

THE PRESENCE OF HOLOCOCOLITHOPHORIDS (CALCAREOUS NANNOPLANKTON) IN THE MARINE ECOSYSTEMS OF ANDROS ISLAND (AEGEAN SEA, GREECE) DURING AUGUST 2001. IMPLICATIONS FOR THEIR USE AS ENVIRONMENTAL AND PALEOECOLOGICAL PROXIES.

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ABSTRACT

Water samples for coccolithophorid analysis were collected in August 2001, from 8 stations along a transect in the gulf of Korthi (Andros Island, Aegean sea). Samples were collected from 0-120m water-depth. Holococcolithophorid absolute abundances usually range between 7.29×10^3 and 0.06×10^3 cells/l. The derived distribution patterns indicate that holococcolithophorids bearing holococcoliths with convex cover above the tube, may constitute a significant part of the summer flora in the uppermost photic zone of the coastal waters of Andros island, showing affinities to shallower environments.

KEY WORDS: morphological groups, living coccolithophores, holococcolithophorids, coastal environments.

1. INTRODUCTION

Coccolithophores are unicellular marine phytoplankton -motile or non-motile cocoid forms- belonging to biflagellate golden-brown algae, which produce minute calcium carbonate plates called coccoliths. The coccoliths, which cover their cell surface, constitute the single most important component of deep-sea sediments and provide floral and biomarker signals for interpreting global change in the geological record. The coccoliths can be divided into two groups: the heterococcoliths, consisting of calcite elements of differing size, shape and orientation and the holococcoliths, which are constructed of calcite microcrystals (crystallites) of uniform size. Coccolithophorid life cycles are not well known, primarily because only a limited number of species have been successfully cultured and in most cases, phase changes occur only sporadically and unpredictably.

Coccolithophores form a major component of the marine micro- and nanoplankton and are one of the main open ocean primary producers. They play a significant role in the CO_2 - O_2 exchanges between the ocean and the atmosphere, seriously effecting on both the biological and the carbonate pumps (Sikes *et al.*, 1994) and producing an additional feedback to climate changes (Westbroek *et al.*, 1993).

The ocean and the atmosphere are tightly linked in the global climate system and any changes in either can affect the other. The cycling of carbon in the ocean is tentatively studied in order processes that control the size and distribution of the ocean carbon reservoir. They also observe the effects that human activities are having on these processes, such as the increase in CO_2 in the atmosphere, which is contributing to rising temperatures. Our ability to predict and perhaps to alter the course of climate change requires a detailed understanding of the ways in which carbon in the ocean is transformed, transported, recycled or buried in the sediments of the sea floor. One route that carbon takes into the deep ocean is via what is called the "biological pump". This pathway begins as Phytoplankton, the single-celled organisms that form the base of the oceanic food web, take up CO_2 and nutrients through the process of photosynthesis and form organic matter.

Consequently research trends focus mainly on phytoplankton and in particular on calcareous nanoplankton -which is one of the most of abundant groups of extant phytoplankton.

Therefore the increase interest of micropaleontological studies in nanoplankton paleoecology and paleoceanography has been paralleled by a renaissance

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of studies of extant nannoplankton, with an increase focus on ecological aspects (Young *et al.*, 2000).

Triantaphyllou *et al.* (in press) investigate the spatial distribution, species composition of recent holococcolithophorids in coastal environments (E. Andros island, middle Aegean Sea). This is the first attempt to group holococcolithophorid species in the calcareous nannoplankton communities from the middle Aegean Sea marine ecosystems. In the present study, we will try to determine the holococcolithophorids, from Andros ecosystems, particular in terms of certain morphological groups and investigate possible relationships of these groups with certain environmental parameters (distribution in the water column, effect of sea bottom depth etc.).

