MORPHOLOGICAL VARIATIONS OF SELECTED COCCOLITH SPECIES IN A SEDIMENT TRAP NORTH OF THE CANARY ISLANDS

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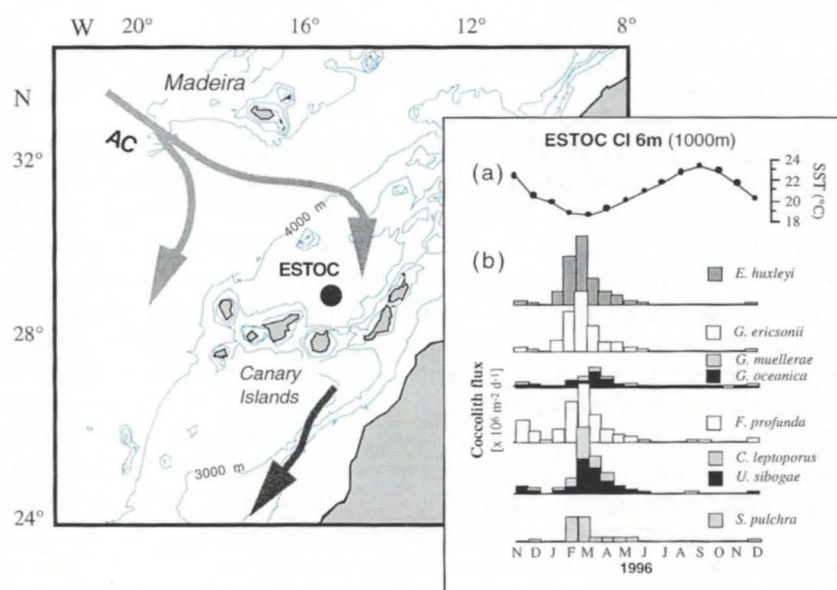**khb@mail.sedpal.uni-bremen.de*

Abstract: Biometrical analyses were performed on nearly 3 200 specimens of distinct coccolith species from the time-series station ESTOC (European Station for Time-series in the Ocean, Canary Islands). Originally begun for calculation of modern species-specific carbonate fluxes, this study was further intensified, both to improve our knowledge of the morphological variability for each of the investigated species, and to check the seasonal size-variations of the various species. Besides the dominant taxa *Emiliania huxleyi* and *Florisphaera profunda*, intensive measurements of various parameters have been made on *Calcidiscus leptoporus*, *Gephyrocapsa* spp., *Helicosphaera carteri*, *Syracosphaera pulchra*, and *Umbilicosphaera sibogae*. Generally, the species are unimodally distributed, with respect to length/diameter, and show only slight seasonal variation.

Introduction

Changes in the morphology of microfossil hard parts, as the basis for taxonomic identification, are most commonly used for reconstructions of evolutionary patterns and processes, especially within coccolithophores (*e.g.* Samtleben, 1980; Young, 1990; Wei, 1992; Baumann, 1995; Kameo & Takayama, 1999; Knappertsbusch, 2000). However, for the interpretation of evolutionary development, it is important to know the present morphological variability as well as the biogeographical distribution of the species. At present, this has been worked out only for very few, abundant coccolithophore species/genera, such as *Emiliania huxleyi* (Young & Westbroek, 1991), *Gephyrocapsa* spp. (Bollmann, 1997) and *Calcidiscus leptoporus* (Knappertsbusch *et al.*, 1997).

Figure 1: Location of the sediment trap mooring ESTOC (CI6m) and main surface-water currents (AC - Azores Current, CC - Canary Current). Additional data on the right-hand side include (a) monthly mean sea-surface temperature (SST) for the sediment trap mooring location (29.1°N, 15.5°W) for the period November 1995 to December 1996, and (b) the coccolith flux data (not to scale!) of the investigated species (from Sprengel *et al.*, 2000).

Changes in morphology through time do not necessarily indicate evolution. Size can be controlled genotypically, as has been shown to be important within *E. huxleyi*, but may also reflect ecological conditions within other species (Young & Westbroek, 1991; Baumann, 1995; Knappertsbusch *et al.*, 1997). The overall morphology of many species often varies with size, and strong size variation is evident in both living and fossil samples (Young & Westbroek, 1991). Study of size variation in living oceanic coccolithophore species is therefore a prerequisite, both in improving our knowledge of the morphological range of the species, and in applying this knowledge to palaeontological and palaeoceanographical studies.

