *nishidae* co-occurs with *Ceratolithus cristatus* var. *cristatus*.

The new combination coccospheres found in the present study having heterococcoliths of *Alisphaera* and *Canistrolithus* with different coccoliths of the genus *Polycrater* appear reasonable. *Polycrater* is considered a nannolith bearing coccolithophore qualified as "*incertae sedis*" and *Alisphaera* and *Canistrolithus* are considered two heterococcolithophore species having coccoliths with a high similar structure (Jordan & Chamberlain, 1993).

The combined specimens appear to have the coccospheres of *Alisphaera* and *Canistrolithus* covering the *Polycrater* nannoliths (see Plates 87 and 88) and that should be homologous with *Neosphaera-Ceratolithus*. Both types of nannolith heterococcolith combinations appear to have the nannolith phase growing inside the heterococcolith phase. Circumstantial evidence supporting the feasibility that the *Alisphaera* and *Canistrolithus* can develop inside and then eject *Polycrater* coccospheres, is the observation in the plankton samples of some *Alisphaera* coccospheres having an unusual circumflagellar extra sized opening. But against the *Neosphaera-Ceratolithus* distribution in surficial waters, *Alisphaera* prefers a deep position in the column whilst *Polycrater* usually inhabits surficial waters (see Chapter V).

RELIABILITY AND SIGNIFICANCE OF THE HOLOCOCCOLITH-HOLOCOCCOLITH COMBINATIONS

The holococcolith-holococcolith combination coccospheres look similar to the heterococcolith-holococcolith combination coccospheres, but there is a significant difference in that the two coccolith types involved are closely similar and even there are transitional coccolith forms. Both pairs, *Syracolithus catilliferus - S. confusus* and *Zygosphaera bannockii - Corisphaera* sp type A, present the coccoliths with related morphologies, but having one coccolith type more robust (*Syracolithus catilliferus, Zygosphaera bannockii*) and the other with perforations (*S. confusus, Corisphaera* sp type

A). Such characteristics suggests that these combinations might be simply an unusual example of intraspecific variation, with no definite life-cycle significance.

In the case of *Zygosphaera bannockii* - *Corisphaera* sp type A, the two holococcolith types are very similar, differing essentially in terms of the presence/absence of openings. All our specimens show clear examples of the two normal morphologies, but in addition intermediate morphologies occur, with small pores. Given this, it seems likely that these specimens are simply examples of intra-specific variation, analogous for instance to the variable degree of calcification described in *Emiliania huxleyi* (Young and Westbroek 1991). It is worth noting that the classification of the two morphotypes in different genera is a reflection of the rather artificial nature of much of holococcolith taxonomy, as discussed by Kleijne (1991).

For the Syracolithus catilliferus with S. confusus combination, the two "species" again differ essentially in the presence of pores in the upper part of S. confusus, and the close identity of the species was noted by Kleijne (1991). In this paper a combination of *Helicosphaera carteri* and Syracolithus catilliferus is presented, whilst Lecal-Schlauder (1961) figured a combination of *H. carteri* and what appears to be S. confusus. An interesting analogy is provided by Coccolithus pelagicus, Rowson et al. (1986) showed that this species produces two apparently discrete holococcolith types - "Crystallolithus hyalinus" and "C. braarudii". The "hyalinus" morphotype is a solid disk whilst "braarudii" is perforate, so there is an obvious parallelism with the two other cases discussed here.

The evidence is variable but in each of these three situations a single heterococcolith species is associated with two holococcolith "species" *Syracosphaera* sp. *aff.* type K with *Corisphaera* sp type A and Z. *bannockii*; *H. carteri* with *Syracolithus catilliferus* and *S. confusus; Coccolithus pelagicus* with "Crystallolithus hyalinus" and "C. braarudii". In each case the two holococcolith "species" differ essentially in the presence/absence of perforations and therefore it seems reasonable to assume that they might represent examples of variation in the degree of calcification, occurring independently of either life-cycles or genotypic variation.

ECOLOGICAL IMPLICATIONS

The Helicosphaera carteri - Syracolithus catilliferus association appears to occupy two different ecological niches in the same geographic area: S. catilliferus lives near the surface while H. carteri occupies deeper waters (usually, it is found at more than 20 meters depth). The studied area presents a well developed deep chlorophyll maximum (DCM) between 40 and 70 m depth, during the stratification period (Estrada, 1985, 1991; Margalef and Estrada, 1987). Possibly, the preference of H. carteri for deep waters can be related to the presence of higher nutrient concentrations there (several authors suggest that H. carteri prefers relatively nutrient-rich waters: Pujos, 1992; Giraudeau, 1992; Flores et al. 1995 and Flores et al. 1997). Moreover holococcolithophores appear to live mainly in oligotrophic waters (Kleijne, 1993). It can be speculated that this H. carteri / S. catilliferus depth zonation is the result of a life-cycle strategy.

A more detailed information on distribution of these coccolithophores is given in Chapter V. Overall, however, there is a clear tendency for the holococcoliths to occur in the upper water column with the heterococcoliths somewhat lower. So, it seems likely that as in other protists, such as dinoflagellates (Garcés et al. 1998) or *Phaeocystis* (Lancelot and Rousseau 1994), the various life-cycle phases will prove to have separate ecological adaptations and so allow the species to survive under and exploit a range of ecological conditions.

IS THE WESTERN MEDITERRANEAN A SEA FAVORABLE TO THE PRODUCTION OF COMBINATION COCCOSPHERES? DOES THE WESTERN MEDITERRANEAN AREA FAVOUR THE PHASE CHANGES IN COCCOLITHOPHORES?

The combination coccospheres recorded come from a wider geographical area but reviewing all the recorded observations of combination coccospheres it is noticeable that an extraordinary proportion of them come from the Western Mediterranean (see Cros et al. 2000). This is a relatively well studied area, but numerous meticulous studies of living coccolithophore assemblages have been undertaken around the world without finding combination coccospheres. It might be possible that conditions in the Western Mediterranean may in some way favour frequent phase changes and consequently may increase the relative frequency of combination coccospheres in the water.

Since Mediterranean is a small sea which present strong physic-chemical gradients and holds high and abruptly changes in the physical conditions it would be understandable that it can induce frequent phase changes if these are already related to the changing conditions. Moreover, the Mediterranean contains a very high diversity of species (Margalef, 1997) and in general terms it is an oligotrophic sea and as noted by Kleijne (1991) holococcolithophores are more common in oligotrophic environments. In addition there is usually a well developed deep chlorophyll maximum which may favour life-cycles adapted to different water conditions. Or, only is the good climate and facilities for mixing waters and populations of this area which favoured a major number of findings and records? Further coccolithophore studies should allow us to answer these questions.

V. DISTRIBUTION OF IDENTIFIED SPECIES IN NW MEDITERRANEAN WATERS

V.1. CRUISES MESO-95 AND FRONTS-95: AN APPROACH TO THE SPATIAL DISTRIBUTION OF SOME COCCOLITHOPHORES.

CRUISE MESO-95: DISTRIBUTION IN SURFACE WATERS AND AT 40 m.

Hydrographic data concerning the Meso-95 cruise (30 May to 16 June 1995) are presented in Figure 5.1. The location of sampled stations is presented in Fig. 2.1.

The most abundant species was *Emiliania huxleyi* (Figure 5.2, A and B), present approximately in numbers an order of magnitude higher than the species following in the abundance ranking. *Emiliania huxleyi* was slightly more abundant at 40 m depth than in surface waters; the highest density (16×10^3 cells/l) was at 40m depth at station 112.

Gephyrocapsa ericsonii (Figure 5.2, C and D) tended to be slightly more abundant towards the south-east of the sampled zone (with a maximum of around 3 x 10^3 cells/l at station 161), and near the Balearic Islands. *G. muellerae* was present at lower densities than *G. ericsonii* and was also more abundant near the Balearic Islands (see Fig. 5.2, E and F).

Helicosphaera carteri (Figure 5.3, A and B) was most abundant in the proximity of the Ebro delta and towards the south of the sampled zone, at depths of 40m (4 x 10^3 cells/l at station 115). The highest abundances of *Syracosphaera pulchra* (Figure 5.3, C and D) were near the Iberian Peninsula, particularly in surface waters (maximum 5 x 10^3 cells/l at the surface at station 005). *Syracosphaera molischii*, on the other hand, was typically more concentrated at 40m than at the surface and tended to be more abundant in the central area, between the peninsula and the Balearic Islands.

CRUISE FRONTS-95: VERTICAL DISTRIBUTIONS

Cruise Fronts-95 was held from 17 to 23 June 1995. The location of sampled stations is presented in Fig. 2.1.

Total coccolithophore abundance was higher along the southern transect, including stations 26W, 25W and 24W; holococcolithophores were associated with the uppermost water layers, especially at the offshore stations (see Fig. 5.4).

The highest densities of *Emiliania huxleyi* (Fig. 5.4), the most abundant species, were mainly associated with coastal waters (a maximum of 94 x 10^3 cells/l at station 28C at 30 m in the northern transect and 64 x 10^3 cells/l at station 25W at 5m in the southern transect). *Gephyrocapsa ericsonii*, the second most abundant species, tended to occupy intermediate (30 to 60 metres) positions in the water column, with maxima around 50m depth in both transects (highest density 7 x 10^3 cells/l at station 20I at 50m).

Syracosphaera molischii was clearly associated with mid-depth layers (maximum 8 x 10^3 cells/l at 60m at station 23D), while Syracosphaera pulchra was more abundant in near surface and coastal waters (maximum 14 x 10^3 cells/l at 5m at station 25W).

CHAPTER V

Calyptrosphaera oblonga, the holococcolithophore phase of S. pulchra, was present in very low numbers in the uppermost layers of the same stations in which S. pulchra showed the highest abundances (Fig. 5.6); the maximum density (2 x 10³ cells/l) was at the same station, 25W, and the same depth, 5m. A similar pattern was found in the relative distribution of Helicosphaera carteri and its holococcolithophore phase, Syracolithus catilliferus; H. carteri reached its highest abundances around 60 m depth, while S. catilliferus was more abundant in surface waters, mostly at the same stations (Fig. 5.5). The maximum density of *H. carteri*, 5 x 10^3 cells/l, was recorded at station 20I at 60m, whilst S *catilliferus* was present at 2 x 10^3 cells/l at the same station, but at 10 metres; the maximum abundance of S. catilliferus, 7 x 10³ cells/l, was at station 26W, at 10m. Coronosphaera mediterranea was most abundant around 50m depth and did not occur in the uppermost layers; its holococcolithophore counterpart, Calyptrolithina wettsteinii, showed highest abundances between 20 and 40 meters but was also present in the upper layers (Fig. 5.5). The maximum abundance of C. mediterranea (2 x 10^3 cells/l) occurred at station 26W at 50m; at the same station, at 40m and 10m, the highest densities of C. wettsteinii (around 4 x 10^3 cells/l) were recorded.

The genus *Alisphaera*, which bears heterococcoliths, can form combination coccospheres with the genus *Polycrater*, which possesses a type of coccoliths named nannoliths, and these taxa appear to have the same relative distribution pattern as the hetero-holococcolithophore pairings. Low abundances of *Alisphaera* (from 1 to 2×10^3 cells/l) were present only at two stations, around 50m depth, in the northern transect (Figure 5.6); no specimens of this genus were found in the southern transect. In the northern transect, *Polycrater*, which was more abundant than *Alisphaera*, presented its highest population densities at the same stations as *Alisphaera*, at the same depth or in shallower waters. In the southern transect, *Polycrater* was present above 20m depth at the offshore station, and between surface and 50m depth at the coastal station.

The heterococcolithophore *Umbellosphaera tenuis* was present at low abundances with a very irregular distribution pattern (Fig. 5.6).

Rhabdosphaera clavigera and *Rhabdosphaera xiphos* presented parallel distribution patterns; they occupied the uppermost layers, particularly in the southern transect (Fig. 5.7). The highest densities of *Rhabdosphaera clavigera* were at 5 m, at stations 20I (3×10^3 cells/l) and 26W (4×10^3 cells/l), for the northern and southern transects respectively. *Rhabdosphaera xiphos* was most abundant at 10m at station 23D (9×10^3 cells/l) and at 5m at station 24D (5×10^3 cells/l). *Ophiaster hydroideus* and *Florisphaera profunda* occurred in deep waters; both species, especially the latter, are clearly recognized as typical of the deep part of the photic zone. The maximum abundance of *Florisphaera profunda* (5×10^3 cells/l) was at station 23D at 70-80 m. The genus *Papposphaera* appeared also to be associated with deep water layers (Fig. 5.7).

The holococcolithophores discussed in the previous paragraphs tended to occupy the upper layers of the photic zone. This trend was also clear for *Calyptrosphaera heimdaliae* and members of the genus *Sphaerocalyptra*, but some holococcolithophores, like

Homozygosphaera arethusae and *Calyptrolithophora papillifera*, appeared to prefer intermediate levels within the photic zone.

V.2. CRUISES MESO-96 AND FRONTS-96: FURTHER EXAMPLES OF COCCOLITHOPHORE VERTICAL DISTRIBUTIONS

The physical oceanographic conditions during the Meso 96 (18 June to 3 July 1996) and Fronts 96 (16 to 21 September 1996) cruises are presented in Figs. 5.9 and 5.10 respectively. Tables 5.1 and 5.2 show the taxa found in the Meso-96 and Fronts-96 cruises, with their relative abundances.

In the four transects sampled during Meso-96, the maximum total coccolithophore abundance was recorded at 40 metres depth (71 x 10^3 cells/l at station D4 at 40m), whilst in the Fronts-96 cruise the highest abundances occurred at slightly deeper levels (69 x 10^3 cells/l at station 013 at 68m). In the southern transects of Meso-96, the highest coccolithophore abundances occurred near the coast; maxima at the offshore stations occurred along transects D and G. In the Fronts-96 transect, the highest abundances were recorded at the furthest offshore station.

The distribution of total holococcolithophore abundance was similar to that of total coccolithophores in transects A and G, but not in D, where holococcolithophores were more numerous in surface waters. Holococcolithophore abundances were low in the Fronts-96 transect, sampled in September (Figs. 5.11 and 5.12). Holococcolithophore concentrations ranged from 0 to 9 x 10^3 cells/l in Fronts-96 whilst they were present at densities of 0 to 49 x 10^3 cells/l in Meso-90.

Emiliania huxleyi, the most abundant coccolithophore species, presented in general, and especially in the September transect (Cruise Fronts-96), a similar distribution to that of total coccolithophores. *Gephyrocapsa ericsonii* occurred in intermediate depth waters (Figs. 5.13 and 5.14). The average values for *Emiliania huxleyi* were 9 and 13 x 10^3 cells/l in Meso-96 and Fronts-96 respectively, while the average values for *Gephyrocapsa ericsonii* were 2 and 4 x 10^3 cells/l in Meso-96 and Fronts-96 respectively.

In the Meso-96 cruise, *Helicosphaera carteri* was most abundant at intermediate depths, with more than 5 x 10^3 cells/l in sample D4. The highest concentrations of *Syracolithus catilliferus*, the holococcolithophore phase of *H. carteri*, were in surface waters at the same stations in which *H. carteri* showed its highest abundances (see Fig. 5.15). Both *H. carteri* and *S. catilliferus* were less abundant in the Fronts 96 transect (see Fig. 5.15). The highest values of *H. carteri* in this transect (around 1 x 10^3 cells/l) occurred in deep waters at the offshore station 021.

Coronosphaera mediterranea was present in low densities, mainly around 50m depth. *Calyptrolithina wettsteinii*, the holococcolithophore phase of *C. mediterranea*, was more abundant and occurred in the surface layers (Figs. 5.17 and 5.18).

Table 5.1 Relative abundances (%) of the identified coccolithophore taxa in the 84 samples of Meso-96 (18 June to 3 July 1996). Location of sampled stations is represented in Fig. 2.2.

Emiliania huxleyi	31.80	Syracosphaera nodosa	0.29
Gephyrocapsa ericsonii	6.56	Syracosphaera nana	0.29
Helladosphaera cornifera	5.65	Alisphaera spp.	0.29
Rhabdosphaera xiphos	5.15	Syracosphaera prolongata	0.27
Syracosphaera molischii	4.18	Pappomonas spp.	0.25
Corisphaera spp.	4.05	Syracosphaera histrica	0.23
Helicosphaera carteri	3.18	Syracosphaera anthos	0.21
Rhabdosphaera clavigera	2.97	Palusphaera vandelii	0.21
Umbellosphaera tenuis	2.74	Turrilithus latericioides	0.21
Calyptrosphaera heimdaliae	2.66	Syracosphaera nana ph. HOL.	0.19
Homozygosphaera arethusae	2.56	Gephyrocapsa muellerae	0.17
Syracolithus catilliferus	2.29	Syracosphaera bannockii	0.17
Sphaerocalyptra adenensis	2.12	Calyptrolithina divergens	0.17
Calyptrolithophora papillifera	1.68	Anacanthoica acanthos	0.15
Ophiaster hydroideus	1.58	Syracolithus dalmaticus	0.15
Syracosphaera halldalii (protr.)	1.35	Anthosphaera lafourcadii	0.15
Calyptrolithina wettsteinii	1.31	Zygosphaera hellenica	0.15
Calyptrosphaera cf. heimdaliae (small)	1.08	Syracosphaera noroitica	0.12
Polycrater galapagensis	1.04	Anoplosolenia brasiliensis	0.12
Syracosphaera pulchra	0.98	Gephyrocapsa oceanica	0.10
Florisphaera profunda	0.87	Heterococcolithophore spp.	0.10
Sphaerocalyptra spp.	0.71	Calyptrosphaera oblonga	0.10
Anthosphaera fragaria	0.69	Coccolithophore sp.	0.08
Syracolithus quadriperforatus	0.58	Cyrtosphaera lecaliae	0.08
Algirosphaera robusta	0.52	Gladiolithus flabellatus	0.08
Acanthoica quattrospina	0.52	Syracosphaera lamina	0.06
Papposphaera spp.	0.52	Coronosphaera mediterranea	0.06
Sphaerocalyptra quadridentata	0.52	Helicosphaera pavimentum	0.04
Polycrater spp.	0.46	Syracosphaera marginaporata	0.04
Syracolithus schillerii	0.44	Syracosphaera sp. (estrat.)	0.04
Anthosphaera periperforata	0.44	Poricalyptra aurisinae	0.04
Corisphaera strigilis	0.44	Helicosphaera carteri v. hyalina	0.02
Syracosphaera sp. type D of Kleijne	0.42	Syracosphaera sp. I cf. epigrosa	0.02
Syracolithus confusus	0.42	Syracosphaera delicata	0.02
Gaarderia corolla	0.39	Cyrtosphaera cucullata	0.02
Palusphaera cf. vandelii (robust)	0.39	Acanthoica acanthifera	0.02
Syracosphaera ossa	0.37	Umbilicosphaera sibogae v. sibogae	0.02
Periphyllophora mirabilis	0.33	Calciosolenia murrayi	0.02
Michaelsarsia elegans	0.31	Calcidiscus leptoporus ph. rigidus	0.02
Calyptrosphaera sphaeroidea	0.31	Zygosphaera marsilii	0.02
Corisphaera tyrreniense	0.31	Zygosphaera bannockii	0.02
Syracosphaera cf. dilatata	0.29	Holococcolithophore sp.	0.02

Syracosphaera pulchra occurred mainly in coastal waters, at 40 - 50 m depth; it presented two maxima of 3 x 10^3 cells/l at 40 m at stations D2 and I2. *Calyptrosphaera oblonga*, the holococcolithophore phase of *S. pulchra*, was present only in three samples, two of which also contained *S. pulchra* (Fig. 5.19). In the Fronts-96 transect, *S. pulchra* occurred at all stations, mainly between 20 and 40 m depth (Fig. 5.20); *C. oblonga* was not found in this transect.

Rhabdosphaera clavigera and *Rhabdosphaera xiphos* occupied the upper photic zone and showed similar distributions. In Meso-96 the maximum densities of these two taxa occurred

around 40 m depth (e.g. transect G) or at the surface (e.g. transect A); *R. xiphos* was much more abundant (two to three times more) than *R. clavigera* and appeared to have a slight

Table 5.2. Relative abundance (%) of the identified coccolithophore taxa in the 29 samples of Fronts-96 (16 to 21 September 1996). Location of sampled stations is represented in Fig. 2.2.

Emiliania huxleyi	45.45	Syracosphaera nodosa	0.25
Gephyrocapsa ericsonii	13.29	Syracosphaera prolongata	0.19
Umbellosphaera tenuis	7.59	Palusphaera vandelii	0.19
Rhabdosphaera clavigera	7.27	Acanthoica quattrospina	0.19
Syracosphaera ossa	3.01	Calyptrosphaera heimdaliae	0.19
Syracosphaera pulchra	1.76	Periphyllophora mirabilis	0.19
Syracosphaera molischii	1.69	Calyptrolithina wettsteinii	0.19
Ophiaster hydroideus	1.44	Calyptrolithophora papillifera	0.19
Syracosphaera histrica	1.00	Sphaerocalyptra adenensis	0.19
Algirosphaera robusta	1.00	Corisphaera strigilis	0.19
Corisphaera spp.	1.25	Helicosphaera pavimentum	0.13
Syracosphaera halldalii (protr.)	0.94	Syracosphaera sp. 7 (small coc.)	0.13
Florisphaera profunda	0.94	Michaelsarsia elegans	0.13
Papposphaera spp.	0.88	Oolithotus fragilis	0.13
Homozygosphaera arethusae	0.88	Syracolithus dalmaticus	0.13
Syracosphaera noroitica	0.75	Syracolithus schillerii	0.13
Alisphaera spp.	0.69	Anthosphaera lafourcadii	0.13
Gaarderia corolla	0.63	Helicosphaera carteri v. hyalina	0.06
Cyrtosphaera lecaliae	0.63	Syracosphaera ampliora	0.06
Helicosphaera carteri	0.56	Syracosphaera sp. I cf. epigrosa	0.06
Rhabdosphaera xiphos	0.56	Syracosphaera tumularis	0.06
Syracosphaera cf. dilatata	0.44	Syracosphaera marginaporata	0.06
Syracosphaera sp type D of Kleijne	0.44	Syracosphaera sp. type L of Kleijne	0.06
Ceratolithus cristatus	0.44	Syracosphaera bannockii	0.06
Polycrater galapagensis	0.38	Syracosphaera sp. (estrat.)	0.06
Calyptrosphaera sphaeroidea	0.38	Palusphaera vandelii (robust)	0.06
Helladosphaera cornifera	0.38	Scyphosphaera apsteinii	0.06
Syracosphaera anthos	0.31	Anoplosolenia brasiliensis	0.06
Syracosphaera nana	0.31	Gladiolithus flabellatus	0.06
Coronosphaera mediterranea	0.31	Polycrater spp.	0.06
Neosphaera coccolithomorpha	0.31	Calyptrosphaera cf. heimdaliae (small)	0.06
Anthosphaera fragaria	0.31	Syracolithus catilliferus	0.06

preference for the offshore stations (Fig. 5.21); The highest densities of *R. xiphos* (10 x 10^3 cells/l) were recorded at stations D6 and G6, at 40 m depth. In the Fronts-96 transect, both species, *R. clavigera* and *R. xiphos*, showed their maximum values in the surface layers but, curiously, *R. clavigera* was around six times more abundant than *R. xiphos* (Fig. 5.22).

Alisphaera was present in low concentrations in Meso-96 and Fronts-96, at depths of about 50 m. *Polycrater* was recorded most often in the uppermost layers, but maximum concentrations of this taxa in the transects A and I of Meso-96 were found at 40 m depth (Figs. 5.23 and 5.24).

The holococcolithophore *Calyptrosphaera heimdaliae* and holococcolithophores of the genus *Sphaerocalyptra* appeared to prefer the surface layers. Maximum concentrations of *C. heimdaliae* were observed along transect G, where it exceeded 5 x 10^3 cells/l at stations G2 and G6. *Sphaerocalyptra* was most abundant at station D2, with more than 15×10^3

cells/l. Both taxa, *C. heimdaliae* and *Sphaerocalyptra*, were relatively scarce in September, during the Fronts-96 cruise (Figs. 5.25 and 5.26).

The holococcolithophore *Calyptrolithophora papillifera* showed a clear preference for waters of intermediate depth. Its maximum abundances appeared around 40m depth, with values of 2 and 4 x10³ cells/l in the transects of Meso-96; only very few specimens were found in September. *Homozygosphaera arethusae*, another holococcolithophore species, also showed its highest values at 40 m depth, but occupied also the upper water layers and its distribution pattern was different from that of *C. papillifera*. The highest abundances of *H. arethusae* were along transect A of Meso-96, and the lowest densities during the Fronts-96 transect (Figs. 5.27 and 5.28).

The heterococcolithophore *Syracosphaera molischii* showed a rather irregular distribution pattern, with maximum concentrations at 70m depth at offshore stations (Figs. 5.29 and 5.30). During Meso-96, *Umbellosphaera irregularis*, another heterococcolithophore, was present at highest concentrations at 40 m depth, especially in the offshore waters (Figs. 5.29 and 5.30).

Ophiaster hydroideus occupied deep waters; its highest abundance (18×10^3 cells/l) was measured at station D4 at 70 m depth; very few specimens were observed along transect A. The distribution pattern of *O. hydroideus* was similar during the September transect. The maximum densities of *Papposphaera* were also around 70m depth, particularly in offshore waters (Figs. 5.31 and 5.32).

Florisphaera profunda, a recognized deep photic zone species, occurred mainly in offshore stations, below 50m depth (Fig. 5.33); maximum abundance of this species (14 x 10^3 cells/l) was at station D8 at 70m.

V.3. FANS CYCLE CRUISES: SEASONAL COCCOLITHOPHORE VARIABILITY

FANS-1: AUTUMN COCCOLITHOPHORE DISTRIBUTION OFF THE EBRO RIVER MOUTH

During the autumn cruise (1 to 10 November 1996), the average sea surface temperature was slightly higher than 19°C. The riverine inflow at this time was low (around 124 m³/s, compared to the average discharge of slightly less than 400 m³/s, Guillén & Palanques, 1997). Salinity data and total Chlorophyll-a concentrations are presented in Figure 5.35. This information and a more complete set of oceanographic data can be found in Salat *et al.* (submitted).

Table 5.3 shows the relative abundances of the taxa found in the Fans-1 samples. The most common species were: *Emiliania huxleyi*, *Gephyrocapsa ericsonii*, *Syracosphaera pulchra*, *Rhabdosphaera clavigera* and *Algirosphaera robusta*. Their abundances and the total concentrations of the remaining heterococcolithophore and holococcolithophore taxa are presented for each of the five sampled stations in Fig. 5.36. As can be seen in the figure, station 78b, directly influenced by river input, had high concentrations of *R. clavigera* and *S. pulchra* (at 5m depth maxima of 21 x 10³ cells/l and 12 x 10³ cells/l for *R. clavigera* and *S. pulchra* respectively). *Emiliania huxleyi* was the most abundant species at all the stations

and depths, especially at 60m depth (maximum 45 x 10^3 cells/l at station 64 at 60m). The holococcolithophores occurred mainly in the surface waters of the offshore stations (4 x 10^3 cells/l at 5 m depth at stations 123 and 127) and appeared to be associated with oligotrophic conditions. *A. robusta* and *G. ericsonii* were found particularly at intermediate depths; maximum density of *A robusta* (6 x 10^3 cells/l) was recorded at station 127 (60m) and of *G. ericsonii* (4 x 10^3 cells/l) at station 64 (60m).

Table 5.3. Relative abundance (%) of the identified coccolithophore taxa in the 26 samples of Fans-1 (01 to 10 November 1996). The location of sampled stations is represented in Fig. 2.3.