1.1 GROUPING HOLOCOCOLITHOPHORIDS IN CALCAREOUS NANNOPLANKTON COMMUNITIES

Holococcolith morphology appears rather plastic and yields few features of obvious higher taxonomic significance. Moreover, the fossil record of holococcoliths is limited, especially in the Neogene. Consequently, it is very difficult to predict phylogenetic relationships from holococcolith morphology. Reflecting this, common classifications (e.g. Jordan & Green, 1994; Jordan & Kleijne, 1994) have included the holococcolithophorids in a single family, the Calyptrerosphaera. Cross *et al.* (2000), suggested that heterococcolith-holococcolith combination must have a common origin and that a consistent relationship of coccolith type and life cycle stage is likely. So for the moment the holococcolith and heterococcolith classifications should be seen as independent.

Holococcolithophorids have often been subdivided into monomorphic and dimorphic genera, e. g. Kleijne (1991) and Jordan *et al.* (1995). This system separates some very similar forms and many "monomorphic" species in fact show weak dimorphism (e.g. *Calyptrerosphaera oblonga*). Young *et al.*, (in press) subdivided holococcolithophorids into five groups based on morphology of the body coccoliths. Most holococcoliths consist of a basal tube with more or less vertical walls, typically about half a micron high. The nature of the cover is used as the primary basis for grouping/identification.

GROUP A Holococcoliths without a tube

GROUP B Holococcoliths with a bridge spanning the tube

GROUP C Holococcoliths with convex cover above tube

GROUP D Holococcoliths flat distal cover, +/- central boss

GROUP E Holococcoliths consisting of tube open distally, with or without internal septae

2. OCEANOGRAPHIC SETTING

The surface water circulation pattern of the Aegean Sea is not simple and regular, but changes temporally and seasonally. The complex circulation is due to many factors, such as: the geographical distribution of the various Aegean island chains; the irregular bottom topography throughout the region; inflow of the lower temperature and salinity Black Sea waters; the river outflows from the Greek and Turkish mainland; seasonal changes in the meteorological conditions. The surface water circulation is incorporated, in general, into an anti-clockwise gyre system during winter. In summer, water movement is essentially towards the south (Poulos *et al.*, 1997). Water circulation is controlled by prevailing wind conditions and the thermohaline circulation patterns and their seasonal variability. During the warm period (May-September), the wind field is dominated by the presence of the Etesian wind, blowing mainly from the north, whilst some south-southwesterly winds blow during spring. In the Cyclades islands, there is a >20% frequency of wind speeds ≥ 6 Beaufort and >10% of ≥ 7 Beaufort, during summer (Metaxas, 1973). The annual maximum Sea Surface Temperature (SST) values ($>24^\circ$) occur around August; minimum values ($<13^\circ\text{C}$) are reached in winter. Sea Surface Salinity (SSS) values vary seasonally, ranging from less than 31.0psu to more than 39.0psu.

3. MATERIAL AND METHODS

Water samples for holococcolithophorids analysis were collected in August 2001, from 8 stations along transect towards the gulf of Korthi (E. Andros Is-

land, middle Aegean Sea) (Fig. 1). The period of sampling, summer, was chosen because it is the season when maximum production of holococcolithophorids takes place in the environment. Water samples were collected from a number of depths (0-120m), using a single oceanographic Hydro-bios bottle. For each sampling depth, 1,5l of seawater was filtered on Millipore cellulose nitrate filters (45mm diameter, 0,8µm pore size), using a vacuum filtration system. The filters were open dried and stored in plastic Petri dishes. A piece of each filter approximately 8x8mm² was attached to an copper electron microscope stub using a double-sided adhesive tape and coated with gold. The filters were examined in a Jeol JSM 5600 scanning electron microscope (SEM). To determine the species composition and standing crop the samples were examined with SEM only, because holococcolithophorid species are difficult to recognize with a light microscope, especially when their coccospheres are disintegrated and form heaps of coccoliths on the filter, or when they are present as free coccoliths. The working magnification was 1200x throughout the counting procedure. The absolute abundances of cell densities (cells/l) holococcolithophorids species were calculated following the methodology of Jordan & Winter (2000).

Identification and taxonomy of species follow that outlined by Kleijne (1993), Jordan & Kleijne (1994), Winter & Siesser (1994), Aubry (1999) and Jordan et al. (2000).

