

Living coccolithophores recorded during the onset of upwelling conditions off Oman in the western Arabian Sea

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Abstract A transect off Oman was sampled in early June, 2000 at the onset of upwelling conditions in the north-western Arabian Sea. Living coccolithophores were investigated in 21 samples from five stations with a scanning electron microscope. From 77 identified taxa, several species contributed significant portions to the communities. The overall dominant taxon was *Gephyrocapsa oceanica*, with an average 34%. Absolute abundances reach up to more than 50 000 coccospheres per litre. Highest coccolithophore concentrations probably occur close to the upwelling centres where oceanic and upwelled waters mix. Ecological preferences of several species are refined. *G. oceanica* occurs with different morphotypes and has a preference for elevated nutrient levels. Additionally, this species can cope with unstable surface-water conditions, that is, turbulent waters caused by active upwelling. In tropical regions, *Emiliania huxleyi* may not be regarded as an indicator of upwelling processes, but may be more typical of stable regimes in terms of vertical mixing with relatively high nutrient-availability. The occurrence of the sub-species *Calcidiscus leptoporus* ssp. *quadriperforatus* probably indicates early upwelling conditions. The deep-living *Florisphaera profunda* plays only a minor role in the communities of the western Arabian Sea.

Keywords Arabian Sea, living coccolithophores, upwelling, ecology, environmental conditions

1. Introduction

We report a survey on living coccolithophores in the western part of the Arabian Sea, off the coast of Oman. The samples were collected in early June, 2000 at the onset of upwelling conditions and, therefore, comprise strongly different environmental conditions and contrasting floral assemblages. To date, only a few plankton studies have given information on the changing coccolithophore communities in the Arabian Sea, although Banse (1994) recently proposed that coccolithophores might be the most important primary producers in this region. An overview of species diversity and taxonomy was given by Kleijne *et al.* (1989) and Kleijne (1991, 1992) for the southern Arabian Sea. A study of the central and northern Arabian Sea was conducted by Guptha *et al.* (1995), who investigated four stations on a south-north transect, reaching close to our studied area. Zeltner (2000) studied a large number of water-samples from the northern Indian Ocean and gave a comprehensive overview of the coccolithophore diversity. Further information was provided by Andruleit *et al.* (2003), who investigated living coccolithophores in the northern Arabian Sea that were retrieved at the end of the summer (SW) monsoon in September, 1993. The coccolithophore communities exhibited a rather heterogeneous pattern in terms of species composition in surface-waters. Several species seemed to be able to dominate the communities, but none of them had an overall dominance (Andruleit *et al.*, 2003). Recently, Schiebel *et al.* (2004) studied the coccolithophore communities during the SW-monsoon in the Arabian Sea, in comparison with diatoms and planktonic foraminifers.

They proposed a coupling of nutrient concentration and coccolithophore cell numbers with increasing coccolithophore numbers towards the open ocean, along with decreasing nutrient concentration and increasing stratification of the upper water-column. An overview of coccolithophores in the Arabian Sea, in terms of their production in the photic zone, transformation to settling assemblages, accumulation on the sea-floor, and their final burial in the sediments, is provided by Andruleit *et al.* (in press). A study on sediment-trap samples from the Somali Basin showed that coccolithophores responded to seasonal changes in monsoonal upwelling (Broerse *et al.*, 2000). Also, in the north-eastern Arabian Sea, a sediment-trap study has revealed a strong relationship between the monsoon seasons and the seasonal flux of coccolithophores (Andruleit *et al.*, 2000). For the present investigation, special emphasis was laid on the identification of species and species groups that are characteristic of upwelling conditions. The calibration of species-specific ecological tolerances is aimed at enhancing the potential of coccolithophores for palaeoceanographic reconstructions.

2. Environmental conditions

The Arabian Sea hydrography is controlled by the Indian Ocean monsoon. Environmental gradients change distinctly between the SW-monsoon in summer (June to September) and the NE-monsoon (December to February) in winter. In summer, the steady and strong SW-monsoon generates extensive coastal upwelling and eddy advection over the continental margins, extending up to 400km seaward off the coast of Oman (Brock *et al.*, 1992). In addi-

tion, open-ocean upwelling is induced due to Ekman transport by strong wind-stress (Currie *et al.*, 1973; Brock *et al.*, 1991). At the onset of the SW-monsoon, late in May/early June, due to increasing wind-speeds, upwelling centres originate and spread out. Contemporaneously, phytoplankton growth increases due to the supply of nutrients (Figure 1). Sea-surface temperatures drop significantly from $>29^{\circ}\text{C}$ in the central Arabian Sea down to $<20^{\circ}\text{C}$ in the upwelling centres off Oman (Currie *et al.*, 1973; Hastenrath & Lamb, 1979; Rixen *et al.*, 2000). The cooling of the surface-water is attributed to upwelling (Rixen *et al.*, 2000). Environmental conditions during sampling are intimately connected with the occurrence of coccolithophores and are presented in Section 4, 'Results'.

3. Material and methods

Plankton samples were collected during *Marion Dufresne* Cruise MD-117 in June, 2000 (Kissel & Schulz, 2000). In total, 21 samples from five stations were investigated (Table 1). Water-samples were taken at several depth-intervals with a rosette sampler. Information about water conditions were provided by CTD profiling, together with fluorometer measurements (uncalibrated data). Chlorophyll fluorescence serves as an indicator of phytoplankton concentrations, and thus provides a means of assessing biological activity within the water-column. The water from each depth was filtered through fleece-supported, regenerated cellulose filters (Sartorius®, $0.45\mu\text{m}$ pore-width) using a vacuum pump. Without further washing, rinsing or chemical conservation, the filters were dried in an oven at 40 to 50°C for at least four hours. The filters were then stored in plastic Petri dishes and kept dry with silica gel. Coccolithophore cell-densities were determined with a scanning electron microscope (SEM), usually at 10kV . For that purpose, a small piece of the dried filter was cut out, fixed on an SEM stub, and sputtered with gold. The number of individuals and the species composition were determined by identifying and counting coccospheres on measured transects at magnifications of $2000\times$ and/or $3000\times$. Generally, it was aimed to count 300 specimens. Cell-densities per litre of water were calculated as follows:

$$\text{Coccolithophore concentration (no./l)} = \frac{F \cdot C}{A \cdot V},$$

where F = effective filtration area [mm^2], C = number of

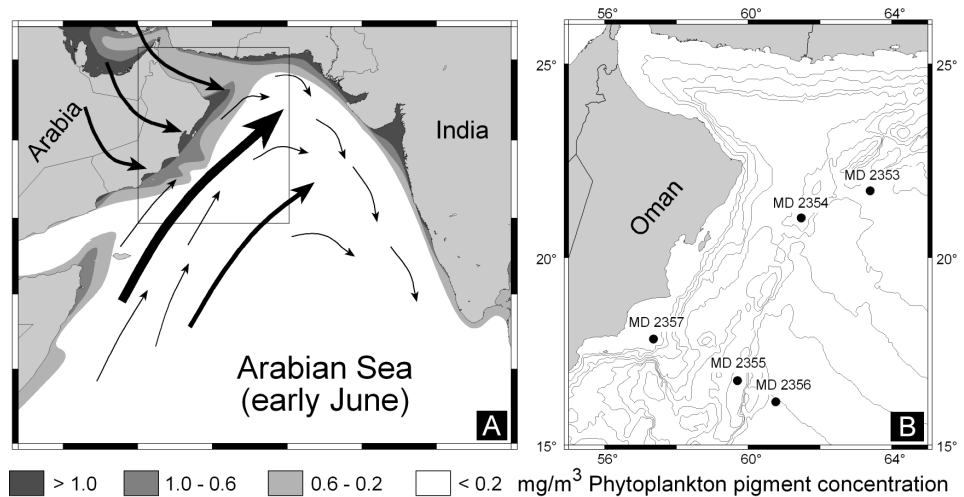


Figure 1: A) Wind and surface-water circulation and phytoplankton pigment concentration (modified after http://daac.gsfc.nasa.gov/CAMPAIGN_DOCS/OCDST/classic_scenes/04_classics_arabian.html) in the Arabian Sea in early June, 2000 at the onset of upwelling conditions (large arrows = winds, small arrows = currents). B) Bathymetry with location of samples

coccospheres, A = investigated filter area [mm^2], and V = filtered volume (l).

For each sample, we applied the Shannon Information Function as a reasonable measure of heterogeneity (diversity). At one station, diatoms greatly dominated the plankton communities. This qualitative observation was noted and is commented on the text.

We performed a cluster analysis (centroid linkage method; distance metric is 1-Pearson Correlation Coefficient) on the relative abundances of species. Taxa with only sporadic occurrence and low cell-densities were excluded.

Digital images are archived in the BGR palaeontology image database. Stubs are stored in the BGR SEM collection.