Emiliania huxleyi	61.24	Syracosphaera prolongata	0.25
Rhabdosphaera clavigera	6.64	Syracosphaera anthos	0.19
Algirosphaera robusta	3.38	Syracosphaera delicata	0.19
Gephyrocapsa ericsonii	2.83	Alisphaera spp.	0.19
Syracosphaera pulchra	2.57	Anthosphaera lafourcadii	0.19
Syracosphaera ossa	2.19	Calyptrolithophora papillifera	0.19
Corisphaera spp.	1.69	Helladosphaera cornifera	0.19
Umbellosphaera tenuis	1.69	Calcidiscus leptoporus	0.13
Syracosphaera molischii	1.57	Syracosphaera nodosa	0.13
Papposphaera spp.	1.50	Syracosphaera noroitica	0.13
Homozygosphaera arethusae	1.25	Syracosphaera bannockii	0.13
Cyrtosphaera lecaliae	1.19	Sphaerocalyptra quadridentata	0.13
Syracosphaera halldalii (protr.)	1.13	Corisphaera strigilis	0.13
Palusphaera vandelii	1.06	Syracosphaera ampliora	0.06
Polycrater spp.	0.94	Syracosphaera marginaporata	0.06
Gaarderia corolla	0.75	Syracosphaera nana	0.06
Syracosphaera cf. dilatata	0.69	Calciopappus spp.	0.06
Rhabdosphaera xiphos	0.69	Umbilicosphaera hulburtiana	0.06
Acanthoica quattrospina	0.69	Umbilicosphaera sibogae v. sibogae	0.06
Ceratolithus cristatus	0.69	Discosphaera tubifera	0.06
Helicosphaera carteri	0.44	Calciosolenia murravi	0.06
Syracosphaera histrica	0.44	Anoplosolenia brasiliensis	0.06
Syracosphaera sp. I cf. epigrosa	0.32	Gladiolithus flabellatus	0.06
Michaelsarsia elegans	0.31	Anthosphaera periperforata	0.06
Coronosphaera mediterranea	0.31	Calyptrolithina wettsteinii	0.06
Ophiaster hydroideus	0.31	Corisphaera tyrreniense	0.06
Neosphaera coccolithomorpha	0.25	Heterococcolithophore spp.	0.06
Calyptrosphaera sphaeroidea	0.25		

FANS-2: WINTER COCCOLITHOPHORE DISTRIBUTION OFF THE EBRO RIVER MOUTH

During the winter cruise (04 to 14 February 1997), the average sea surface temperature was near 12.7°C. The riverine inflow at this time was high (around 1873 m³/s). Salinity data and total Chlorophyll-a concentrations are presented in Figure 5. 37 (and in Salat *et al.*, submitted).

The high river discharges caused low salinity at stations M01, J03 and M03; the other stations, J07, M07 and N07 and J13 were less influenced by river water. Total Chlorophyll *a* concentrations were high (with an average of 1 μ g l⁻¹ at the surface) and there was no recognizable deep chlorophyll maximum (DCM).

Table 5.4 shows the taxa identified in the Fans-2 samples, with their relative abundances. The concentrations of the main species and groups are presented for each station in Fig.5.38. The coccolithophore community was dominated by *Emiliania huxleyi*. At stations J03, M01 and M03, directly influenced by river input, important concentrations of *Syracosphaera pulchra* were recorded, particularly in the upper layers (maximum of 9 x 10^3 cells/l at station M03 at 5m) in which the lowest salinity waters of riverine influence were found. At the further offshore stations *Syracosphaera molischii* was more abundant than *S. pulchra*. Holococcolithophores were scarce at all stations and depths (they were only registered at stations J03 and N07, with densities lower than 1 x 10^3 cells/l). Total coccolithophore abundances decreased markedly below 40 m depth; this fact could be related to the high amounts of suspended sediment, which exceeded 10 mg/l south of the river mouth, at about 60 m depth (Salat *et al.*, submitted).

Table 5.4. Relative abundance (%) of the identified coccolithophore taxa in the 30 samples of Fans-2 (04 to 14 February 1997). The location of sampled stations is represented in Fig. 2.3

0.27
0.21
0.16
0.16
0.11
0.11
0.11
0.11
0.05
0.05
0.05
0.05
0.05
0.05
0.05
0.05

FANS-3: SUMMER COCCOLITHOPHORE DISTRIBUTIONS OFF THE EBRO RIVER MOUTH

During the summer cruise (13 to 15 July 1997), the average sea surface temperature was higher than 22°C. The riverine inflow at this time was low (around 133 m³/s). Salinity data and Chlorophyll *a* concentrations are presented in Figure 5.39 (and in Salat *et al.*, submitted).

The hydrographic conditions during Fans-3 were typical for the summer in the NW Mediterranean; Chlorophyll *a* concentrations were low at the surface and there was a rather sharp DCM (see Fig. 5.39). Stations K03 and K05 were most influenced by the riverine water.

Table 5.5 shows the taxa found during Fans-3 and their relative abundances. The abundances of the main species and groups at each station are shown in Fig. 5.40. The coccolithophore community was very diverse, and *Emiliania huxleyi* was less abundant than in the other two cruises. There were important concentrations of holococcolithophores (maximum of 31×10^3 cells/l at station M11 at 5m), with *Calyptrolithina wettsteinii* as one

of the abundant species, especially in the uppermost layers (5 x 10^3 cells/l at station M11 at 5m). *Rhabdosphaera clavigera* and *Rhabdosphaera xiphos* were abundant in the offshore samples under minor river influence. The maximum concentration of *R. clavigera* (16 x 10^3 cells/l) was recorded at station K12 at 25 m, and that of *R. xiphos* (5 x 10^3 cells/l) at the same station, K12, at 40 m. Very high coccolithophore abundances were recorded at 60 m depth, coinciding with the DCM. *S. molischii* was present in high quantities at 60 m depth at stations K03 (21 x 10^3 cells/l) and K05 (10 x 10^3 cells/l).

Table 5.5. Relative abundance (%) of the identified coccolithophore taxa in the 30 samples of Fans-3 (13 to 15 July 1997). The location of sampled stations is represented in Fig. 2.3.

Emiliania huxleyi	46.78	Cyrtosphaera lecaliae	0.35
Rhabdosphaera clavigera	12.02	Palusphaera vandelii	0.30
Syracosphaera molischii	4.98	Umbellosphaera tenuis	0.30
Corisphaera spp.	3.77	Alisphaera spp.	0.25
Rhabdosphaera xiphos	2.62	Ophiaster hydroideus	0.25
Calyptrolithina wettsteinii	2.57	Calyptrosphaera cf. heimdaliae (small)	0.25
Homozygosphaera arethusae	2.06	Syracolithus schillerii	0.25
Syracosphaera pulchra	2.01	Zygosphaera hellenica	0.25
Syracolithus confusus	2.01	Gephyrocapsa ericsonii	0.25
Helicosphaera carteri	1.76	Sphaerocalyptra quadridentata	0.20
Syracosphaera halldalii (protr.)	1.36	Helladosphaera cornifera	0.20
Polycrater galapagensis	1.16	Corisphaera tyrreniense	0.20
Syracolithus catilliferus	1.11	Syracosphaera cf. dilatata	0.15
Calyptrosphaera sphaeroidea	0.86	Syracosphaera sp. I cf. epigrosa	0.15
Acanthoica quattrospina	0.80	Syracosphaera marginaporata	0.15
Polycrater spp.	0.75	Gaarderia corolla	0.15
Sphaerocalyptra adenensis	0.70	Palusphaera cf. vandelii (robust)	0.15
Syracosphaera nana	0.65	Calcidiscus leptoporus ph. rigidus	0.15
Calyptrolithophora papillifera	0.65	Syracosphaera tumularis	0.10
Syracosphaera ossa	0.60	Syracosphaera prolongata	0.10
Anthosphaera fragaria	0.60	Anoplosolenia brasiliensis	0.10
Zygosphaera bannockii (HOL)	0.60	Syracosphaera nana (HOL)	0.10
Syracosphaera nodosa	0.55	Helicosphaera carteri v. hyalina	0.05
Calyptrosphaera heimdaliae	0.55	Syracosphaera sp. type L Kleijne	0.05
Syracosphaera bannockii	0.50	Syracosphaera sp. (estrat.)	0.05
Calciosolenia murrayi	0.50	Syracosphaera sp. (small cocc.)	0.05
Papposphaera spp.	0.50	Michaelsarsia elegans	0.05
Syracolithus quadriperforatus	0.50	Algirosphaera robusta	0.05
Syracosphaera histrica	0.40	Florisphaera profunda	0.05
Coronosphaera mediterranea	0.40	Pappomonas spp.	0.05
Sphaerocalyptra spp.	0.40	Calyptrosphaera dentata	0.05
Syracosphaera anthos	0.35	Anthosphaera periperforata	0.05

GENERAL REMARKS ON THE FANS CRUISES

Several clear trends in coccolithophore distribution can be discerned from the Fans cruises, especially if the results of the three cruises are compared.

It is noticeable that in the chlorophyll-rich winter waters, with no DCM, *Emiliania huxleyi* occurred at high relative abundances and holococcolithophores were scarce. By contrast, holococcolithophores were very abundant in the nutrient-poor and well-stratified summer

waters, with a well developed DCM. Large numbers of different types of heterococcolithophores were present in Autumn samples. The presence of *Syracosphaera pulchra* was associated with coastal waters influenced by land runoff and river discharges.

The highest abundances of coccolithophores observed were in the coastal station K03 of the summer cruise at 60 m depth; high densities of *Emiliania huxleyi* at this station (and in the neighbouring K05), together with the presence of high quantities of *Syracosphaera molischii* rather than *Syracosphaera pulchra* suggest the effect of an intrusion of nutrient-rich waters from the shelf break into deeper offshore layers during this summer cruise.

V.4. DISCUSSION OF THE ECOLOGICAL BEHAVIOUR OF SOME SPECIES.

The observations presented above indicate that certain coccolithophore taxa show preferences for particular depth layers and water masses. It can be noted also that the abundance of certain species is strongly related to season.

DEPTH AFFINITIES

Since the study of Lohmann (1902) in Mediterranean waters, the vertical distribution of coccolithophores has been reported for various areas and a classification into three main depth zones following light availability criteria has been proposed: upper photic zone (UPZ), middle photic zone (MPZ) and lower photic zone (LPZ) (Okada & Honjo, 1973; Winter *et al.*, 1994; Jordan & Chamberlain, 1997; Jordan & Winter, 2000). In a study conducted in the Pacific Ocean, Okada & Honjo (1973) recognized an additional layer, the upper-middle photic zone (UMPZ), between the UPZ and the MPZ. In subtropical waters, the boundary UPZ-MPZ has been located at a depth of 80 m and the boundary MPZ-LPZ at a depth of 120 meters (Winter *et al.*, 1994; Jordan & Chamberlain; 1997), but it is recognized that these boundaries depend on latitude (Okada & Honjo, 1973) and on local conditions (Jordan & Winter, 2000).

The present study shows clearly that some species prefer particular water depths; this characteristic might be related to the high stratification of Mediterranean waters in summer. Some of the coccolithophore species analyzed here show narrower vertical preferences than previously described from other areas; it should be noted also that the boundaries between depth zones are all nearer to the surface than those reported in the literature.

According to the studied transects in the Catalano-Balearic Sea, five vertical zones can be tentatively proposed:

1- UPZ. The upper photic zone (0-30 m depth) contains the holococcolithophores Syracolithus catilliferus, Calyptrosphaera heimdaliae, Calyptrosphaera oblonga. Calyptrolithina wettsteinii, Rhabdosphaera clavigera, Rhabdosphaera xiphos and Polycrater spp. inhabit this zone or slightly deeper layers (upper-middle photic zone).

2- U-MPZ. The upper-middle photic zone (between 30 and 40 m depth) shares *Calyptrolithina wettsteinii*, *Rhabdosphaera clavigera*, *Rhabdosphaera xiphos* and *Polycrater* spp. with the UPZ and contains other species which clearly prefer this zone:

Calyptrolithophora papillifera, Homozygosphaera arethusae and Umbellosphaera tenuis; the U-MPZ contains the highest abundances of *Emiliania huxleyi* and *S. pulchra*.

CHAPTER V

3- **MPZ.** The middle photic zone (between 40 and 60 m depth) contains *Syracosphaera molischii*, *Helicosphaera carteri*, *Gephyrocapsa ericsonii*, *Coronosphaera mediterranea* and *Alisphaera spp*. The highest total coccolithophore abundances are found in this zone, at around 50 m depth.

4- U-LPZ. The upper-lower photic zone (between 60 and 80 m depth) contains the species *Ophiaster hydroideus* and *Papposphaera* spp. which show maximum abundances around 70 m depth.

5- LPZ. *Florisphaera profunda* is typical of the lower photic zone, reaching maximum abundances at depths of 80 to 100 m, or occasionally deeper.

The presence of holococcolithophore taxa in the UPZ has been repeatedly reported, but the preferences of some species, such as *Calyptrolithophora papillifera* and *Homozygosphaera arethusae*, for sub-surface layers is reported here for the first time.

The two species of the genus *Rhabdosphaera*, *R. clavigera* and *R. xiphos*, show an affinity for upper water layers, as recognized by Okada & Honjo (1973), in Pacific waters, for *R. clavigera*.

Umbellosphaera tenuis was considered a MPZ species by Okada & Honjo (1974), who recorded highest abundances between 50 m and 100 m; Winter *et al.* (1994) also recorded maximum concentrations of this species in the MPZ in subtropical environments (80 - 120 m depth). In the Mediterranean samples studied here, *U. tenuis* presented maximum densities mainly around 40 m depth, and therefore it has been considered as an U-MPZ inhabitant.

Emiliania huxleyi has been considered as lacking depth preference (Jordan & Chamberlain, 1997) and as an omnipresent species (Hagino *et al.*, 2000); Okada & Honjo (1973) recognized that this species may be found over a very wide range of conditions, but noticed its preference for the upper-middle euphotic layer. Such a preference was reported also by Reid (1980) and has been corroborated in the studied Mediterranean samples. In the present work, *E. huxleyi* type C and especially the overcalcified *E. huxleyi* specimens (see Plate 37, Fig. 6) are usually found in waters deeper than 60m, while type A, which is the most common in the studied samples, prefers the uppermost waters. Comparable observations were made by Hagino *et al.* (2000), who pointed out the preference of type C for deep waters.

Syracosphaera molischii, Helicosphaera carteri, Gephyrocapsa ericsonii, Coronosphaera mediterranea and Alisphaera spp. are here recognized as inhabiting the MPZ. While Coronosphaera was recognized previously as belonging to the MPZ (Jordan & Chamberlain, 1997), Helicosphaera and Alisphaera were considered, in subtropical waters, either as taxa without depth preference (Winter et al., 1994) or with a preference for the UPZ (Jordan & Chamberlain, 1997). S. molischii had not previously been ascribed to any group, but the Syracosphaera genus is reported to inhabit different photic layers (Jordan &

Chamberlain, 1997). *Gephyrocapsa* is considered as lacking depth preference in subtropical waters (Jordan & Chamberlain, 1997); *G. ericsonii* is considered as an omnipresent species in the Equatorial Pacific Ocean (Hagino *et al.*, 2000); but Okada & Honjo (1973) recognized *Gephyrocapsa* sp. A as inhabiting the middle photic layer.

In the studied Mediterranean samples, *Ophiaster hydroideus* and *Papposphaera* spp. were found just above the LPZ, in what is termed here the U-LPZ. *Ophiaster* was considered as an UPZ species in the Equatorial Pacific (Hagino *et al.*, 2000) while it appeared to belong to the MPZ assemblage in subtropical waters (Jordan & Chamberlain, 1997). *Papposphaera* was not included in any of the subtropical photic groups.

Florisphaera profunda, as the name suggests, is considered here and in the literature as a well defined LPZ species (Okada & Honjo, 1973; Winter *et al.*, 1994; Jordan & Chamberlain, 1997; Hagino *et al.*, 2000; Jordan & Winter, 2000); Jordan & Winter (2000) consider the dominance of *F. profunda* as a characteristic of the LPZ, such that the depth distribution of this species signals the depth of the LPZ.

Jordan & Winter (2000) suggest that changes in overlaying upper photic waters may affect the communities below, producing variations in the LPZ position. I agree with this suggestion. In the Mediterranean waters studied here all the described photic zone layers are recognizable, but their depth positions are displaced upwards with respect to those described for subtropical areas.

It is noteworthy that the specimens of the Helicosphaera carteri - Syracolithus catilliferus pairing occupy two different depth layers in the same geographic area: S. catilliferus is found near the surface (in summer samples highest abundances were in the UPZ) while H. carteri occupies deeper waters (in summer samples highest abundances in the MPZ). This relationship can be seen in the same stations (Cruises Fronts-95, Meso-96 and Fronts-96) and even in the poorly preserved samples of Meso-95 Cruise, it was possible to observe that H. carteri was more abundant at 40 m depth than at surface. The preference of relatively deep waters by Helicosphaera carteri has not been recorded before and in the Western-Central Equatorial Pacific Ocean this species has been considered as belonging to the UPZ group (Hagino et al., 2000). The area studied here presents a well developed deep chlorophyll maximum (DCM) between 40 and 70 m depth, during the stratification period (Estrada, 1985, 1991; Margalef & Estrada, 1987). Possibly, the preference of H. carteri for deep waters can be related to the presence of higher nutrient concentrations; in this context, Giraudeau (1992) associated this species to low-salinity nutrient-rich waters and Ziveri et al. (1995) linked H. carteri abundances to high coccolithophore productivity. The affinity of S. catilliferus for the UPZ agrees with the reported affinity of holococcolithophores for the UPZ (Jordan & Winter, 2000 and references therein). As holococcolithophores appear to live mainly in oligotrophic waters (Kleijne, 1993), it can be speculated that this H. carteri / S. catilliferus depth zonation is linked to a life-cycle strategy, with the heterococcolith phase inhabiting relatively rich, deep waters and the holococcolith phase subsisting in poorer but better illuminated layers.

Other well known hetero-holococcolithophore pairings were not present in high enough quantities to corroborate or reject this hypothesis of relationship of depth preferences with a life-cycle strategy. Of the association *Syracosphaera pulchra – Calyptrosphaera oblonga*, only *S. pulchra* was present in relatively high abundances, while of *Coronosphaera mediterranea – Calyptrolithina wettsteinii*, relatively high numbers of the holococcolith phase *C. wettsteinii* were recorded, but few *C. mediterranea*.

WATER MASS AFFINITIES

It is well recognized that coccolithophore assemblages change with latitude; several biogeographic zones have been established in association with latitudinal areas and in relationship with the main ocean surface currents (McIntyre & Bé, 1967; Okada & Honjo, 1973). The Mediterranean Sea is connected to the Atlantic, within the so-called subtropical zone (McIntyre & Bé, 1967; Winter *et al.*, 1994). Studies dealing with particular areas have shown the association of different coccolithophore communities with different water masses and hydrographical features (Samtleben & Schröder, 1992).

Some species appeared to have affinities for the different water masses that were recognized in the studied area. *Emiliania huxleyi* which occurred everywhere, appeared to have the highest abundances in coastal waters. *Gephyrocapsa ericsonii* and more clearly *G*. *muellerae* (see Fig. 5.2) and *G*. *oceanica* tended to be found near the Balearic Islands, within waters of Atlantic origin. These records agree with the observations of Knappertsbusch (1993), who considered *Gephyrocapsa oceanica* as a tracer for Atlantic surface waters in the Mediterranean Sea. In the present study, *Syracosphaera pulchra* appeared to prefer coastal waters, while *Syracosphaera molischii* tended to be associated with higher salinity Mediterranean waters, offshore of the shelf break front. *Rhabdosphaera clavigera* and *Rhabdosphaera xiphos* inhabited the same zones, but *R*. *xiphos* showed a slight preference for more offshore waters.

SEASONAL DISTRIBUTION

Examination of the Fans cruises as well as the Meso-96 and Fronts-96 cruises reveals strong seasonal changes.

Holococcolithophores were very important in early summer (29.6 and 17.5 % of the total cell numbers in Meso-96 and Fans-3, respectively); their abundance decreased through the autumn and ended up being very low in winter (in the cruise Fans-2, in February, they represented only 0.1% of the total coccolithophore abundance). These data are in agreement with Broerse *et al.* (2000) who found the maximum fluxes of holococcolithophore taxa in August, at 48° in the North Atlantic.

Emiliania huxleyi presents a completely opposite trend to that of holococcolithophores. In the Fans cycle, *E. huxleyi* showed a relative abundance of 61.2 % of the total coccolithophores in November and reached 78.6 % in February; in summer its relative abundance was 46.8 %. *E. huxleyi* showed even lower relative abundances in the early summer cruise Meso-96 (31.8%) and the late summer cruise Fronts-96 (45.45%). These
lower abundances might be explained by the overall more oligotrophic conditions outside the influence of river runoff of the Meso and Fronts cruise areas relative to the Fans zone. In accordance with these findings, Reid (1980) noticed the highest abundances of *Emiliania* in winter samples from the North Pacific Central Gyre, at 28°N, and Winter *et al.* (1979) found the lowest abundances in August in the Gulf of Elat. Sediment trap data from the North Atlantic at 29°N (Sprengel *et al.*, 2000) and 34°N (Broerse *et al.*, 2000) reported the highest *E. huxleyi* fluxes from January to March, while at 48°N they occurred later in April (Broerse *et al.*, 2000; Ziveri *et al.*, 2000). Blooms of *Emiliania* are regularly observed during early summer in the northern North Atlantic near Iceland (Holligan *et al.*, 1983, 1993; Simó & Pedrós, 2000). The time delay in the development of phytoplankton proliferations at higher latitudes is well known (Margalef, 1945) and explains the difference in the time of development of *Emiliania* to looms around 60° in the North Atlantic (early summer) and that of proliferations at lower latitudes (around February).

Rhabdosphaera clavigera and *Rhabdosphaera xiphos* show marked variations in abundance at different times of the year; they tend to show higher concentrations in summer and only *R. clavigera* appears to be relatively important in autumn. Neither *R. clavigera* nor *R. xiphos* occur in significant numbers in winter (they showed respectively values of 0.05 and 0.27 % in February). Winter *et al.* (1979) found the highest abundances of *Rhabdosphaera* in August, in the Gulf of Elat.

The genus *Polycrater* showed a clear affinity for summer conditions; it reached 1.5 % (Meso-95) and 1.9 % (Fans-3) of the total abundance in early and mid summer, 0.44 % (Fronts-96) in late summer, and 0.94 % (Fans-1) in autumn; there were no registered presences in winter.

EMILIANIA HUXLEYI

Emiliania huxleyi, the most ubiquitous coccolithophore in today's ocean (McIntyre & Bé, 1967; Winter, 1982), was the most abundant species found in the present study. *E. huxleyi* is considered as a typical coccolithophore of the first stages of the planktonic succession. The winter cruise Fans-2, with relatively low coccolithophore diversity (see Table 5.4), had the highest relative abundance of *E. huxleyi* (78.58 %); both characteristics, low diversity and high number of the dominant species, are typical of the first stages of succession (Margalef, 1974). The directly river-influenced area of Fans cruises presented a high proportion of *E. huxleyi*. In offshore and stratified conditions, *E. huxleyi* grows well in the upper-middle photic zone (U-MPZ), near the richer waters of the deep chlorophyll maximum (DCM). All these preferences corroborate the *r*- ecological strategy of *Emiliania* which is reflected in the literature (Margalef, 1974, 1978; Young, 1994, and references herein).

The most abundant morphotype of *E. huxleyi* in these NW Mediterranean waters was the type A which tended to inhabit the most superficial waters; type C and the overcalcified type tended to live in deeper layers.

HOLOCOCCOLITHOPHORES

Holococcolithophores tend to appear in early summer and grow in the nutrient-poor and well illuminated surface waters of the stratified summer conditions. Moreover holococcolithophore abundances are not directly related with temperature, as can be inferred from their distributions; lower abundances of holococcolithophores were recorded during cruise Fronts-96 relative to Meso-96, despite similar water temperatures. The relative abundances of holococcolithophores is strongly related to high overall diversity of species; holococcolithophores were abundant in the samples which also contained a large number of hetereococcolithophore species (see Tables 1-5).

The different depth preferences of the heterococcolithophore *Helicosphaera carteri* and its related holococcolithophore, the former *Syracolithus catilliferus*, might illustrate an ecological survival strategy. The liklehood that holococcolithophores are haploid stages and heterococcolithophores diploid, suggested by Billard (1994), supports such an hypothesis; the haploid stages appear to need less nutrients than the diploid stages (Lewis, 1985) and an haplo-diploid cycle is considered as an adaptation to an environment that is seasonally variable or that contains two different ecological niches (Valero *et al.*, 1992). For these reasons, the haploid stage in the life cycle of coccolithophores could be an adaptation to colonize nutrient-poor surface waters during the stratification period.



Fig. 5.1. Horizontal distribution of temperature, in °C, (A) and salinity (B) during the Cruise Meso-95 at 5m depth. (From Salat, unpublished).



Fig. 5.2.- Abundances of selected coccolithophores during Meso-95 cruise (30 May to 16 June 1995).
A: *Emiliania huxleyi* distribution at surface; B: *E. huxleyi* distribution at 40 m depth;
C: *Gephyrocapsa ericsonii* distribution at surface; D: *G. ericsonii* distribution at 40 m depth;
E: *G. mullerae* distribution at surface; F: *G. mullerae* distribution at 40 m depth.





Fig. 5.3.- Abundances of selected coccolithophores during Meso-95 cruise (30 May to 16 June 1995).
A: *Helicosphaera carteri* distribution at surface; B: *H. carteri* distribution at 40 m depth; C: *Syracosphaera pulchra* distribution at surface; D: *S. pulchra* distribution at 40 m depth; E: *S. molischii* distribution at surface; F: *S. molischii* distribution at 40 m depth.
Legend:

 $\square <100 \text{ cells } l^{-1} \square 100 - 1,000 \text{ cells } l^{-1} \square >1,000 \text{ cells } l^{-1}$



Fig. 5.4. Distribution (in cells l^{-1}) of total coccolithophores, total holococcolithophores, *Emiliania huxleyi*, *Gephyrocapsa ericsonii* and *Syracosphaera molischii* along the northern (left) and southern (right) transects of the Fronts-95 cruise (17 - 23 June 1995). See Fig. 2.1 for the situation of the stations.



Fig. 5.5. Distribution (in cells l^{-1}) of *Helicosphaera carteri*, *Syracolithus catilliferus*, *Coronosphaera mediterranea* and *Calyptrolithina wettsteinii* along the northern (left) and southern (right) transects of the Fronts-95 cruise (17 - 23 June 1995). See Figs. 2.1 for the situation of the stations.



Fig. 5.6. Distribution (in cells 1^{-1}) of *Syracosphaera pulchra*, *Calyptrosphaera oblonga*, *Alisphaera* spp., *Polycrater* spp. and *Umbellosphaera tenuis* in the northern (left) and southern (right) transects of the Fronts-95 cruise (17 - 23 June 1995). See Fig. 2.1 for the situation of the stations.



Fig. 5.7. Distribution (in cells 1^{-1}) of *Rhabdosphaera clavigera*, *Rhabdosphaera xiphos*, *Ophiaster hydroideus*, *Papposphaera* spp. and *Florisphaera profunda* along the northern (left) and southern (right) transects of the Fronts-95 cruise (17 - 23 June 1995). See Fig. 2.1 for the situation of the stations.



Fig. 5.8. Distribution (in cells l^{-1}) of *Calyptrosphaera heimdaliae, Sphaerocalyptra* spp., *Calyptrolithophora papillifera* and *Homozygosphaera arethusae* along the northern (left) and southern (right) transects of the Fronts-95 cruise (17 - 23 June 1995). See Figs. 2.1 for the situation of the stations.



Fig. 5. 9. Hydrographic data of Meso-96 cruise (18 June - 3 July 1996). A, B, C and D represent temperatures (°C) at 5, 40,70 and 100 m depth respectively. E, F, G and H represent the salinity at 5, 40, 70 and 100 m depth respectively. In A there are figured the sampled stations.



Fig.5.10. Distribution of temperature in …C (A) and distribution of salinity (B), along the transect visited during Fronts-96 cruise. The numbers on top of the upper axis indicate the stations.



Fig. 5.11. Distribution (cells I^{-1}) of total coccolithophores (left) and holococcolithophores (right) along the transects A, D, G and I of the Meso-96 cruise (18 June - 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.12. Distribution (in cells l^{-1}) of total coccolithophores (left) and holococcolithophores (right) along the main transect of Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for situation of stations and hydrographic data respectively.