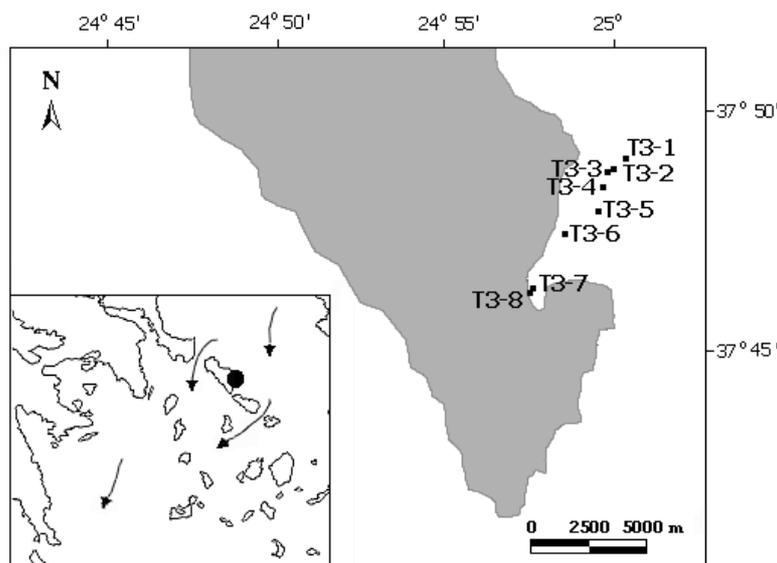


Fig.1. Map of the study area, at middle Aegean Sea, with generalized current patterns during summer (based on Lacombe & Tchernia, 1972) and location of the sampled stations at southeastern Andros island.

4. TOTAL STANDING CROP AND CELL DENSITIES

Coccolithophores were present in all the studied samples. The absolute abundance of the total nanoplankton varied between 13.64×10^3 cells/l (Stn T3-3, 15m depth) and 1.92×10^3 cells/l (Stn T3-1, 120m depth), whereas holococcolithophorid assemblages reaching sometimes more than 50% of the total standing crop, varied between 7.29×10^3 cells/l and 0.06×10^3 cells/l (Table I). The significantly lower population at the latter Stn indicates the negative correlation of coccolithophore densities with depth (Table I). Our results corroborate the findings of Kleijne (1991) who collected surface water samples along an east west transect of the Mediterranean during the summer of 1985, resulting at holococcolithophorid percentages reaching 50-70% of the total coccolithophore count, which in abundance was generally low ($<10^4$ /l). Additionally Haidar & Thierstein (2001) calculated the holococcolithophorid cell densities off Bermuda as less than 13×10^3 , encountering them mostly in the upper photic zone.

Fig. 2 reveals the tendency to increasing holococcolithophorid abundances towards shallower environments at 5m depth comparing to heterococcolithophorid species whereas at 15m holococcolithophorids seem to show a more or less stable

distribution pattern at all Stns. On the other hand the holococcolithophorid abundances at 5m are almost negatively correlated to those at 45m.

Stations	Longitude	Latitude	Water depth (m)	Coccolithophorids (x10 ³ cells/l)	Heterococcoliths (x10 ³ cells/l)	Holococcoliths (x10 ³ cells/l)
T3-1	37°49'01''	25°00'31''	0	4,05	2,60	1,44
			5	13,43	12,00	1,43
			15	12,72	7,51	5,20
			45	14,7	7,41	7,29
			90	6,75	6,31	0,44
T3-2	37°48'48''	25°00'02''	120	1,92	1,86	0,06
			0	8,70	6,50	2,20
			5	12,64	8,24	4,41
			15	11,08	7,18	3,9
			45	5,93	5,25	0,68
T3-3	37°48'46''	24°59'58''	90	3,36	2,88	0,48
			0	3,08	1,54	1,54
			5	6,70	3,68	3,02
			15	13,64	8,67	4,97
			45	7,40	4,56	2,84
T3-4	37°48'28''	24°59'41''	90	3,72	2,89	0,83
			0	3,70	2,91	0,79
			5	8,48	5,70	2,77
			15	10,28	5,91	4,38
			45	11,34	6,83	4,51
T3-5	37°47'56''	24°59'20''	60	5,94	4,84	1,10
			0	2,48	1,90	0,58
			5	7,30	4,10	3,20
			15	5,97	4,05	1,93
			45	13,58	9,32	4,26
T3-6	37°47'24''	24°58'45''	0	8,38	5,88	2,50
			5	10,38	5,00	5,38
			15	11,17	6,94	4,24
			45	1,99	1,99	-
			90	4,24	2,70	1,54
T3-7	37°46'40''	24°57'44''	5	8,26	5,20	3,05
			15	8,92	4,29	4,62
			25	7,93	3,30	4,62
			0	7,80	4,53	3,27
			5	11,95	6,36	5,59
T3-8	37°46'34''	24°57'23''	7	8,32	4,62	3,70