In the present study, samples from a year-round moored sediment trap (CI6m) at 1 000m water-depth, from 60 nautical miles north of Gran Canaria (Figure 1) were investigated in order to measure the morphological variation of selected coccolith species. This study was originally undertaken to provide a more exact determination of modern species-specific carbonate fluxes (Sprengel *et al.*, 2000), by using mean-length data of various species in a formula given by Young & Ziveri (2000). Besides providing information on the seasonal succession of species, sediment trapping also gives the opportunity to study seasonal variation in the morphology of coccoliths. Therefore, this aspect has been much intensified in the latter part of the work.

The mooring is located in the Eastern Boundary Current regime of the subtropical North Atlantic gyre. This is a transition zone between relatively nutrient-rich waters along the North African continent to the east and more oligotrophic waters of the North Atlantic gyre to the west and, thus, seems to be well-suited to address the above-mentioned problems. The monthly averaged sea-surface

temperatures (SSTs) for 1996 show a 'normal' North Atlantic seasonality, with minimum SSTs (18.6°C) in February and March, and maximum SSTs (up to 23.5°C) in September (Figure 1). Maximum coccolith fluxes recorded at ESTOC are closely related to the period of lowest SSTs and highest pigment concentration (Sprengel *et al.*, 2000). Highest fluxes of >4500x10^6 coccoliths m^{-2}d^{-1} were observed in late winter/early spring, whereas lowest values of <20x10^6 coccoliths m^{-2}d^{-1} generally occurred during summer months (Sprengel *et al.*, 2000; Figure 1). *Emiliania huxleyi*,

Figure 2: Scatter plots and frequency distribution (of the coccolith diameter, at 0.25µm intervals) of all *C. leptoporus* coccoliths measured. Measured parameters are indicated in the SEM picture.

Florisphaera profunda and *Gephyrocapsa ericsonii* dominated the coccolithophore assemblages, whereas all other species generally contributed <10% to the community. Variation in the relative species composition was low, reflecting similar seasonal flux patterns of the different species during the entire sampling period.

Besides the most abundant species, *E. huxleyi* and *F. profunda*, we have selected *Gephyrocapsa* spp., *Calcidiscus leptoporus*, *Umbilicosphaera sibogae*, *Helicosphaera carteri* and *Syracosphaera pulchra*, displaying an overview of styles of the main morphological variations of coccoliths. Basic aims of this study are: (1) to measure (and numerically classify) the morphological variability for each of the investigated species; and (2) to check the seasonal distribution of the morphological varieties. This study was conducted in conjunction with the EU-funded TMR-project, CODENET, which, among other tasks, aims to study coccolith morphology and determine ecophenotypic and genotypic variability of selected species.

Materials and Methods

For this study, 16 of the 20 samples from the time-series sediment trap, CI6m, were chosen, all of which had already been counted for coccolith content (Sprengel *et al.*, 2000). The individual sampling intervals of the mooring is about three weeks. For coccolithophore analysis, aliquots of each sample were wet-split by means of an electrical rotary sample divider (Fritsch, Laborette 27) using tap-water as the split medium. The samples were filtered onto polycarbonate membrane filters (Schleicher & Schuell^{TM} 47mm diameter, 0.45µm pore-size) using a vacuum pump. Thereby a monolayer of all sediment particles was created which was than investigated under the scanning electron microscope (SEM) (for more details see Sprengel *et al.*, 2000).