Fig. 5.13. Distribution (in cells l^{-1}) of *Emiliania huxleyi* (left) and *Gephyrocapsa ericsonii* (right) along the transects A, D, G and I of the Meso-96 cruise (18 June - 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.14. Distribution (in cells l^{-1}) of *Emiliania huxleyi* (left) and *Gephyrocapsa ericsonii* (right) along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5.15. Distribution (in cells l⁻¹) of *Helicosphaera carteri* (left) and *Syracolithus catilliferus* (right) along the transects A, D, G and I of the Meso-96 cruise (18 June- 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.16. Distribution (in cells l⁻¹) of *Helicosphaera carteri* (left) and *Syracolithus catilliferus* (right) along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5.17. Distribution (in cells l^{-1}) of *Coronosphaera mediterranea* (left) and *Calyptrolithina wettsteinii* (right) along the transects A and I, and *C. wettsteinii* (right) along the transect D and G of the Meso-96 cruise (18 June- 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.18. Distribution (in cells l^{-1}) of *Coronosphaera mediterranea* (left) and *Calyptrolithina wettsteinii* (right) along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5.19. Distribution (in cells 1⁻¹) of *Syracosphaera pulchra* (left) and *Calyptrosphaera oblonga* (right) along the transects A, D and I, and *S. pulchra* (left) along the transect G of the Meso-96 cruise (18 June - 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Distance from the coast (Km) Fig. 5.20. Distribution (in cells l⁻¹) of *Syracosphaera pulchra* (left) along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5.21. Distribution (in cells 1⁻¹) of *Rhabdosphaera clavigera* (left) and *Rhabdosphaera xiphos* (right) along the transects A, D, G and I of the Meso-96 cruise (18 June - 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.22. Distribution (in cells 1^{-1}) of *Rhabdosphaera clavigera* (left) and *Rhabdosphaera xiphos* (right) along the main transect of the Fronts-96 cruise (16 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5.23. Distribution (in cells l^{-1}) of *Alisphaera* (left) and *Polycrater* (right) along the transects A, D and G and *Polycrater* (right) along transect I of the Meso-96 cruise (18 June - 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.24. Distribution (in cells l^{-1}) of *Polycrater* along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5.25. Distribution (in cells l^{-1}) of *Calyptrosphaera heimdaliae* (left) and *Sphaerocalyptra* spp. (right) along the transects A, D, G and I of the Meso-96 cruise (18 June- 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.26. Distribution (in cells l^{-1}) of *Calyptrosphaera heimdaliae* (left) and *Sphaerocalyptra* spp. (right) along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for situation of the stations and hydrographic data respectively.



Fig. 5.27. Distribution (cells l^{-1}) of *Calyptrolithophora papillifera* (left) and *Homozygosphaera arethusae* (right) along the transects A, D, G and I of the Meso-96 cruise (18 June - 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.28. Distribution (cells Γ^1) of *Calyptrolithophora papillifera* (left) and *Homozygosphaera arethusae* (right) along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5.29. Distribution (in cells l^{-1}) of *Syracosphaera molischii* (left) and *Umbellosphaera tenuis* (right) along the transects A, D, G and I of the Meso-96 cruise (18 June - 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.30. Distribution (in cells l^{-1}) of *Syracosphaera molischii* (left) and *Umbellosphaera tenuis* (right) along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5.31. Distribution (in cells l^{-1}) of *Ophiaster hydroideus* (left) and *Papposphaera* spp. (right) along the transects A, D, G and I of the Meso-96 cruise (18 June - 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.32. Distribution (in cells l^{-1}) of *Ophiaster hydroideus* (left) and *Papposphaera* spp. (right) along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5.33. Distribution (in cells l⁻¹) of *Florisphaera profunda* along the transects D and I of the Meso-96 cruise (18 June - 3 July 1996). See Figs. 2.2 and 5.9 for the situation of the stations and hydrographic data respectively.



Fig. 5.34. Distribution (in cells l^{-1}) of *Florisphaera profunda* along the main transect of the Fronts-96 cruise (16 - 21 September 1996). See Figs. 2.2 and 5.10 for the situation of the stations and hydrographic data respectively.



Fig. 5. 35 Salinity at 5 m depth and chlorophyll during Fans-1 Cruise (1-10 Nov. 96)



Fig. 5. 36. Abundances of several coccolithophore species and groups at the five stations sampled during Fans-1 cruise (01-08 November 1996). The stations are ordered from the coast to the open sea. See Figs. 2.3 for the situation of the stations and 5.35 for salinity and chlorophyll data.



Fig. 5. 37 Salinity at 5 m and Chlorophyll during Fans-2 Cruise (4-14 Feb. 97)



Fig. 5. 38. Abundances of several coccolithophore species and groups at the seven stations sampled during Fans-2 cruise (04-14 February 1997). The stations are ordered from the coast to the open sea. See Fig. 2.3 for the situation of the stations and 5.37 for salinity and chlorophyll data.



Fig. 5. 39 Salinity at 5 m depth and Chlorophyll during Fans-3 Cruise (13-15 Jul. 97)



Fig. 5. 40. Abundances of several coccolithophore species and groups at the five stations sampled during Fans-3 cruise (13-15 July 1997). The stations are ordered from the coast to the open sea. See Fig. 2.3 for the situation of the stations and 5.39 for salinity and chlorophyll data. N.B. The graphic of 60 m is a different scale of the others, to can represent nicely the high values of the station KO3.

VI. CALCAREOUS NANNOPLANKTON IN SURFACE SEDIMENTS

VI.1. REMAINS OF SEDIMENT FORMING ORGANISMS

The sediment samples studied were rich in remains of biological origin, mainly the hard parts of phytoplankton, and in particular the calcium carbonate producing groups (see Plates 90 and 91). Sample 1 was an exception, being poor in material of organic origin.

The remains of calcareous nannoplankton were present in all sediments studied, mostly as isolated coccoliths but exceptionally as whole coccospheres (e.g. *Emiliania*, *Gephyrocapsa*, *Calcidiscus* and *Umbilicosphaera*; Plate 91 shows a coccosphere of *Emiliania huxleyi* from sample 15). Other phytoplankton remains consisted mainly of calcareous thecae of Dinophyceae (especially of *Thoracosphaera* spp.). Diatom frustules were notably scarce and appeared corroded.

Although the methodology used was designed for the study of nannoplankton and should underrepresent zooplankton remains, some well-preserved calcareous shells of foraminifera were found; by contrast, siliceous remains from radiolaria were scarce and corroded.

VI.2. CALCAREOUS NANNOPLANKTON

The most common species of coccolith found in the sediments was *Emiliania huxleyi*, followed by *Gephyrocapsa muellerae* and then *G. oceanica*, *Calcidiscus leptoporus*, *Syracosphaera pulchra*, other *Syracosphaera* spp., *Florisphaera profunda*, *Helicosphaera carteri*, *Umbellosphaera tenuis*, *Rhabdosphaera clavigera*, *Gladiolithus flabellatus* and *Discosphaera tubifera*.

E. huxleyi contributed from 68.2 to 80.7% of the coccoliths observed, except in sample 1 where this species accounted for 62.1%. The contribution of *Gephyrocapsa* ranged from 8.2 to 20.4%. In general, *Gephyrocapsa* values increased when *Emiliania* decreased except at certain stations, such as sample 1, where both were poorly represented.

Most of the sediments contained significant amounts of calcareous nannoplankton remains, although sample 1 had a high proportion of terrigenous components with only a few coccoliths which showed signs of damage, especially those of *Emiliania*.

Overall, the relative abundance of *Emiliania* (see Fig. 6.1, A) tended to decrease from the Iberian margin to the Balearic Islands (i.e. from the west to the east), although some exceptions were found, like station 16 and particularly station 1, which had the lowest percentage of *Emiliania* (62,1%). Following an opposite trend, *Gephyrocapsa* relative abundance increased from the Iberian margin to the Balearic Islands (see Fig. 6.1, B).

The other genera found were present at much lower concentrations and showed variable distribution patterns. *Umbilicosphaera*, for example, consisted between 0.0 and 1.9% of coccoliths, with higher values in the centre towards the northeast with a maximum in sample 17 (see Fig. 6.2, A). *Rhabdosphaera* ranged from 0.0 to 2.3% of coccoliths, the lower values near the Iberian margin, with an apparent absence in sample 1; the largest area with the higher percentages of this species was just to the north of Mallorca (see Fig. 6.2, B). *Calcidiscus* showed a general tendency for higher values towards the northeast (see Fig. 6.3, A) although its highest value of 5.6% occurred in sample 1; the other samples ranged from 0.0 to 3.0%. In general, *Helicosphaera* had higher values in the centre towards the north, but showed a maximum of 11.3% in sample 1 (see Fig. 6.3, B); in the other samples the contribution of this species ranged from 0.2 to 3.7%.



Fig. 6.1.- Distribution of coccoliths in surficial sediments. (A) Relative frequency of *Emiliania huxleyi*; (B) Relative frequency of the genus *Gephyrocapsa*.





Fig. 6.2.- Distribution of coccoliths in surficial sediments. (A) Relative frequency of the genus *Umbilicosphaera*; (B) Relative frequency of the genus *Rhabdosphaera*.





Fig. 6.3.- Distribution of coccoliths in surficial sediments. (A) Relative frequency of the genus *Calcidiscus*; (B) Relative frequency of the genus *Helicosphaera*.

VI.2. DISCUSSION

GENERAL TRENDS OF CALCAREOUS NANNOPLANKTON DISTRIBUTION

The distribution of calcareous nannoplankton in the sediments of the Catalano-Balearic Sea showed, in general, a pattern with bands of abundance roughly parallel to the shore.

Emiliania huxleyi is the most abundant species in this area. Its relative abundance decreases by about 10% from the west to the east, while *Gephyrocapsa*, the second most abundant genus, has the opposite trend (i.e. increases by about 10% from the west to the east). *Gephyrocapsa* abundance appears to be related to the stratified and warmer water masses of Atlantic origin, an observation in accordance with that of Knappertsbusch (1993b) who reported *Gephyrocapsa oceanica* as a tracer for Atlantic surface waters in the Mediterranean Sea.

Rhabdosphaera distribution was also related to the warmer water masses of Atlantic origin. Umbilicosphaera shows a distribution pattern with low values near the margins of the Iberian Peninsula and Balearic Islands, and a clear increase at the centre and the northeast of the basin; the coincidence of its distribution in the Catalan Sea with the dome-like structure in the middle of the basin (Margalef, 1985b; Estrada, 1985; Estrada & Margalef, 1988) is in agreement with the preference of Umbilicosphaera for salty and relatively nutrient-rich waters (Roth, 1994). Helicosphaera distribution has an increasing trend towards the northern centre of the basin with low values near the margins; sample 1, near the Iberian Peninsula and under direct influence of runoff from the Ebro river, is an exception. Sample 1 also shows the highest Calcidiscus content; coccoliths of both Calcidiscus and Helicosphaera are considered highly solution-resistant (Shneidermann, 1977) and are among the more robust species preferentially preserved under dissolution and reworking conditions (Findlay, 1998). Geological research in this area (Alonso et al., 1991) revealed a slope with sedimentary instability promoting reworking and carriage of sediments from the shelf. These environmental circumstances may favour, and can explain, the high proportion of these highly solution-resistant coccoliths in this area.

LACK OF SILICEOUS REMAINS

The sediments of the Catalano-Balearic Sea are noteworthy for the high proportion of calcium carbonate and the scarcity of siliceous remains. Most of the siliceous skeletal remains found were corroded, suggesting that biogenic opal is easily dissolved in this area. Emelianov & Shimkus (1986) reported that the accumulation rates of amorphous silica in Mediterranean sediments are 50 - 100 times less than those of CaCO₃.

There are, however, exceptions to this general pattern. In recent sediments collected in spring from a canyon floor (NW Mediterranean), coincident with a period of high planktonic production in the overlaying waters and likely fast sedimentation, an unusual presence of siliceous remains inside a brownish biodeposit which also contained intact coccospheres was observed (Rioux-Gobin *et al.*, 1995). These observations do not contradict the general trends of the scarcity of biogenic opal (Emelyanov and Shimkus, 1986; Cros, 1995). It is known that a rapid transportation of material can maintain intact coccospheres (Andruleit, 1997, 2000; Broerse, 2000; Broerse *et al.* 2000) and that fast sedimentation may prevent silica dissolution. It is reasonable to accept that the silicate concentration must be high in the interstitial water of these spring diatom-rich sediments, and consequently that opal remains would not be subject to high dissolution rates.

Except for these highly productive spots, with associated fast sedimentation processes, in general the high temperatures and relatively high pH of Mediterranean deep water must tend to promote the rapid dissolution of siliceous skeletons (Emelyanov and Shimkus,

1986), but not the calcareous remains. In the sedimentary register, coccoliths seems to be better preserved in warmer than in colder periods (Vazquez et al, 1991, Vazquez & Zamarreño, 1993 and references therein; Lototskaya, 1999). The peculiar hydrochemical conditions of the Mediterranean, with a high super-saturation of waters with respect to calcite (Emelyanov and Shimkus, 1986), may also control the preservation of the carbonate remains.

SCARCITY OF THE LOW SOLUTION-RESISTANT COCCOLITHS

Very few holococcoliths have been found in these sediment samples in clear contrast to the abundance of heterococcoliths. This observation is in agreement with previous reports of the scarcity of holococcoliths in surface (Bartolini, 1970; Knappertsbusch, 1993; Riaux-Gobin *et al.*, 1995) and deep (last 100k years) sediments of the Western Mediterranean (Flores *et al.*, 1997). The fact that holococcoliths are present and common in water column samples (see Chapter V) indicates that the scarcity of this kind of coccoliths in the sediments must be the result of their recognized low preservation potential (Tappan, 1980; Samtleben & Schröder, 1992; Riaux-Gobin *et al.*, 1995).

Such differences in preservation characteristics can also be found at the species level. For example, the genus *Gephyrocapsa* is mainly represented in sediments by *G. muellerae* and *G. oceanica*, which are rare in the water column; in contrast *G. ericsonii*, the most common *Gephyrocapsa* species in the water column, is scarcely represented in the sediments.

Previous reports on the dissolution of delicate species can be found in the literature (Samtleben & Schröder, 1992; Ziveri *et al.*, 2000; Broerse *et al.*, 2000). Ziveri *et al.* (2000) reported that the relative abundance of the delicate coccoliths of *Oolithotus fragilis* decreased from 3% of total coccoliths at 1 Km depth, to less than 0.5 % at 3.7 Km depth in the Northeastern Atlantic. By contrast, the same authors noted that the group of solution-resistant species *Emiliania huxleyi*, *Gephyrocapsa muellerae*, *Calcidiscus leptoporus* and *Coccolithus pelagicus*, increased their relative abundance from 65% at 1 Km depth to 95% at 3.7 Km depth. Ziveri *et al.* (2000) also reported that selective dissolution continues in the sediments, therefore increasing the relative frequencies of the solution resistant species (*C. leptoporus* can increase from 10-15% in trap samples to 15–40% in sediments).

COCCOLITHUS PELAGICUS

The presence of *Coccolithus pelagicus* in the Mediterranean Sea is well documented in the Pleistocene sediments of the area (Matias, 1990) and in the Pliocene to Holocene sediments near the Balearic Islands (Vazquez, 1988; Flores et al., 1997). However, only one coccolith was found in the sediment samples of the present study; similarly, Riaux-Gobin (1995) reported the presence of C. pelagicus in recent sediments of the Gulf of Lions as occasional. In fact, in our samples, which corresponded mainly to the period of summer stratification, no record of this species was made from the water column. This discordance between the presence in the sediment record reported in the quoted literature and their absence in our water column samples might be explained if this species would occur in infrequent bursts of production (see Cachao & Moita, 2000, and references therein) or if it prefers low temperatures as it is explained in Vazquez (1988) and references therein or only in cold waters of high productivity as is pointed out in Mateu (1986). The fact that the massive coccoliths of C. pelagicus are highly resistant to dissolution and the coccospheres of this species are particularly resistant (Samtleben & Schröder, 1992) would help to explain their presence in older sediments. The absence of C. pelagicus in the studied water column samples might suggest a decrease in the abundance of this species in present day
NW Mediterranean waters. Further evidence with studies of winter samples is required to support this hypothesis.

COCCOLITH REGISTER VERSUS COCCOLITHOPHORE PRODUCTION

The nannoplankton content in the sediments reflects the coccolithophore community of the overlaying waters, but in a biased way, with overrepresentation of the highly resistant and underrepresentation of the less resistant species. From this study it appears clear, considering the differences in nannoplankton composition in water column and sediment samples, that differences in dissolution rate play a key role in the structure of nannoplankton assemblages in sediments.

Nevertheless, the main trends in the composition of nannoplankton communities in overlaying waters are, in general, accurately reflected in the sediments, as was the case in the study of Samtleben & Schröder (1992). Since the distribution of different nannoplankton species is determined to a large extent by water mass characteristics, relative abundance of coccoliths in sediments provides a proxy for the horizontal distribution of different water masses. The facts that calcium carbonate preservation is good in the Mediterranean Sea, and that the sediments constitute an integrated record of water column production over seasonal cycles mean the study of the coccolith sedimentary record in this area offers a valuable tool for tracking the horizontal variability and understanding the behaviour of different water masses through time.

VII. COCCOLITH CHEMISTRY

BACKGROUND

The chemical environment of the Mediterranean Sea is suitable for the preservation of calcium carbonate remains. Mediterranean sediments contain, therefore, a high quantity of coccoliths (Bartolini, 1970; Emelyanov & Shimkus, 1986; Mateu, 1985; Müller, 1985; Vazquez & Zamarreño, 1993; Cros, 1995, see also chapter VI).

The biological calcareous particles introduce elements, mainly carbon and calcium, at deep waters by dissolution of sinking particles (Lal, 1977). But when coccoliths enter the sediments, the chemical elements that they contain are removed from active geobiochemical cycles (Westbroek et al., 1994). It is thus useful to know the elemental composition of the coccoliths in order to evaluate losses to geobiochemical cycles due to these algae.

Only few chemical studies have been undertaken on coccoliths. The main difficulty has been the extremely small size of the coccoliths, which consist mainly of low magnesium (<4% Mg) calcite (Siesser, 1977; Siesser & Winter, 1994). It has been demonstrated that growth conditions can explain large differences in the molar proportions of Ca:C in *Emiliania huxleyi* coccoliths (Fagerbakke *et al.*, 1994), and that the Sr/Ca ratio can be related to growth conditions and calcification, providing a potential tool for the prediction of past changes in productivity (Stoll *et al.*, 2000). Other factors, such as the presence of an acidic polysaccharide, can also play a regulatory role in the biomineralization process of the cell (Westbroek *et al.*, 1989).

ELEMENTAL COMPOSITION

The present study attempts to evaluate the elemental composition of very different groups of coccolithophores by analyzing specimens of different coccolithophore species, and comparing them to other phytoplankton groups which present hard skeletons (i.e., the diatom *Thalasionema* sp. and the dinoflagellate *Prorocentrum balticum*).

The analyzed specimens came from station 147 of the MESO-95 cruise, a sample which contained a high quantity of coccoliths. The X-ray microanalysis technique employed provides a qualitative overview of the elements with atomic weight higher than 23 (sodium).

The coccoliths consist of calcium carbonate. With the microanalyzer employed, high quantities of calcium, when present, can give rise to secondary false phosphorus (P) signals; such false peaks were corrected by adjusting the software controlling the microanalyzer.

Blank filters showed little response to the X-ray microanalysis (Fig. 7.1, A). Figures 7.1 B and C show the analyses corresponding to the diatom and the dinoflagellate, respectively. While the diatom presented a high signal of Si and small peaks of S, Ca and Fe (Fig. 7.1, B), the dinoflagellate gave clear signals of Cl, Si and Ca and traces of Al, Mg, K and Cu (Fig. 7.1, C).

The analysis of coccolithophores indicated a high proportion of Ca and minor signals mainly of Si, S and Cl (see Figs. 7.2 and 7.3). Most species gave signals of Al and several presented signals of Ag. Repeated signals of P and Mg were also identified.

The comparison of the elemental composition of the different phytoplankton groups studied shows the expected presence of large signals of Ca in coccolithophores and of Si in diatoms. Moreover, a clear presence of S is noticeable in the coccolithophores, especially in the holococcolithophores; this element is less abundant in the diatom and particularly in the dinoflagellate. The presence of S might be related to the production of DMS, an important molecule in the sulphur cycle.

The presence of the elements Al and Ag should be considered with caution, because the EM stubs used were of Al, and colloidal Ag was used to mount the filters on the stubs. The P signals were particularly strong in *E. huxleyi* and *Calyptrosphaera heimdaliae* specimens (Fig. 7.2, D and 7.3, H respectively), but due to the technical problems with these signals (see the above remarks) we consider that such signals should also be considered cautiously.

The Mg signal is imperceptible in heterococcolithophore specimens of *E. huxleyi* (Fig. 7.2, D), *Syracosphaera pulchra* (Fig. 7.2, E) and *Rhabdosphaera clavigera*, (Fig. 7.2, F), but this element was obviously present in holococcolithophore specimens of *Calyptrolithina wettsteinii* (Fig. 7.3, G), *Calyptrosphaera heimdaliae* (Fig. 7.3, H) and *Helladosphaera cornifera* (Fig. 7.3, I). These results suggest the presence of Mg cations inside the carbonate reticules of the holococcolithophores.

DISCUSSION

Siesser (1977), using an electron microprobe to analyze individual coccoliths, did not find detectable amounts of magnesium in the calcite. In our study we have observed the presence of Mg signals in holococcoliths, but not in heterococcoliths. As the coccoliths studied in Siesser (1977) were mainly *Coccolithus pelagicus* and *Reticulofenestra* in sediment samples, the probable lack of holococcoliths may explain the absence of Mg signals in this study.

Previous studies on the chemical composition of *E. huxleyi* coccoliths, focussed especially on Ca:C relationships (Fagerbakke *et al.*, 1994), reported the presence of signals of Na, Mg, S and Cl. However, the correlation of such elements compared with C, O and Ca suggested to these authors that very likely these elements came from seawater contamination. It is not clear if the high Mg content of holococcoliths observed in our study is real or the result of contamination (which may be supposed to be accentuated in holococcoliths due to the high surface area / volume ratio of their structure). If the presence of Mg is confirmed, it may explain the low preservation potential of holococcolithophores since high magnesium calcite is the least stable carbonate mineral and is considered highly fragile (Siesser, 1971). Further studies using finer techniques with emphasis on minimizing contamination are necessary to confirm these preliminary results.



Fig. 7.1. X-ray diagrams: A. a blank; B. a diatom, *Thalassionema;* C. a dinoflagellate, *Prorocentrum.* The capture analysis time was of 100 s.



 Fig. 7.2. X-ray diagrams of Heterococcolithophores: D. Emiliania huxleyi,
 E. Syracosphaera pulchra; F. Rhabdosphaera clavigera. The capture analysis time was of 100 s.



 Fig. 7.3. X-ray diagrams of Holococcolithophores: G. Calyptrolithina wettsteinii;
 H. Calyptrosphaera heimdaliae; I. Helladosphaera cornifera. The capture analysis time was of 100 s.

Although the results obtained are very promising, they can be considered only as preliminary due to the limitations of the technique used, particularly since it was not possible to accurately quantify the elemental composition. Problems with the analysis of P in the presence of abundant calcium were mentioned above. It appears, however, that P may well be present in coccoliths; Siesser (1977) also detected this element and was quite confident with his analysis. This issue is critical in the Mediterranean, where P is a key limiting nutrient (Margalef, 1985a), and it is thus very important to know the role of these organisms in the biogeochemical cycle of P, both in the water column and in the sediments. Further evidence of the potential involvement of coccolithophores in the P cycle comes from the reports of relatively high growth rates of *E. huxleyi* in P-depleted environments (Egge & Heimdal, 1994; Heimdal *et al.*, 1994), and its competitive success for phosphate (Riegmann *et al.*, 2000). Since *E. huxleyi* is the most abundant coccolithophore in the NW Mediterranean, the relevance, for ecological purposes, of the accurate quantification of the P content in this species becomes evident.

CONCLUSIONS

1.- In order to study coccolithophores, it is necessary to ensure that no dissolution of coccoliths occurs through any of the methodological steps. Fixing the samples or even rinsing them with distilled water can dissolve coccoliths and produce unsatisfactory results. Processing the samples with or without fixation (even with neutralized fixatives) produces the preservation of very different components of coccolithophore communities. Losses of 39 to 69 % of the coccolithophores occurred in the fixed samples; these percentages reached 75 % and even up to 100 % when holococcolithophores were considered.

2.- The present study describes and figures 166 coccolithophores (including different taxonomic and morphotype entities); among these, only 102 had well established Linnean names, while 40 have been figured or described here for the first time. The description of 20 additional forms has been improved.

3.- The taxonomy of the complex genus *Syracosphaera* has been clarified as far as possible. Some species have been redescribed (e.g. *S. nana*, *S. tumularis*). A new species, *Syracosphaera delicata* sp. nov., has been identified. The exothecal coccoliths of 11 taxa have been recognized for the first time: *Syracosphaera* sp. I cf. *S. epigrosa* (Kleijne, 1993), *S. marginaporata*, *S.* sp. II cf. *S. epigrosa* (Kleijne, 1993), *S. tumularis*, S. sp. (aff. *S. orbiculus*, ovoid; this work), S. sp. (aff. *S. orbiculus*, spherical; this work), S. sp. (aff. *S. nana*, very small; this work), *S. cf. dilatata*, *S.* sp. type D (Kleijne, 1993), *S. noroitica* and *S.* sp. type G (Kleijne, 1993).

4.- It has been found that the family *Papposphaeraceae*, formerly associated with cold waters, is present in the Mediterranean with several possible new species and even a possible new genus.

5.- Seven heterococcolithophore – holococcolithophore combinations have been established with a high degree of confidence and seven additional possible associations have been identified. The well established associations are: *Helicosphaera carteri* with *Syracolithus catilliferus*, *Syracosphaera pulchra* with *Calyptrosphaera oblonga*, *Syracosphaera anthos* with *Periphyllophora mirabilis*, *Coronosphaera mediterranea* with *Calyptrolithina wettsteinii*, *Syracosphaera nana* with holococcoliths, *Acanthoica quattrospina* with *Holococcolithophore sp.* and *Syracosphaera* sp. *aff.* type K of Kleijne with *Corisphaera* sp. type A of Kleijne (now *Syracosphaera bannockii* comb. nov.).

Two holococcolithophores involved in these combinations have also been found forming associations with other holococcolithophore forms: *Syracolithus catilliferus* with *Syracolithus confusus* and *Corisphaera* sp. type A of Kleijne with *Zygosphaera bannockii*. In both cases, the two holococcolith types differ essentially in the presence / absence of pores.

Two new associations of nannolith-bearing coccolithophores with heterococcolithophores have been found: *Polycrater* spp. with *Alisphaera* spp. and *Polycrater* galapagensis var A (with dots) with *Canistrolithus* sp. 1.

6.- In the summer oligotrophic waters of the NW Mediterranean, *Helicosphaera carteri*, the heterococcolithophore phase of the well established combination with *Syracolithus catilliferus*, tends to occupy the mid-depths of the photic zone, whilst *Syracolithus catilliferus* inhabits the nutrient-poor surface waters of the same stations; such relative distribution might be indicative of an ecological life-cycle strategy.

7.- The spatial and seasonal variations of the coccolithophore community have been described for different areas of the Catalano-Balearic Sea. Several taxa present a marked vertical stratification during the summer period.

8.- X-ray microanalysis of the elemental composition of the coccoliths suggests a higher content of magnesium in the holococcoliths than in the heterococcoliths.

9.- The surface sediments of the Catalano-Balearic Sea contain a high proportion of calcium carbonate relative to siliceous remains. Most of the scarce siliceous skeletal remains were corroded, suggesting that biogenic opal is easily dissolved in this area.

10.- The coccolithophore remains found in the sediments show a pattern of species distribution with well marked bands, more or less parallel to the coast, reflecting the distribution of the different water masses in the area.

11.- The calcareous nannoplankton community found in the sediments reflects the coccolithophore community of the overlying waters, but with over-representation of some species with highly resistant coccoliths and under-representation of the species with poorly resistant coccoliths. Dissolution appears to be an important agent controlling nannoplankton conservation in the sediments.