4. Results

4.1 Physical data and diversity

Temperature and salinity data from all stations exhibited a clear trend in surface-water conditions (Figure 2). Warmest temperatures with highest salinities were found at Station MD 2353. At southerly-located, and especially more westerly-located, stations, surface-water temperatures and salinities decreased significantly. Lowest values were reached at Station MD 2357. The top of the thermocline depth (defined as the depth where the temperature is 1°C cooler than at the sea-surface [Hastenrath & Merle, 1987]) varied between about 20m to 40m. Fluorometer data underline the exceptional status of Station MD 2357, with several times higher values than at the other stations. Similarly to the temperature and salinity values, the diversity (Shannon Function) of the coccolithophore communities decreased in a south-westerly direction and exhibited the lowest diversities at Station MD 2357.

4.2 Coccolithophore data

A total of 77 taxa were identified in this study, with sev-

Station	Date	lat. (N)	long. (E)	Depth (m)	C. lept.	E. hux.	F. prof.	G. ocea.	O. ant.	P. vand.	Syr. spp.	Umb. spp.	Holoc.	Other	Count
MD 2353	07/06/00	21.750	63.387	10	0	52	0	3952	0	2496	2652	3172	3432	988	323
Water-depth: 3180m				25	0	47	0	4324	0	799	2303	4183	2256	1504	331
				50	195	3445	130	5395	910	0	1690	0	325	9945	342
				80	0	51	1836	646	578	0	17	0	17	153	195
				140	20	0	0	400	20	0	0	0	0	0	22
MD 2354	08/06/00	21.043	61.477	20	0	29	0	0	29	1682	1769	3248	2059	841	335
Water-depth: 2740m				40	0	150	0	300	525	450	2775	11925	3375	3825	311
				60	0	580	0	3335	20735	145	7685	11455	725	8845	369
				120	87	87	2407	261	1682	0	203	58	0	4234	311
MD 2355	09/06/00	16.705	59.711	25	0	1102	0	9860	0	1624	2494	3886	290	1856	370
Water-depth: 2420m				38	0	2050	0	6100	1100	500	2850	0	650	6150	389
				70	294	504	6846	1260	4158	126	126	0	84	3570	405
				90	0	117	8463	546	2028	0	273	0	0	1170	329
MD 2356	10/06/00	16.123	60.759	30	0	1224	0	18564	204	612	2652	4386	1836	4998	339
Water-depth: 4020m				40	83	1079	83	12284	8881	332	2656	1328	83	6557	389
				70	100	225	2300	1975	2075	0	175	0	0	800	310
				100	117	208	1456	1209	1131	0	65	0	0	195	338
MD 2357	11/06/00	17.834	57.393	10	5781	564	0	35391	1692	0	141	0	0	3243	332
Water-depth: 345m				30	5192	0	0	27848	1062	0	236	0	0	4012	325
				40	6500	0	0	23600	800	0	0	0	0	1600	325
				75	108	27	486	1557	315	0	81	0	0	351	316

Table 1: Locations of, and data for, the investigated water-samples. Species abundance = coccospheres per litre

eral species that contribute significant portions of the communities. Absolute abundances reach up to >50 000 coccospheres per litre at intermediate water-depths (Station MD 2354, 50m). The overall dominant taxon was *Gephyrocapsa oceanica*, with an average 34%. This species exhibited at least three different morphotypes, with respect to different structures of the central area, tube, and collar (Plate 1, Figures 1-3). Due to a high and variable diversity, several species are not shown individually for the sake of clarity and comparability between the samples. However, all taxa of importance for the aim of this study (see Introduction) are either depicted on the figures or mentioned in the text. The genus *Syracosphaera* consists of 19 species, but none of them had a clear dominance within this group. In contrast, *Umbellosphaera* spp. comprises only the two species *U. irregularis* and *U. tenuis*, with the former one as the dominant taxon of this genus in our samples. The holococcolithophore group is very heterogeneous, with 20 different taxa, all with sporadic and mainly rather low occurrences. All identified species are listed alphabetically, with full citations, in Appendix A (data are shown in Table 1). Selected taxa are illustrated on the plates.

Results from all stations are briefly described below (Figure 3):

Station MD 2353: In the samples above the thermocline, *G. oceanica*, *Palusphaera vandellii*, *Syracosphaera* spp., *U. irregularis*, *U. tenuis* and holococcolithophores contributed large proportions to the communities. Below the thermocline, solely at this station, *Calciosolenia murrayi* occurred in high amounts. Cell-densities reach, at most, 22 000 coccospheres per litre at 50m water-depth.

Station MD 2354: Here again, *P. vandellii*, *Syracosphaera* spp., *Umbellosphaera* spp. and holococcolithophores contributed significantly to the communities, while *G. oceanica* was absent in the upper water-column. Below the thermocline, the highest cell-density of all samples, with 53 500 coccospheres per litre, was reached. Especially *Oolithotus antillarum* occurred in high abundances at this depth. Similarly to Station MD 2353, species of *Syracosphaera* spp. and *Umbellosphaera* spp. were abundant, even below the thermocline. The sample at 20m water-depth is the only one where *U. tenuis* dominates over *U. irregularis*.

Station MD 2355: At this station, *G. oceanica* was the dominant species in the upper water-column but also other species contributed significantly. Below the thermocline, *Florisphaera profunda* and *O. antillarum* were the main components of the communities. Generally, intermediate to high cell-densities, between 10 000 and 20 000

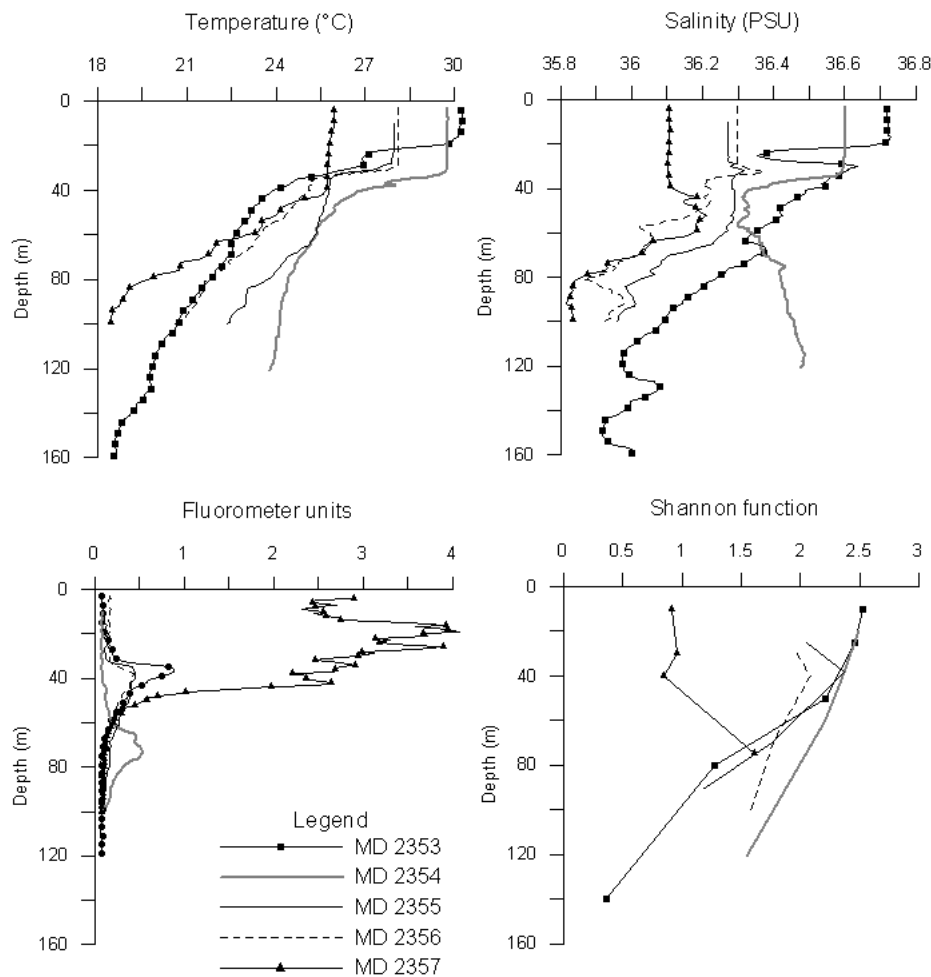


Figure 2: Shipboard-derived data of temperature, salinity and fluorometer units (Kissel & Schulz, 2000). Additionally, the Shannon Information Function as a reasonable measure of heterogeneity (diversity) is depicted

cells per litre, were reached at this station.

Station MD 2356: The species compositions at this station were rather similar to the ones found at Station MD 2355. The main differences were due to somewhat higher total cell-densities in the upper water-column and lower ones below the thermocline.

Station MD 2357: In all samples, *G. oceanica* was by far the most abundant species, with more than 75% at 10m water-depth. Even in the deepest sample, at 75m water-depth, this taxon still dominated the community, whilst *F. profunda* only contributed a minor proportion. The second most abundant species was *Calcidiscus leptoporus* (Plate 1, Figures 8, 9) that almost solely occurred at this station. A repeated counting only of specimens of this species in the sample from 10m revealed an overwhelming dominance of the subspecies *C. leptoporus* ssp. *quadriperforatus* (= *C. leptoporus* large), with more than 97%. Interestingly, coccospheres of this species were often found together (Plate 1, Figure 9), which possibly indicates a status of ongoing cell-division. *Umbilicosphaera foliosa* was only found in rather low numbers at all stations, but had a slight maximum in the samples here. No

further species could be identified with indicative abundance variations with respect to the exceptional environmental conditions.