Measurements were made using a Zeiss DMS 940A SEM. For all species, distal shield length and width, or the
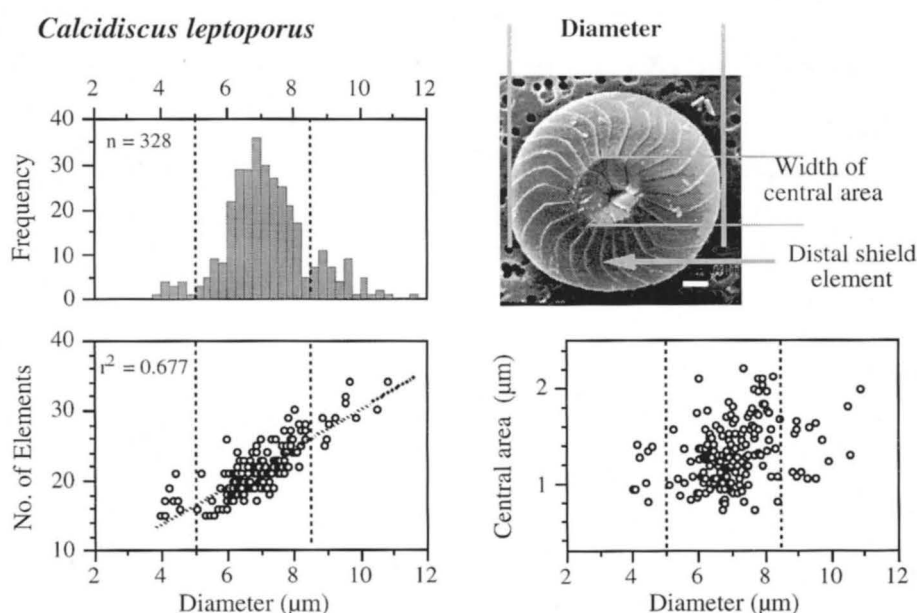
diameter of the distal shield, of about 30 to 50 randomly chosen specimens were measured. In addition, various other parameters were measured or counted, such as the size of the central area (*C. leptoporus*, *E. huxleyi*, *Gephyrocapsa* spp. and *U. sibogae*) and the number of distal shield elements (*C. leptoporus*, *E. huxleyi* and *U. sibogae*). All measurements were made directly on the TV-screen at a magnification of 5 000x or 10 000x by using an internal Zeiss measuring system. This leads to a resolution of about 0.1-0.2µm. An attempt was made to measure coccoliths in different areas of the SEM-mounts by moving from one measured specimen to the next unmeasured specimen.

Results and Discussion

Variability of the species:

Coccospheres of *Calcidiscus leptoporus* (Murray & Blackman, 1898) Loeblich & Tappan, 1978 consist of tightly interlocked coccoliths. These placoliths are mostly circular or slightly elliptical in plan-view, with the distal shields displaying dextrally-imbricated and sigmoidally-shaped sutures. *C. leptoporus* was thought to have a holococcolith stage (*C. leptoporus* f. *rigidus*) in its life-cycle (Kleijne, 1991; Cortés, 2000). However, Geisen *et al.* (2000) recently found combination coccospheres of *C. leptoporus* together with *Syracolithus quadriperforatus* and tentatively explained the combination of two holococcoliths associated with one heterococcolithophorid by cryptic speciation in the group.

The morphology of a total of 328 individual placoliths of the heterococcolith-bearing stage of the *C. leptoporus* group fell into three indistinct clusters of <5.0µm, 5.0 to ~8.5µm, and >8.5µm (Figure 2). Overall, the diameters of the distal shield range from 3.9µm to 11.5µm and the number of elements from 15 to 34 (Table 1). However, the majority of measurements are between 6.0µm to 8.0µm and 18 to 28 distal shield elements. In addition, a strong correlation (r^2 = 0.677) of the coccolith diameter and the number of

		Counts (in μm/in °)	Minimum (in μm/in °)	Maximum (in μm/in °)	Mean (in μm/in °)	Standard Deviation
C. leptoporus	Diameter	328	3.97	11.55	7.21	1.27
	No. of elements	159	15	34	22	3.89
	Pore width	173	0.08	2.21	1.32	0.34
E. huxleyi	Length	803	2.38	4.43	3.33	0.33
	Width	516	2.01	3.56	2.78	0.29
	No. of elements	512	22	40	31	3.56
	Pore length	516	0.79	2.07	1.4	0.21
F. profunda	Length	497	1.59	5.95	2.78	0.76
	Width	393	0.94	3.99	1.83	0.48
G. ericsonii	Length	122	1.44	2.94	1.97	0.23
	Width	62	1.18	2.34	1.58	0.18
	Pore length	62	0.65	1.47	1.04	0.15
	Bridge angle	62	20	55	34.29	7.96
G. muellerae	Length	62	2.94	3.82	3.45	0.24
	Width	43	2.42	3.16	2.88	0.21
	Pore length	43	1.2	1.92	1.68	0.2
	Bridge angle	43	13	33	21.5	6.01
G. oceanica	Length	81	3.94	5.91	4.99	0.5
	Width	71	3.25	5.15	4.27	0.47
	Pore length	71	1.74	3.34	2.46	0.35
	Bridge angle	71	45	81	64.27	7.82
H. carteri	Length	223	4.75	12.84	9.13	1.44
	Width	100	4.93	7.91	5.95	0.73
S. pulchra	Length	484	3.88	8.42	5.87	0.7
	Width	282	2.75	6.28	4.15	0.58
U. sibogae var. foliosa	Diameter	452	2.91	5.99	4.42	0.49
	Central area	263	1.77	3.57	2.58	0.29
	Pore size	357	1.02	2.83	1.70	0.25
	No. of elements	99	17	33	28	2.71
U. sibogae var. sibogae	Diameter	118	4.43	6.97	5.93	0.44
	Central area	95	1.59	3.3	2.61	0.30
	Pore size	99	0.81	2.18	1.54	0.29
	No. of elements	50	22	35	32	2.38