REFERENCES

- Alcober, J. and Jordan, R.W., 1997. An interesting association between *Neosphaera* coccolithomorpha and Ceratolithus cristatus (Haptophyta). Eur. J. Phycol. 32: 91-93.
- Alonso, B., Palanques, A., Canals, M. and Rehault, J.P., 1991. The Valencia Valley: Origin and Evolution of a "Mid-Ocean Channel" Sea Valley type in the Northwestern Mediterranean. In: 3ème Congrès Français de Sédimentologie. Brest (Novembre 1991): pp. 3-6.
- Andruleit, H., 1997. Coccolithophore fluxes in the Norwegian-Greeland Sea: seasonlity and assemblage alteration. Marine Micropaleontology 31: 45-64.
- Andruleit, H.A., 2000. Dissolution-affected coccolithophore fluxes in the central Greenland Sea (1994/1995). Deep-Sea Research II, 47: 1719-1742.
- Aubry, M.-P., 1989. Phylogenetically based calcareous nannofossil taxonomy: implications for the interpretation of geological events. In: Nannofossils and their aplications: Proceedings INA Conference. London 1987. Ed. by J. A. Crux & S. E. van Heck. Ellis Horwood. Chichester: pp. 21-40
- Bartolini, C., 1970. Coccoliths from sediments of the western Mediterranean. Micropaleontology 16 (2): 129-154.
- Bé, W.H. and Anderson, R.O., 1976. Preservation of planktonic foraminifera and other calcareous plankton. In: Zooplankton fixation and preservation. Ed. by: H.F. Steedman. The Unesco Press. Paris: pp. 250-258.
- 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: The Haptophyte Algae. Ed. by J.C. Green and B.S.C. Leadbeater, Systematics Association Special Volume 51, Clarendon Press, Oxford: pp. 167-186.
- 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: The Micropaleontology of the Oceans. Ed. by: B.M. Funnel & W.R. Riedel. Cambridge University Press. Cambridge. pp. 611-624.
- Bollmann, J., 1997. Morphology and biogeography of *Gephyrocapsa* coccoliths in Holocene sediments. Marine Micropaleontology, 29: 319-350.
- Borsetti, A.M. and Cati, F., 1972. Il nannoplancton calcareo vivente nel Tirreno centromeridionale. Giornale di Geología (2), 38 (II): 395-452.
- Borsetti, A.M. and Cati, F., 1976. Il nannoplancton calcareo vivente nel Tirreno centromeridionale. Parte II. Giornale di Geologia (2), 40 (I): 209-240.
- Borsetti, A.M. and Cati, F., 1979. Il nannoplancton calcareo vivente nel Tirreno centromeridional. Parte III. Giornale di Geologia (2), 43 (I): 157-174.
- Boudreaux, J.E. and Hay, W.W., 1969. Calcareous nannoplankton and biostratigraphy of the late Pliocene-Pleistocene-Recent sediments in the Submarex cores. Revista Española de Micropaleontología 1 (3): 249-292.
- Bown, P.R. 1998. Calcareous nannofossil biostratigraphy. Chapman and Hall, Cambridge. 314 pp.
- Bown, P.R. and Young, J.R., 1997. Mesozoic calcareous nannoplankton classification. Journal of Nannoplankton Research 19 (1): 21-36.
- Bown, P.R. and Young, J.R., 1998. Introduction. In: Calcareous nannofossil biostratigraphy. Ed. by: P.R. Bown. Chapman & Hall. London: pp. 1-15.

- Braarud, T., Deflandre, G., Halldal P. and Kamptner, E., 1955. Terminology, nomenclature, and systematics of the Coccolithophoridae. Micropaleontology 1 (2): 157-159.
- Bramlette, M.N. and Martini, E., 1964. The great change in calcareous nannoplankton fossils between the Maestrichtian and Danian. Micropaleontology, 10 (2): 291-322.
- Brassell, S.C., Eglinton, G., Marlowe, I.T., Pflaumann, U., Sarnthein, M., 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.
- Broerse, A.T.C. 2000. Coccolithophore export production in selected ocean environments. Published PhD. Faculty of Earth Sciencies. Vrije Universiteit. Amsterdam.
- Broerse, A.T.C., Brummer, G.-J.A. and J.E. van Hinte, 2000a. Coccolithophore export production in response to monsoonal upwelling of Somalia (northwestern Indian Ocean. Deep-Sea Research II, 47: 2179-2205.
- Broerse, A.T.C., Ziveri, P., van Hinte, J. E., and Honjo, S., 2000b. Coccolithophore export production, species composition, and coccolith-CaCO₃ fluxes in the NE Atlantic (34°N 21°W and 48°N 21°W). Deep-Sea Research II, 47: 1877-1905.
- Broerse, A.T.C., Ziveri, P., and Honjo, S., 2000c. Coccolithophore (-CaCO₃) flux in the Sea of Okhotsk: seasonality, settling and alteration processes. Marine Micropaleontology, 39 (Special Issue: Nannoplankton Ecology and Palaeoecology): 179-200.
- Cachao, M. and Moita, M.T., 2000. Coccolithus pelagicus, a productivity proxy related to moderate fronts off Western Iberia. Marine Micropaleontology, 39 (Special Issue: Nannoplankton Ecology and Palaeoecology): 131-155.
- Cavalier-Smith, T., 1981. Eucaryote kingdoms, seven or nine?. BioSystems, 14: 461-481.
- Cavalier-Smith, T., 1986. The Kingdom Chromista: Origin and Systematics. In: Progress in Phycological Research. Ed. by: F.E. Round and D.J. Chapman. vol. 4, pp. 309-347. Biopress Ltd. Bristol.
- Cavalier-Smith, T., 1989. The Kingdom Chromista. In: The Chromophyte Algae. Problems and Perspectives. Ed. by: J.C. Green, B.S.C. Leadbeater, and W.I. Diver. Clarendon Press. Oxford. pp. 381-407
- Cavalier-Smith, T., 1993. Kingdom Protozoa and its 18 phyla. Microbiological Reviews, 57: 953-94.
- Cavalier-Smith, T., 1994. Origin and relationships of Haptophyta. In: The Haptophyte Algae. Ed. by J.C. Green and B.S.C. Leadbeater. Systematics Association Special Volume 51. Clarendon Press. Oxford: pp. 413-435
- Cavalier-Smith, T., 1998. A revised six-kingdom system of life. Biological Reviews of the Cambridge Philosophical Society, 73 (3): 203-266.
- Charlson, R.J., Lovelock, J.E., Andreae, M.O. and Warren, S.G., 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. Nature 326: 655-661.
- Chrétiennot-Dinet, M.-J., 1990. Atlas du phytoplancton marin, volume 3, (A. Sournia, ed.). Editions du C.N.R.S., Paris.
- Chrétiennot-Dinet, M.-J., Sournia, A., Ricard, M. and Billard, C. 1993. A classification of the marine phytoplankton of the world from class to genus. Phycologia 32: 159-179.
- Christensen, T. 1962. Alger. In: Botanik Bd 2, Systematisk Botanik. Nr. 2. Ed. by: T.W. Böcher, M. Lange and T. Sorensen. Munksgaard. Copenhagen, pp. 1-178.
- Christensen, T., 1990. The Chromophyta, past and present. In: The chromophyte algae: problems and perspectives. Ed by: J.C. Green, B.S.C. Leadbeater, and W. L. Diver. Systematics Association Special Volume 38, Clarendon Press. Oxford: pp. 1-12.

- Cohen, C.L.D., 1964. Coccolithophorids from two Caribbean deep-sea cores. Micropaleontology 10 (2): 231-250.
- Cohen, C.L.D. and Reinhardt, P., 1968. Coccolithophorids from the Pleistocene Caribbean deep-sea core CP-28. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 131: 289-304.
- Copeland, H.F., 1956. The classification of Lower Organisms. Pacific Books. Palo Alto.
- Cortés, M.Y., 2000. Further evidence for the heterococcolith-holococcolith combination *Calcidiscus leptoporus - Crystallolithus rigidus*. Marine Micropaleontology 39 (Special Issue: Nannoplankton Ecology and Palaeoecology): 35-37.
- Cros, L. 1995. Calcareous nannoplankton in surficial sediments of the Catalano-Balearic Sea. (Northwestern Mediterranean). In: 5th INA Conference in Salamana 1993. Proceedings. Ed. by: J.A. Flores and F.J. Sierro. Universidad de Salamanca. Salamanca: pp. 47-59.
- Cros, L. 2000. Variety of exothecal coccoliths of *Syracosphaera*. Journal of Nannoplankton Research 22 (1): 41-51.
- Cros, L., Kleijne, A., Zeltner, A., Billar, C. and Young, J.R., 2000. New examples of holococcolith-heterococcolith combination coccospheres and their implications for coccolithophorid biology. Marine Micropaleontology 39 (Special Issue: Nannoplankton Ecology and Palaeoecology): 1-34.
- Deflandre, G. 1952. Classe des Coccolithophoridés. (Coccolithophoridae Lohmann, 1902). Traite de Zoologie 1. Ed. by: P. P. Grassé. Masson. Paris: pp. 439-470.
- Deflandre, G. and Fert, C., 1953. Aplication du microscope électronique a l'étude des coccolithophoridés. Extrait du Bulletin de la Société d'Histoire Naturelle de Toulouse, T. 88, fasc. 3-4: pp. 301-313.
- Deflandre, G. and Fert, C., 1954. Observations sur les coccolithophoridés actuels et fossiles en microscopie ordinaire et électronique. Annales de Paléontologie 40: 115-176.
- Delgado, M. and Fortuño, J.-M., 1991. Atlas de Fitoplanton del Mar Mediterráneo. Sci. Mar. 55 (Supl. 1): 1-133.
- Egge, J.K. and Heimdal, B.R., 1994. Blooms of phytoplankton including *Emiliania huxleyi* (Haptophyta). Effects of nutrient supply in different N:P ratios. Sarsia 79: 333-348.
- Ehrenberg, C.G. 1836. Bemerkugen uber feste mikroscopische anorganische Formen in den erdigen und derben Mineralien. Bericht. Verh. K. Preuss. Akad. Wiss. Berlin: pp. 84-85.
- Emelyanov, E.M. and Shimkus, K.M. 1986. Geochemistry and Sedimentology of the Mediterranean Sea. D. Reidel Publishing Company. Dordrecht: 553 pp.
- Estrada, M. 1985. Deep phytoplankton and chorophyll maxima in the Western Mediterranean. In: Mediterranean Marine Ecosystems. Ed. by: Moraitou-Apostolopou, M., and Kiortsis, V., Plenum Press. London: pp. 247-277.
- Estrada, M., 1991. Phytoplankton assemblages across a NW Mediterranean front: Changes from winter mixing to spring stratification. In: Homage to Ramon Margalef or, Why there is such pleasure in studying nature. Ed. by: J.D. Ros and N. Prat. Oecologia aquatica, 10, pp. 157-185
- Estrada, M., 1996. Primary production in the northwestern Mediterranean. Science Marine, 60 (Supl. 2): 55-64.
- Estrada i Miyares, M., 1999. Hidrodinàmica i fitoplàncton en el Mar Català. Memorias de la Real Academia de Ciencias y Artes de Barcelona. Núm. 961, Vol. LVIII, nº 6: pp. 189-241.

- Estrada, M. and Margalef, R. 1988. Supply of nutrients to the Mediterranean photic zone along a persistent front., Oceanologica Acta, Special Issue, 9: 133-142.
- Estrada, M. and Salat, J., 1989. Phytoplankton assemblages of deep and surface water layers in a Mediterranean frontal zone. In: Topics in Marine Biology. Ed. by: J.D. Ros. Sci. Mar. 53 (2-3): pp. 203-214.
- Fagerbakke, K.M., Heldal, M., Norland, S., Heimdal, B.R., and Batvik, H., 1994. *Emiliania huxleyi*. Chemical composition and size of coccoliths from enclosure experiments and a Norwegian fjord. Sarsia 79: 349-355.
- Farinacci, A., 1971. Round Table on calcareous Nannoplankton. In: Proceedings of the II Planktonic Conference, Roma 1.970. Ed. by: A. Farinacci. Ed. Tecnoscienza. Roma: pp. 1343-1369.
- Findlay, C.S. 1998., Living and Fossil Calcareous Nannoplankton from the Australian Sector of the Southern Ocean: Implications for Paleoceanography. PhD, University of Tasmania.
- Flores, J.A., Sierro, F.J., Vázquez, A., Zamarreño, I., 1993. Late Quaternary Coccoliths from a Western Mediterranean Core Palaeoceanographic and Palaeoenvironmental Implications. INA Newsleter, 15 (2): 63
- Flores, J.A., Sierro, F.J. and Raffi, I., 1995. Evolution of the calcareous nannofossil assemblage as a response to the paleoceanographic changes in the Eastern equatorial Pacific from 4 to 2 Ma (Leg 138, Sites 849 and 852). In: L. Mayer, N. Pisias, T. Janecek et al., Proc. ODP, Init. Rept., 138. College Station, TX (Ocean Drilling Program) pp. 163-176.
- Flores, J. A., Sierro, F. J., Francés, G., Vázquez, A. and Zamarreño, I. 1997. The last 100.000 years in the western Mediterranean: sea surface water and frontal dynamics as revealed by coccolithophores. Marine Micropaleontology. 29: 351-366.
- Font i Ferré, J., 1986. La circulació general a la Mar Catalana. Tesi Doctoral. Universitat de Barcelona.
- Font, J., Julià, A., Rovira, J., Salat, J. and Sánchez-Pardo, J., 1986-1987. Circulación marina en la plataforma continental del Ebro determinada a partir de la distribución de masas de agua y los microcontaminantes orgánicos en el sedimento. Acta Geologica Hispanica 21-22: 483-489.
- Font, J., Salat, J. and Tintoré, J. 1988. Permanent features of the circulation in the Catalan Sea. Oceanologica Acta, Special Issue, 9: 51-57.
- Fresnel, J., 1989. Les Coccolithophorides (Prymnesiophyceae) du littoral: Genres: *Cricosphaera, Pleurochrysis, Cruciplacolithus, Hymenomonas et Ochrosphaera.* Ultrastructure, cycle biologique, systématique. Thèse de Doctorat d'Etat Sciences, Université de Caen.
- Fresnel, J., 1994. A heteromorphic life cycle in two coastal coccolithophorids, *Hymenomonas lacuna* and *Hymenomonas coronata* (Prymnesiophyceae). Canadian Journal of Botany 72: 1455-1462.
- Fresnel, J. and Billard, C., 1991. *Pleurochrysis placolithoides* sp. nov. (Prymnesiophiceae), a new marine coccolithophorid with remarks on the status of cricolith-bearing species. Br. phycol. J. 26: 67-80.
- Gaarder, K.R., 1962. Electron microscope studies on holococcolithophorids. Nytt Magasin for Botanikk, 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 Magasin for Botanikk 17 (2): 113-126.

- Gaarder, K.R., and Hasle, G.R., 1971. Coccolithophorids of the Gulf of Mexico. Bulletin of Marine Science 21: 519-544.
- Gaarder, K.R., and Heimdal, B.R., 1977. A revision of the genus *Syracosphaera* Lohmann (Coccolithineae). "Meteor" Forsch.-Ergebnisse, Reihe D (24): 54-71.
- Gaarder, K.R., and Ramsfjell, E. 1954. A new coccolithophorid from northern waters. *Calciopappus caudatus* n. gen., n. sp. Nytt. Magasin for Botanikk 2: 155-156.
- Gallagher, L.T., 1989. *Reticulofenestra*: A critical review of taxonomy, structure and evolution. In: Nannofosils and their aplications. Ed. by: J.A. Crux and S.E. van Heck. Ellis Horwood, Chichester: pp. 41-75.
- Garcés, E., Delgado, M., Masó, M., Camp, J., 1998. Life history and in situ growth rates of *Alexandrium taylori* (Dinophyceae). J. Phycol. 34, 880-887.
- Gartner, S. and Bukry, D. 1969. Tertiary holococcoliths. Journal of Paleontology, 43: 1213-1221.
- Gayral, P., and Fresnel, J., 1983. Description, sexualité et cycle de développement d'une nouvelle Coccolithophoracée (Prymnesiophyceae): *Pleurochrysis pseudoroscoffensis* sp. nov. Protistologica 19 (2): 245-261.
- Giraudeau, J., 1992. Distribution of Recent nannofossils beneath the Benguela system: southwest African continental margin. Marine Geology, 108: 219-237.
- Giraudeau, J., and Bailey, G.W., 1995. Spatial dynamics of coccolithophore communities during an upwelling event in the Southern Benguela system. Continental Shelf Research, v. 15, n°. 14: pp. 1825-1852.
- Gran, H.H., 1912. Pelagic plant life. In: The Depths of the Ocean. Ed. by: J. Murray and J. Hjort. Macmillan. London. pp. 307-386.
- Green, J.C. and Jordan, R.W., 1994. Systematic history and taxonomy. In: In: The Haptophyte Algae. d. by J. C. Green and B. S. C. Leadbeater, Systematics Association Special Volume 51, Clarendon Press, Oxford: pp. 1-21.
- Green, J.C., Course, P.A., and Tarran, G.A., 1996. The life-cycle *Emiliania huxleyi*: A brief review and a study of relative ploidy levels analysed by flow cytometry. Journal of Marine Systems 9: 33-44.
- Green, J.C., Perch-Nielsen, K., and Westbroek, P., 1989. Phylum Prymnesiophyta. In: Handbook of the Protoctista, Ed. by: L. Margulis, J. Corliss, M. Melkoniam and D. Chapman. Jones and Bartlett. Boston. pp 293-317.
- Guillén, J., Palanques, A., 1997. A historical perspective of the morphological evolution in the lower Ebro river. Environmental Geology, 20 (3/4): 174-180.
- Haeckel, E., 1866. Generelle Morphologie der Organismen. Reimer. Berlin.
- Haeckel, E., 1894. Sistematische Phylogenie der Protisten und Pflanzen. Reimer. Berlin.
- Hagino, K., and Okada, H., 1998. *Gladiolithus striatus* sp. nov. (Prymnesiophyceae), a living coccolithophore from the lower photic zone of the Pacific Ocean. Phycologia 37 (4): 246-250.
- Hagino, H., Okada, H. and Matsuoka, H., 2000. Spatial dynamics of coccolithophore assemblages in the Equatorial Western-Central Pacific Ocean. Marine Micropaleontology 39 (Special Issue: Nannoplankton Ecology and Palaeoecology): 53-72.
- Halldal, P., 1953. Phytoplankton investigations from weather ship M in Norwegian Sea, 1948-49. Hvalrädets Skrifter 38: 1-91.
- Halldal, P., and Markali, J., 1954a. Morphology and microstructure of coccoliths studied in the electron microscope. Observations on *Anthosphaera robusta* and *Calyptrosphaera papillifera*. Nytt Magasin for Botanikk 2: 117-121.
- Halldal, P. and Markali, J., 1954b. Observations on coccoliths of Syracosphaera mediterranea Lohm., S. pulchra Lohm., and S. molischi Schill. in the electron

microscope. Extrait du Journal du Conseil International pour l'Exploration de la Mer 19 (3): 329-336.

- Halldal, P. and Markali, J., 1955. Electron microscope studies on coccolithophorids from the Norwegian Sea, the Gulf Stream and the Mediterranean. Avhandlinger Utgitt Av Det Norske Videnskaps-Akademi i Oslo I. Mat.-Naturv. Klasse 1: 1-30.
- Hallegraeff, G.M. 1984. Coccolithophorids (calcareous nanoplankton) from Australian waters. Botanica Marina 27: 229-247.
- Hay, W.W., Mohler, H.P., and Wade, M.E., 1966. Calcareous nannofossils from Nal'chik (northwets Caucasus). Ecologae Geologicae Helvetiae, 59: 379-399.
- Hay, W.W., Mohler, H.P., Roth, P.H., Schmidt, R.R. and Bourdeaux, J.E. 1967. Calcareous nannoplankton zonation of the Cenozoic of the Gulf Coast and Caribbean-Antillean area, and transoceanic correlation. Transactions of the Gulf Coast Association of Geological Societies 17: 428-480.
- Heimdal, B.R., 1973. Two new taxa of recent coccolithophorids. "Meteor" Forschungsergebnisse Reihe, D, 13: 70-75.
- Heimdal, B.R., 1982. Validation of the names of some species of *Zygosphaera* Kamptner. INA Newsletter, 4: 52-56.
- Heimdal, B.R., 1993. Modern Coccolithophorids. A Guide to Naked Flagellates and Coccolithophorids. In C. R. Tomas Eds., Marine Phytoplankton pp. 147-243. London: Academic Press, Inc.
- Heimdal, B.R., and Gaarder, K.R., 1980. Coccolithophorids from the northern part of the eastern central Atlantic. I. Holococcolithophorids. "Meteor" Forschungsergebnisse Reihe, D, 32: 1-14.
- Heimdal, B.R., and Gaarder, K.R., 1981. Coccolithophorids from the northern part of the eastern central Atlantic. II. Heterococcolithophorids. "Meteor" Forschungsergebnisse Reihe, D, 33: 37-69.
- Heimdal, B.R., Egge, J.K., Veldhuis, M.J.W., and Westbroek, P., 1994. The 1992 Norwegian *Emiliania huxleyi* experiment. An overview. Sarsia 79: 285-290.
- Hibberd, D.J., 1972. Chrysophyta: definition and interpretation. British Phycological Journal, 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. Botanical Journal of the Linnean Society 72: 55-80.
- Hibberd, D.J. 1980. Prymnesiophytes (=Haptophytes). In: Phytoflagellates. Ed. by: E.R. Cox. Developments in Marine Biology, 2: 273-317 Elsevier North Holland. Amsterdam.
- Hodgkinson, R. L. 1991. Microfossil processing: a damage report. Micropaleontology 37 (3): 320-326.
- Holligan, P.M., Viollier, M., Harbour, D.S., Camus, P. and Champagne-Philippe, M., 1983. Satellite and ship studies of coccolithophore production along a continental shelf edge. Nature 304: 339-342.
- Holligan, P.M. Fernandez, E., Aiken, J., Balch, W.M., Boyd, P., Burkill, P.H.. Finch, M., Groom, S.B., Malin, G., Muller, K., Purdie, D.A., Robinson, C., Trees, C.C., Turner, S.M., van der Wal, P., 1993. A biogeochemical study of the coccolithophore *Emiliania huxleyi* in the North Atlantic. Global Biogeochemical Cycles 7: 879-900.
- Honjo, S., 1976. Coccoliths: production, transportation and sedimentation. Marine Micropaleontology 1: 65-79.
- Honjo, S. and Okada, H. 1974. Community structure of coccolithophores in the photic layer of the mid-Pacific. Micropaleontology, 20 (2): 209-230.

- Hori, T. and Green, J.C., 1985. An ultrastructural study of mitosis in non-motile coccolithbearing cells of *Emiliania huxleyi* (Lohm) Hay and Mohler (Prymnesiophyceae). Protistologica 21 (1): 107-120.
- Hori, T., and Inouye, I., 1981. The ultrastructure of mitosis in *Cricosphaera roscoffensis* var. *haptonemifera* (Prymnesiophyceae). Protoplasma 106: 121-135.
- Inouye, I., and Kawachi, M., 1994. The haptonema. In: The Haptophyte Algae. Ed. by J.C. Green and B.S.C. Leadbeater, Systematics Association Special Volume 51, Clarendon Press, Oxford: 73-89
- Inouye, I., and Pienaar, R.N., 1984. New observations on the coccolithophorid *Umbilicosphaera sibogae* var. *foliosa* (Prymnesiophyceae) with reference to cell covering, cell structure and flagellar apparatus. British Phycological Journal 19: 357-369.
- Inouye, I., and Piennar, R.N., 1988. Light and electron microscope observations of the type species of *Syracosphaera*, *S. pulchra* (Prymnesiophyceae). British Phycological Journal 23: 205-217.
- Jafar, S.A., and Martini, E., 1975. On the validity of the calcareous nannoplankton genus *Helicosphaera*. Senckenbergiana Lethaea 56 (4/5): 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). Mémories de la Societé Géologique de France 152: 1-317.
- Jerkovic, L. 1970. Noëlaerhabdus nov. gen. type d'une nouvelle famille de Coccolithophoridés fossiles: Noëlaerhabdaceae du Miocène supérieur de Yougoslavie. Comptes Rendus (Hebdomadaires des Séances) de l'Académie des Sciences, Paris, Serie D, 270: 468-470.
- Jordan, R.W., 1991. Problems in the taxonomy and terminology of living coccolithophorids. INA Newsletter 13 (2): 52-53.
- Jordan, R.W. and Chamberlain, A.H.L., 1993a. *Canistrolithus valliformis* gen. et sp. nov. (Syracosphaeraceae, Prymnesiophyta) a comparison with the genus *Alisphaera*. Phycologia, 32 (5): 373-378.
- Jordan, R.W. and Chamberlain, A.H.L. 1993b. Vexillarius cancellifer gen. et sp. nov. and its possible affinities with other living coccolithophorids. In: Nannoplankton Research Vol. 2. Proceedings of the Fourth INA Conference, Prague 1991, Ed. by: B. Hamrsmíd and J. R. Young. MND. Hodonín. pp. 305-325.
- Jordan, R.W. and Chamberlain, A.H.L., 1997. Biodiversity among haptophyte algae. Biodiversity and Conservation 6: 131-152.
- Jordan, R.W., and Green, J.C., 1994. A check-list of the extant Haptophyta of the world. J. mar. biol. Ass. U. K. 74: 149-174.
- Jordan, R.W., and Kleijne, A. 1994. A classification system for living coccolithophores. In: Coccolithophores. Ed. by: A. Winter and W.G. Siesser. Cambridge University Press. Cambridge: pp. 83-105.
- Jordan, R.W., and Winter, A., 2000. Assemblages of coccolithophorids and other living microplankton off the coast of Puerto Rico during January-May 1995. Marine Micropaleontology 39 (Special Issue: Nannoplankton Ecology and Palaeoecology): 113-130.
- Jordan, R.W., and Young, J.R., 1990. Proposed changes to the classification system of living coccolithophorids. INA Newsletter 12 (1): 15-18.
- Jordan, R.W., Kleijne, A. and Heimdal, B.R., 1993. Proposed changes to the classification system of living coccolithophorids III. INA Newsletter 15 (1): 18-21.

- Jordan, R.W., Kleijne, A., Heimdal, B.R. and Green, J.C., 1995. A Glossary of the extant Haptophyta of the world. J. Mar. biol. Ass. U.K. 75: 769-814.
- Jordan, R.W., Knappertsbusch, M., Simpson, W.R., and Chamberlain, A.H.L., 1991. *Turrilithus latericioides* gen. et sp. nov., a new coccolithophorid from the deep photic zone. British Phycological Journal 26: 175-183.
- Kamptner, E., 1927. Beitrag zur Kenntnis adriatischer Coccolithophoriden. Archiv für Protistenkunde, 58: 173-184.
- Kamptner, E., 1937. Neue und bemerkenswerte Coccolithineen aus dem Mittelmeer. Archiv für Protistenkunde, 89: 279-316.
- Kamptner, E., 1941. Die Coccolithineen der Südwestküste von Istrien. Naturhistorischen Museum in Wien, Annalen, 51: 54-149.
- Kamptner, E., 1943. Zur Revision der Coccolithineen-Spezies *Pontosphaera huxleyi* Lohm. Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenchaftliche Klasse 80: 43-49.
- Kamptner, E., 1950. Über den submikroskopischen Aufbau der Coccolithen. Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenchaftliche Klasse, 87: 152-158.
- Kamptner, E., 1954. Untersuchungen über den Feinbau der Coccolithen. Archiv für Protistenkunde, 100:1-90.
- Kamptner, E., 1956. Morphologische Betrachtungen uber Skelettelemente der Coccolithineen. Osterreichische Botanische Zeitschrift, 103, 142-163.
- Kamptner, E., 1963. Coccolithineen-Skelettreste aus Tiefseeablagerungen des Pazifischen Ozeans. Naturhistorisches Museum in Wien, Annalen, 66: 139-204.
- Kamptner, E., 1967. Kalkflagellaten Skelettreste aus Tiefseeschlam des Sudatlantisken Ozeans. Naturhisttorischen Museum in Wien, Annalen, 71: 117-198.
- Keller, M.D., Bellows, W.K., and Guillard, R.R.L., 1989. Dimethyl sulfide production in marine phytoplankton. In: Biogenic sulfur in the environment, (ed. E. S. Saltzman and W. J. Cooper). American Chemical Society, Washington: pp. 183-200.
- Klaveness, D., 1972a. *Coccolithus huxleyi* (Lohmann) Kamptner. I.- Morphological investigations on the vegetative cell and the process of coccolith formation. Protistologica 8 (3): 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*. Norwegian Journal of Botany 20 (2-3): 151-162.
- Klaveness, D., and Paasche, E., 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. Marine Micropaleontology 17: 1-76.
- Kleijne, A. 1992. Extant Rhabdosphaeraceae (coccolithophorids, class Prymnesiophyceae) from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. Scripta Geologica 100: 1-63.
- Kleijne, A., 1993. Morphology, taxonomy and distribution of extant coccolithophorids (Calcareous nannoplankton) Published PhD. Vrije Universiteit, Amsterdam. Drukkerij FEBO, Enschede. Katwijk. The Netherlands, pp. 321.
- Knappertsbusch, M.W. 1989. Morphological evolution of the Neogene coccolith group *Calcidiscus macintyrei*. INA Newsl. 11 (2): 74-75.
- Knappertsbusch, M.W., 1990. Geographic distribution of modern coccolithophorids in the Mediterranean Sea and morphological evolution of *Calcidiscus leptoporus*. Ph.D. Diss. Swiss Federal Inst. of Tech. Zurich ETH. pp. 141

- Knappertsbusch, M., 1993a. *Syracosphaera noroiticus* sp. nov., and *S. marginaporata* sp. nov., (Syracosphaeraceae, Prymnesiophyta), new coccolithophorids from the Mediterranean Sea and North Atlantic Ocean. J. Micropalaeontol. 12 (1): 71-76.
- Knappertsbusch, M., 1993b. Geographic distribution of living and Holocene coccolithophores in the Mediterranean Sea. Marine Micropaleontology 21: 219-247.
- Lal, D., 1977. The Oceanic Microcosm of Particles. Science, 198, nº 4321: 997-1009.
- Lancelot, C., and Rousseau, V., 1994. Ecology of *Phaeocystis*: the key role of colony forms. In: The Haptophyte Algae. Ed. by: J.C. Green and B.S.C. Leadbeater, Systematics Association Special Volume 51, Clarendon Press, Oxford: pp. 229-245.
- 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. Annales de l'Institut Océanographique, 26: 255-362.
- Lecal-Schlauder, J., 1954. Richesse en microplancton estival des eaux Méditerranéennes de Port-Vendres a Oran. Vie et Milieu, 3: 13-95.
- Lecal-Schlauder, J., 1961. Anomalies dans la composition des coques de flagelles calcaires. Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord, 52: 63-66.
- Lecal, J., 1965a. Coccolithophorides littoraux de Banyuls. Vie et Milieu, 16 (1-B): 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 (3-4): 305-387.
- Lemmermann, E. 1903. Das Phytoplankton des Meeres. II. Beitrag. Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen, 17, 341-418..
- Lemmermann, E. 1908. Flagellatae, Chlorophyceae, Coccosphaerales und Silicoflagellatae. In: "Nordisches Plankton. Botanischer Teil" Ed. by: K. Brandt and C. Apstein. Lipsius & Tischer. Kiel & Leipzig: pp. 1-40.
- Lewis, W. Jr., 1985. Nutrient scarcity as an evolutionary cause of haploidy. The American Naturalist, 125: 692-701.
- Loeblich, A.R., Jr., and Tappan, H., 1963. Type fixation and validation of certain calcareous nannoplankton genera. Proceedings of the Biological Society of Washington, 76: 191-196.
- Loeblich, A.R., Jr., and Tappan, H., 1966. Annotated index and bibliography of the calcareous nannoplankton. Phycologia, 5 (2/3): 81-216.
- Loeblich, A.R., Jr., and Tappan, H., 1968. Annotated index and bibliography of the calcareous nannoplankton. 2. Journal of Paleontology 42: 584-598.
- Loeblich, A.R., Jr., and Tappan, H., 1978. The coccolithophorid genus *Calcidiscus* Kamptner and its synonyms. Journal of Paleontology 52: 1390-1392.
- Lohmann, H., 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, Zugleich ein Beitrag zur Kenntnis des Mittelmeerauftriebs. Archiv für Protistenkunde 1: 89-165.
- Lohmann, H., 1903. Neue Untersuchungen über den Reichthum des Meeres an Plankton und über die Brauchbartkeit der vershiedenen Fangmethoden. Zugleich auch ein Beitrag zur Kenntnis des Mittelmeerauftriebs. Wissenschaftliche Meeresuntersuchungen. Abteilung Kiel, N.F. 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.