Overall, cell-densities with up to 46 800 cells per litre were high but not highest when compared to the other stations. In contrast to all other stations, diatoms occurred in much higher numbers than coccolithophores.

5. Interpretation and discussion

Temperature and salinity data suggest that Stations MD 2353 and MD 2354 were furthestmost from the upwelling centres. Stations MD 2355 and MD 2356 seemed to be located closer to the upwelling area, whereas physical conditions at Station MD 2357 indicate a position at, or close to, the upwelling. The species composition and abundance of coccolithophore communities support this classification. Most coccolithophore species tend to be more K-selected, and therefore are

more important components of communities in warm, stratified, nutrient-poor waters and less important in nutrient-rich waters (r-selected species) (Brand, 1994; Young, 1994). High amounts of oceanic, K-selected species occurred in the samples at Stations MD 2353 and MD 2354 above the thermocline, whilst r-selected species were absent or rare. At Stations MD 2355 and MD 2356, similar species compositions were observed, but the r-selected species *G. oceanica* was already the dominant species, and at Station MD 2357, this species dominated the communities by far. In consequence, the diversity (Shannon Function) decreased accordingly.

5.1 Ecological tolerances of coccolithophore species

Gephyrocapsa oceanica is known to represent high nutrient levels, especially in tropical to subtropical seas (McIntyre & Bé, 1967; Okada & Honjo, 1977; Bollmann, 1997). Under the strong influence of monsoon climates, this species is more abundant than any other placolith-bearing coccolithophore species (Cheng & Wang, 1997; Andruleit *et al.*, 2000) and was even attributed to indicat-

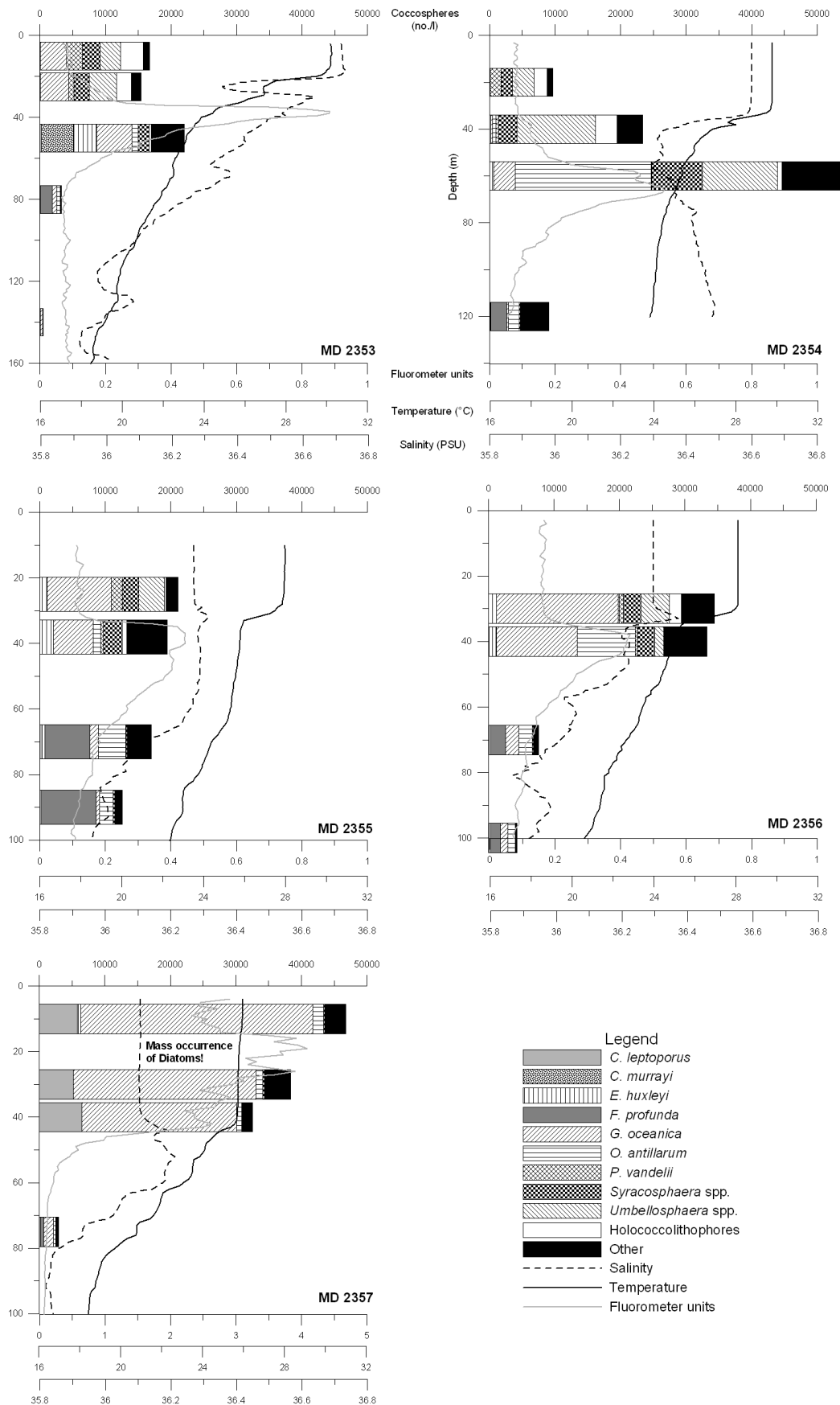


Figure 3: Coccolithophore data for the investigated sites, with profiles of temperature, salinity, and fluorometer units

ing maximum upwelling conditions (Broerse *et al.*, 2000). Several studies in the Arabian Sea have confirmed the preference of *G. oceanica* for elevated nutrient levels (Houghton & Guptha, 1991; Andruleit *et al.*, 2000; Broerse *et al.*, 2000; Andruleit & Rogalla, 2002). The present study additionally emphasises that *G. oceanica* can cope with unstable surface-water conditions, *i.e.* turbulent waters caused by active upwelling. A cluster analysis underlines the exceptional status of this species (Figure 4). Together with *Umbellosphaera foliosa* and

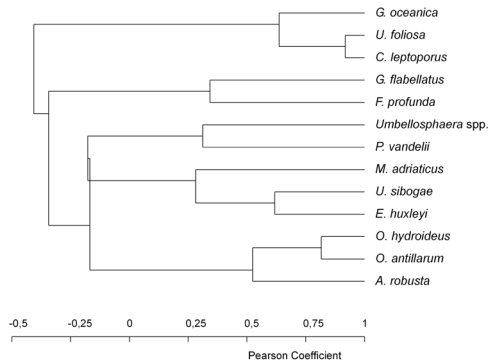


Figure 4: Cluster analysis (centroid linkage method; distance metric is 1-Pearson Correlation Coefficient) on the cell-densities of the most important taxa

Calcidiscus leptoporus, it forms a group with the greatest distance from all other taxa.

C. leptoporus also contributed significantly to the communities in the upwelling area and appeared in the same cluster as *G. oceanica* (Figure 4). This observation suggests that, at least, the subspecies *C. leptoporus* ssp. *quadriperforatus* (= *C. leptoporus* large) is not related to oligotrophic conditions. The use of *C. leptoporus* as an indicator of low nutrient levels, as still proposed by Schiebel *et al.* (2004), has, therefore, to be questioned. Already, a plankton analysis from the North Atlantic has revealed the affinity of large *Calcidiscus* cells with nutrient-rich conditions (Renaud & Klaas, 2001). Renaud *et al.* (2002) showed that only the small and large morphotypes occurred in the Arabian Sea, with the latter dominating this genus. Also, other studies have suggested that increased abundances of *C. leptoporus* may be indicative of high productivity (Ziveri *et al.*, 1995; Flores *et al.*, 1997; Kinkel *et al.*, 2000; Henderiks & Renaud, 2004). However, one has to bear in mind that the differentiation of all taxa within the genus of *Calcidiscus* is essential for ecological specifications or usage as palaeoenvironmental indicators. According to our study, the high abundance of this species probably indicates early upwelling conditions. The common occurrence of *C. leptoporus* ssp. *quadriperforatus* in the state of ongoing cell-division probably indicates rapid and ongoing reproduction of this species during this stage.

According to Young (1994), *C. leptoporus*, *G. oceanica* and, additionally, *U. foliosa* belong to the placolith-

bearing coccolithophores which superficially may exhibit an erratic biogeographical distribution worldwide, but all typical environments exhibit similar ecological conditions in that they are all eutrophic. The present study provides strong evidence that all three species are indicators of nutrient-rich conditions.