Table 1: Statistics showing the morphological variability of the selected coccolith species at CI6m. Note that in a first phase of the study only measurements of lengths/diameters were made, resulting in different counts per parameter.

elements is obvious, whereas the diameter of the central area is less clearly correlated to the coccolith diameter (Figure 2).

In total, our data confirm several previous observations of *C. leptoporus* morphology (*e.g.* McIntyre & Bé, 1967; Bartolini, 1970; Baumann, 1990; Kleijne, 1993; Knappertsbusch *et al.*, 1997). In particular, the clustering of the coccolith measurements into three different morphotypes with minimum overlap at 5μm and 8μm by Knappertsbusch *et al.* (1997) and by Kleijne (1993) is very similar to our findings. The authors have not found good correlation between these morphotypes and single environmental parameters. Nevertheless, Knappertsbusch *et al.* (1997) also showed that individual assemblage plots might differ significantly from different regions, with either large, intermediate or small coccoliths dominating. Thus, the strong dominance in frequency of the intermediate morphotypes in samples of CI6m is not surprising.

Conspicuous differences of the morphotypes occur in the inner part of the shield, especially in the filling of the central area. We have found that in the small- and medium-sized placoliths (types A and C, respectively, of Kleijne (1993)), the radial elements extend inward into the central pore. In contrast, the central area is filled with a ring-like solid structure, without visible sutures, leaving only a small central pore in the large-sized morphotype (type B of Kleijne (1993)). In addition, variation in suture shape has also to be included in distinguishing between the different morphotypes (Kleijne, 1993).
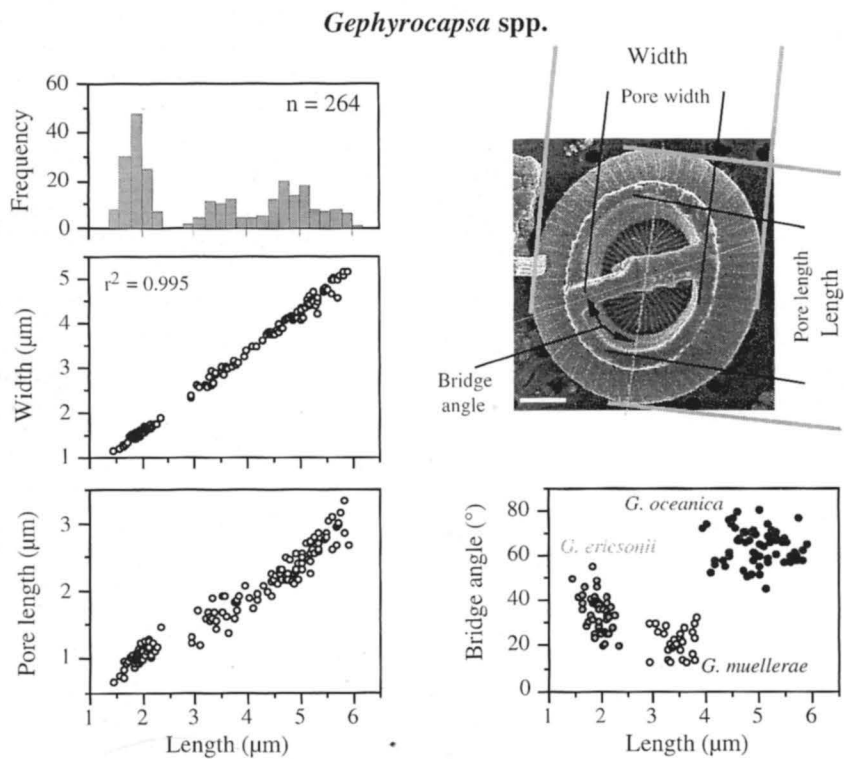
Emiliania huxleyi (Lohmann, 1902) Hay & Mohler, 1967 *in* Hay *et al.*, 1967 forms spherical coccospheres consisting of <10 to upto >50 partially interlocked placoliths. These oval placoliths typically are formed of T-shaped elements and have an elliptical central area. Young & Westbroek (1991) distinguished between different varieties of *E. huxleyi* (types A, B, C, and var. *corona*), although they stated that biometrical analyses do not separate these types easily. *E. huxleyi* in general is the most abundant living coccolithophore and has extremely broad ecological affinities, occurring in all of the main oceanic conditions. Large-scale blooms which mainly consist of *E. huxleyi* are regularly observed during early summer in the northern North Atlantic (*e.g.* Holligan *et al.*, 1993; Brown & Yoder, 1994). This species is easy to maintain in culture and has been subjected to intensive studies, combining observations from culture and oceanic populations (*e.g.* Watabe & Wilbur, 1966; Westbroek *et al.*, 1989; Young & Westbroek, 1991; Westbroek *et al.*, 1993; Young, 1994).