Universitaet Berlin, Veröffentlichungen des Instituts für Meereschundund, Geogr.-Naturwissenschaft 1 (viii): 1-92.

- Lohmann, H., 1913. Beitäge zur Charakterisierung des Tier- und Pflanzenlebens in den von der "Deutschland" wahrend ihrer Fahrt nach Buenos Aires Durchfahrenen Gebieten des Atlantischen Ozeans. II. Teil. Internationale Revue der gesamten Hydrobiologie und Hydrographie 5: 343-372.
- Lohmann, H., 1919. Die Bevölkerung des Ozeans mit Plankton nach den Ergebnissen der Zentrifugenfänge während der Ausreise der "Deutschland" 1911. Archiv für Biontologie 4: 1-617.
- Lohmann, H., 1920. Die Bevölkerung des Ozeans mit plankton. Nach den Ergebnissen der Zentrifugenfängen während der Ausreise der Deutschland 1911. Arch. Biontolo. Berl., 4 (1916-1919): 1-617.
- Lototskaya, A., 1999. Mid-latitude North Atlantic climate between 150.000 and 100.000 years BP. Published PhD. Vrije Universiteit. Amsterdam: pp. 171.
- Malin, G., and Kirst, G.O., 1997. Algal production of dimethyl sulfide and its atmospheric role. Journal Phycology 33: 889-896.
- Manton, I., and Leedale, G.F., 1963. Observations on the microanatomy of *Crystallolithus hyalinus* Gaarder and Markali. Arch. Mikrobiol. 47: 115-136.
- Manton, I., and Leedale, G.F., 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 Oates, K., 1975. Fine-structural observations on *Papposphaera* Tangen from the southern hemisphere and on *Pappomonas* gen. nov. from South Africa and Greenland. British Phycological Journal, 10: 93-109.
- Manton, I. and Oates, K., 1980. *Polycrater galapagensis* gen. et sp. nov., a putative coccolithophorid from the Galapagos Islands with an unusual aragonitic periplast. British Phycological Journal, 15: 95-103.
- Manton, I. and Oates, K., 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 Oates, K., 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., Sutherland, J., and McCully, M., 1976. Fine structural observations on coccolithophorids from South Alaska in the genera *Papposphaera* Tangen and *Pappomonas* Manton and Oates. British Phycological Journal, 11: 225-234.
- Manton, I., Sutherland, J., and Oates, K., 1976. Arctic coccolithophorids: two species of *Turrisphaera* gen. nov. from West Greeland, Alaska, and the Northwest Passage. Proc. R. Soc. Lond. B 194: 179-194.
- Manton, I., Bremer, G., and Oates, K., 1984. Nanoplankton from the Galapagos Islands: *Michaelsarsia elegans* Gran and *Halopappus adriaticus* Schiller (coccolithophorids) with special reference to coccoliths and their unmineralized components. Phil. Trans. R. Soc. Lond. B, 305: 183-199.
- Margalef, R., 1945. Fitoplancton nerítico de la Costa Brava catalana (Sector de Blanes). Publicaciones sobre Biología Mediterranea. Instituto Español de Estudios Mediterraneos 1: 7-48.
- Margalef, R., 1974. Ecología. Ediciones Omega S.A. Barcelona: pp. 951.

- Margalef, R., 1978. Life forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta, 1: 493-509.
- Margalef, R., 1985a. Introduction to the Mediterranean. In: Western Mediterranean (Key environments). Ed. by: R. Margalef, Pergamon Press. Oxford: pp. 1-16.
- Margalef, R., 1985b. Environmental control of the mesoscale distribution of primary producers and its bearing to primary production in the Western Mediterranean. In: Mediterranean Marine Ecosystems. Ed. by: M. Moraitou-Apostolopoulou and V. Kiortsis Plenum Press. London: pp. 213-229.
- Margalef, R., 1989. Els ecosistemes pelàgics. In: Història Natural dels Països Catalans, volum 14 (Sistemes naturals). Fundació Enciclopèdia Catalana. Barcelona: pp. 73-118.
- Margalef, R. 1997. Our Biosphere. Excellence in Ecology, 10, Ed. by. O. Kinne. Ecology Institute. Oldendorf/Luhe Germany. pp. 176.
- Margalef, R., and Ballester A., 1967. Fitoplancton y producción primaria de la costa catalana, de junio de 1965 a junio de 1966. Inves. Pesq., 31: 165-182.
- Margalef, R. and Estrada, M., 1987. Synoptic distribution of summer microplankton (Algae and Protozoa) across the principal front in the Western Mediterranean. Inv. Pesq. 51 (1): 121-140.
- Margulis, L. and Schwartz, K.V., 1982. Five Kingdoms. An illustrated guide to the phyla of life on earth. W. H. Freeman and Company. San Francisco.
- Markali, J. and Paasche, E. 1955. On two species of *Umbellosphaera*, a new marine coccolithophorid genus. Nytt Magasin for Botanikk 4: 95-100.
- Marlowe, I.T., Green, J.C., Neal, A.C., Brassell, S.C., Eglinton, G. and Course, P.A., 1984. Long chain $(n-C_{37}-C_{39})$ alkenones in the Prymnesiophyceae. Distribution of alkenones and other lipids and their taxonomic significance. British Phycological Journal, 19: 203-216.
- Martini, E., and Müller, C., 1972. Nannoplankton aus dem nordlichen Arabischen Meer,. "Meteor" Forschungs-Ergebnisse, (serie C), 10: 63-74.
- Mateu, G., 1985, Nannoplancton calcáreo pliocuaternario del Mar Balear (Mediterráneo Occidental: Implicaciones cronoestratigráficas y paleobiogeográficas). Revista Española de Micropaleontologia, 17 (2): 167-200.
- Matias i Sendra, M.I., 1982. Els cocolitofòrids del Pliocé de Papiol (Baix Llobregat). Tesi de Llicenciatura. Universitat de Barcelona. 194 pp.
- Matias i Sendra, M.I., 1990 Els nanofossils calcaris del Pliocé de la Mediterrània Nord-Occidental. Tesi Doctoral, Universitat de Barcelona. 241 pp.
- McIntyre, A. and Bé, A.W.H., 1967. Modern coccolithophoridae of the Atlantic Ocean I. Placoliths and cyrtholiths. Deep-Sea Research 14: 561-597.
- Medlin, L.K., Barker, G.L.A., Campbell L. Green, J.C., Hayes, P.K., Marie, D., Wrieden, S. and Vaulot, D. 1996. Genetic characterisation of *Emiliania huxleyi* (Haptophyta). Journal of Marine Systems 9: 13-32.
- Müller, C., 1985. Late Miocene to recent Mediterranean. Biostratigraphy and paleoenvironments based on calcareous nannoplankton. In: Geological Evolution of the Mediterranean Basin. Ed. by: D.J. Stanley. and F.-C. Wezel, Springer Verlag. New York: pp. 471-485
- Murray, G., and Blackman, V.H., 1898. On the nature of the coccospheres and rhabdospheres. Philosophical Transactions of the Royal Society of London (B). 190: 427-441.
- Nishida, S., 1979. Atlas of Pacific Nannoplanktons. NOM (News of Osaka Micropaleontologists), Special Paper, 3: 1-31 and 23 plates.
- Nishida, S., 1986. Nannoplankton flora in the Southern Ocean, with special reference to siliceous varieties. Mem. Natl Inst. Polar Res., Spec. Issue, 40: 56-68.

- Norris, R.E., 1965. Living cells of *Ceratolithus cristatus* (Coccolithophorineae). Arch. Protistenk. Bd. 108: 19-24.
- Norris, R.E., 1983. The family position of *Papposphaera* Tangen and *Pappomonas* Manton & Oates (Prymnesiophyceae) with records from the Indian Ocean. Phycologia 22 (2): 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 Honjo, S., 1973. The distribution of oceanic coccolithophorids in the Pacific. Deep-Sea Research, 20: 355-374.
- Okada, H., and McIntyre, A., 1977. Modern coccolithophores of the Pacific and North Atlantic Oceans. Micropaleontology, 23 (1): 1-55.
- Okada, H. and McIntyre, A., 1979. Seasonal distribution of modern coccolithophores in the Western North Atlantic Ocean. Marine Biology 54: 319-328.
- Okada, H. and McIntyre, A., 1980. Validation of *Florisphaera profunda* var. *elongata* (2). International Nannoplankton Association Newsletter, 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. Zoologischer Anzeiger 23: 198-200.
- Paasche, E., and Klaveness, D., 1970. A physiological comparison of coccolith-forming and naked cells of *Coccolithus huxleyi*. Arch. Mikrobiol. 73 : 143-152.
- Papenfuss, G.F., 1955. Classification of the Algae. In: A century of progress in the natural sciencies, 1853-1953, California Academy of Sciencies. San Francisco: pp. 115-124.
- Parke, M. and Adams, I. 1960. The motile (*Crystallolithus hyalinus* Gaarder & 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. & Dixon, P.S., 1976. Check-list of British marine algae third revision. Journal of the Marine Biological Association of the United Kingdom, 56: 527-94.
- Parke, M. and Green, J.C., 1976. Haptophyta. Haptophyceae. In: Chek-list of British marine algae- Third revision (Ed. by: M. Parke & P.S. Dixon). Journal of the Marine Biological Association of the United Kingdom 56 : 551-555.
- Perch-Nielsen, K., 1985a. Mesozoic calcareous nannofossils. In: Plankton Stratigraphy. Ed. by: H.M. Bolli, J.B. Saunders and K. Perch-Nielsen. Cambridge University Press. Cambridge. pp. 329-426.
- Perch-Nielsen, K., 1985b. Cenozoic calcareous nannofossils In: Plankton Stratigraphy. Ed. by: H.M. Bolli, J.B. Saunders and K. Perch-Nielsen. Cambridge University Press. Cambridge: pp. 427-555.
- Piennar, R.N., 1994. Ultrastructure and calcification of coccolithophores. In: Coccolithophores Ed. by: A. Winter & W. G. Siesser, Cambridge University Press. Cambridge: pp. 13-37.
- Pinot, J.-M., Tintoré, J. and Gomis, D., 1994. Quasi-synoptic mesoscale variability in the Balearic Sea. Deep-Sea Research I 41 (5/6): 897-914.
- Prieur, L. 1979. Structures hydrologiques, chimiques, biologiques dans le bassin Liguro-Provenzal. Rapp. Comm. int. Mer Médit, 25/26 (7): 75-76
- Prieur, L. and Tiberti, M. 1985 Identification et echelles des processus physiques et biologiques responsables de l'heterogeneite spatiale pres du front de Mer Ligure. Rapp. Comm. int. Mer Médit 29, (3): 35-36.

- Pujos, 1992. Calcareous nannofossils of Plio-Pleistocene sediments from the northwestern margin of tropical Africa. In: Upwelling Systems: Evolution Since the Early Miocene. Ed. by: C.P. Summerhayes, W.L. Prell and K.C. Emeis. Geol. Soc. Spec. Publ., 64:343-359.
- Rayns, D.G., 1962. Alternation of generations in a coccolithophorid, *Cricosphaera carterae* (Braarud & 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 (2): 151-176.
- Riaux-Gobin, C., Chrétiennot-Dinet, M.J. and Descolas-Gros, C., 1995. Undamaged sedimented coccolithophorids in a deep environment (continental slope of the Gulf of Lions). Marine Geology 123: 239-252.
- Riegman, R., Stolte, W., Noordeloos, A.N. and Slezak, D., 2000. Nutrient uptake and alkaline phophatase (EC 3:1:3:1) activity of *Emiliania huxleyi* (Prymnesiophyceae) during growth under N and P limitation in continuous cultures. Journal of Phycology 36: 87-96.
- Roth, P.H., 1994. Distribution of coccoliths in oceanic sediments. In: Coccolithophores. Ed. by: A. Winter & W. G. Siesser. Cambridge University Press. Cambridge: pp. 199-218.
- Rowson, J.D., Leadbeater, B.S.C. and Green, J.C. 1986. Calcium carbonate deposition in the motile (*Crystallolithus*) phase of *Coccolithus pelagicus* (Prymnesiophyceae). Br. phycol. J., 21: 359-370.
- Salat, J. 1995. The interaction between the Catalan and Balearic currents in the southern Catalan Sea. Oceanologica Acta 18 (2): 227-234.
- Salat, J. 1996. Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. Sci. Mar. 60 (supl. 2): 21-32.
- Salat, J. and Cruzado, A. 1981. Masses d'eau dans la Méditerranée occidentale: Mer Catalane et eaux adjacentes. In Rapp. Comm. int. Médit. 27, 6: 201-209.
- Salat, J., Garcia, M.A., Cruzado, A., Palanques, A., Arin, L., Gomis, D., Guillén, J., de León, A., Puigfábregas, J., Sospedra, J. and Velazquez, Z. R. (submitted). Seasonal changes of water mass structure and shelf slope exchanges at the Ebro shelf (NW Mediterranean).
- Samtleben, C., 1980. Die Evolution der Coccolithophoriden-Gattung *Gephyrocapsa* nach Befunden im Atlantik. Päleontologische. Zeitschrift 54 (1/2): 91-127.
- Samtleben, C. and Schöder, A., 1990. Coccolithophoriden-Gemeinschaften und Coccolithen-Sedimentation im Europäischen Nordmeer: Zur Abbildung von planktischer Zönosen im Sediment. Ber. Sonderforschungsbereich. Kiel. 313, 25: 1-52.
- Samtleben, C., and Schröder, A., 1992. Living coccolithophore communities in the Norwegian-Greenland Sea and their record in sediments. Marine Micropaleontology 19: 333-354.
- Samtleben, C., Baumann, K.-H. and Schröder-Ritzrau, A. 1995. Distribution, composition and seasonal variation of coccolithophore comunities in the northern North Atlantic.
 In: 5th INA Conference in Salamanca 1.993. Proceedings. Ed. by: J. A. Flores and F. J. Sierro, Universidad de Salamanca, Salamanca: pp. 219-235.
- 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. Biologia Marina. Acta Científica Venezolana 41: 152-158.

- Sánchez-Suárez, I.G., 1992. Coccolithophorids (Haptophyta) from the South-Eastern Caribbean Sea: II Order Syracosphaerales. Biologia Marina. Acta Científica Venezolana 43: 109-124
- 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(1): 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, pls 1-9.
- Schiller, J. 1930. Coccolithineae. In: Kryptogamen-Flora von Deutschland, Österreich und der Schweiz Ed. by: L. Rabenhorst 10: 89-267. Akademische Verlagsgesellschaft. Leipzig.
- Schlauder, J., 1945. Reserches sur les flagellés calcaires de la baie d'Alger. Univ. d'Alger, Dipl. Fac. Sci., Université d'Alger: 1-51.
- Schneiderman, N. 1977. Selective dissolution of recent coccoliths in the Atlantic Ocean. In: Ocean Micropaleontology. Ed. by: A.T.S. Rammsay. Academic Press. London: pp. 1009-1053.
- Siesser, W.G., 1971. Mineralogy and diagenesis of some South African coastal and marine carbonates. Mar. Geol., 10: 15-38.
- Siesser, W.G., 1977. Chemical Composition of Calcareous Nannofossils. South African Journal of Science 73: 283-285.
- Siesser, W.G., 1994. Historical background of coccolithophore studies. In: Coccolithophores. Ed. by: A. Winter & W.G. Siesser. Cambridge University Press. Cambridge: pp. 1–11.
- Siesser, W.G., 1998. Calcareous nannofosil Genus *Scyphosphaera*: structure, taxonomy, biostratigraphy, and phylogeny. Micropaleontology, 44 (4): 351-384.
- Siesser, W.G. and Winter, A. 1994. Composition and morphology of coccolithophore skeletons. In: Coccolithophores. Ed. by: A. Winter & W. G. Siesser. Cambridge University Press. Cambridge: pp. 51-62.
- Simó, R., and Pedrós-Alió, C., 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 Young, J.R., 2000. First direct documentation of associations of *Ceratolithus cristatus* ceratoliths, hoop-coccoliths and *Neosphaera coccolithomorpha* planoliths. Marine Micropaleontology, 39 (Special Issue: Nannoplankton Ecology and Palaeoecology): 39-41.
- Sprengel, C., Baumann, K.-H. and Neuer, S., 2000. Seasonal and interannual variation of coccolithophore fluxes and species composition in sediment traps north of Gran Canaria (29°N 15°W). Marine Micropaleontology, 39 (Special Issue: Nannoplankton Ecology and Palaeoecology): 157-178.
- Stacey, V. J., and Pienaar, R. N., 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. Woods Hole Oceanographic Institution. Ed. by: S. Honjo. Ocean Biocoenosis Series, 1: pp. 1-85.
- Stoll, H., Klaas, C., Probert, I., Ziveri, P., Encinar, J.R., Alonso, I.G., 2000. Sr/Ca of coccolith carbonate: testing the stories of the smallest carbonate repositories. 8th INA Conference. Bremen 2000. Abstracts. Journal of Nannoplankton Research, 22(2): 142.

- Stosch, H.A. von. 1955. Ein morphologischer Phasenwechel bei einer Coccolithophoride. Sonderdruck aus die Naturwissenschanften 42 423 :1 y 2.
- Stosch, H.A. von, 1967. Chrysophyta. In: Vegetative Florpflaunzung, Parthenogenese und Apogamie bei Algen. Ed. by: Ettl, H., Muller, D.G., Neumann, K., Stosch, H.A. von, Weber, W. Springer-Verlag, Berlin, Heidelberg, N.Y., pp. 637-656, fig. 27-36
- Tangen, K., 1972. Papposphaera lepida, gen. nov., sp. nov, a new marine coccolithophorid from Norwegian coastal waters. Norwegian Journal of Botany 19 (3-4): 171-178.
- Tappan, H. 1980. Haptophyta, coccolithophores, and other calcareous nannoplankton. In: The Paleobiology of plant protists. Ed. by: H. Tappan. Freeman. San Francisco. California: pp. 678-803.
- Theodoridis, S., 1984. Calcareous nannofossil biostratigraphy of the Miocene and revision of the helicoliths and discoasters. Utrecht Micropaleontological Bulletins, 32; 1-271.
- Thomsen, H.A., 1980. Two species of *Trigonaspis* gen. nov. (Prymnesiophyceae) from West Greenland. Phycologia 19 (3): 218-229.
- Thomsen, H.A., 1981. Identification by electron microscopy of nanoplanktonic coccolithophorids (Prymnesiophyceae) from West Greenland, including the description of *Papposphaera sarion* sp. nov. Br. phycol. J. 16: 77-94.
- Thomsen, H.A., and Oates, K., 1978. *Balaniger balticus* gen et sp. nov. (Prymnesiophyceae) form Danish Coastal Waters. J. mar. biol. Ass. U.K. 58: 773-779.
- Thomsen, H.A., and Buck, K.R., 1998. Nanoflagellates of East Pacific coastal Waters: Morphology, taxonomy, and biogeography of weakly calcified coccolithophorids (Prymnesiophyceae). Cryptogamie Algol. 19: 29-48.
- Thomsen, H.A., Østergaard, J.B. and Hansen, L.E., 1991. Heteromorphic life histories in Arctic coccolithophorids (Prymnesiophyceae). J. Phycol. 27: 634-642.
- Thomsen, H.A., Buck, K.R. and Chavez, F.P., 1994. Haptophytes as components of marine phytoplankton. In: The Haptophyte Algae. Ed. by: J.C. Green & B.S.C. Leadbeater. Systematics Association Special Volume 51. Clarendon Press, Oxford: pp. 187-208..
- Thomsen, H.A., Buck, K.R., Coale, S.L., Garrison, D.L. and Gowing, M.M., 1988. Nanoplanktonic coccolithophorids (Prymnesiophyceae, Haptophyceae) from the Weddell Sea, Antarctica. Nordic Journal of Botany 8: 419-436.
- Throndsen, J., 1972. Coccolithophorids from the Caribbean Sea. Norwegian Journal of Botany 19 (1): 51-60.
- Throndsen, J., 1978. Preservation and storage. In: Phytoplankton manual. Monographs on Oceanographic methodology 6. Ed. by: A. Sournia. Publ. Unesco. Paris: pp. 69-74.
- Tintoré J., Wang D.P., La Violette P.E., 1990. Eddies and thermohaline intrusions of the shelf / slope front off the northeast Spanish coast. J. of Geoph. Res., 95: 1627-1633.
- Valero, M., Richerd, S., Perrot, V. and Destombe, C. 1992. Evolution of alternation of haploid and diploid phases in life cycles. Trends in Ecology and Evolution 7 (1): 25-29
- Vázquez Martinez, A., 1988. Procesos sedimentarios y diagenéticos en los sedimentos carbonatados hemipelágicos del Margen Sur-Balear. Tesis Doctoral, Programa de Doctorado de Ciencias del Mar. UPC-CSIC. Barcelona
- Vázquez, A., Zamarreño, I., Reyes, E. and Linares, J., 1991. Late Quaternary climatic changes on the southwestern Balearic slope (Western Mediterranean): isotopic, faunal and mineralogical relationships. Palaeogeogr., Palaeoclimatol., Palaeoecol., 81: 215-227.
- Vázquez, A. and Zamarreño, I., 1993. Late Quaternary hemipelagic carbonate oozes on the southwestern Balearic slope (western Mediterranean). Mar Geol., 112: 71-87.

- Volkmen, J.K., Eglinton, G., Corner, E.D.S., Forsberg, T.E.V., 1980. Long-chain alkenes and alkenones in the marine coccolithophorid *Emiliania huxleyi*. Phytochemistry 19: 2619-2622.
- Vrid-de Jong, E.W. de., Emburg, P.R.V. and Vrind, J.P.M. de, 1994. Mechanisms of calcification: *Emiliania huxleyi* as model system. In: The Haptophyte Algae. Ed. by: J.C. Green & S.B.C. Leadbeater. Systematics Association Special Volume 51, Clarendon Press, Oxford: pp. 149-166.
- Wallich, G.C. 1877. Observations on the coccosphere. Annals and Magazine of Natural History, (Series 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. Annales du Jardin botanique de Buitenzorg (ser. 2), 17 (2): 126-141.
- Westbroek, P. 1991. Life as a geological force. Dynamics of the Earth. Norton, New York (Commonwealt Fund Book Program), 240p. (Traduida al català per Marta Vigo, 1998. La vida com a força geològica. Dinàmica de la Terra. Ed. Proa.
- Westbroek, P., Young, J.R. and Linschooten, K., 1989. Coccolith production (Biomineralization) in the marine alga *Emiliania huxleyi*. J. Protozool. 36 (4): 368-373.
- Westbroek, P., Hinte, J.E. van, Brummer, G.-J., Veldhuis, M., Brownlee, C., Green, J.C., Harris, R. and Heimdal, B. R., 1994. *Emiliania huxleyi* as a key to biosphere-geosphere interactions. In: The Haptophyte Algae. Ed. by: J. C. Green & B. S. C. Leadbeater. Systematics Association Special Volume 51. Clarendon Press. Oxford: pp. 321-334.
- Whittaker, R.H. and Margulis, L., 1978. Protist classification and the kingdoms of organisms. BioSystems 10: 3-18.
- Winter, A., 1982. Paleonvironmental interpretation of quaternary coccolith assemblages from the Gulf of Aqaba (Elat), Red Sea. Revista Española de Micropaleontología XIV: 291-314.
- Winter, A. and Siesser, W.G., 1994. Atlas of living coccolithophores. In: Coccolithophores. Ed. by: A. Winter & W.G. Siesser. Cambridge University Press. Cambridge: pp. 107-159.
- Winter, A., Jordan, R.W. and Roth, P.H., 1994. Biogeography of living coccolithophores in ocean waters. In: Coccolithophores. Ed. by: A. Winter & W.G. Siesser. Cambridge University Press. Cambridge: pp. 161-177.
- Winter, A., Reiss, Z. and Luz, B., 1978. Living *Gephyrocapsa protohuxleyi* in the Gulf of Elat. Marine Micropaleontology 3: 295-298.
- Winter, A., Reiss, Z. and Luz, B. 1979. Distribution of living coccolithophore assemblages in the Gulf of Elat ('Aqaba). Marine Micropaleontology 4: 197-223.
- Young, J.R., 1989. Observations on heterococcolith rim structure and its relationship to developmental processes. In: Nannofossils and their aplications Ed. by: J. A. Crux & S. E. van Heck. Ellis Horwood. Chichester: pp. 1-20
- Young, J.R., 1992a. The description and analysis of coccolith structure: Nannoplankton Research Vol. 1. Proceedings of the Fourth INA Conference, Prague 1991, Ed. by: B. Hamrsmíd and J. R. Young. MND. Hodonín: pp. 35-71.
- Young, J.R., 1992b. Report Terminology working group meeting, London April 1992. INA Newsletter 14 (1): 6-8.
- Young, J.R., 1994. Functions of coccoliths. In: Coccolithophores, Ed. by: A. Winter and G. Siesser, Cambridge University Press. Cambridge: pp. 63-82.
- Young, J.R. 1998. Neogene. In: Calcareous Nannofossil Biostratigraphy. Ed. by: P.R. Bown. Chapman & Hall. London: pp. 225-265.