The species *Florisphaera profunda* and, especially, *Gladiolithus flabellatus* played only a minor role in the communities of the western Arabian Sea. This agrees well with the finding of Andruleit & Rogalla (2002), that *F. profunda* has a positive correspondence to the mixed-layer depth which is shallowest in the study region and deepens to the east and south. The occurrence of both species in one cluster indicates similar ecological demands. A wide range of different conditions may control the occurrence and abundance of *F. profunda* (Jordan, 2002). Our study underlines the common thread that it is an indicator of low productivity in surface-waters.

Taxa such as *Umbellosphaera* spp. or holococcolithophores have been found to be negatively correlated to upwelling conditions (Kleijne, 1991). Their occurrence is usually confined to stable, open-ocean conditions above the thermocline (Kleijne *et al.* 1989, 1993; Andruleit *et al.*, 2003). In our study, these species were found below the thermocline, too. This observation may be explained by instabilities in the water stratification due to the onset of upwelling. In corroboration, *F. profunda* rarely dominated the communities below the thermocline. Since *Palusphaera vandellii* clustered together with *Umbellosphaera* spp., similar ecological tolerances may be deduced.

Although *Emiliania huxleyi* is the most ubiquitous coccolithophore species in the world ocean (McIntyre & Bé, 1967; Winter & Siesser, 1994) and is able to form strong blooms (Holligan *et al.*, 1983; 1993), it was not found to dominate the communities in the northern Arabian Sea. Generally, the distribution of this species was found to be largely independent of water temperature and thermocline depth (Samtleben *et al.*, 1995a, b), and cells become very abundant in a nutrient-rich environment, such as along the edges of the subtropical gyres or along the outer continental shelves (Brand, 1994). In equatorial regions, however, this species may not be regarded as an indicator of upwelling processes, but may be more typical of stable régimes in terms of vertical mixing with relatively high nutrient-availability (Lampert *et al.*, 2002). In more temperate regions, the ubiquitous *E. huxleyi* seems to be more successful and outnumbers *G. oceanica* even in upwelling areas (Mitchell-Innes & Winter, 1987; Giraudeau & Bailey, 1995). The co-occurrence of *Umbellosphaera sibogae* in the same cluster (Figure 4) as *E. huxleyi* indicates some correspondence in the ecological demands of the two species. Furthermore, the taxa *U. sibogae* and *U. foliosa*, which were recently emended into separated species according to molecular genetic data (Young *et al.*, 2003), indeed seem to inhabit different ecological niches.

Although other phytoplankton were not the focus of this study, the high numbers of diatoms, together with the fluorometer data, clearly indicate that, at Station MD 2357, coccolithophores were not the dominant group. Despite much higher chlorophyll concentrations than at the other stations, coccolithophore abundances remain rather constant. Diatom numbers seem to be positively related to nutrient concentration and negatively related to coccolithophore abundances, while coccolithophore numbers increased towards more nutrient-depleted and stratified surface-waters (Schiebel *et al.*, 2004). A dominance of coccolithophores might be restricted to environmental settings where biological conditions allow chlorophyll maxima only at greater depth (Winter *et al.*, 1994). This observation indicates that coccolithophores are generally K-selected taxa in relation to other phytoplankton groups. Exceptions are the taxa *G. oceanica* and *C. leptoporus* ssp. *quadriperforatus*, which appear to be more r-selected. According to the fluorometer profiles, it appears likely that, at the stations remote from the upwelling area,

al., in press).

6. Conclusions

Absolute coccolithophore abundances range from 10 000 to >50 000 coccospheeres per litre in the upper water-column. Highest coccolithophore concentrations probably occur close to the upwelling centres where oceanic and upwelled water mix. A total of 77 taxa were identified in this study, with several species that contribute significant portions to the communities. The overall dominant taxon was *Gephyrocapsa oceanica*, with an average 34%.

We conclude that *G. oceanica* has a preference for elevated nutrient levels and, additionally, can cope with unstable surface-water conditions, *i.e.* turbulent waters caused by active upwelling. The occurrence of the subspecies *Calcidiscus leptoporus* ssp. *quadriperforatus* (*C. leptoporus* large) probably indicates early upwelling conditions. In equatorial regions, *Emiliania huxleyi* may not be regarded as an indicator of upwelling processes, but appears to be more typical for stable regimes in terms of

vertical mixing with relatively high nutrient-availability. The deep-living *Florisphaera profunda* played only a minor role in the communities of the western Arabian Sea, emphasising the common thread that it is an indicator of low productivity in surface-waters.

High amounts of diatoms outnumbered coccolithophores at, or in close proximity to, active upwelling. This underlines that coccolithophores are generally K-selected taxa in relation to other phytoplankton.

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References

- Andruleit, H.A., von Rad, U., Bruns, A. & Ittekkot, V. 2000. Coccolithophore fluxes from sediment traps in the north-eastern Arabian Sea off Pakistan. *Marine Micropaleontology*, **38**: 285-308.
- Andruleit, H. & Rogalla, U. 2002. Coccolithophores in surface sediments of the Arabian Sea in relation to environmental gradients in surface waters. *Marine Geology*, **186**: 505-526.
- Andruleit, H., Rogalla, U. & Stäger, S. In press. From living communities to fossil assemblages: origin and fate of coccolithophores in the northern Arabian Sea. *Micropaleontology*.
- Andruleit, H., Stäger, S., Rogalla, U. & Cepek, P. 2003. Living coccolithophores in the northern Arabian Sea: ecological tolerances and environmental control. *Marine Micropaleontology*, **49**: 157-181.
- Banase, K. 1994. On the coupling of hydrography, phytoplankton, zooplankton, and settling organic particles offshore in the Arabian Sea. In: D. Lal (Ed.). *Biogeochemistry of the*

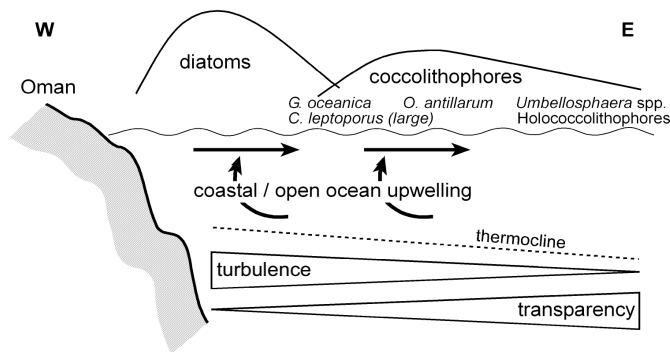


Figure 5: Schematic coccolithophore succession (diatoms are shown in addition) on a schematic transect through the upwelling area perpendicular to the coast of Oman. Modified after Zeltner (2000) and references therein

coccolithophore communities composed of taxa such as *P. vandellii*, *U. irregularis* and *U. tenuis* had a greater portion of the phytoplankton biomass. Highest coccolithophore concentrations probably occur close to the upwelling centres where oceanic and upwelled water mix (Giraudeau & Bailey, 1995). Generally, the results of our study support the findings of Zeltner (2000), concerning the coccolithophore succession on a schematic transect through the upwelling area off Oman (Figure 5). However, the overall contribution of coccolithophores to phytoplankton abundance and biomass is rather low in the Arabian Sea. The phytoplankton community structure is dominated by prokaryote taxa and only diatoms are sometimes able to contribute significantly to phytoplankton standing stocks (Tarran *et al.*, 1999). Although coccolithophores might not be among the most important phytoplankton constituents in the Arabian Sea, their fossil record bears unique potential for successful monitoring and reconstruction of palaeoenvironmental changes (Andruleit *et*