Table I. Location of depth profile samples, sampling depth and total standing stock of heterococcolithophorids and holococcolithophorids.

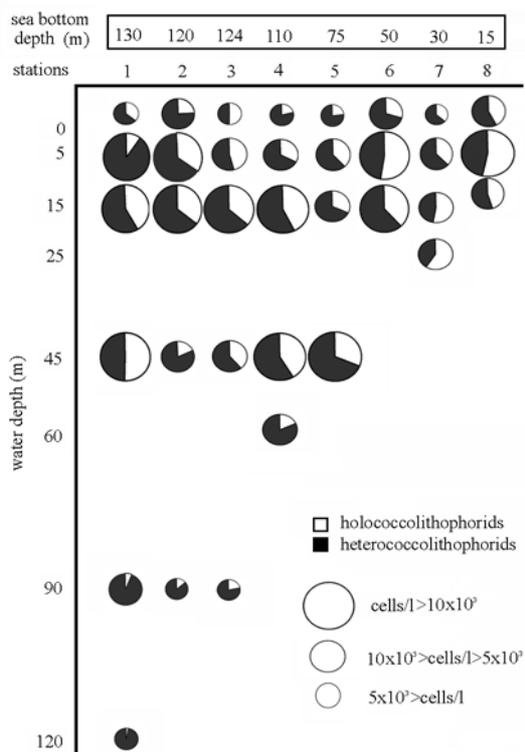


Fig. 2. Vertical relative abundance of heterococcolithophorids vs holococcolithophorids at the sampled stations. Note the different bottom depths corresponding to each station.

Stations	T3-1						T3-2					T3-3					T3-4					T3-5				T3-6				T3-7				T3-8		
Water depth (m)	0	5	15	45	90	120	0	5	15	45	90	0	5	15	45	90	0	5	15	45	60	0	5	15	45	0	5	15	45	0	5	15	25	0	5	7
Holococcolithophorids %	35,7	10,6	40,1	49,4	6,6	3,1	25,3	34,9	35,1	11,7	14,4	50	45	36,4	37,7	22,1	21,4	32,7	42,2	39,6	18,4	23,3	47,7	30,5	21,8	28,5	50,8	37,3	0	36,5	37	51,7	57,3	38,3	46,6	44,4
Group A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2,4	0	1	1,1	0	0,6	0	0	1	3,6	0	0	0,8	0
Group B	11,9	2,4	11	27	1,1	3,1	2,54	9,8	11,7	2,9	9	17,8	18,3	13,5	20,6	4,4	7,1	12,7	22,4	14,5	0	13,4	10,3	6,4	12,3	11,4	10,9	9,2	0	15,9	11	7,4	16,7	11,1	5,6	8,9
Group C	23,8	2,5	24,7	16,8	3,3	0	15,2	22,8	22,6	5,8	3,6	25	26,7	19,5	14,4	13,3	10,7	20	17,4	16,4	14,8	6,6	31,8	21,7	2	13,8	35,4	25,8	0	16	22	40,7	35,8	17,3	35,4	35,5
Group D	0	5,7	4,4	4,8	2,2	0	7,59	2,3	0,4	2	0	7,2	0	3,4	2,7	4,4	3,6	0	2,4	4,8	3,6	3,3	3,2	2,4	5,4	1,1	2,7	1,7	0	4,6	3	0	3,6	1,23	4	0
Group E	0	0	0	0,8	0	0	0	0	0,4	1	1,8	0	0	0	0	0	0	0	0	3,9	0	0	0	0	1,1	1,1	1,8	0	0	0	0	0	1,2	8,64	0,8	0