- Young, J.R. and Bown, P.R., 1997a. Higher classification of calcareous nannofossils. Journal of Nannoplankton Research 19 (1): 15-20.
- Young, J.R. and Bown, P.R., 1997b. Cenozoic calcareous nannoplankton classification. Journal of Nannoplankton Research 19 (1): 36-47.
- Young, J.R. and Westbroek, P., 1991. Genotypic variation in the coccolithophorid species *Emiliania huxleyi*. Marine Micropaleontology 18: 5-23.
- Young, J.R., Bergen, J.A., Bown, P.R., Burnett, J.A., Fiorentino, A., Jordan, R.W., Kleijne, A., Niel, B. van, Romein, A.J.T. and Salis, K. von, 1997. Guidelines for coccolith and calcareous nannofossil terminology. Palaeontology 40: 875-912.
- Young, J.R., Jordan, R.W. and Cros, L., 1998. Notes of nannoplankton systematics and life-cycles *Ceratolithus cristatus*, *Neosphaera coccolithomorpha* and *Umbilicosphaera sibogae*. Journal of Nannoplankton Research 20 (2): 89-99.
- Young, J.R., Davis, S.A., Bown, P.R. and Mann, S., 1999. Coccolith ultrastructure and biomineralisation. Journal of Structural Biology 126: 195-215.
- Ziveri, P., Thunell, R.C., Rio, D., 1995. Export production of coccolithophores in an upwelling region: Results from San Pedro Basin, Southern California Borderlands. Marine Micropaleontology, 24: 335-358.
- Ziveri, P., Broese, A.T.C., Hinte, J.E. van, Westbroek, P. and Honjo, S., 2000. The fate of coccoliths at 48°N 21°W, northeastern Atlantic. Deep-Sea Research II 47: 1853-1875.

Plate 1. *Helicosphaera* Scale bars = 1μ m

1-4. *Helicosphaera carteri* (Wallich) Kamptner var. *carteri* 1. *H. carteri* var. *carteri* coccosphere. Fronts-95, 23D, 50m.

2. Large coccosphere of H. carteri var. carteri. Fronts-95, 20I, 60m.

3. Coccosphere of H. carteri var. carteri showing coccoliths with two central pores and one

coccolith with a longitudinal slit (lower middle). Fans-1, 127, 25m.

4. Helicolith in proximal view (Catalano-Balearic Sea, 1990, (Fronts 90 - Est. 118))



Plate 2. Helicosphaera

Scale bars = $1\mu m$

1, 3, 5. Helicosphaera carteri var. hyalina (Gaarder) Jordan et Young

1. Coccosphere with helicoliths having the central area filled by needle-shaped elements. Meso-96, G2, 50m.

3. Complete coccosphere. Fans-3, K03, 60m.

5. Detail of a collapsed coccosphere showing coccoliths in distal view (centre), some in proximal view (left) and one in lateral view (right). Fans-3, K03, 40m.

2. Helicosphaera carteri var. wallichii (Lohmann) Theodoridis

2. Complete coccosphere. Fans-1, 123, 60m

4, 6. Helicosphaera pavimentum Okada et McIntyre

4. Complete coccosphere showing coccoliths with one or two aligned central slits; note the narrow flange of the helicoliths. Meso-96, I6, 90m.

6. Detail showing a coccolith with two central pores. Meso-95, 178, 40m.



Plate 3. Scyphosphaera

Scale bars = $1\mu m$

1-5. Scyphosphaera apsteinii Lohmann

- 1. Coccosphere of S. apsteinii with cribriliths and two lopadoliths. Fronts-95, 18P, 30m.
- 2. Disintegrated coccosphere with one lopadolith and cribriliths. Fans-1, 123, 40m.

3. Well formed coccosphere with one lopadolith in an equatorial position and another located internally. (Catalano-Balearic Sea, Fronts-92-93)

- 4. Detail of figure 3 showing clearly the internal lopadolith.
- 5. Lopadolith showing characteristic convex outline. Fans-2, M07, 60m.
- 6. Scyphosphaera apsteinii f. dilatata Gaarder
- 6. Some cribriliths and one lopadolith without distal decrease in width. Fronts-96, 027, 45m.



Plate 4. Anoplosolenia brasiliensis (Lohmann) Deflandre

Scale bars indicated in each figure.

1. Complete coccosphere. Fronts-95, 25W, 30m.

2. Detail of figure 1; note that these rhomboliths have few but wide laths.

3. Apical zone of another coccosphere with tapering end. Meso-96, G4, 5m.

4. Detail of figure 3; note the few but wide laths that characterize the Anoplosolenia rhomboliths found in these samples.


Plate 5. Calciosolenia murrayi Gran

Scale bars indicated in each figure.

1. Complete coccosphere. Fans-3, K03, 66m.

2. Detail of figure 1 showing the apical area.

3. Complete coccosphere with few apical spines. Fans-3, M11, 75m.

4. Detail of figure 3. Note the apical spines which appear to be transformed scapholiths (rhomboliths).

5. Detail of figure 3 showing rhomboliths with overlapping laths (upper middle) and other rhomboliths with highly transformed plate-like laths (lower part of the figure).

6. Detail of figure 3 with rhomboliths having real plates instead of laths.



Plate 6. Acanthoica

Scale bars indicated in each figure.

1-3. Acanthoica acanthifera Lohmann, ex Lohmann

1. Collapsed coccosphere. Fans-1, 123, 5m.

2. Detail of figure 1 showing tilted radial laths and slightly compressed sacculiform protrusion.

3. Complete coccosphere having body coccoliths with large sacculiform protrusion. Fans-3, K12, 25m.

4-6. Acanthoica quattrospina Lohmann

4. 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, 40m.

5. 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, 40m.

6. Detail of the body coccoliths. Fans-1, Est. 100, 40m.



Plate 7. Algirosphaera and Anacanthoica

Scale bars indicated in each figure.

1-4. Algirosphaera robusta (Lohmann) Norris

1. Complete coccosphere in apical view showing three joined circum-flagellar petaloid coccoliths, closing the flagellar opening. Fronts-95, 23D, 60m.

2. 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 (bottom). Fronts-95, 23D, 60m.

3. Detail of some coccoliths showing the large central protrusion and a radial cycle of laths in the basal part. Fronts-95, 23D, 60m.

4. Complete coccosphere in lateral view showing variable sized coccoliths, most with a pore in the central protrusion. Fans-1, 100, 5m.

5-6. Anacanthoica acanthos (Schiller) Deflandre

5. Complete coccosphere. Hivern-99, Est. 25, 60m.

6. Detail of figure 5 showing body coccoliths with a relatively wide rim.



Plate 8. Cyrtosphaera

Scale bars indicated in each figure.

1-2. Cyrtosphaera aculeata (Kamptner) Kleijne

1. Complete coccosphere. Fans-3, K03, 40m.

2. 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, Est. 25, 60m.

3-4. Cyrtosphaera lecaliae Kleijne

3. Complete coccosphere with the vari-monomorphic coccoliths. Fronts-96, 039, 10m.

4. Detail of figure 3 showing several coccoliths with slender laths and the highly sloped protrusion tipped by a small central papilla.

5-6. Cyrtosphaera cucullata (Lecal-Schlauder) Kleijne

5. Coccosphere with two detached coccoliths (upper right) showing their proximal side. Meso-96, G6, 40m.

6. 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, 5m.



Plate 9. Discosphaera and Palusphaera

Scale bars indicated in each figure.

1-2. Discosphaera tubifera (Murray et Blackman) Ostenfeld

1. Complete coccosphere showing the rhabdoliths with trumpet-like central structure. Hivern-99, Est. 25, 20m.

2. Detail with coccoliths having detached central structures. Note the small spine inside the central pore which was also shown by Kleijne (1992); each spine might be a small central papilla of the rhabdolith with organic remains which may help to maintain the join between the central structure and the basal part of these special rhabdoliths (see the resemblance of such spines with the central papilla in *Cyrtosphaera lecaliae* of plate 8, 4). Meso-95, 132, 5m.

3, 5. Palusphaera vandeli Lecal, emend. R.E. Norris

3. Collapsed coccosphere. Meso-96, D4, 40m.

5. Detail with a rhabdolith showing thin styliform central structure. Hivern-99, Est. 25, 60m.

4-6. Palusphaera sp. 1 (type robusta)

4. Coccosphere with coccoliths having thick styliform spines. Fans-3, M11, 75m.

6. Detail of several rhabdoliths in proximal view with several small nodes around the central pore. Fronts-95, 23D, 60m.



Plate 10. Rhabdosphaera

Scale bars indicated in each figure.

1-3. Rhabdosphaera clavigera Murray et Blackman

1. Complete coccosphere with endothecal rhabdoliths having styliform central structure which is characteristic of the specimens originally described as *R. stylifera*. Meso-95, 023, 5m.

2. Complete coccosphere with endothecal rhabdoliths having styliform central structures which end in small 'wings'; this morphotype was originally described as *R. stylifera* var. *capitellifera*. Fans-3, M11, 5m.

3. Detail showing exothecal coccoliths (without the styliform central structure) covering the bases of the endothecal rhabdoliths. Notice one detached endothecal rhabdolith showing the proximal side with central pore (upper left). Fronts-96, 027, 15m.

4-6. Rhabdosphaera xiphos (Deflandre and Fert) Norris

4. Complete coccosphere. Meso-96, I3, 40m.

5. A group of endothecal rhabdoliths showing a large proximal pore and slender styliform central structure; note the characteristic basal collar of the styliform central process. An exothecal coccolith in distal view (lower middle) shows the characteristic star-like central structure. Meso-95, 156, 5m.

6. Detail with endothecal and exothecal coccoliths. Notice the base of endothecal rhabdoliths is smaller and more rounded than that of exothecal coccoliths. Fans-3, K03, 40m.



Plate 11. Calciopappus

Scale bars indicated in each figure.

1-3. Calciopappus rigidus Heimdal in Heimdal et Gaarder

1. Slightly collapsed coccosphere. Fans-1, 78b, 5m.

2. Detail of the apical area of the coccosphere figured in 1, 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 (right), and body caneoliths (bottom). The whorl coccoliths partially cover the base of the spine-like appendages.

3. Complete coccosphere. Barcelona harbour, surface waters; Picasso workshop, July 98.

4-6. Calciopappus sp. 1 (very small)

4. Coccosphere with lightly calcified body coccoliths, curved spines and characteristic whorl coccoliths each with two spines. Meso-96, E8, 100m.

5. Coccosphere with very lightly calcified body coccoliths and curved spines. Cruise Fronts-95, 24W, 70m.

6. Detail of figure 5 with 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 70° .



Plate 12. Michaelsarsia

Scale bars indicated in each figure.

1-6. Michaelsarsia elegans Gran, emend. Manton et al.

1. Coccosphere with appendages. Fans-1, 123, 60m.

2. Detail of figure 1 showing body caneoliths with robust wall and central structure.

3. Detail of figure 4 showing body caneoliths and three small rhomboid circum-flagellar muroliths (lower left) with central protrusion.

4. Coccosphere with the four types of coccoliths: body caneoliths, small rhomboid circumflagellar caneoliths with spine, whorl coccoliths and detached link coccoliths which belong to the appendages. Fronts-96, 038, 60m.

5. Detail of the apical area of the coccosphere figured in 6, 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*).

6. Elongated coccosphere. Fans-3, K03, 66m.



Plate 13. Ophiaster

Scale bars indicated in each figure.

1-4. Ophiaster formosus Gran, sensu Gaarder 1967.

1. Coccosphere with appendages. Fronts-95, 20I, 80m.

2. Detail showing lightly calcified body caneoliths, circum-flagellar caneoliths with a robust spine and part of one osteolith (lower left). Fronts-95, 20I, 80m.

3. 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, 80m.

4. Coccosphere with circum-flagellar coccoliths with short spines (top), body caneoliths and appendages in antapical position. Fans-2, M07, 25m.

5-6. Ophiaster hydroideus (Lohmann) Lohmann emend. Manton et Oates

5. Coccosphere with circum-flagellar coccoliths with long spines (centre right), body caneoliths and osteoliths mostly detached. Fans-3, K12, 75m.

6. 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, 60m.



Plate 14. Coronosphaera

Scale bars indicated in each figure.

1-3. Coronosphaera binodata (Kamptner) Gaarder, in Gaarder et Heimdal.

1. Collapsed coccosphere. Meso-95, 147, 5m.

2. Complete coccosphere with circum-flagellar caneoliths with spine (top). Meso-95, 117, 5m.

3. 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, 5m.

4-6. Coronosphaera mediterranea (Lohmann) Gaarder, in Gaarder et Heimdal.

4. Detail with body caneoliths and one circum-flagellar caneolith (centre left) which has a strong squared spine; there is a caneolith in proximal view (lower middle), and three in distal view (right side of the figure). 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, 60m.

5. Complete coccosphere bearing five circum-flagellar caneoliths with spine. Fronts-96, 021, 20m.

6. Complete coccosphere. Fronts-95, 19T, 40m.



Plate 15. Gaarderia

Scale bars indicated in each figure.

1-7. Gaarderia corolla (Lecal) Kleijne.

1. Coccosphere showing endothecal and exothecal caneoliths. Fans-3, Est. K05, 40m.

2. 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, 10m.

3. Detail showing large exothecal coccoliths in distal view (bottom of the figure), variablesized 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, 25m.

4. Exothecal coccolith in proximal view showing no bilateral symmetry. Fronts-96, 027, 5m.

5. Detail with an endothecal caneolith in distal view (left) showing the strong sinistral obliquity of the rim elements and another endothecal caneolith in latero-proximal view (right). Fronts-96, 038, 45m.

6. Complete coccosphere with well developed exotheca. Fans-1, 127, 25m.

7. Coccosphere with slightly broken exothecal coccoliths which show the strong sinistral obliquity of the elements of the petaloid distal flange. Fans-2, M01, 10m.



Plate 16. Syracosphaera

Scale bars indicated in each figure.

1-2. Syracosphaera ampliora Okada et McIntyre

1. Complete coccosphere with monomorphic coccoliths. (Catalano-Balearic Sea, Fronts-92).

2. Detail of caneoliths with the characteristic centrally widened laths. Fans 1, 127, 40m.

3-6 Syracosphaera anthos (Lohmann) Janin

3. Complete coccosphere with overlapping exothecal coccoliths. Meso-96, G6, 70m.

4. Collapsed coccosphere with body caneoliths, circum-flagellar caneoliths with spine and exothecal coccoliths. Fronts-96, 039, 60m.

5. 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, 70m.

6. 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, 60m.



Plate 17. Syracosphaera dilatata group

Scale bars indicated in each figure.

1-6. Syracosphaera cf. dilatata Jordan Kleijne and Heimdal

1. Whole coccosphere showing detached apical exothecal caneoliths, near the circum-flagellar caneoliths with spine. Meso-96, I2, 40m.

2. Detail of the figure 1 with body caneoliths (lower left), four circum-flagellar caneoliths with spine (one partially hidden) and exothecal caneoliths (top) which are larger and more fragile than the body caneoliths. Note that all coccolith types have a proximal, a distal and a beaded mid-wall flange.

3. 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, 10m.

4. Detail with body caneoliths (right) and exothecal caneoliths (left). The exothecal caneoliths have higher and thinner walls. Meso-96, D4, 40m. Note that figures 3 and 4 are to the same scale.

5. Coccosphere with three circum-flagellar caneoliths with spine and several detached exothecal caneoliths. Hivern-99, Est. 25, 20m.

6. Collapsed coccosphere (to the same scale as figure 5) showing coccoliths with narrower distal flange and wider central area than the other specimens shown in this plate. Meso-95, 005, 5m.



Plate 18. Syracosphaera halldalii Gaarder ex Jordan et Green

Scale bars indicated in each figure.

1-3. S. halldalii (tooth-like form)

1. Monothecate coccosphere 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, 5m.

2. Detail with body caneoliths and two circum-flagellar caneoliths with spine. Fronts-96, 013, 10m.

3. Detail with three body caneoliths in distal view showing the wide and smooth distal flange which has small inward tooth-like protrusions. Meso-95, 147, 5m.

4-6. S. halldalii (finger-like form)

4. Monothecate coccosphere showing several circum-flagellar caneoliths with spine (upper left). Notice that this figure is to the same scale as figure 1. Hivern-99, Est. 25, surface waters.

5. Detail of figure 4 showing several body caneoliths (lower right) and several circum-flagellar caneoliths with spine; one of which, in side view, shows the high and straight wall.

6. Detail of body coccoliths: several in distal view showing the ribbed distal flange with the finger-like inward protrusions; the two body coccoliths in side view show the well developed wall framed by the two flanges. This figure is to the same scale as figure 3 and the smaller size of these coccoliths compared to those of the "tooth-like" form can easily be seen. Meso-96, G6, 40m.



Plate 19. Syracosphaera

Scale bars indicated in each figure.

1-2 Syracosphaera histrica Kamptner

1. Complete coccosphere with exothecal coccoliths covering the coccosphere. Meso-95, 161, 5m.

2. 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, 5m.

3-6. Syracosphaera lamina Lecal-Schlauder

3. Coccosphere with remains of the exothecal coccoliths (upper middle). Fronts-95, 23D, 70m.

4. Complete coccosphere showing the characteristic shape of this species. Fronts-95, 23D, 80m.

5. Detail of the figure 3 with body caneoliths having the characteristic keel-shaped central structure and the thin (sub)circular exothecal coccoliths (centre right) covering the caneoliths.

6. Detail with body caneoliths in distal view and one in proximal view (upper right). Meso-96, I3, 100m.



Plate 20. Syracosphaera

Scale bars = $1 \mu m$.

1-4. Syracosphaera marginaporata Knappertsbusch

1. 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, 75m.

2. Detail showing body caneoliths in distal view with the characteristic row of pores between the smooth central area and the flange (bottom), 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, 60m.

3. Detail showing the complex undulating exothecal coccoliths in distal view, partially covering spine-bearing caneoliths. Hivern-99, Est. 25, 60m.

4. Detail showing two circum-flagellar caneoliths with broken distal flanges and four-tipped spines. Fans-2, J03, 10m.

5-8. Syracosphaera molischii Schiller

5. 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, 70m.

6. Complete coccosphere showing considerable morphological variation among the body caneoliths. Fronts-95. 28C, 5m.

7. Detail of the internal part of a broken coccosphere with body coccoliths in proximal view (left), one partially formed coccolith (lower left) and exothecal coccoliths in proximal view with the characteristic small nodes in the central area (right). Fans-2, J03, 10m.

8. Coccosphere detail showing the apical area with five circum-flagellar caneoliths, a well developed flagellar opening and body caneoliths with a well developed central structure and internal protrusions of the distal flange. Meso-96, G6, 100m.



Plate 21. Syracosphaera nana (Kamptner) Okada & McIntyre

Scale bars = $1 \mu m$.

1-4. Syracosphaera nana heterococcolith phase

1. Ovoid coccosphere showing body caneoliths with the central area formed like a sloping roof, and one exothecal coccolith (upper left). Fans-3, M11, 60m.

2. Collapsed coccosphere with two caneoliths with very small spines (centre left) and exothecal coccoliths (upper left) most of which are detached. Fronts-95, 23D, 50m.

3. Detail with four caneoliths having small rounded spines and body caneoliths (lower left) showing hunchbacked shape as described by Kamptner (1941). Fronts-95, 20I, 60m.

4. 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, 70m.

5-6. Syracosphaera nana holococcolith phase

5. Complete coccosphere showing laminoliths as body holococcoliths. Meso-96, G6, 5m.

6. Detail of the apical area of a coccosphere showing a large flagellar opening and zygolithlike circum-flagellar holococcoliths. Fronts-95, 26W, 30m.



Plate 22. Syracosphaera nodosa group

Scale bars = $1 \mu m$.

1-4. Syracosphaera nodosa Kamptner

1. Complete coccosphere with exothecal coccoliths which show conspicuous radial cycle with sinistral obliquity. Fronts-95, 23D, 50m.

2. Detail with two 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, 45m.

3. Detail of figure 4 showing the endothecal body caneoliths with straight radial laths which link the elongated central connecting structure with the well developed external connecting ring.

4. 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, 35m.

5-7. Syracosphaera aff. nodosa

5. Complete coccosphere strongly resembling *S. nodosa* but with larger coccosphere and coccolith (both body caneoliths and exothecal coccoliths) size. Note that this figure has the same scale as figure 1. Hivern-99, Est. 25, 60m.

6. 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 (left) show the angular central structure and the two in proximal view (centre right) show the central area bordered by a low ridge as in *S. nodosa*. Note that this figure has the same scale as figure 2, highlighting the larger size of these coccoliths in comparison with those of *S. nodosa*. Hivern-99, Est. 25, 60m.

7. 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. Note that this figure is to the same scale as figure 4 for easy comparison of size. Meso-95, 132, 5m.


Plate 23. Syracosphaera noroitica Knappertsbusch

Scale bars = $1 \mu m$.

1. Coccosphere showing apical circum-flagellar caneoliths with long double-ended spine, varimorphic body caneoliths with robust spine near the apical pole and with no central spine at the antapical pole. Fronts-95, 19T, 40m.

2. 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, 66m.

3. Coccosphere showing varimorphic body caneoliths, circum-flagellar caneoliths with long spine and large exothecal caneoliths around the endotheca, mostly detached. The exothecal caneoliths have high walls with nodes forming a proximal flange. Meso-96, E 3/4, 70m.

4. Detail of apical area showing body caneoliths with robust spines (lower right), five circumflagellar caneoliths with double-ended long spines, which resemble the horns of a snail (centre); and an exothecal caneolith with nodes forming the proximal flange (upper left). Fronts-96, 013, 66m.

5. Detail of the antapical area with body caneoliths showing the double-layered wall and a well developed proximal flange, and caneoliths with lateral spines which appear to be the continuation of laths. Meso-96, 18, 70m.

6. Detail with antapical caneoliths (left) and four exothecal caneoliths showing the characteristic proximal nodes (right). Meso-96, I8, 70m.



Plate 24. Syracosphaera ossa (Lecal) Loeblich Jr. et Tappan

Scale bars = $1 \mu m$.

1. Coccosphere with body caneoliths showing the characteristic smooth distal flange and circum-flagellar caneoliths with the characteristic flattened spines. Meso-95, 161, 5m.

2. Complete coccosphere in apical view showing the complex undulating exothecal coccoliths around the flagellar area. Fronts-96, 027, 5m.

3. Coccosphere in antapical view showing the high variability in size and morphology of the body caneolith central structures and the presence of two coccoliths with short spines. Workshop Picasso, T5, July 98, surface waters off Barcelona.

4. Detail of the flattened spines of the circum-flagellar caneoliths which are tipped by four small, very thin projections (left) and one exothecal coccolith in proximal view (right) showing the complex-shaped rim and the elliptical central area which possesses two small nodes and is bordered by two parenthesis-like slits. Meso-95, 136, surf.

5. Detail of the two spine-bearing caneoliths and one complex undulating exothecal coccolith (upper middle) and several body caneoliths, mostly in distal and side view; near the top right corner there is a partially covered caneolith in proximal view. Fronts-96, 038, 15m.

6. 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, 20m.



Plate 25. Syracosphaera prolongata group

Scale bars = $1 \mu m$.

1-4. Syracosphaera prolongata Gran ex Lohmann (sensu Throndsen)

1. 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, 10m.

2. 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, 10m.

3. Detail of body caneoliths in distal view (bottom) which show a filament crossing the laths and smooth distal flange; one body caneolith, partially covered, in proximal view showing the three flanges (centre left); four exothecal caneoliths (top), two in proximal and two in distal view. Meso-96, A3, 40m.

4. Detail showing body caneoliths (left) and an exothecal caneolith, presumably in proximal view, showing the nodes which form the proximal flange, the slender laths and the hollow part of the central structure (right); a long spine belonging to a circum-flagellar caneolith is poking through the laths. Meso-96, A3, 40m.

5-8. *Syracosphaera prolongata* Gran ex Lohmann (*sensu* Heimdal et Gaarder)

5. Detail of the body caneoliths showing laths which appear to be composed of two parts and the characteristic twisted central structure. Meso-96, G4, 70m.

6. Complete elongated coccosphere showing exothecal caneoliths near the apical area. Meso-96, G4, 70m.

7. Detail showing two exothecal caneoliths; one showing the characteristic twisted central structure and a very narrow distal flange (left), the other, presumably in proximal view, showing the beaded proximal flange (right). Meso-96, F4, 70m.

8. Detail of the circum-flagellar caneoliths showing an uneven base with three well developed flanges. Meso-96, F4, 70m

Note that figures 3, 4 and 5 are to the same scale, highlighting the larger size of coccoliths of *S. prolongata sensu* Heimdal and Gaarder.



Plate 26. Syracosphaera

Scale bars = $1 \mu m$.

1-5. Syracosphaera pulchra Lohmann

1. Obpyriform coccosphere showing body caneoliths, five circum-flagellar caneoliths with spine, and vaulted exothecal coccoliths, mostly on the left side. Meso-95, 005, 5m.

2. Detail with body caneoliths and some exothecal vaulted coccoliths showing the central depression. Meso-96, G6, 5m.

3. Detail of the apical area showing six circum-flagellar caneoliths with robust, bifurcate ended spines. Fans-1, 100, 25m.

4. Detail showing one malformed body caneolith with overgrown flanges (upper left), one well-formed body caneolith in proximal view (top) and several in distal view (bottom); the central area of these body caneoliths is almost filled with thin laths. Meso-95, 114, 5m.

5. Detail with two exothecal vaulted coccoliths: in distal view showing the composed central area (left) and in proximal view showing the central hollow spine (right). Meso-96, G4, 40m.

6-7. Syracosphaera rotula Okada et McIntyre

6. Collapsed coccosphere with endothecal caneoliths (mostly in the right side of the figure) and some larger wheel-shaped exothecal coccoliths. Hivern-99, Est. 25, 20m.

7. Detail of one exothecal coccolith in proximal view showing the central area composed of two plates and bordered by a low ridge (as in the *S. nodosa* group), the laths showing obliquity (as in *S. nodosa* group) and the rim bent suggesting a transitional form between exothecal disc-like coccoliths and caneoliths. Hivern-99, Est. 25, 20m.



Plate 27. Syracosphaera tumularis Sánchez-Suárez

Scale bars = $1 \mu m$.

1. Collapsed coccosphere composed of monomorphic body caneoliths. Fronts-95, 19T, 60m. 2. 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, 75m.

3. Coccosphere with endothecal caneoliths and thin subcircular exothecal coccoliths (four on the coccosphere and others detached). Fronts-96, 019, 75m.

4. Detail of figure 3 showing the endothecal caneoliths partially covered by thin subcircular exothecal coccoliths, the central area of which is constructed by two angular plates and is surrounded by a cycle of joined wide and short laths with a wide rim with slight indentations.

5. Detail of figure 1 with one endothecal caneolith in proximal view showing two central straight longitudinal ridges.

6. Exothecal coccolith in proximal view showing a ridge bordering the central plates (this kind of construction is present in *S. nodosa* exothecal coccoliths). Fronts-96, 019, 75m

7. Exothecal coccolith in distal view showing slightly sinistral obliquity of the radial cycle which joins the rim and the central plates. Fronts-96, 019, 75m.



Plate 28. Syracosphaera sp. type D Kleijne 1993

Scale bars = $1 \mu m$.

1. Complete coccosphere with the exothecal caneoliths mostly detached surrounding the coccosphere. Hivern-99, Est. 25, 60m.

2. Collapsed coccosphere showing the body caneoliths (centre), four circum-flagellar caneoliths with a long spine and large exothecal caneoliths around the coccosphere, particularly near the apical area. Meso-96, I6, 70m.

3. Detail with the three types of caneoliths: some endothecal body caneoliths in lateral view showing the wall with a proximal, a distal and a mid-wall flange, the latter seemingly formed by a fold (upper left); an exothecal caneolith in lateral view with a very high wall with both a proximal and a flaring distal flange, but no mid-wall flange (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, 80m.

4. Detail of figure 7 with an exothecal caneolith in distal view showing the ribbed outer part of the distal flange and a very tenuous central structure. Meso-96, I4, 70m.

5. Detail of figure 7 with endothecal body caneoliths in distal view showing the distal flange with two different kind of ribs and a thick elongated central structure. Note that this figure is to the same scale as figure 4, demonstrating that endothecal caneoliths are smaller but more robust. Meso-96, I4, 70m.

6. Detail of a coccosphere showing the body caneoliths (upper right) and exothecal caneoliths with higher and thinner walls. Meso-96, G4, 70m.

7. 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, 70m.



Plate 29. Syracosphaera

Scale bars = $1 \mu m$.

1-4. Syracosphaera sp. type G Kleijne 1993

1. Collapsed coccosphere with varimorphic body caneoliths, some circum-flagellar caneoliths in apical position and some detached exothecal caneoliths (top). Fronts-96. 013, 75m.

2. Detail of figure 1 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 right) in distal view showing slender laths and a relatively high, distally crenalated wall.