- Arabian Sea. *Proc. Indian Acad. Sci. (Earth Planet. Sci.)*, **103**(2): 125-161.
- Bollmann, J. 1997. Morphology and biogeography of *Gephyrocapsa* coccoliths in Holocene sediments. *Marine Micropaleontology*, **29**: 319-350.
- Brand, L.E. 1994. Physiological ecology of marine coccolithophores. In: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press, Cambridge: 39-49.
- Brock, J.C., McClain, C.R., Anderson, D.M., Prell, W.L. & Hay, W.W. 1992. Southwest monsoon circulation and environments of Recent planktonic foraminifera in the northwestern Arabian Sea. *Paleoceanography*, **7**(6): 799-813.
- Brock, J.C., McClain, C.R., Luther, M.E. & Hay, W.W. 1991. The Phytoplankton Bloom in the Northwestern Arabian Sea During the Southwest Monsoon of 1979. *Journal of Geophysical Research*, **96/C11**: 20 623-20 642.
- Broerse, A.T.C., Brummer, G.-J.A. & van Hinte, J.E. 2000. Coccolithophore export production in response to monsoonal upwelling off Somalia (northwestern Indian Ocean). *Deep-Sea Research II*, **47**: 2179-2205.
- Cheng, X. & Wang, P. 1997. Controlling factors of coccolith distribution in surface sediments of the China seas: marginal sea nannofossil assemblages revisited. *Marine Micropaleontology*, **32**: 155-172.
- Currie, R.I., Fisher, A.E. & Hargreaves, P.M. 1973. Arabian Sea Upwelling. In: B. Zeitzschel & S.A. Gerlach (Eds). *The Biology of the Indian Ocean*. Springer-Verlag, Berlin, Heidelberg, New York: 38-52.
- Flores, J.-A., Sierro, F.J., Fancés, G., Vázquez, A. & Zamarréño, 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.
- Giraudeau, J. & Bailey, G.W. 1995. Spatial dynamics of coccolithophore communities during an upwelling event in the Southern Benguela system. *Continental Shelf Research*, **15**(14): 1825-1852.
- Guptha, M.V.S., Mohan, R. & Muralinath, A.S. 1995. Living coccolithophorids from the Arabian Sea. *Riv. It. Paleont. Strat.*, **100**(4): 551-574.
- Hastenrath, S. & Lamb, P.J. 1979. *Climatic atlas of the Indian Ocean, Part I: Surface climate and atmospheric circulation*. Wisconsin University Press: 1-14.
- Hastenrath, S. & Merle, J. 1987. Annual cycle of subsurface thermal structure in the tropical Atlantic Ocean. *J. Phys. Oceanogr.*, **17**: 1518-1538.
- Henderiks, J. & Renaud, S. 2004. Coccolith size increase of *Calcidiscus leptoporus* offshore Morocco during the Last Glacial Maximum: an expression of enhanced glacial productivity. *Journal of Nannoplankton Research*, **26**(1): 1-12.
- Holligan, P.M., Fernández, E., Aiken, J., Balch, W.M., Boyd, P., Burkill, P.H., Finch, M., Groom, S.B., Malin, G., Muller, K., Purdi, 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**(4): 879-900.
- Holligan, P.M., Viollier, M., Harbour, D.S., Camus, P. & Champagne-Philippe, M. 1983. Satellite and ship studies of coccolithophore production along a continental shelf edge. *Nature*, **304**: 339-342.
- Houghton, S.D. & Guptha, M.V.S. 1991. Monsoonal and fertility controls on Recent marginal sea and continental shelf coccolith assemblages from the western Pacific and northern Indian oceans. *Marine Geology*, **97a**: 251-259.
- Jordan, R.W. 2002. Environmental applications of calcareous nannofossils. In: S.K. Haslett (Ed.). *Quaternary Environmental Micropaleontology*. Arnold, London: 185-206.
- Kinkel, H., Baumann, K.-H. & Cepek, M. 2000. Coccolithophores in the equatorial Atlantic Ocean: response to seasonal and Late Quaternary surface water variability. *Marine Micropaleontology*, **39**: 87-112.
- Kissel, C. & Schulz, H. 2000. Transit Encens-Sheba. R.V. Marion Dufresne, Colombo (Sri Lanka – Salalah (Oman), June 3rd 2000 – June 12th 2000, unpublished cruise report MD-117.
- 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 Geol.*, **100**: 1-63.
- Kleijne, A. 1993. *Morphology, taxonomy and distribution of extant coccolithophorids (calcareous nannoplankton)*. PhD thesis, Amsterdam Free University, Netherlands: 321pp.
- Kleijne, A., Kroon, D. & Zevenboom, W. 1989. Phytoplankton and Foraminiferal Frequencies in Northern Indian Ocean and Red Sea Surface Waters. *Netherlands Journal of Sea Research*, **24**(4): 531-539.
- Lampert, L., Quéguiner, B., Labasque, T., Pichon, A. & Lebreton, N. 2002. Spatial variability of phytoplankton composition and biomass on the eastern continental shelf of the Bay of Biscay (north-east Atlantic Ocean). Evidence for a bloom of *Emiliania huxleyi* (Prymnesiophyceae) in spring 1998. *Continental Shelf Research*, **22**: 1225-1247.
- McIntyre, A. & Bé, A.W.H. 1967. Modern Coccolithophoridae of the Atlantic Ocean. I. Placoliths and Cyrtoliths. *Deep-Sea Research*, **14**: 561-597.
- Mitchell-Innes, B.A. & Winter, A. 1987. Coccolithophores: a major phytoplankton component in mature upwelled water off the Cape Peninsula, South Africa in March, 1983. *Marine Biology*, **95**: 25-30.
- Okada, H. & McIntyre, A. 1977. Modern coccolithophores of the Pacific and North Atlantic Oceans. *Micropaleontology*, **23**(1): 1-55.
- Renaud, S. & Klaas, C. 2001. Seasonal variations in the morphology of the coccolithophore *Calcidiscus leptoporus* off Bermuda (N. Atlantic). *Journal of Plankton Research*, **23**: 779-795.
- Renaud, S., Ziveri, P. & Broerse, A.T.C. 2002. Geographical and seasonal differences in morphology and dynamics of the coccolithophore *Calcidiscus leptoporus*. *Marine Micropaleontology*, **46**: 363-385.
- Rixen, T., Haake, B. & Ittekkot, V. 2000. Sedimentation in the western Arabian Sea: the role of coastal and open-ocean upwelling. *Deep-Sea Research II*, **47**: 2155-2178.
- Samtleben, C., Baumann, K.-H. & Schröder-Ritzrau, A. 1995. Distribution, composition, and seasonal variation of coccolithophore communities in the Northern Atlantic. In: J.-A. Flores & F.J. Sierro (Eds). *Proceedings 5th INA Conference, Salamanca, 1993*: 219-235.
- Samtleben, C., Schäfer, P., Andruleit, H., Baumann, A., Baumann, K.-H., Kohly, A., Matthiessen, J. & Schröder-Ritzrau, A. ('Synpal' Working Group) 1995. Plankton in the

- Norwegian-Greenland Sea: from living communities to sediment assemblages - an actualistic approach. *Geologische Rundschau*, **84**: 108-136.
- Schiebel, R., Zeltner, A., Treppke, U.F., Waniek, J.J., Bollmann, J., Rixen, T. & Hemleben, C. 2004. Distribution of diatoms, coccolithophores and planktic foraminifers along a trophic gradient during SW monsoon in the Arabian Sea. *Marine Micropaleontology*, **51**: 345-371.
- Tarran, G.A., Burkill, P.H., Edwards, E.S., Malcolm, E. & Woodward, S. 1999. Phytoplankton community structure in the Arabian Sea during and after the SW monsoon, 1994. *Deep-Sea Research II*, **46**: 655-676.
- Winter, A., Jordan, R.W. & Roth, P. 1994. Biogeography of living coccolithophores in ocean waters. In: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press, Cambridge: 161-177.
- Winter, A. & Siesser, W.G. 1994. *Coccolithophores*. Cambridge University Press, Cambridge: 242pp.
- Young, J. 1994. Function of coccoliths. In: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press, Cambridge: 63-82.
- Young, J., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I. & Østergaard, J.B. 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research, Special Issue*, **1**: 125pp.
- Zeltner, A. 2000. Monsoonal influenced changes of coccolithophore communities in the northern Indian Ocean - alteration during sedimentation and record in surface sediments. *Tübinger Mikropaläontologische Mitteilungen*, **22**: 1-102.
- 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.
- Appendix A: Taxonomic list**
- The taxonomic list includes all taxa identified during the present study. Identification followed Young *et al.* (2003) and Kleijne (1993), in which full references can be found.
- Acanthoica quattrosipina* Lohmann, 1903
Algirosphaera robusta (Lohmann, 1902) Norris, 1984
Alisphaera extenta Kleijne *et al.*, 2002
Alisphaera gaudii Kleijne *et al.*, 2002
Alisphaera ordinata (Kamptner, 1941) Heimdal, 1973
Alisphaera pinnigera (Kleijne *et al.*, 2002)
Alveosphaera bimurata (Okada & McIntyre, 1977) Jordan & Young, 1990
Anthosphaera lafourcadii (Lecal, 1967) Kleijne, 1991
Calcidiscus leptoporus (Murray & Blackman, 1898) Loeblich & Tappan, 1978
Calcidiscus leptoporus ssp. *quadriperforatus* (Kamptner, 1937) Geisen *et al.*, 2002 (= *C. leptoporus* large)
Calciopappus rigidus Heimdal in Heimdal & Gaarder, 1981
Calciosolenia brasiliensis (Lohmann, 1919) Young in Young *et al.*, 2003
Calciosolenia murrayi Gran, 1912
Calyptrolithina divergens (Halldal & Markali, 1955) Heimdal, 1982
Calyptrolithina multipora (Gaarder in Heimdal & Gaarder, 1980) Norris, 1985
Calyptrolithophora papillifera (Halldal, 1953) Heimdal in Heimdal & Gaarder, 1980
Calyptriosphaera oblonga Lohmann, 1902
Corisphaera gracilis Kamptner, 1937
Coronosphaera mediterranea (Lohmann, 1902) Gaarder in Gaarder & Heimdal, 1977
Cyrtosphaera lecaliae Kleijne, 1992
Discosphaera tubifera (Murray & Blackman, 1898) Ostenfeld, 1900
Emiliania huxleyi (Lohmann, 1902) Hay & Mohler, 1967
Florisphaera profunda Okada & Honjo, 1973
Gephyrocapsa ericsonii McIntyre & Bé, 1967
Gephyrocapsa oceanica Kamptner, 1943
Gephyrocapsa? sp. type A *sensu* Kleijne, 1993
Gladiolithus flabellatus (Halldal & Markali, 1955) Jordan & Chamberlain, 1993
Heladosphaera cornifera (Schiller, 1913) Kamptner, 1937
Helicosphaera carteri (Wallich, 1877) Kamptner, 1954
Homozygosphaera triarcha Halldal & Markali, 1955
Michelsarsia adriaticus (Schiller, 1914) Manton *et al.*, 1984
Michelsarsia elegans Gran, 1912 emend. Manton *et al.*, 1984
Oolithotus antillarum (Cohen, 1964) Reinhardt in Cohen & Reinhardt, 1968
Oolithotus fragilis (Lohmann, 1912) Martini & Müller, 1972
Ophiaster hydroideus (Lohmann, 1903) Lohmann, 1913 emend. Manton & Oates, 1983
Palusphaera vandellii Lecal, 1965 emend. Norris, 1984
Pappomonas sp. type 2 Cros & Fortuño, 2002
Papposphaera lepida Tangen, 1972
Papposphaera sp. Tangen, 1972
Polycrater galapagensis Manton & Oates, 1980
Poricalyptra aurisinae (Kamptner, 1941) Kleijne, 1991
Poricalyptra magnaghii (Borsetti & Cati, 1976) Kleijne, 1991
Reticulofenestra sessilis (Lohmann, 1912) Jordan & Young, 1990
Rhabdosphaera clavigera Murray & Blackman, 1898
Sphaerocalyptra adenensis Kleijne, 1991
Sphaerocalyptra quadridentata (Schiller, 1939) Deflandre, 1952
Syracolithus catilliferus (Kamptner, 1937) Loeblich & Tappan, 1963
Syracolithus dalmaticus (Kamptner, 1927) Deflandre, 1952
Syracolithus sp. Deflandre, 1952
Syracosphaera anthos (Lohmann, 1912) Jordan & Young, 1990
Syracosphaera corolla Lecal, 1966
Syracosphaera delicata Cros *et al.*, 2000
Syracosphaera dilata Jordan *et al.*, 1993
Syracosphaera epigrosa Okada & McIntyre, 1977
Syracosphaera florida Sánchez-Suárez, 1990
Syracosphaera halldalii Gaarder in Gaarder & Hasle, 1971 ex Jordan & 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 orbiculus Okada & McIntyre, 1977
Syracosphaera ossa (Lecal, 1966) Loeblich & Tappan, 1968
Syracosphaera pirus Halldal & Markali, 1955
Syracosphaera prolongata Gran, 1912 ex Lohmann, 1913
Syracosphaera pulchra Lohmann, 1902
Syracosphaera rotula Okada & McIntyre, 1977
Turrilithus latericioides Jordan *et al.*, 1991
Umbellosphaera irregularis Paasche in Markali & Paasche, 1955