The morphology of a total of 803 individual coccoliths of *E. huxleyi* shows a clear unimodal distribution with a maximum centred at 3.3μm (Figure 3). Overall, distal shield lengths are 2.4 to 4.4μm, the widths are 2.0 to 3.6μm, and the number of T-shaped elements range between 22 and 40 (Table 1). Length and width of the distal shield are extremely well correlated ($r^2 = 0.93$) and a good correlation also exists between the length of the distal shield and both numbers of radial elements and size of the central area ($r^2 = 0.68$ and $r^2 = 0.548$, respectively). Varieties as given by Young & Westbroek (1991) have not been distinguished here. However, since most of the coccoliths had a grill of curved rods in the central area (see SEM picture in Figure 3), the majority of the measured specimens are probably type A coccoliths. A few specimens, with delicate rays and open (dissolved?) central areas or with remains of a tiny plate, indicate that forms of *E. huxleyi* type C also occur.

Despite an increasing base of knowledge on *E. huxleyi*, we still know little about its variability in coccolith morphology. The types of variation observed in the present study indicate that genotypic variation, as has been described by Young & Westbroek (1991) for *E. huxleyi* as a whole, is not obvious. The population in this area seems to be morphologically relatively homogeneous, a finding that has been made for other regions as well, especially in the North Atlantic (Young, 1994). Thus, there might only have been one genotype present in this area.

Florisphaera profunda Okada & Honjo, 1973 forms subspherical coccospheres with overlapping, flat coccoliths (nannoliths), forming a rosette when looking in top-view. Each single nannolith is a polygonal plate without any ornamentation. Generally, two varieties of *F. profunda* (var. *profunda* and var. *elongata*) could be distinguished (Okada & Honjo, 1973; Okada & McIntyre, 1977). Together with a few other species, it is the main contributor to the so-called deep-water assemblage (~60 to ~180m water-depth) of low- to mid-latitudes (Okada & Honjo, 1973; Nishida, 1979; Reid, 1980). In sediment assemblages, this species has often been overlooked. However, recently *F. profunda* has gained increasing attention, since it was shown to be a useful

Emiliania huxleyi

Figure 3: Coccolith size variation data and frequency distributions (at 0.25μm intervals) of various parameters measured in *E. huxleyi*. Measured parameters are indicated in the SEM picture of this species (representing a type A variety).

coccoliths, resulting in a correlation coefficient of only $r^2 = 0.269$. Possibly, this is due to the fact that both varieties of *F. profunda* are present in the investigated samples, with var. *elongata* forming larger coccoliths (*e.g.* Reid, 1980).

The presented results of the study of morphological variation in *F. profunda* are rather preliminary, but give a first impression of the size-variability of this species. A wide range in size of the nannoliths has already been described and has lead to the subdivision of this species (Okada & Honjo, 1973). However, from the presented data, this subdivision seems a little questionable, although we have not measured the variation on coccospheres.

palaeoproductivity indicator (*e.g.* Molfino & McIntyre, 1990; Ahagon *et al.*, 1993; Bassinot *et al.*, 1997; Okada & Matsuoka, 1996). The nutrient availability is controlled by the depth of the nutricline, which can be monitored by the abundance of *F. profunda* (Molfino & McIntyre, 1990).