Table II. Percentages of the morphological groups at all sampled stations

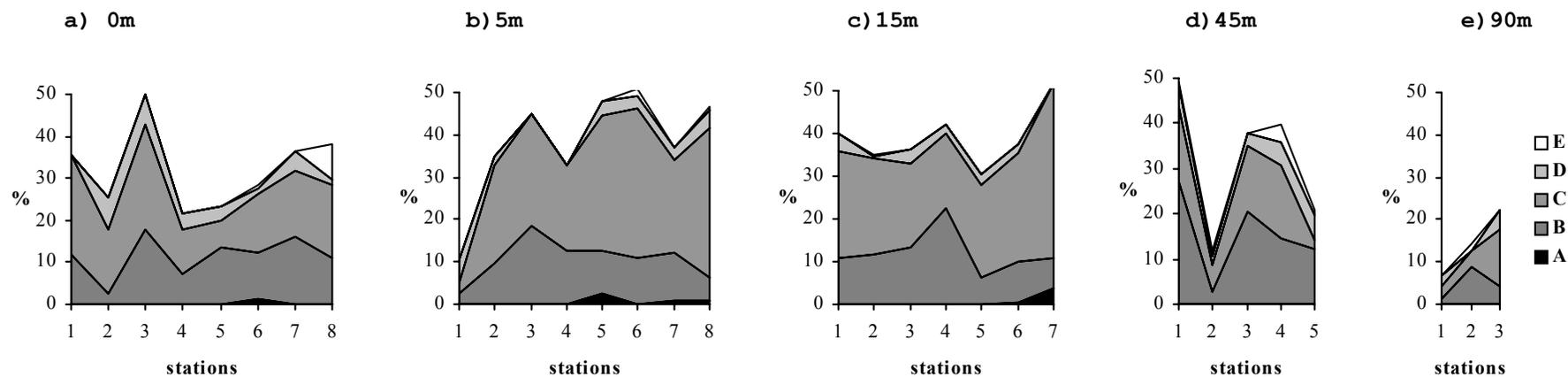


Fig.4. Abundances of holococcolithophorid morphological groups at all depths

5. ABUNDANCE CHANGES OF HOLOCOCOLITHOPHORE GROUPS IN THE WATER COLUMN

The enormous diversity of holococcolithophorid species reported by Heimdal & Gaarder (1980), Norris (1985) and Kleijne (1991) is also confirmed by the present study for the middle Aegean Sea.

Concerning the grouping of holococcolithophorids, based on morphological criteria, the following species have been assigned to groups A,B,C,D,E, respectively:

GROUP A: *Anthosphaera* sp., *A. lafourcadii* and *A. periperforata*.

GROUP B: *C. gracilis*, *C. strigilis*, *C. tyrrheniensis*, *H. cornifera* (Pl.I, fig.2), *H. arethusae* (Pl.I, fig.4), *H. spinosa*, *H. triarcha* (Pl.I, fig.13), *P. mirabilis* (Pl.I, fig.15) and *P. poritectum*.