- Umbellosphaera tenuis* (Kamptner, 1937) Paasche in Markali & Paasche, 1955
Umbilicosphaera anulus (Lecal, 1967) Young & Geisen in Young *et al.*, 2003
Umbilicosphaera foliosa (Kamptner, 1963) Geisen in Sáez *et al.*, 2003
Umbilicosphaera hulburtiana Gaarder, 1970
Umbilicosphaera sibogae (Weber-Van Bosse, 1901) Gaarder, 1970
Zygospaera bannockii (Borsetti & Cati, 1976) Heimdal, 1982
Zygospaera marsilii (Borsetti & Cati, 1976) Heimdal, 1982

Plate 1

- 1: Morphotype of *Gephyrocapsa oceanica* with a delicate bridge and a large central-opening filled with a well-developed grille (Image # 2224; MD 2355, 90m)
- 2: Morphotype of *Gephyrocapsa oceanica* with a stronger bridge and a small central-opening (compared to morphotype of Figure 1) with marginal pores (Image # 2301; MD 2357, 10m)
- 3: Coccospheres of *Gephyrocapsa oceanica* with a strong bridge, a large central-opening, and a prominent tube and collar. The coccospheres seem to be multilayered with only loosely-attached coccoliths (Image # 2542; MD 2356, 30m)
- 4: Intact coccosphere of *Umbilicosphaera hulburtiana* (Image # 2509; MD 2356, 30m)
- 5: Partially-broken coccosphere of *Umbilicosphaera sibogae* (Image # 2821; MD 2355, 25m)
- 6: Two coccospheres of *Umbilicosphaera foliosa* (Image # 2433; MD 2355, 38m)
- 7: Coccosphere of *Emiliana huxleyi* (Image # 2543; MD 2356, 30m)
- 8: *Calcidiscus leptoporus* small (Image # 2259; MD 2355, 90m)
- 9: Two specimens of *Calcidiscus leptoporus* ssp. *quadriperforatus* (= *C. leptoporus* large), probably in a status just after cell division (Image # 2320; MD 2357, 10m)
- 10: Morphotype of *Florisphaera profunda* with short coccoliths (Image # 2387; MD 2355, 90m)
- 11: Morphotype of a rosette-like coccosphere of *Florisphaera profunda* with elongate coccoliths (Image # 2390; MD 2355, 90m)
- 12: Two well-preserved coccospheres of *Alisphaera unicornis* (Image # 2432; MD 2355, 38m)

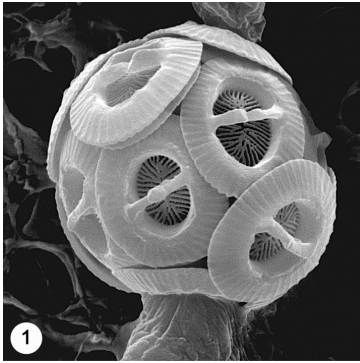
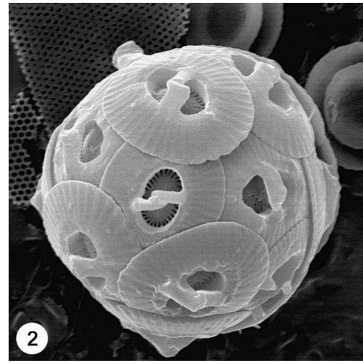
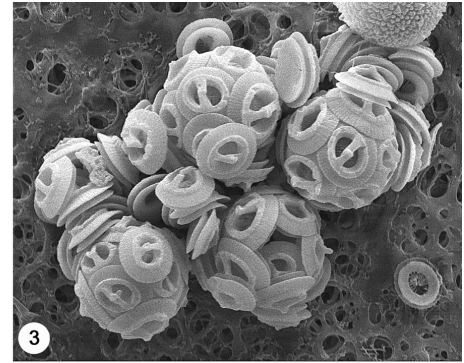
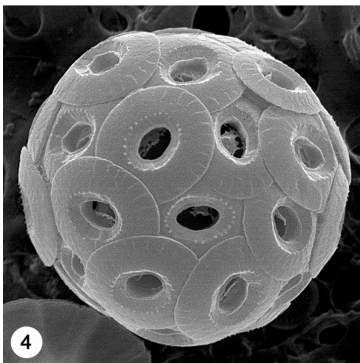
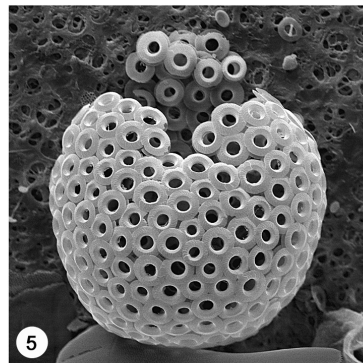
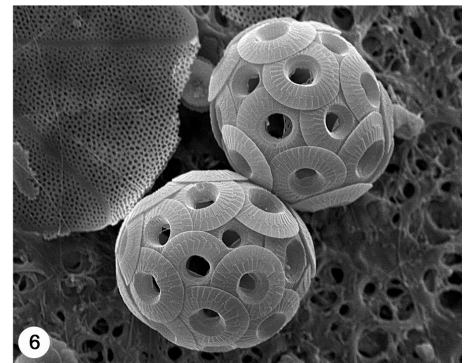
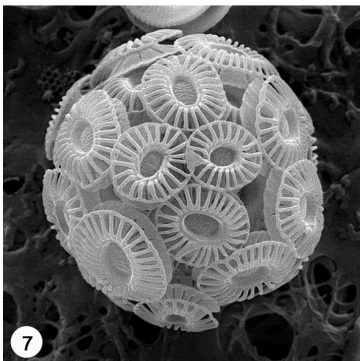
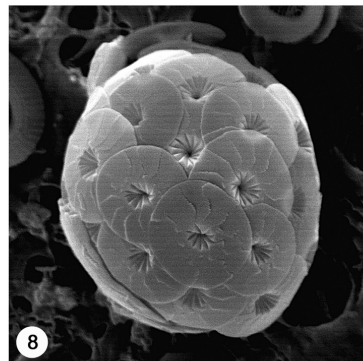
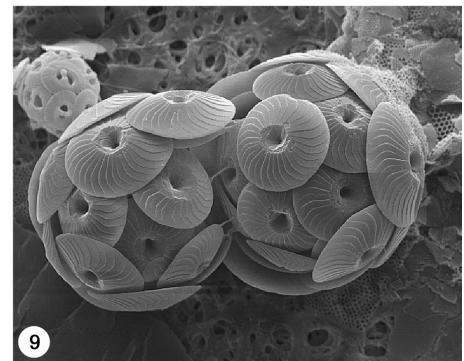
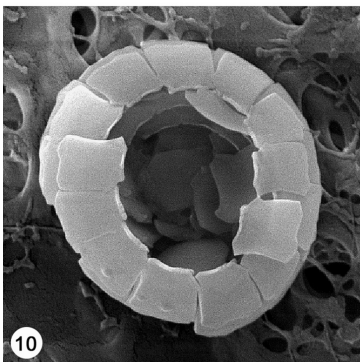
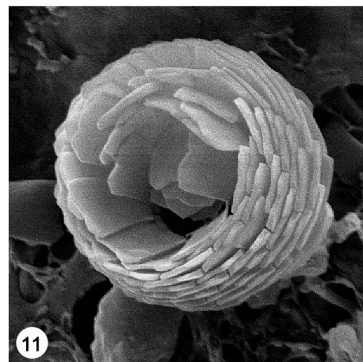
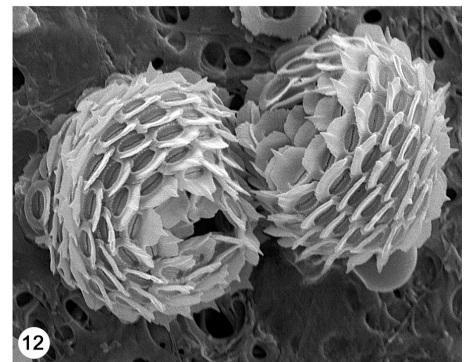
Plate 1Scale-bars = 3 μ m*Gephyrocapsa oceanica**Gephyrocapsa oceanica**Gephyrocapsa oceanica**Umbilicosphaera hultburtiana**Umbilicosphaera sibogae**Umbilicosphaera foliosa**Emiliana huxleyi**Calcidiscus leptoporus* small*Calcidiscus leptoporus* large*Florisphaera profunda**Florisphaera profunda**Alisphaera unicornis*