The length and width of the nannoliths are easily measurable morphometrical parameters in *F. profunda*. Therefore, and due to the high relative abundance in settling assemblages of the Canary Islands, 496 specimens were measured in the present study. The distribution shows a unimodal pattern with a maximum centred at about 2.8μm (Figure 4). Overall, coccolith lengths are 1.6 to 5.9μm, the maximum widths are 0.9 to 4.0μm (Table 1). Obviously, there is a great variability in the scatterplot (Figure 4), especially of coccoliths >3.5μm in length. Thus, a rather low correlation exists between the length and the width of the

Their increased value as a proxy for nutrients could possibly advance to a study of the morphological diversity of the whole population.

All extant species of the genus *Gephyrocapsa* Kamptner, 1943 build spherical coccospheres of oval placoliths with a bridge crossing the central area. The number of extant species within the genus is still a point of debate and, besides, has often been confused due to different taxonomic concepts. This is rather surprising, since Bréhéret (1978) and Samtleben (1980) have already demonstrated that *Gephyrocapsa* species could relatively easily be distinguished by a combination of morphological parameters, such as the placolith length and bridge-angle. Recently, morphological analysis of Holocene *Gephyrocapsa* assemblages revealed six dominant morphological associations (Bollmann, 1997), which the author described informally, since he reserved judgement on whether these corresponded to discrete species or at least in part to ecophenotypes.

For this study, our aims were to test whether the three species of *Gephyrocapsa* (*G. ericsonii* McIntyre & Bé, 1967, *G. muellerae* Bréhéret, 1978, *G. oceanica* Kamptner, 1943), which were distinguished by Sprengel *et al.* (2000) in the investigated samples, could be separated by morphological measurements. We measured the lengths of 264 specimens and the width, bridge-angle and central-area size of 136 of these. Overall, lengths and widths of the placoliths are extremely well correlated ($r^2 = 0.995$) and a trimodal distribution pattern can be observed in the length data (Figure 5). A bivariate plot of length *vs.* bridge-angle clearly

Figure 4: Coccolith size variation data of all measured *F. profunda*.

Figure 5: Coccolith size variation data and frequency distributions (at 0.2μm intervals) of various parameters measured in *Gephyrocapsa* spp. Measured parameters are indicated in the SEM picture (representing a *G. oceanica*).

length and width of the coccolith (both including and excluding the wing: Figure 6) measured on a total of 223 specimens. Most coccoliths are between 6.2μm and 12.2μm in length and range from 4.4 to 7.9μm in width. Length and width are relatively well correlated to each other ($r^2 = 0.586$). *H. carteri* seems to be unimodally distributed with respect to coccolith length. However, since we have not included the central-area structure as a morphological feature in this study, different intraspecific varieties have possibly been analysed together. This might be the case even though a conspicuous unimodal frequency distribution was observed. Nevertheless, results are promising to intensify study on the morphological variability of this species.

The coccosphere of *Syracosphaera pulchra* Lohmann, 1902 is dithecate, and consists of an endothecal layer of elliptical, basin-

seperates the three modes into discrete clusters. These clusters correspond to the above-mentioned species. *G. ericsonii* coccoliths are 1.4 to 2.9μm long, ≤2.3μm wide, and have medium-large bridge-angles of about 20-55° (Table 1). *G. muellerae* coccoliths are medium-sized, 2.9 to 3.8μm long and have a typical small bridge-angle of 13-33°, whereas large-sized *G. oceanica* are 3.9μm to 5.9μm long and have a large bridge-angle, generally >50° (Figure 5).

Thus, our measurements exactly fit into the 'traditional' scatterplot-scheme of bridge-angle *vs.* length presented by Samtleben (1980). In addition, although difficult to combine, the observed species could be identical to morphotype associations GM, GC and GE/GL as introduced by Bollmann (1997), with his ecological interpretation fitting relatively nicely into the observed composition of the *Gephyrocapsa* assemblage.