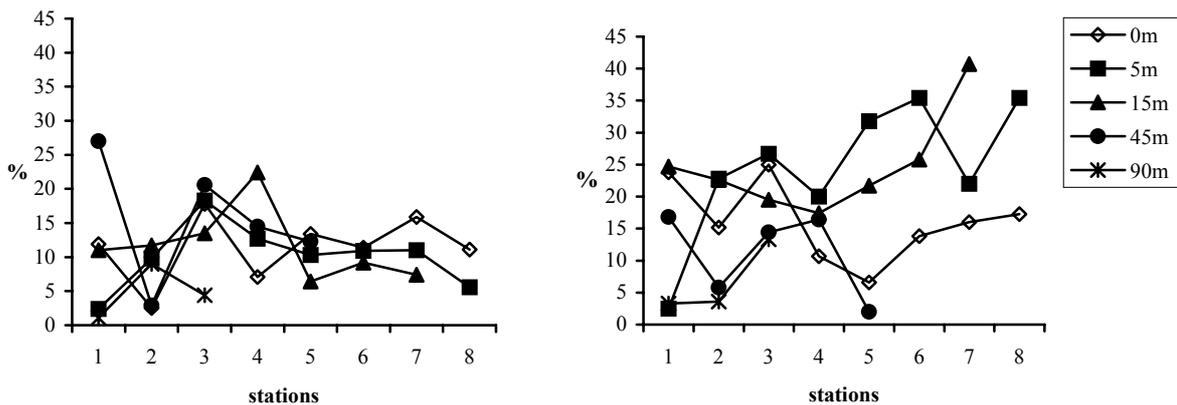
GROUP C: *C. divergens* f. *tuberosa* (Pl.I, fig.9), *C. heimdalaе*, *C. oblonga* (Pl.I, fig.7), *C. pirus* (Pl.I, fig.11), *C. sphaeroidea* (Pl.I, fig.3), *G. amitakarenae*, *S. quadridentata* (Pl.I, fig.1) and *Sphaerocalyptra* sp. 2.

GROUP D: *C. multipora* (Pl.I, fig.12), *C. wettsteinii*, *C. papillifera*, *C. dentata*, *P. aurisinae* (Pl.I, fig.6), *P. gaarderae*, *P. issellii*, *S. catilliferus*, *S. confuses* (Pl.I, fig.5), *S. ponticuliferus*, *Z. amoena*, *Z. bannockii* and *Z. helvetica* (Pl.I, fig.10)

GROUP E: *C. blokii*, *C. concava*, *Calicasphaera* sp. (Pl.I, fig.8), *S. schilleri* and *S. quadriperforatus* (Pl.I, fig.14)

The group abundances have been calculated at all sampled depth (Table II, Fig.3), providing the following results:

Group B and C (mostly characterized by the presence of *S. quadridentata*/*C. oblonga* and *H. cornifera* respectively) dominate the assemblages at the surface samples (Fig.3a), followed by Group D and showing maximum at Stn T3-3. Group E is only represented at Stn T3-8. At 5m depth Group B still shows max at Stn T3-3, but Group C, which dominates now the nannoflora assemblages peaks at Stns T3-3, T3-5, T3-6 and T3-8, showing a tendency to increase towards shallower environments. The same tendency is also observed at 15m, but at 45m there is an abrupt decline of Group C and Group B remains the dominant assemblage followed by Groups D and E. All groups show minimum abundance at this depth, at Stn T3-2. Finally at 90m all groups are rather faintly represented, but Group C still remains more or less dominant.



a) GROUP B

b) GROUP C

Fig.4. Relative abundances of holococcolithophorid Groups B and C

Fig. 4 reveals a slight tendency of Group B to decrease towards shallower environments, whereas Group C is clearly increasing, except of the water depth 45m.

DISCUSSION. CONCLUSIONS

The spatial distribution of holococcolithophorid morphological groups points out that species bearing holococcoliths with a bridge spanning the tube (Group B) dominate the nannoflora assemblages in water depths from 45m and below, showing decreasing tendencies towards shallower environments.

On the other hand species bearing holococcoliths with convex cover above tube (Group C) prefer the ecological niche of the uppermost euphotic zone (0-45m) and increase significantly when sea bottom depth is declining.

Holococcoliths without a tube (Group A), with a tube open distally (Group E), or bearing flat distal cover (Group D) consist a minor component of the extant nanoplankton communities, during late summer 2001, at coastal environments of middle Aegean Sea. These results are in good agreement with Triantaphyllou et al. (in press) findings concerning the individual holococcolithophorid species vertical distribution.

It is hoped that future sampling will shed further light on the regional dynamics in relationship to seasonality and annual cycling of coccolithophores in the middle Aegean Sea, as the understanding the ecology of these species is of great interest to biostratigraphy and paleoceanography.

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Appendix A

Index of taxa

Group A:

Anthosphaera lafourcadii (Lecal, 1967) Kleijne, 1991
Anthosphaera periperforata Kleijne, 1991
Anthosphaera sp.