Plate 2

- 1: Intact coccosphere of *Rhabdosphaera clavigera* (Image # 2806; MD 2355, 25m)
- 2: Coccosphere of *Michaelsarsia adriaticus* with only partially-damaged apparatus of circumflagellar coccoliths (Image # 2212; MD 2354, 60m)
- 3: Coccosphere of *Calciopappus rigidus* with streamlined circumflagellar coccoliths. Several coccospheres exhibited such behaviour, supporting the idea of the flotation-related function of coccoliths (Young, 1994) (Image # 2420; MD 2355, 38m)
- 4: Only partially-broken coccosphere of the delicate species *Palusphaera vandellii* (Image # 2425; MD 2355, 38m)
- 5: Coccosphere of *Calciopappus rigidus* with normal (cf. Figure 3) shape of circumflagellar coccoliths (Image # 2524; MD 2356, 30m)
- 6: *Calciopappus rigidus*. Magnified sector of Figure 5 (Image # 2525; MD 2356, 30m)
- 7: Intact coccosphere of *Umbellosphaera irregularis* (Image # 2089; MD 2353, 25m)
- 8: Intact coccosphere of *Umbellosphaera tenuis* (Image # 2573; MD 2354, 20m)
- 9: Intact coccosphere of *Syracosphaera pulchra* (Image # 2093; MD 2353, 25m)
- 10: Intact coccosphere of *Syracosphaera ossa* (Image # 2016; MD 2353, 50m)
- 11: Intact coccosphere of *Coronosphaera mediterranea* (Image # 2080; MD 2353, 25m)
- 12: Partially-damaged coccosphere of *Syracosphaera prolongata* (Image # 2517; MD 2356, 30m)

Plate 3

- 1: Magnified part of *Calciosolenia murrayi*, showing body coccoliths (cf. Figures 2 and 3) (Image # 2033; MD 2353, 50m)
- 2: Magnified part of *Calciosolenia brasiliensis*, showing body (left) and apical (right) coccoliths (cf. Figures 1 and 3) (Image # 2036; MD 2353, 50m)
- 3: Coccospheres of *Calciosolenia murrayi* (top left) and *Calciosolenia brasiliensis* (centre). The differences in size and shape of the coccospheres are obvious (Image # 2034; MD 2353, 50m)
- 4: Well-preserved coccosphere of *Alveosphaera bimurata* (Image # 2217; MD 2355, 90m)
- 5: Magnified section of *Syracosphaera pirus* (cf. Figure 6) (Image # 2107; MD 2353, 25m)
- 6: Collapsed coccosphere of *Syracosphaera pirus* (cf. Figure 5) (Image # 2106; MD 2353, 25m)
- 7: Intact coccosphere of *Helicosphaera carteri* var. *carteri* (Image # 2557; MD 2354, 20m)
- 8: Intact coccosphere of *Homozygosphaera triarcha* (Image # 2099; MD 2353, 25m)
- 9: Intact coccosphere of *Discosphaera tubifera* (Image # 2540; MD 2356, 30m)
- 10: Intact coccosphere of *Poricalyptra aurisinae* (Image # 2696; MD 2354, 40m)
- 11: Intact coccosphere of *Calyptrolithina multipora* (Image # 2568; MD 2354, 20m)
- 12: Intact coccosphere of *Calyptrosphaera oblonga* (Image # 2571; MD 2354, 20m)