Helicosphaera carteri (Wallich, 1877) Kamptner, 1954 forms coccospheres with large, elliptical coccoliths (helicoliths), with a helical flange terminated by an expanded wing. Three varieties of *H. carteri* (vars *carteri*, *hyalina* and *walichii*) are conventionally recognised in the extant calcareous nannoplankton, based on the helicolith central-area structure (*e.g.* Young, 1998), although it is not clear whether this variation is genotypically controlled. Cros *et al.* (2000) have found combination coccospheres of *H. carteri* heterococcoliths with *Syracolithus catilliferus* holococcoliths, from which they infer that the two morphospecies are life-cycle phases of a single biological species.

The length of the helicolith is the most easily measurable morphometrical parameter in *H. carteri*. Therefore, in the present study, data is mainly presented as total coccolith

shaped caneoliths and an exothecal layer of dome-shaped cyrtoliths. The exothecal coccoliths have a very low preservation potential so that we have only measured the endothecal coccoliths. Combination coccospheres occur with both the holococcolithophorids *Calyptrosphaera oblonga* and *Daktylethra pirus*. These combination coccospheres can have various possible causes. Cros *et al.* (2000) argued that this might indicate a particularly complex life-cycle. However, the association of two holococcoliths, which do not occur on the same cell, with one hetero-coccolithophorid is probably due to cryptic speciation in *S. pulchra* morphology (Geisen *et al.*, 2000).

In our study, we have measured only length and width of the endothecal caneoliths. The measurements on a total of 484 caneoliths show a clear unimodal distribution pattern (Figure 7). In general, the population was consistently characterised by medium-sized coccoliths, most of them 5-7μm long and 3.5-5μm wide. Overall, the length of the caneoliths ranges from 3.9μm to 8.4μm, and the width from 2.7 to 6.3μm (Table 1). The lengths and widths are strongly correlated to each other, with a correlation coefficient of $r^2 = 0.846$ (Figure 7).

Detailed morphological data on *S. pulchra* does not, to our knowledge, exist so far, although it is the most robust *Syracosphaera* species and is characteristic of temperate to subtropical coccolithophore assemblages (Jordan & Chamberlain, 1997). Therefore, the present study gives a first basis for the morphometrical characterisation of this species.

Umbilicosphaera sibogae Weber-van Bosse, 1901 forms non-motile, spherical coccospheres covered with circular placoliths. It contains two varieties, most probably
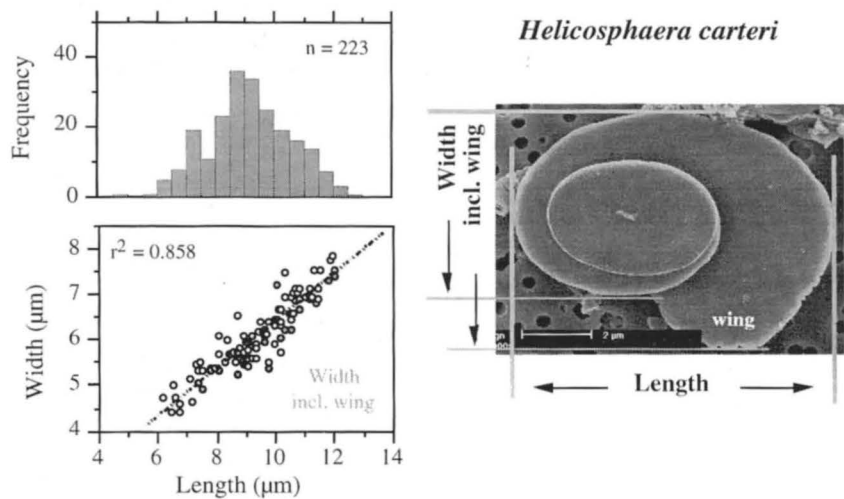
Helicosphaera carteri