3. Detail of figure 1 showing the varimorphic endothecal body caneoliths with the columnar central structure and one with no central structure (upper right).

4. 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 right), and some exothecal caneoliths with nodes forming a distal flange (top corners). Meso-96, A5, 70m.

5-6. Syracosphaera sp. type L Kleijne 1993

5. Complete spherical coccosphere showing the endothecal caneoliths and the small and thin exothecal coccoliths all around the coccosphere. Meso-95, 023, 5m.

6. Detail of figure 5 showing the muroliths (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.



Plate 30. Syracosphaera

Scale bars = $1 \mu m$.

1-2. Syracosphaera sp. 2 (slender)

1. Complete 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, 60m.

2. Detail showing some body endothecal caneoliths (lower left) with no central structure, exothecal coccoliths with a smooth distal side positioned around the flagellar area, and, partially hidden, some circum-flagellar caneoliths with long spines tipped by four small wings. Fans-1, Est. 123, 40m.

3-6. Syracosphaera sp. 3 (rods on the laths)

3. Coccosphere showing body caneoliths with irregularly distributed nodes and rods on the laths, and some simple undulating exothecal coccoliths (upper right). Meso-96, E8, 40m.

4. Complete 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, Est. 25, 60m.

5. Detail with body caneoliths in proximal view (left) and in distal view with irregularly distributed nodes on the laths (upper right). Fronts-95, 18P, 5m.

6. Detail showing one simple undulating exothecal coccolith with two parenthesis-like large slits around the central area and several endothecal caneoliths in proximal, side and distal views with regularly distributed rods on the laths. Note that this figure has the same scale as figure 5. Fans-1, 123, 60m.



Plate 31. Syracosphaera

Scale bars = $1 \mu m$.

1-3. Syracosphaera sp. 4 (now, S. delicata sp. nov.)

1. 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, Est. 25, 60m.

2. Detail showing two 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, 10m.

3. Detail of figure 1 showing two caneoliths with a small spine and a low and fragile wall (which is easily deformed and broken).

4-7. Syracosphaera sp. 5, aff. S. sp. type K of Kleijne (now S. bannockii comb. nov.)

4. Coccosphere showing body and circum-flagellar caneoliths. Hivern-99, Est. 25, 60m.

5. Complete coccosphere showing body caneoliths, four circum-flagellar caneoliths and a ribbon of exothecal coccoliths around the coccosphere. Hivern-99, Est. 25, 5m.

6. 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, 40m.

7. 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, 40m.



Plate 32. Syracosphaera

Scale bars = $1 \mu m$.

1-4. Syracosphaera sp. 6 (with stratified coccoliths)

1. Coccosphere with body caneoliths with a smooth central area, surrounded by numerous exothecal coccoliths on the filter. Meso-96, D8, 70m.

2. Collapsed coccosphere showing body caneoliths, one circum-flagellar caneolith with spine and three exothecal coccoliths in proximal view (upper right). Meso-96, D8, 70m.

3. Detail of figure 1 showing body caneoliths with a very thick wall and smooth central area.

4. Detail of the exothecal coccoliths showing a stratified distal side and a smooth proximal side (centre right). Fronts-96, 021, 90m.

5-8. Syracosphaera sp. 7 (aff. S. nana, laths with sinistral obliquity)

5. Collapsed coccosphere with body caneoliths, three circum-flagellar caneoliths and exothecal coccoliths (top). Fronts-96, 013, 60m.

6. Detail of figure 5 showing two oval exothecal coccoliths.

7. Detail of figure 5 showing three body caneoliths in distal view with a very low rim, laths with sinistral obliquity and no central structure.

8. Collapsed coccosphere showing body caneoliths and five circum-flagellar caneoliths each with a small spine. Fronts-95, 23D, 50m.



Plate 33. Syracosphaera

Scale bars = $1 \mu m$.

1-2. Syracosphaera sp. 8 (aff. to orbiculus (ovoid))

1. 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, 10m.

2. Coccosphere showing endothecal body caneoliths with a flat central structure and circum-flagellar caneoliths with short and pointed spines. Fans-2, M03, 5m.

Remarks: These two specimens appear to belong to one species but minor morphological differences and the absence of exothecal coccoliths in the specimen illustrated in figure 2 lead to the possibility that they might not belong to the same taxa.

3-5. Syracosphaera sp. 9 (aff. to orbiculus (spherical))

3. Spherical coccosphere showing body caneoliths, circum-flagellar caneoliths with robust and long spines and many detached exothecal coccoliths on the filter. Hivern-99, Est. 25, 40m.

4. Coccosphere showing endothecal coccoliths; the body caneoliths have a nearly flat and thin central connecting structure, straight laths, notable external connecting ring and a high and smooth wall; the circum-flagellar caneoliths possess robust spines with pointed endings. Hivern-99, Est. 25, 5m.

5. Characteristic asymmetrical exothecal coccoliths with the rim bent on two sides. Hivern-99, Est. 25, 20m.



Plate 34. *Alisphaera*

Scale bars = $1 \mu m$.

1-2. Alisphaera capulata Heimdal, in Heimdal et Gaarder

1. Collapsed coccosphere showing coccoliths with a characteristic extension. Fronts-96, 013, 60m.

2. Detail of coccoliths with a base plate filling the central area and a characteristic sinistrally inclined extension of the wider flange. Meso-96, A3, 40m.

3-4. Alisphaera sp. (with extended wider flange)

3. Detail of figure 4 showing coccoliths with a broad pointed extension of the wide distal flange.

4. Complete coccosphere in apical view (all coccolith extensions directed to the centre of the coccosphere). Fans-2, M03, 10m.

5-6. Alisphaera sp. (with small coccoliths)

5. Complete coccosphere with small coccoliths. Meso-96, E 3/4, 70m.

6. Detail showing coccoliths with a longitudinal slit in the central area; some of these coccoliths show a characteristic small vertical, flat, triangular protrusion. Fronts-96, 013, 60m.



Plate 35. Alisphaera

Scale bars = $1 \mu m$.

1-2. Alisphaera sp. (with a five sided extension)

1. Complete coccosphere showing coccoliths with a characteristic extension. Hivern-99, Est. 25, 80m.

2. Detail with coccoliths having a central area with a longitudinal slit and a wider distal flange that has a more or less five-sided extension. Fronts-95, 23D, 50m

3-4. Alisphaera sp. (with a beak-like protrusion)

3. Complete coccosphere showing coccoliths with a small pointed beak-like protrusion. Fans-1, 64, 25m.

4. Detail of figure 3 showing coccoliths with a longitudinal slit and a wider distal flange that has a spine-like extension.

5-6. Alisphaera unicornis Okada et McIntyre

5. Complete coccosphere showing coccoliths with a pointed protrusion. Hivern-99, Est. 25, 60m.

6. Detail of figure 5 showing coccoliths with a longitudinal irregularly shaped slit and a pointed horn-like protrusion on the wider distal flange.



Plate 36. Canistrolithus

Scale bars = $1 \mu m$.

1-4. Canistrolithus sp.1

1. Coccosphere 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, 84m.

2. Detail of figure 1 showing coccoliths with and without a lateral squared protrusion which finishes in a pointed spine.

3. Detail of figure 1 with part of the coccosphere and detached coccoliths in proximal and lateral view (bottom and right side of the figure).

4. Detail of figure 1 showing coccoliths with a high wall and notably asymmetric distal flanges constructed of conspicuous elements.



Plate 37. Emiliania huxleyi Hay et Mohler in Hay et al.

Scale bars = $1 \mu m$.

1. Complete type A coccosphere showing placoliths with a central area constructed of curved rods. The morphology of the placoliths allows a complete indentation of the coccoliths, thus forming a robust coccosphere. Fronts-96, 021, 20m.

2. Complete type A coccosphere showing placoliths with a central area that has a slight sieve-like appearance. Meso-95, 142, 5m.

3. Complete type C coccosphere showing small placoliths with a thin sieve-like plate in the central area. There are four detached placoliths: one in distal view (centre right), another in proximal-lateral view, showing the two shields (upper right) and two in proximal view which are partially covered by the coccosphere. Meso-95, 119, 70m.

4. 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, 50m.

5. Complete coccosphere showing placoliths with no central area, but having some remains of a possibly organic plate in one coccolith (upper left). Meso-95, 142, 40m.

6. Complete coccosphere showing placoliths with a filled central area having an overcalcified appearance. Fronts-96, 013, 90m.



Plate 38. Emiliania huxleyi Hay et Mohler in Hay et al.

Scale bars = $1 \mu m$.

1. Multilayered coccosphere, the coccoliths in the outer layers remaining imbricated due to the placolith structure. Meso-95, 115, 40m.

2. Two whole type A coccospheres. Meso-95, 015, 5m.

3. 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, 60m.

4. A coccolith-ring, more developed than that figured in 3, surrounded by type A coccoliths. Fans 2, J03, 10m.

5. Detail of coccolith structure showing clearly the anti-clockwise imbrication of the inner tube elements. Meso-95, 119, 70m.

6. Detail of coccolith structure showing clearly the inward growth of the inner tube elements. Meso-95, 119, 70m.



Plate 39. Gephyrocapsa

Scale bars = $1 \mu m$.

1. Gephyrocapsa oceanica Kamptner

1. 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, 5m.

2. Gephyrocapsa muellerae Bréhéret

2. Complete coccosphere with medium sized coccoliths which have a bridge that diagonally crosses the central area. Meso-95, 119, 70m.

3-6. Gephyrocapsa ericsonii McIntyre et Bé

3. 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, 5m.

4. Complete coccosphere of the type *protohuxleyi* showing distal shields built up of T-elements, like *Emiliania huxleyi*. This morphotype was considered as a different species by some authors. Meso-95, 023, 5m.

5. Complete coccosphere of the type *protohuxleyi* showing the T-elements in the distal shield and a thin thorn, which grows from the tube, in some coccoliths. Meso-95, 015, 5m.

6. Complete coccosphere of the type *protohuxleyi* "with thorn" showing very high bridges and long thorns which are perpendicular to the shield and grow from the tube of the placolith. Meso-95, 178, 40m.



Plate 40. Reticulofenestra and Gephyrocapsa

Scale bars = $1 \mu m$.

1. Reticulofenestra parvula (Okada et McIntyre) Biekart, var. parvula

1. 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, 5m.

2-4. Gephyrocapsa

2. *Gephyrocapsa* coccosphere possessing a coccolith without a bridge which strongly resembles *Reticulofenestra* coccoliths. Meso-95, 161, 40m.

3. Gephyrocapsa coccosphere possessing two coccoliths without bridges. Fans-2, J03, 25m.

4. *Gephyrocapsa ericsonii* type *protohuxleyi* coccosphere possessing a coccolith without a bridge which strongly resembles *Emiliania* coccoliths. Meso-95, 147, 5m.


Plate 41. *Calcidiscus leptoporus* (Murray et Blackman) Loeblich et Tappan Scale bars = $1 \mu m$.

1, 3 and 5. Calcidiscus leptoporus HET (heterococcolith phase)

1. Subcircular coccosphere showing the tightly interlocked coccoliths. Fans-2, N07, 25m.

3. Detail with two placoliths in distal view and six in proximal view which show the manner in which coccoliths imbricate. Fans-2, J03, 40m.

5. Detail of a placolith showing the narrow central area and the laevogyral curvature of the distal shield sutures. Fans-3, K12, 150m.

2, 4 and 6. Calcidiscus leptoporus HO (holococcolith phase, see Kleijne, 1991)

NB. This holococcolith-bearing phase was described previously as *Crystallolithus rigidus* Gaarder (Heimdal et Gaarder, 1980).

2. Coccosphere composed of irregularly elliptical crystalloliths. Fans-3, K12, 40m.

4. Detail showing coccoliths 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, 5m.

6. Detail with coccoliths in distal view which have a base layer of crystallites arranged in an hexagonal meshwork having six-sided perforations and an upper layer consisting of a variable number of single crystallites that are not connected with each other and cover perforations of the base layer. Fans-3, K12, 40m.



Plate 42. Oolithotus and Umbilicosphaera

Scale bars = $1 \mu m$.

1. Oolithotus antillarum (Cohen) Reinhardt, in Cohen et Reinhardt

1. Collapsed coccosphere with two partially covered placoliths in proximal view showing the small eccentrically placed proximal shield. Fronts-96, 021, 90m.

2. Oolithotus fragilis (Lohmann) Martini et Müller

2. 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, 40m.

3. Umbilicosphaera hulburtiana Gaarder

3. Complete coccosphere with elliptical placoliths having an elliptical opening which is surrounded distally by small nodes. Hivern-99, Est. 76, 20m.

4. Umbilicosphaera sibogae var. foliosa (Kamptner) Okada et McIntyre ex Kleijne

4. Complete coccosphere. Several placoliths have a characteristic small spine placed inside the central opening. Hivern-99, Est. 64, 30m.

5-6. Umbilicosphaera sibogae var. sibogae (Weber-van Bosse) Gaarder

5. Collapsed coccosphere consisting of many circular placoliths which have a large circular central opening. Fans-1, 127, 25m.

6. Detail with placoliths showing a distal shield slightly smaller than the proximal shield. Hivern-99, Est. 25, 60m.



Plate 43. Papposphaera lepida Tangen

Scale bars = $1 \mu m$.

1. Complete coccosphere, slightly collapsed. Meso-96, D6, 70m.

2. 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 which connects with the distal structure; a distal structure (calyx) in proximal view which shows the wristlet in the centre and the characteristic arrangement of the four elements or lobes (upper centre). Fronts-95, 20I, 80m.

3. 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, 70m.

4. Complete coccosphere with slightly varimorphic pappoliths. Meso-96, G4, 70m.

5. Collapsed coccosphere showing pappoliths with squared distal structures. Fans-1, 64, 81m.

6. Collapsed coccosphere with very small flower-like pappoliths. Fronts-96, 013, 75m.



Plate 44. Papposphaera

Scale bars = $1 \mu m$.

1-2. Papposphaera sp. type 1

1. Complete coccosphere showing small varimorphic pappoliths. Meso-96, I4, 100m.

2. Detail with pappoliths which consist of a spine without wristlet and a distal structure composed of four small rectangular elements. Fans-1, 127, 75m.

3-4. Papposphaera sp. type 2

3. Dimorphic coccosphere with varimorphic body pappoliths. Fans-1, 127, 100m.

4. Detail of figure 3 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.

5-6. Papposphaera sp. type 3

5. Coccosphere with varimorphic pappoliths. Fronts-95, 23D, 50m.

6. Detail of figure 5 showing the long shafts of the pappoliths which are tipped by four more or less rhomboidal elements.



Plate 45. Papposphaera

Scale bars = $1 \mu m$.

1-2. Papposphaera sp. type 4

1. Coccosphere showing varimorphism. Fans-3, M11, 75m.

2. Detail of the figure 1 with pappoliths that show a spine tipped by four distally serrated triangular elements.

3-4. Papposphaera sp. type 5

3. Complete coccosphere. Fronts-96, 013, 75m.

4. Detail with varimorphic pappoliths which have a propeller-like distal structure. Fans-1, 123, 75m.

5-6. ?Papposphaera sp. type 6

5. Coccosphere with varimorphic coccoliths. Fans-1, 100, 60m.

6. Detail of figure 5 showing pappolith-like base, no clear shaft and a distal structure consisting of three joined distally widened blade-like elements.



Plate 46. Papposphaera as Turrisphaera phase

Scale bars = $1 \mu m$.

1-2. Papposphaera as Turrisphaera phase sp. type A

1. Collapsed coccosphere showing varimorphic holococcoliths. Meso-96, E8, 100m.

2. Detail of figure 1 showing apple-core shaped holococcoliths.

3-4. Papposphaera as Turrisphaera phase sp. type B

3. Collapsed coccosphere with characteristic leaf-like holococcoliths. Meso-96, E3/4, 70m.

4. Detail of figure 3 showing holococcoliths with an apple-core like proximal side which is suddenly flattened becoming a distally spatulate leaf-like structure.



Plate 47. Pappomonas

Scale bars = $1 \mu m$.

1. Pappomonas sp. type 1

1. Detail showing some pappoliths with a long spine tipped by four small rods, and others without the central spine. Meso-96, D6, 100m.

2. Pappomonas sp. type 2

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, 40m.

3-4. Pappomonas sp. type 3

3. Dimorphic coccosphere with 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, 70m

4. Detail of figure 3 showing the long pappoliths with a flower-like distal calyx.

5. ?Pappomonas sp. type 4

5. 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, 25m.

6. ?Pappomonas sp. type 5

6. 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, 100m.

Note that figures 5 and 6 are to the same scale for size comparison.



Plate 48. Genus type A

Scale bars = $1 \mu m$.

1. Genus type A, species type 1

1. Monomorphic coccosphere with coccoliths showing long and sharp spines. Meso-96, D8, 100m.

2. Genus type A, species type 2

2. Coccosphere with coccoliths having a long central process with a characteristic feather-like distal structure. Fronts-96, 013, 90m.

3-4. Genus type A, species type **3**

3. Coccosphere with varimorphic coccoliths having a curved central process which becomes a hollow distal structure with pointed ends. Meso-96, I6, 70m.

4. 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, 80m.

5-6. Genus type A, species type 4

5. Coccosphere with varimorphic coccoliths which have a curved, hollow, straight-ended central process. Meso-96, I6, 70m.

6. Coccosphere with the same characteristics but of smaller size. The detached coccolith at the top of the figure appears to have a diagonal cross-bar in the base plate. Fronts-95, 25W, 70m.



Plate 49. Ceratolithus cristatus Kamptner

Scale bars = $1 \mu m$.

1. The large *Ceratolithus* nannolith with remains of the hoop-like coccoliths. Fans-1, 123, 25m.

2. The hoop-like coccoliths inside a cracked coccosphere of the former *Neosphaera* coccolithomorpha coccoliths. Fronts-96, 013, 10m.

3. A large *Ceratolithus cristatus* forma *rostratus* nannolith (see the '*rostrum*' protrusion, upper middle), a *Ceratolithus* nannolith of the forma *simplex* (left), three planoliths of the former *Neosphaera coccolithomorpha*, and remains of the hoop-like coccoliths inside the concave part of one planolith. Fans-1, 123, 40m.

4. Detail with hoop-like coccoliths and part of a ceratolith (lower right corner). Fronts-96, 013, 10m.

5. Collapsed coccosphere of the former *Neosphaera coccolithomorpha* showing the planoliths in proximal, distal and side views. Fronts-96, 013, 10m.

6. 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, 30m.



Plate 50. Genera incertae sedis

Scale bars = $1 \mu m$.

1-2. Umbellosphaera tenuis Paasche in Markali et Paasche, emend. Gaarder in Heimdal and Gaarder

1. Complete coccosphere showing macrococcoliths. Fronts-96, 021, 10m.

2. Coccosphere showing macrococcoliths and micrococcoliths which are smaller and have a large elliptical central area (central part of the figure). Fronts-96, 013, 60m.

3-4. Gladiolithus flabellatus (Halldal and Markali) Jordan and Chamberlain

3. Complete coccosphere in antapical view showing the small and flat elliptical lepidoliths partially covering the base of the tubular coccoliths. Fronts-95, 23D, 80m.

4. Detail with lepidoliths composed of two platelets joined by a suture line through the short axis of the lepidolith and the tubular coccoliths with very small spines on the distal side. Fronts-95, 23D, 70 m.

5-6. *Turrilithus latericioides* Jordan et al.

5. Complete coccosphere with the tower-shaped coccoliths. Meso-96, F2, 100m.

6. 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, 70m.



Plate 51. Florisphaera

Scale bars = $1 \mu m$.

1-5. Florisphaera profunda Okada and Honjo

1. Complete coccosphere in apical view showing the flower-like arrangement of the coccoliths. Fronts-96, 039, 160m.

2. Complete coccosphere in antapical view. Fronts-96, 021, 90m.

3. Collapsed coccosphere of the *elongata* type. Meso-95, 119, 70m.

4. Collapsed coccosphere of the profunda type. Fronts-95, 23D, 80m.

5. 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, 100m.

6. Florisphaera ?sp.

6. Collapsed coccosphere with more or less square coccoliths with irregular borders and a notable distal spine. Meso-96, D8, 70m.



Plate 52. Polycrater

Scale bars = $1 \mu m$.

1-2. Polycrater galapagensis Manton et Oates

1. Complete coccosphere with the small coccoliths arranged in slightly curved rows. Meso-95, 015, surf.

2. Detail of figure 1 showing the squared bowl-shaped coccoliths which usually have been called nannoliths due to their unusual structure.

3-4. Polycrater galapagensis var. A (with dots)

3. Complete coccosphere. Meso-95, 147, surf.

4. Detail of figure 3 showing coccoliths with dots on the distal part of the smaller half.

5-6. Polycrater sp. 1 (with slit)

5. Collapsed coccosphere. Fronts-95, 20I. 20m.

6. Detail of figure 5 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).



Plate 53. Polycrater

Scale bars = $1 \mu m$.

1-2. Polycrater sp. 2 (with holes, Gaudí architecture)

1. Coccosphere showing coccoliths with elongated holes. Fans-3, K03, 25m.

2. Detail of figure 1 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).

3-4. *Polycrater* sp. 3 (with lip-like borders)

3. Collapsed coccosphere showing small coccoliths with rounded borders on the distal flange. Fronts-95, 24W, 5m.

4. Detail of figure 3 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.

5-6. *Polycrater* sp. 4 (minimum?)

5. Coccosphere showing numerous very small coccoliths. Meso-96, E3/4, 40m.

6. Detail of figure 5 showing the very small and simple coccoliths.



Plate 54. Polycrater

Scale bars = $1 \mu m$.

1-2. Polycrater sp. 5 (spinous, two petal-like structures very modified)

1. Coccosphere with a spiny shape like a sea urchin due to the very modified shape of the coccoliths. Meso-96, E3/4, 70m.

2. Detail of figure 1 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. There are two coccoliths with a squared ladle appearance (centre left).

3-6. *Polycrater* **sp. 6** (two petal-like structures very modified, the other two lacking)

3. Coccosphere showing the spiny appearance. Meso-96, D6, 5m.

4. Detail of figure 3 showing the coccoliths; half of the petal-like part of the coccoliths narrows to form a rod-like extension and the other half is missing; the sepal-like part does not appear to be modified (upper right).

5. Coccosphere showing the very modified "polycrater" coccoliths. Meso-96, D6, 40m.

6. Detail showing the distal rods and the sepal-like proximal part of the coccoliths (upper middle, centre right by the hole in the filter, and lower left corner) Meso-96, A3, 40m.



Plate 55. Anthosphaera

Scale bars = $1 \mu m$.

1-3. Anthosphaera fragaria Kamptner, emend. Kleijne

1. Complete coccosphere with dimorphic coccoliths; the large, broad fragarioliths are positioned apically (upper part of figure). Fans-3, M11, 5m.

2. 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, 20m.

3. Coccosphere on which the most distal part of the fragarioliths is slightly broken. Fans-3, K12, 40m

4. Anthosphaera cf. fragaria Kamptner, emend. Kleijne

4. Coccosphere showing small sized coccoliths with large pores in both calyptrolith-like body coccoliths and circum-flagellar fragarioliths. Fronts-95, 23D, 50m.

5-6. Anthosphaera lafourcadii (Lecal) Kleijne

5. Complete coccosphere showing body coccoliths with perforations and fragarioliths having a broad but short process. Fans-1, 127-141, 25m.

6. Complete coccosphere with coccoliths showing the roughly-packed arrangement of the crystallites. Fans-1, 100, 25m.



Plate 56. Anthosphaera periperforata Kleijne

Scale bars = $1 \mu m$.

1-2. Type 1

1. 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, 40m.

2. Detail with body coccoliths and, in the centre of the figure, two fragarioliths with pointed endings to the distal protrusion. Meso-96, G2, 20m.

3-4. Type 2

3. Complete coccosphere showing fragarioliths with very pointed endings and having body coccoliths with a small distal spine. Meso-96, E3/4, 40m.

4. Detail showing body coccoliths having columns which appear to support the distal dome; the fragarioliths have a pointed protrusion and long rows of crystallites which connect the distal part of the protrusion with the end of the basal ring (see upper part of the figure). Fronts-95, 23D, 30m.

5-6. Type 3

5. Coccosphere with very perforated coccoliths. Meso-96, E3/4, 40 m.

6. Detail of figure 5 showing body coccoliths formed by rows of crystallites, a connecting basal ring of two crystallites width and a connecting distal part tipped by a central spine. The fragarioliths, in the upper part of the figure, are partially disintegrated.



Plate 57. Anthosphaera and Calicasphaera

Scale bars = $1 \mu m$.

1-2. Anthosphaera sp. type A (very ornamented (origami art))

1. Coccosphere with dimorphic coccoliths having very ornamented apical fragarioliths and body coccoliths which resemble origami paper boats. Fronts-95, 23D, 50m.

2. Detail showing a fragariolith (centre left) with rows of crystallites forming 'spines' along the distal part of the blade, the central one being the longest. Several ornamented calyptrolith-like body coccoliths are figured, some in proximal view, showing a tear in the central part of the base plate, and others in distal and lateral view, showing a basal ring and columns of crystallites supporting the paper boat shaped distal part. Fronts-95, 23D, 50m.

3-6. Calicasphaera

3 and 5. Calicasphaera concava Kleijne

3. Coccosphere with calicaliths in distal and proximal view. Fronts-96, 039, 40m.

5. Detail of figure 3 showing the concave wall of the calicaliths widening to form a broad distal opening.

4 and 6. Calicasphaera blokii Kleijne

4. Coccosphere with calicaliths mostly in distal view, with two detached calicaliths showing the elliptical proximal side (lower middle/right). One calicalith in side view (upper middle) shows the convex distal wall. Fans-3, K03, 10m.

6. Detail of figure 4 with calicaliths in distal view showing concentric rows of large crystallites.



Plate 58. Calyptrolithina

Scale bars = $1 \mu m$.

1-2. Calyptrolithina divergens (Halldal et Markali) Heimdal var. divergens

1. Coccosphere showing only the body calyptroliths. Fronts-95, 23D, 50m.

2. Detail of figure 1 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.

3-4. Calyptrolithina divergens var. tuberosa (Heimdal) Jordan et al.

3. 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, 25m.

4. Detail showing a transverse row of zygoliths with a bridge tipped by a central protrusion, and the perforated body calyptroliths. Fronts-95, 23D, 10m.

5-6. Calyptrolithina wettsteinii (Kamptner) Kleijne

NB. C. wettsteinii is now considered as the holococcolith phase of Coronosphaera mediterranea (see Chap. IV)

5. Complete coccosphere 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 and a rounded central protrusion. Fans-3, M11, 5m.

6. 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 real zygoliths. Meso-95, 147, surf.


Plate 59. Calyptrolithophora

Scale bars = $1 \mu m$.

1-2. Calyptrolithophora gracillima (Kamptner) Heimdal

1. Coccosphere showing a flagellar area surrounded by zygolith-like calyptroliths and body coccoliths which are calyptroliths. Fans-1, 100, 40m.

2. 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-top corner of the figure. Fronts-95, 23D, 50m.

3-6. Calyptrolithophora papillifera (Halldal) Heimdal in Heimdal et Gaarder

3. Coccosphere showing a notable flagellar opening. Fans-1, 100, 25m.

4. Coccosphere showing the circum-flagellar calyptroliths having characteristic rows of crystallites on the distal surface. Meso-96, I8, 40m.

5. Detail showing the flat body calyptroliths and a prominent hump-like square-sided circum-flagellar calyptrolith (upper left corner) which shows the characteristic parallel rows of crystallites. Meso-95, 163, 40m.

6. Detail of figure 3 showing the hexagonal arrangement of crystallites in the body calyptroliths, which have a slightly protruding rim.



Plate 60. Calyptrosphaera

Scale bars = $1 \mu m$.

1-2. Calyptrosphaera cialdii Borsetti et Cati

1. Coccosphere with monomorphic coccoliths. Fans-3, K03, 25m.

2. Detail of figure 1 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).

3-4. Calyptrosphaera heimdaliae R.E. Norris, orthog. emend. Jordan et Green

3. 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, 30m.

4. 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, 5m.

5-6. Calyptrosphaera sp. type 1 (smaller tholifera/heimdaliae)

5. Collapsed coccosphere with calyptroliths similar to those of *C. heimdaliae*, but smaller and having more numerous and smaller lateral pores. Fans-3, K05, 5m.

6. Coccosphere possessing the characteristics of the specimen figured in 5, but having more calyptroliths with smaller and more numerous lateral pores. Fronts-96, 027, 10m.



Plate 61. Calyptrosphaera

Scale bars = $1 \mu m$.