Group B

Corisphaera gracilis Kamptner, 1937
Corisphaera strigilis Gaarder, 1962
Corisphaera tyrreniensis Kleijne, 1991
Helladosphaera cornifera (Schiller, 1913) Kamptner, 1937
Homozygosphaera arethusae (Kamptner, 1941) Kleijne, 1991
Homozygosphaera spinosa (Kamptner, 1941) Deflandre 1952
Homozygosphaera triarcha Halldal & Markali, 1955
Periphyllophora mirabilis (Schiller, 1925) Kamptner, 1937
Poritectolithus poritectum (Heimdal in: Heimdal and Gaarder, 1980) Kleijne, 1991

Group C

Calyptrolithina divergens f. *tuberosa* (Heimdal in: Heimdal and Gaarder, 1980) Heimdal, 1982
Calyptrosphaera heimdala Norris, 1985
Calyptrosphaera oblonga Lohmann, 1902
Calyptrosphaera pirus Kamptner, 1937
Calyptrosphaera sphaeroidea Schiller, 1913
Gliscolithus amitakarenae Norris, 1985
Sphaerocalyptra quadridentata (Schiller, 1913) Deflandre, 1952
Sphaerocalyptra sp. 2 Cross, 2001

Group D

Calyptrolithina multipora (Gaarder in: Heimdal and Gaarder, 1980) Norris, 1985
Calyptrolithina wettsteinii (Kamptner, 1937) Kleijne, 1991
Calyptrolithophora papillifera (Halldal, 1953) Heimdal in: Heimdal and Gaarder, 1980
Calyptrosphaera dentata Kleijne, 1991
Poricalyptra aurisinae (Kamptner, 1941) Kleijne, 1991
Poricalyptra gaarderae (Borsetti & Cati, 1976) Kleijne, 1991
Poricalyptra issellii (Borsetti & Cati, 1976) Kleijne, 1991
Syracolithus catilliferus (Kamptner, 1937) Deflandre 1952
Syracolithus confusus Kleijne, 1991
Syracolithus ponticuliferus (Kamptner, 1941) Kleijne & Jordan, 1990
Zygosphaera amoena Kamptner, 1937
Zygosphaera bannockii (Borsetti & Cati, 1976) Heimdal, 1982
Zygosphaera hellenica Kamptner, 1937

Group E

Calicasphaera blokii Kleijne, 1991
Calicasphaera concava Kleijne, 1991
Calicasphaera sp.
Syracolithus quadriperforatus (Kamptner, 1937) Gaarder, 1962
Syracolithus schilleri (Kamptner, 1927) Loeblich & Tappan, 1963

LATE I

1 *Sphaerocalyptra quadridentata* (Schiller) Deflandre, sample T3-6-45m. 2 *Helladosphaera cornifera* (Schiller) Kamptner, sample T3-1-45m. 3 *Calyptrosphaera sphaeroidea* Schiller, sample T3-7-0m. 4 *Homozygosphaera arethusae* (Kamptner) Kleijne, sample T3-1-45m. 5 *Syracolithus confusus* Kleijne, sample T3-5-5m. 6 *Poricalyptra aurisinae* (Kamptner) Kleijne, sample T3-5-45m. 7 *Calyptrosphaera oblonga* Lohmann, sample T3-1-45m. 8 *Calicasphaera* sp., sample T3-5-15m. 9 *Calyptrolithina divergens* f. *tuberosa* (Heimdal) Heimdal, sample T3-2-15m. 10 *Zygosphaera hellenica* Kamptner, sample T3-5-15m. 11 *Calyptrosphaera pirus* Kamptner, sample T3-5-45m. 12 *Calyptrolithina multipora* (Gaarder) Norris, sample T3-1-45m. 13 *Homozygosphaera triarcha* Halldal & Markali, sample T3-2-5m. 14 *Syraco-*

lithus quadriperforatus (Kamptner) Gaarder, sample T3-6-5m. 15 *Periphyllophora mirabilis* (Schiller) Kamptner, sample T3-2-90m.

PLATE I