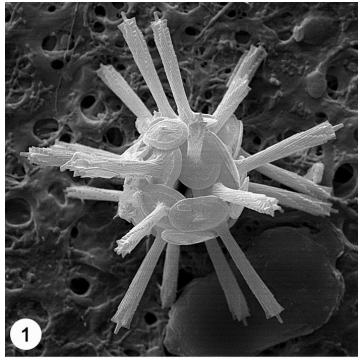
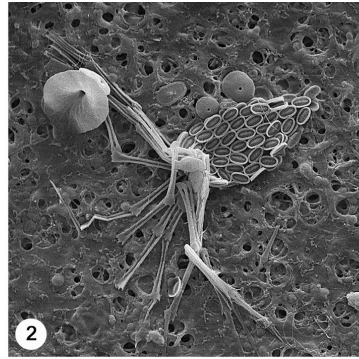
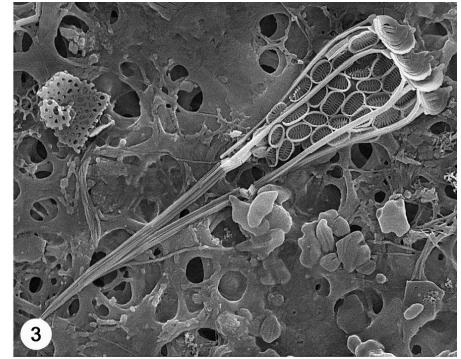
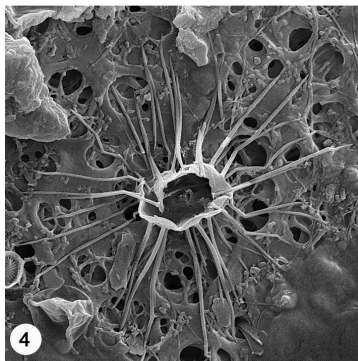
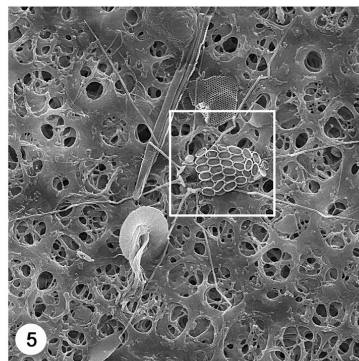
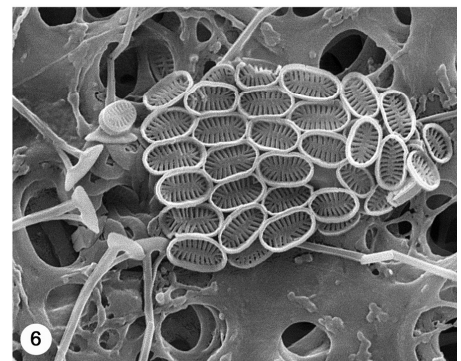
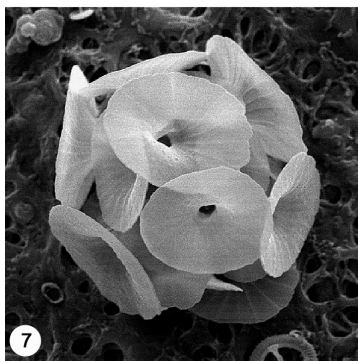
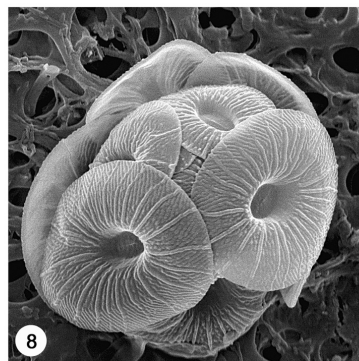
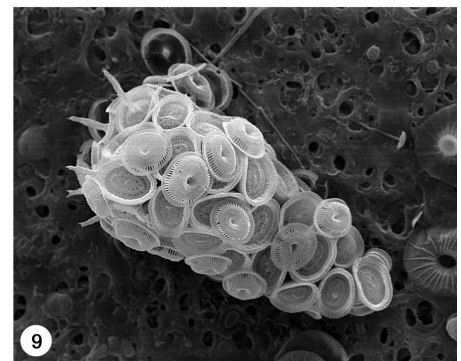
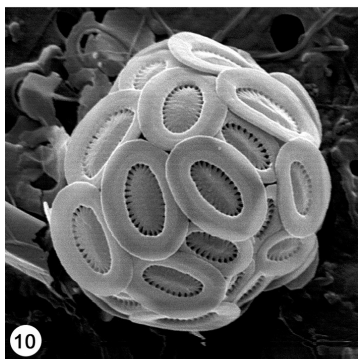
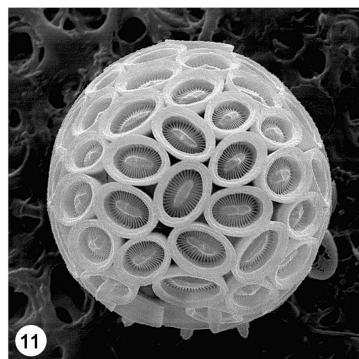
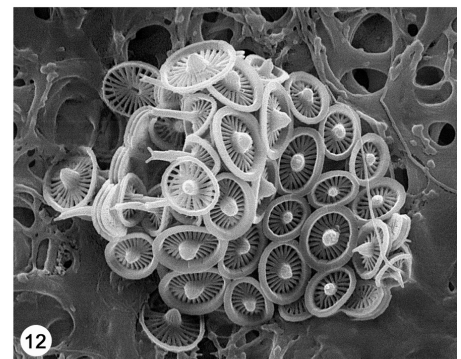
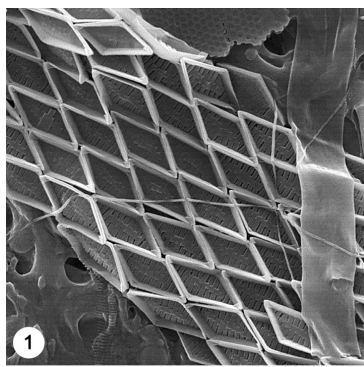
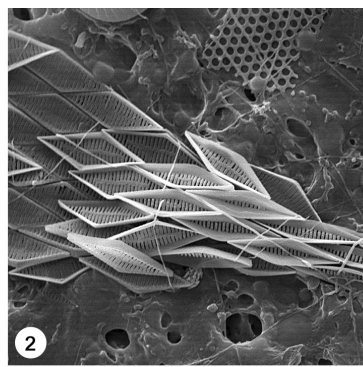
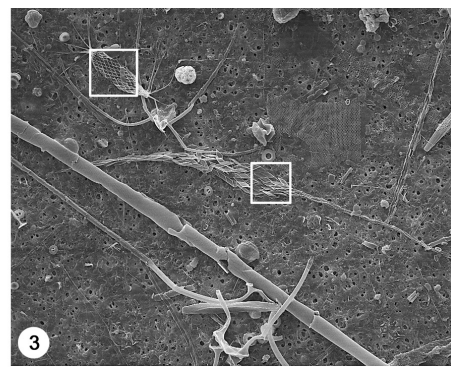
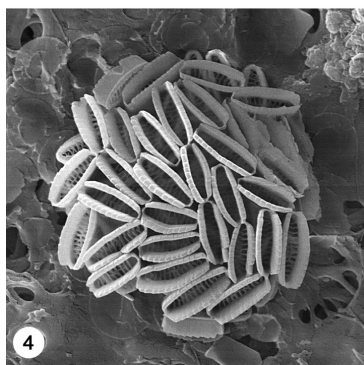
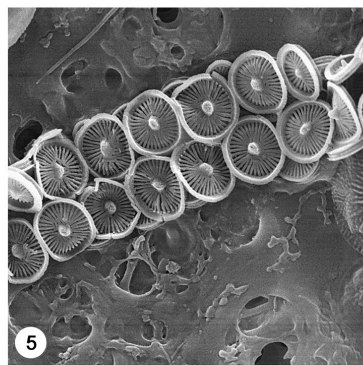
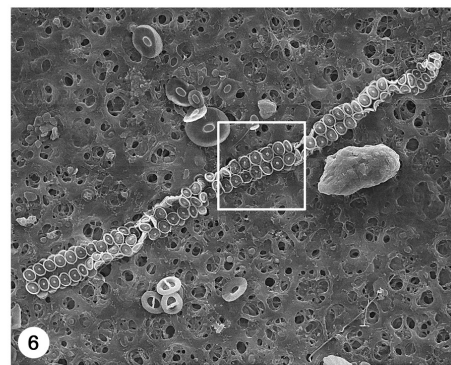
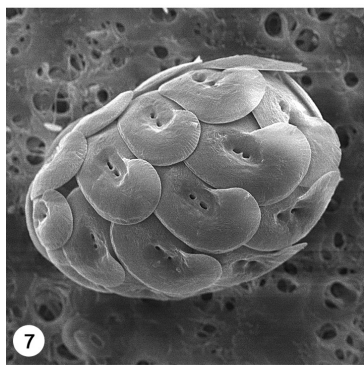
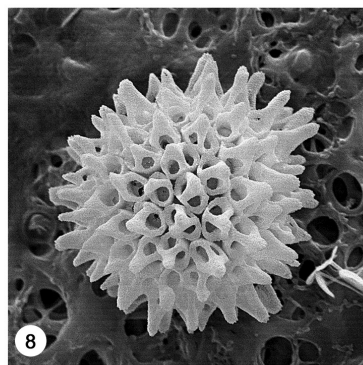
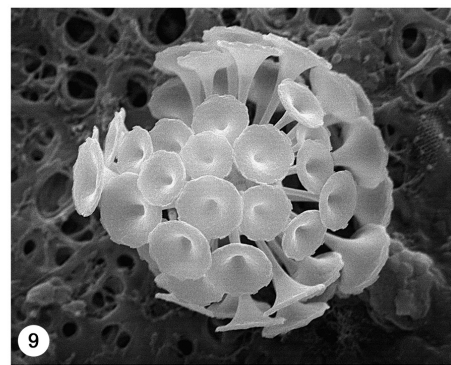
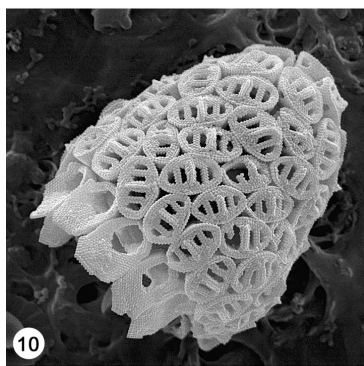
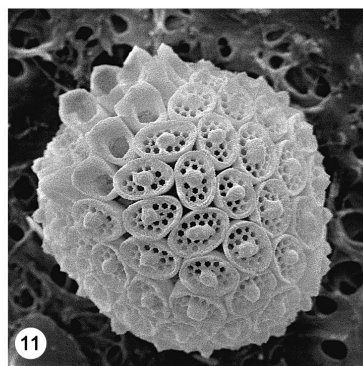
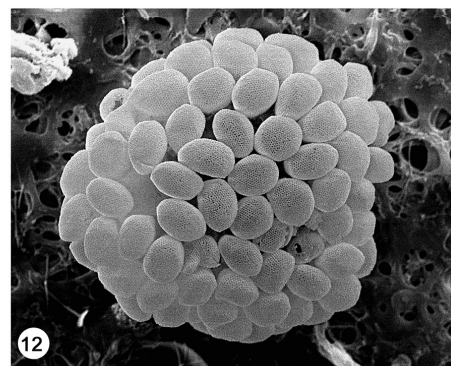
Plate 2Scale-bars = 3 μ m*Rhabdosphaera clavigera**Michaelsarsia adriaticus**Calciopappus rigidus**Palusphaera vandellii**Calciopappus rigidus**Calciopappus rigidus**Umbellosphaera irregularis**Umbellosphaera tenuis**Syracosphaera pulchra**Syracosphaera ossa**Coronosphaera mediterranea**Syracosphaera prolongata*

Plate 3Scale-bars = 3 μ m*Calciosolenia murrayi**Calciosolenia brasiliensis**C. murrayi* (top) & *C. brasiliensis* (centre)*Alveosphaera bimurata**Syracosphaera pirus**Syracosphaera pirus**Helicosphaera carteri**Homozygosphaera triarcha**Discosphaera tubifera**Poricalypta aurisinae**Calyptrolithina multipora**Calyptosphaera oblonga*