1-2. Calyptrosphaera dentata Kleijne

1. Coccosphere with monomorphic coccoliths. Fans-3, K07, 25m.

2. Detail of figure 1 showing calyptroliths with a central area surface having six-sided regularly arranged perforations and a thick rim with a tooth-like protrusion.

3-4. Calyptrosphaera oblonga Lohmann

NB. C. oblonga is now considered to be the holococcolith phase of Syracosphaera pulchra (see Chap. IV)

3. Complete coccosphere with circum-flagellar calyptroliths having a distal protrusion (upper middle) which is absent in the other calyptroliths. Workshop Picasso, Est. T1, July 1998.

4. Detail of calyptroliths: the basal part consists of a ring three crystallites wide and only one crystallite high, and a presumably organic baseplate (half missing in the calyptrolith in the upper right corner of the figure); 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, 5m.

5-6. Calyptrosphaera sphaeroidea Schiller

5. Coccosphere with globular calyptroliths; the coccoliths in side view show a basal ring one crystallite thick. Meso-95, 023, 5m.

6. Detail of a coccosphere showing irregularly constructed calyptroliths which are not completely closed distally. Fans-1, 100, 5m.



Plate 62. Corisphaera

Scale bars = $1 \mu m$.

1-2. Corisphaera strigilis Gaarder

1. Coccosphere with dimorphic coccoliths. Meso-96, G6, 5m.

2. Detail showing flat body coccoliths with thick bridge (lower right corner) and circum-flagellar coccoliths with a leaf-like pointed extension (left). Fronts-95, 23D, 30m.

3-4. Corisphaera tyrrheniensis Kleijne

3. Coccosphere with several slightly disintegrated coccoliths. Note the zygolith (centre left) which resembles the zygoliths of *Zygosphaera marsilii* (see *Z. marsilii* in Plate 73, figs. 5 and 6). Meso-96, G6, 40m.

4. Detail showing the delicate, perforated construction of the zygoliths. Fans 3, M11, 25m.

5-6. Corisphaera sp. type A of Kleijne (1991)

NB. *Corisphaera* sp. type A of Kleijne is now considered to be the holococcolith phase of *Syracosphaera bannockii* (see Chap. IV)

5. Slightly collapsed coccosphere. Note the possible residual parts of the flagella that appear to emerge from the flagellar area. Fronts-95, 18P, 5m.

6. 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, D8, 40m.



Plate 63. Corisphaera

Scale bars = $1 \mu m$.

1. Corisphaera cf. gracilis

1. Coccosphere with dimorphic coccoliths. Fronts-96, 013, 30m.

2. Corisphaera sp. 1 (aff. type A of Kleijne, 1991)

2. Coccosphere with dimorphic coccoliths; body zygoliths have a low and very narrow bridge. Fronts-96, 039, 10m.

3. Corisphaera sp. 2 (aff. type A of Kleijne, 1991 and C. gracilis)

3. 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, 40m.

4. Corisphaera sp. 3 (double-layered body zygoliths)

4. Slightly collapsed coccosphere with dimorphic coccoliths; body zygoliths with doublelayered wall and undulated bridge, circum-flagellar zygoliths with high and pointed bridge. Meso-96, I4, 40m.

5. Corisphaera sp. 4 (body zygoliths with pointed bridge)

5. 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, 20m.

6. Corisphaera sp. 5 (ornamented circum-flagellar coccoliths)

6. 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, 20m.



Plate 64. Daktylethra and Helladosphaera

Scale bars = $1 \mu m$.

1-3. Daktylethra pirus (Kamptner) Norris

1. Collapsed coccosphere showing calyptroliths with a vaulted distal protrusion and pores around the rim. Meso-95, 178, 40m.

2. Detail of figure 1 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. One calyptrolith in distal view (lower right).

3. Detail of figure 1 with calyptroliths in side view showing a complex rim and the pores at the base of the vaulted protrusion which has a distal point which is characteristic of the circum-flagellar calyptroliths.

4-7. Helladosphaera cornifera (Schiller) Kamptner

4. 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, 5m.

5. Large coccosphere with helladoliths at both apical and antapical poles, thus possibly representing a pre-division stage. Meso-96, G6, 40m.

6. Detail showing helladoliths with a high, double-layered process which has a pointed angular tip and a pore in the base. Meso-95, 147, 5m.

7. Detail of zygoliths showing high bridges with thick intersections with the tube. Fans-3, K03, 25m.



Plate 65. *Homozygosphaera and Periphyllophora* Scale bars = $1 \mu m$.

1-2. Homozygosphaera arethusae (Kamptner) Kleijne

1. Complete coccosphere showing body zygoliths with broad bridges apical circum-flagellar zygoliths with higher bridges adorned with a distal protrusion (upper middle). Fans-1, 123, 5m.

2. 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, 40m.

3-4. Homozygosphaera triarcha Halldal and Markali

3. Coccosphere having three-arched coccoliths. The higher coccoliths have an adorned distal tip (e.g. upper centre). Workshop Picasso, Est. T4, July 1998.

4. Detail showing the disposition of the arches. Workshop Picasso, Est. T4, July 1998.

5-6. Periphyllophora mirabilis (Schiller) Kamptner

NB. *P. mirabilis* is now considered to be the holococcolith phase of *Syracosphaera anthos* (see Chap. IV)

5. Complete coccosphere showing the presumed flagellar opening (centre). Workshop Picasso, Est. T4, July 1998.

6. Detail showing helladolith structure with the double-layered protrusion and double-layered tubes. Meso-95, G2, 20m.



Plate 66. Poricalyptra

Scale bars = $1 \mu m$.

1-3. Poricalyptra aurisinae (Kamptner) Kleijne

1. Complete coccosphere showing body calyptroliths with transverse slits and circum-flagellar helladoliths. Fans-3, K12, 60m.

2. Detail with body calyptroliths in lateral view (left) showing the perforated wall and in distal view (right) showing the transverse slits and a central transverse protrusion with crystallites. Meso-95, 163, 40m.

3. Detail of helladoliths. Meso-96, E2, 5m.

4-6. Poricalyptra isselii (Borsetti and Cati) Kleijne

4. Detail of calyptroliths in distal view (top) showing six perforations and a small transverse row of crystallites and in lateral view (lower left) showing perforations in the wall. Meso-95, 161, 5m.

5. Large coccosphere with body calyptroliths only, several of which are partially disintegrated. Meso-95, 161, 5m.

6. Detail with two helladoliths. Meso-95, 161, 5m.



Plate 67. Poritectolithus

Scale bars = $1 \mu m$. **1-2.** *Poritectolithus* sp. 1

1. Coccosphere having flat and thin calyptroliths and helladoliths without tube. Fronts-95, 24W, 30m.

2. Detail of figure 1 with body coccoliths distally covered by rows of crystallites and circumflagellar coccoliths resembling helladoliths but lacking the tube and possessing a pointed protrusion.

3-4. Poritectolithus tyronus Kleijne

3. Coccosphere with low body calyptroliths and irregularly shaped circum-flagellar helladoliths. Fans-3, K12, 75m.

4. Detail of figure 3 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.

5-6. Poritectolithus poritectus (Heimdal) Kleijne, orthog. emend. Jordan et Green

5. Coccosphere with helladoliths and varimorphic calyptroliths, higher and more vaulted near the apical area. Meso-96, E2, 70m.

6. Detail of figure 5 showing helladoliths and calyptroliths with protruding rim.



Plate 68. Poritectolithus

Scale bars = $1 \mu m$.

1-2. Poritectolithus sp. 2

1. Coccosphere with zygoliths as body coccoliths, the bridges of which are constructed by arches of crystallites. Fronts-95, 23D, 60m.

2. Detail of figure 1 showing circum-flagellar coccoliths with a broad but not very high protrusion.

3-6. Poritectolithus (details for comparison)

Note that the four figures are to the same scale to facilitate comparison.

3. Poritectolithus sp. 1

Detail with the low calyptroliths. Fronts-95, 24W, 30m.

4. Poritectolithus tyronus

Detail with the slightly vaulted calyptroliths showing the distal rows of crystallites symmetrically arranged in pairs (each row of apparently triangular crystallites is symmetrically matched by a neighboring row). Fans-3, K12, 75m.

5. Poritectolithus poritectus

Detail with the calyptroliths showing the same characteristic of symmetry among neighboring rows. Meso-96, E2, 70m.

6. Poritectolithus sp. 2

Detail with a body zygolith (upper left) showing the bridge constructed of rows of crystallites. Fronts-95, 23D, 60m.



Plate 69. Sphaerocalyptra

Scale bars = $1 \mu m$.

1-2. Sphaerocalyptra quadridentata (Schiller) Deflandre

1. Coccosphere with some body calyptroliths slightly broken. Fronts-96, 013, 10 m.

2. 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, 5m.

3-4. Sphaerocalyptra cf. adenensis Kleijne

3. Completely collapsed coccosphere showing high variability in the size of body calyptroliths and three large circum-flagellar calyptroliths (upper right). Fans-3, K03, 10m.

4. Detail with calyptroliths showing the packed crystallites arranged in more or less concentric rows and the single-layered base. Meso-96, A5, 5m.

5-6. Sphaerocalyptra sp. 1

5. Coccosphere showing body and circum-flagellar calyptroliths. Fans-3, K03, 10m.

6. 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, 5m.



Plate 70. Sphaerocalyptra

Scale bars = $1 \mu m$.

1-2. Sphaerocalyptra sp. 1 (with few crystallites in distal)

NB. This taxa is now considered to be the holococcolith phase of *Acanthoica quattrospina* (see Chap. IV)

1. Completely collapsed coccosphere showing body calyptroliths and two circum-flagellar calyptroliths (centre right). Fans-2, N07, 10m.

2. Detail of figure 1 with calyptroliths in proximal view (upper left, lower left) showing the wide basal ring of around 3-5 rows of crystallites, the calyptroliths in distal view (right) have angular crystallites that scarcely cover the distal face, circum-flagellar calyptroliths (centre left, partially hidden) have a large distal protrusion.

3. Sphaerocalyptra sp. 2

3. Disintegrated coccosphere showing cone-shaped body calyptroliths with very thin pointed endings; circum-flagellar coccoliths are higher and more robust (top). Meso-96, D6, 5m.

4-6. Sphaerocalyptra sp. 3

4. Coccosphere with very perforated and pointed coccoliths which are formed by columns of crystallites. Fronts-95, 28C, 20m.

5. 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, 50m.

6. 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, 40m.



Plate 71. Sphaerocalyptra

Scale bars = $1 \mu m$.

1-2. Sphaerocalyptra sp. 4

1. Collapsed coccosphere with characteristic circum-flagellar coccoliths which possess a robust stick-like protrusion. Fronts-95, 23D, 30m.

2. Detail of figure 1 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.

3-4. Sphaerocalyptra sp. 5

3. Coccosphere with perforated, highly diverse-shaped calyptroliths. Meso-96, I8, 40m.

4. Detail of figure 3 showing the pointed circum-flagellar coccoliths and the rounded body calyptroliths which are constructed of large crystallites.

5-6. Sphaerocalyptra sp. 6

5. Coccosphere with pointed circum-flagellar coccoliths and very simple body coccoliths, most of which have lost the cover. Meso-92, E3-4, 40m.

6. Detail with very thin and high body coccoliths (left) and body coccoliths which seem to be calyptroliths with the distal cover missing. Fronts-95, 20I, 20m.



Plate 72. Syracolithus

Scale bars = $1 \mu m$.

1-2. Syracolithus catilliferus (Kamptner) Deflandre

NB. S. catilliferus is now considered to be the holococcolith phase of *Helicosphaera carteri* (see Chap. IV)

1. Coccosphere with a notable flagellar area. Meso-96, G6, 5m.

2. Detail showing laminoliths which are solid coccoliths with a sharply pointed distal protrusion (see the coccolith in distal view in the lower left corner). Meso-95, 147, 5m.

3. Syracolithus confusus Kleijne

NB. S. confusus is now considered to be the perforated holococcolith phase of *Helicosphaera* carteri (see Chap. IV)

3. 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, 5m.

4. Syracolithus dalmaticus (Kamptner) Loeblich et Tappan

4. Coccosphere with coccoliths which show a thick cover and a hollow central part. Hivern-99, Est. 69, 40m.

5. Syracolithus schilleri (Kamptner) Kamptner

5. Coccosphere with a flagellar opening (centre); the coccoliths have 8 to 16 pores (perforations through the laminolith) and a central protrusion. Meso-96, A5, 5m.

6. Syracolithus quadriperforatus (Kamptner) Gaarder

6. Coccosphere with very high and perforated laminoliths. Meso-95, 023, 5m.



Plate 73. Zygosphaera

Scale bars = $1 \mu m$.

1-2. Zygosphaera amoena Kamptner

1. Complete coccosphere showing circum-flagellar zygoliths (top) with double-layered wall and body laminoliths. Fans-3, K12, 60m.

2. 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, 40m.

3-4 Zygosphaera bannockii (Borsetti and Cati) Heimdal

NB. Z. bannockii is now considered to be the holococcolith phase of Syracosphaera bannockii (see Chap. IV)

3. Coccosphere with body coccoliths with a transverse ridge; part of one apical zygolith is seen at the top of the figure. Fans-1, 100, 40m.

4. Detail showing two circum-flagellar zygoliths with a high and broad protrusion (top) and zygoform body laminoliths. Fans-1, 100, 25m.

5-6. Zygosphaera marsilii (Borsetti and Cati) Heimdal

5. Coccosphere showing microperforate appearance of coccoliths. Hivern-99, Est. 25, 20m.

6. 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, 5 m.



Plate 74. Zygosphaera

Scale bars = $1 \mu m$.

1-6. Zygosphaera hellenica Kamptner

1. Complete coccosphere showing body laminoliths only. Meso-95, 023, surf.

2. Complete coccosphere showing body laminoliths, several with pores, and two circum-flagellar zygoform coccoliths (upper left). Workshop Picasso, Est. T4, July 1998.

3. 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, 5m.

4. Detail with laminoliths in distal view showing the ordered arrangement of crystallites and one laminolith in side view (upper left) showing the rim with a row of perforations. Meso-95, 023, 5m.

5. Collapsed coccosphere; coccoliths of unusual appearance. Fronts-95, 28C, 20m.

6. Detail of figure 5 with body laminoliths (left) and circum-flagellar zygolith-like laminoliths (right) showing the irregular crystallite arrangement which gives the coccosphere this unusual appearance.



Plate 75. Unidentified species

Scale bars = $1 \mu m$.

1-2. Holococcolithophore sp. 1 (Coccoliths with two small pores in proximal side)

1. Holococcolithophore that appears highly related to the genus *Sphaerocalyptra*, but possesses only monomorphic coccoliths; no larger calyptroliths were found in the specimens studied. Meso-96, D4, 5m.

2. Detail with holococcoliths in distal and proximal view. The proximal side of the coccoliths has two diagonally arranged pores and the basal plate seems to be solid, more closely resembling a laminolith than a calyptrolith, a ring of crystallites typically being visible on the proximal side of the base of the latter. In distal view the coccoliths could be considered to be either calyptroliths with an underdeveloped cover or laminoliths with a central mound of crystallites. Fronts-95, 23D, 5m.

3-4. Holococcolithophore sp. 2 (Coccoliths of *Anthosphaera* affinity?)

3. Coccosphere with dimorphic coccoliths; characteristic circum-flagellar coccoliths and very simple body holococcoliths. Meso-96, G4, 5m.

4. Detail showing apical coccoliths (upper right) which resemble fragarioliths with a slender pointed arch and body coccoliths which seem to be very simple calyptroliths, some with the central mound missing. These characteristics suggest a relationship with *Anthosphaera*. Fans-1, Est 64, 5m.

5-6. Coccolithophore sp. 1 (affinities with Rhabdosphaeraceae family?)

5. 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, 57m.

6. Detail of coccoliths which resemble calyptroliths but without clear crystallites. No clear structural similarities with *Algirosphaera* or *Cyrtosphaera* can be ascertained; the SEM does not provide enough resolution to determine whether they are holococcoliths or heterococcoliths. Meso-96, D8, 70m.



Plate 76. Unidentified species

Scale bars = $1 \mu m$.

1. Coccolithophore sp. 2 (Syracosphaera affinity?)

1. 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. These characters suggest an affinity with *Syracosphaera*, but further specimens are required to establish clear relations. Meso-96, E8, 100m.

2. Coccolithophore sp. 3

2. Very small and rounded coccoliths with a bridge which is higher and centrally pointed on several coccoliths; they present no clear crystallite structure. Meso-96, G4, 70m.

3-4. Unidentified sp. 1

3. Complete cell case showing a honeycomb aspect. Fans-3, K03, 25 m.

4. Detail showing small murolith-like constructions without proximal or distal covers and with a perforated wall. Fronts-95, 23D, 50m.

5-6. Unidentified sp. 2

5. 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. Such detailed structure is homologous to the *Papposphaera* genus. If the 'coccoliths' of this unidentified sp. 2 are proved to be constructed of calcium carbonate, it must be related with Papposphaeraceae family. At present the chemical composition is unknown. Meso-96, D6, 100m. 6. Detail showing the structure of the complex varimorphic stars.


Plate 77. *Helicosphaera carteri* - *Syracolithus catilliferus* combination Scale bars = $2 \mu m$.

- 1. Helicosphaera carteri. Fronts-96, 021, 68m.
- 2. Syracolithus catilliferus. Meso-96, A3, 5m.
- 3. Collapsed coccosphere with H. carteri and S. catilliferus coccoliths. Fronts-95, 24W, 70m.
- 4. Detail of figure 3.
- 5. A well-formed combination coccosphere of *H. carteri* and *S. catilliferus*. Meso-96, G4, 70m.
- 6. Detail of figure 5.



Plate 78. Syracosphaera pulchra - Calyptrosphaera oblonga combination

Scale bars = $2 \mu m$.

Syracosphaera pulchra with vaulted exothecal coccoliths (upper left side), body caneoliths and circum-flagellar caneoliths with bifurcate-tipped spines. Meso-95, 05, 5m.
 Calyptrosphaera oblonga with some body caneoliths of Syracosphaera pulchra (see

arrows). Fronts-96, 021, 20m.

3. Syracosphaera pulchra - Calyptrosphaera oblonga combination as seen in the L. M. (a, the specimen at high focus; b, the specimen at medium focus). Medea-98, Masnou off-shore.
4. The same specimen as in figure 3, seen in the SEM.



Plate 79. Syracosphaera anthos - Periphyllophora mirabilis combination

Scale bars = $2 \mu m$.

1. Syracosphaera anthos showing body caneoliths and circular exothecal coccoliths. Meso-96, G2, 70 m.

2. Periphyllophora mirabilis. Meso-95, 023, surf.

3. Combination coccosphere consisting of body caneoliths (a) and exothecal coccoliths (b) of

S. anthos and holococcoliths of P. mirabilis (c). Meso-95, 178, 40m.

4. Detail of figure 3 showing a layer of *P. mirabilis* holococcoliths covering the caneoliths of *S. anthos*.

5. Coccosphere of P. mirabilis with caneoliths of S. anthos. Meso-96, G4, 40m.

6. Detail of figure 5 showing three caneoliths of S. anthos (see arrows).



Plate 80. Coronosphaera mediterranea - Calyptrolithina wettsteinii combination Scale bars = $2 \mu m$.

1. *Coronosphaera mediterranea* showing the body caneoliths and four circum-flagellar coccoliths around the flagellar opening (F). Meso-95, 118, 40m.

2. *Calyptrolithina wettsteinii* showing the body calyptroliths and zygoliths around the flagellar opening (F). Meso-96, E8, 40m.

3. A combination coccosphere consisting half of *Coronosphaera mediterranea* and half of *Calyptrolithina wettsteinii* coccoliths. Meso-96, I2, 40m.

4. Analogous specimen figured by Kamptner (1941).



Plate 81. Syracosphaera nana - holococcolithophore (HO) combination. Scale bars = $1 \mu m$.

1. *Syracosphaera nana*. Egg-shaped coccosphere of caneoliths and detached exothecal coccoliths (see arrows). Fronts-96, 038, 60m.

2. *Syracosphaera nana* (HO) showing laminoform body coccoliths and the zygolith-like circum-flagellar coccoliths around the flagellar opening (F). Fronts-95, 26W, 30m.

3. Collapsed coccosphere of *Syracosphaera nana* (holococcolith and heterococcolith phases). Fronts-96, 013, 75m.

4. Detail of figure 3 showing the holococcoliths covering heterococcoliths, including both body caneoliths and exothecal coccoliths (arrows).

PLATE 81



Plate 82. Acanthoica quattrospina - holococcolithophore (HO) combination.

Scale bars: 1, 2, 3, $4 = 2 \mu m$; 5, $6 = 1 \mu m$.

1. Acanthoica quattrospina. Fans-2, N7, 5m.

2. Disintegrated coccosphere consisting of body and two circum-flagellar holococcoliths (arrows) of an undescribed species of *Sphaerocalyptra* affinity. Fans-2, N7, 10m.

3. Collapsed coccosphere of the undescribed holococcolithophore with several

heterococcoliths of Acanthoica quattrospina. Fans-2, N7, 5m.

4. Collapsed mixed coccosphere with body rhabdoliths of *Acanthoica quattrospina* which appear to surround the holococcoliths. Fans-2, J3, 10m.

5. Detail of figure 3.

6. Detail of figure 4.



Plate 83. Syracosphaera sp. - Corisphaera type A combination

Scale bars: = $2 \mu m$.

1. Coccosphere of *Syracosphaera* sp. (cf. type K of Kleijne, 1993) showing the body caneoliths and circum-flagellar caneoliths with spines, and detached exothecal coccoliths (arrows). Meso-96, G6, 40m.

2. Collapsed coccosphere of *Corisphaera* sp. type A (Kleijne, 1991) showing the body and the circum-flagellar zygoliths (arrows). Meso-96, D6, 40m.

3. Collapsed coccosphere showing body and circum-flagellar zygoliths of *Corisphaera* sp. type A and caneoliths and a detached exothecal coccolith of *Syracosphaera* sp. Meso-96, G6, 40m.

4. Detail of figure 3 showing two detached exothecal cyrtoliths (arrows) of Syracosphaera sp.



Plate 84. Other possible heterococcolith - holococcolith combinations.

Scale bars = $2 \mu m$.

1. A collapsed mixed coccosphere with a circum-flagellar caneolith (a) and body caneoliths (b) of *Syracosphaera molischii* surrounding the body (c) and circum-flagellar (d) holococcoliths of *Anthosphaera fragaria*. Fronts-95, 20I, 20m.

2. A collapsed coccosphere of *Calyptrolithophora papillifera* surrounded by heterococcoliths of *Syracosphaera histrica*; one circum-flagellar caneolith (a), some body caneoliths (b) and exothecal coccoliths (c). Meso-96, I4, 40m.

3. Heterococcoliths of *Syracosphaera* sp. type D (see Kleijne, 1993) (a) mixed with holococcoliths of *Homozygosphaera arethusae* (b). Fronts-96, 013, 66m.

4. Another mixed group of the same combination of coccoliths as figure 3. Fronts-96, 013, 66m.

5. Mixed collapsed coccosphere with (a) body caneoliths of *Syracosphaera delicata* sp. nov. and (b) body coccoliths of the dimorphic holococcolithophore *Corisphaera* sp. type B (Kleijne 1991). Fans-1, 127, 100m.

6. 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 (arrows). Meso-96, I8, 40m.



Plate 85. Other possible heterococcolith - holococcolith combinations.

Scale bars = $1 \mu m$.

Collapsed *Rhabdosphaera clavigera* coccosphere partially covering a coccosphere of *Sphaerocalyptra quadridentata*. Workshop Picasso July-98, T1 (off. Barcelona), surf.
 Detail of figure 1 showing the *Sphaerocalyptra quadridentata* coccosphere partially surrounded by an intact part of a *Rhabdosphaera clavigera* coccosphere.

3. Disintegrated coccosphere of *Sphaerocalyptra quadridentata* with some exothecal coccoliths of *Rhabdosphaera clavigera*. Workshop Picasso July-98, T5 (off. Barcelona), surf. 4 Coccosphere of *Sphaerocalyptra quadridentata*. Workshop Picasso July-98, T6 (off. Barcelona), surf.

5. Collapsed coccosphere consisting of holococcoliths of *Sphaerocalyptra* sp. and heterococcoliths of an undetermined *Acanthoica* sp. Fans-3, M11, 25m.
6. Detail of figure 5.



Plate 86. Neosphaera coccolithomorpha var. nishidae - Ceratolithus cristatus.

Scale bars = $2 \mu m$.

1. Coccosphere of Neosphaera coccolithomorpha var. nishidae. Fronts-96, 013, 10m.

2. Disintegrated coccosphere of *Ceratolithus cristatus* showing the large ceratolith and a mass of collapsed hoop-like coccoliths. Fronts-96, 013, 10m.

3. Partially disintegrated coccosphere of *Neosphaera coccolithomorpha* var. *nishidae* surrounding hoop-like coccoliths of *Ceratolithus cristatus*. Fronts-96, 013, 10m.

4. Detail of figure 3 showing *Neosphaera* coccoliths covering the hoop-like *Ceratolithus* coccoliths.



Plate 87. Alisphaera - Polycrater

Scale bars = $1 \mu m$.

1. Coccosphere consisting of a combination of *Alisphaera* (upper left) and *Polycrater* sp. (lower right) coccoliths. Fans-3, M11, 5m.

2. Detail of figure 1 showing the layer of *Alisphaera* coccoliths apparently covering the *Polycrater* coccoliths.

3. Detail of figure 1 showing the characteristic Gaudí style structure of *Polycrater* coccoliths.

4. Detail of figure 1 with the *Polycrater* coccoliths covered by *Alisphaera* heterococcoliths.

5. Coccosphere of Alisphaera which appears to cover the remains of a Polycrater

coccosphere. The *Alisphaera* coccoliths closely resemble those of the specimen in figure 1, but with notable tooth-like protrusions; the *Polycrater* coccoliths are significantly smaller than those of the previous specimen. Hivern-99, Est. 25, 40m.

6. Detail of figure 5 showing the small Polycrater coccoliths.



Plate 88. Canistrolithus - Polycrater

Scale bars = $1 \mu m$.

1. Coccosphere of *Polycrater* surrounded by coccoliths of *Canistrolithus* sp.1. Fans-3, K05, 84m.

2. Detail of figure 1 showing the coccoliths of *Canistrolithus* covering the coccoliths of *Polycrater*.

3. Detail of figure 1 showing three coccoliths of *Canistrolithus* with a robust spine and the coccoliths of *Polycrater* with characteristic dots on the smaller petal-like sides.

4. Detail of figure 1 with *Canistrolithus* coccoliths next to, and covering the *Polycrater* coccoliths.

5. Coccosphere of *Canistrolithus* with part of a *Polycrater* coccosphere (left). Fans-3, K05, 84m.

6. Detail of figure 5 with the dotted coccoliths of *Polycrater* apparently covered by coccoliths of *Canistrolithus* (right).



Plate 89. Holococcolith-Holococcolith combination coccospheres

Scale bars = $1 \mu m$.

1 and 2. Syracolithus catilliferus and S. confusus

1. Collapsed coccosphere of *Syracolithus confusus* including coccoliths of *Syracolithus catilliferus* (see arrows); transitional forms can be seen. Meso-96, F2, 5m.

2. Coccosphere of *Syracolithus* consisting of coccoliths of both *S. catilliferus* and *S. confusus*. Meso-96, F2, 5m.

3-6. Zygosphaera bannockii and Corisphaera sp type A of Kleijne (1991)

3. Collapsed coccosphere with body coccoliths of *Zygosphaera bannockii* (arrows) and others of *Corisphaera* sp. type A. Fans-1, 123, 40m.

4. Collapsed coccosphere consisting of coccoliths of *Zygosphaera bannockii* (arrows), others of *Corisphaera* sp. type A and transitional forms. Fans-1, 127, 5m.

5. Coccosphere of *Corisphaera* sp. type A with some coccoliths of *Zygosphaera bannockii* (arrow). Fans-1, 127, 40m.

6. Detail of figure 5 showing clearly a coccolith of Zygosphaera bannockii (arrow).



Plate 90. Sediments from station 3

Scale bar = $3 \mu m$.

General aspect of the sediment sample showing many of the most representative coccoliths. This micrograph corresponds to sediments from station 3 (see Fig. 2.4).



Plate 91. Sediments from station 15

Scale bar = $3 \mu m$.

General aspect of the sediment sample showing many of the most representative coccoliths and a complete coccosphere of *Emiliania huxleyi*. This micrograph corresponds to sediments from station 15 (see Fig. 2.4).