Figure 6: Scatter plots and frequency distribution (at 0.25µm intervals) of all *H. carteri* coccoliths measured. Note that the specimen shown in the SEM picture has an unusually wide wing.
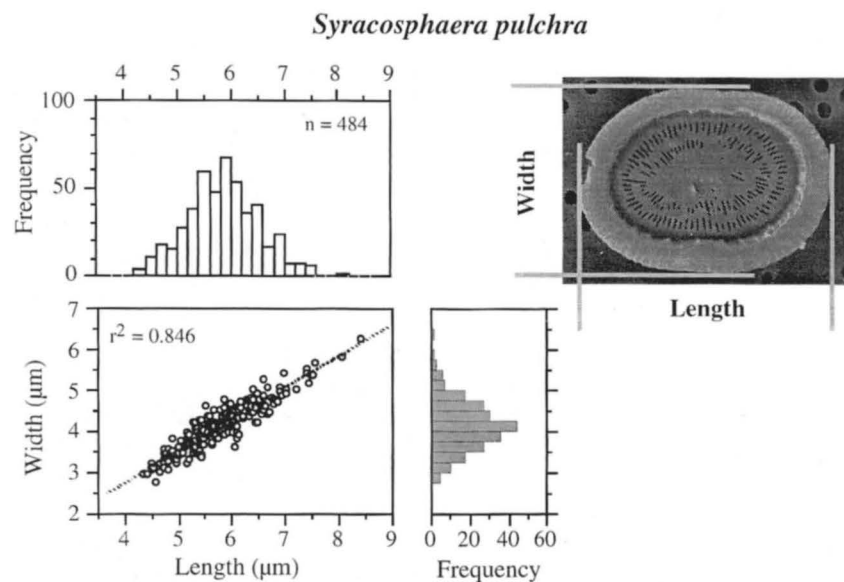
Syracosphaera pulchra

Figure 7: Scatter plots and frequency distribution (at 0.2µm intervals for the coccolith length; at 0.25µm intervals for the coccolith width) of all *S. pulchra* coccoliths measured.

is 2.9µm to 6.0µm in diameter and consists of 21(17)-33 elements (Table 1). Proximal shields are larger than the distal shields, but have not been measured in our study. The distal shield of *U. sibogae* var. *foliosa* is 4.4µm to 7.0µm in diameter, and consists of 26(22)-35 elements. The distribution of each of the varieties is unimodal with peaks centred at 4.4µm (var. *sibogae*) and, less clear, at about 5.9µm (var. *foliosa*), respectively. A good correlation of most of the parameters (pore size, diameter of the central-area, number of distal shield elements) exist with the diameter of the distal shield, with correlation coefficients ranging between $r^2 = 0.49$ and $r^2 = 0.667$ (Figure 8). The absolute range, both of the pore-size and of the central opening, is very similar for both varieties, indicating that the relative proportions with the diameter of the distal shield are smaller for var. *sibogae*.

In general, our findings very well fit to previously published morphological data on *U. sibogae* (*e.g.* Okada & McIntyre, 1977; Kleijne, 1993). Although the morphology of both varieties slightly overlaps, identification usually was never a problem in our samples.

Seasonal variation of morphological associations:
The investigated coccolith species show surprisingly little morphological variation throughout the year, although strong seasonal coccolith fluxes, coinciding with variation in

discrete genotypes, showing distinct variation in coccosphere form: *U. sibogae* var. *sibogae* (Weber-van Bosse, 1901) Gaarder, 1970 forms a large coccosphere with about 40-100 partly interlocked, circular placoliths, which have a relatively large central opening. Proximal shields usually are larger, or as large, as distal shields. The coccosphere of *U. sibogae* var. *foliosa* (Kamptner, 1963) Okada & McIntyre, 1977 is smaller in diameter and consists of <30 tightly interlocked, circular coccoliths with a relatively small central opening, and with proximal shields smaller than distal shields. Detailed descriptions of the coccolith morphology are given in Okada & McIntyre (1977) and Kleijne (1993).

In our study of 569 individual coccoliths, the two varieties show distinct variation in coccolith diameter, element numbers, and size, both of the central area and the pore (Figure 8). The distal shield of *U. sibogae* var. *sibogae*

SST, are well illustrated at ESTOC from November 1995 to November 1996 (Sprengel *et al.*, 2000; Figure 9). In particular, this is the case for the variation in mean length of *E. huxleyi*, which is about 3.3µm throughout the year. The frequency distribution of the single samples, however, display less clear (unimodal) distribution than that of the total population (Figure 3). This is probably an artefact of the lower number of measurements in comparison to the total population. However, the maximum range in size of *E. huxleyi* generally exhibits a pulsating pattern of minor variation during bloom phase, and slightly wider distribution of lengths in pre- and post-bloom samples. Conspicuous variation in size-distribution between single samples of the sediment trap can also be seen in most of the other species, especially in *F. profunda*, without revealing any seasonal pattern. This is in contrast to seasonal trends in species occurrences, with highest
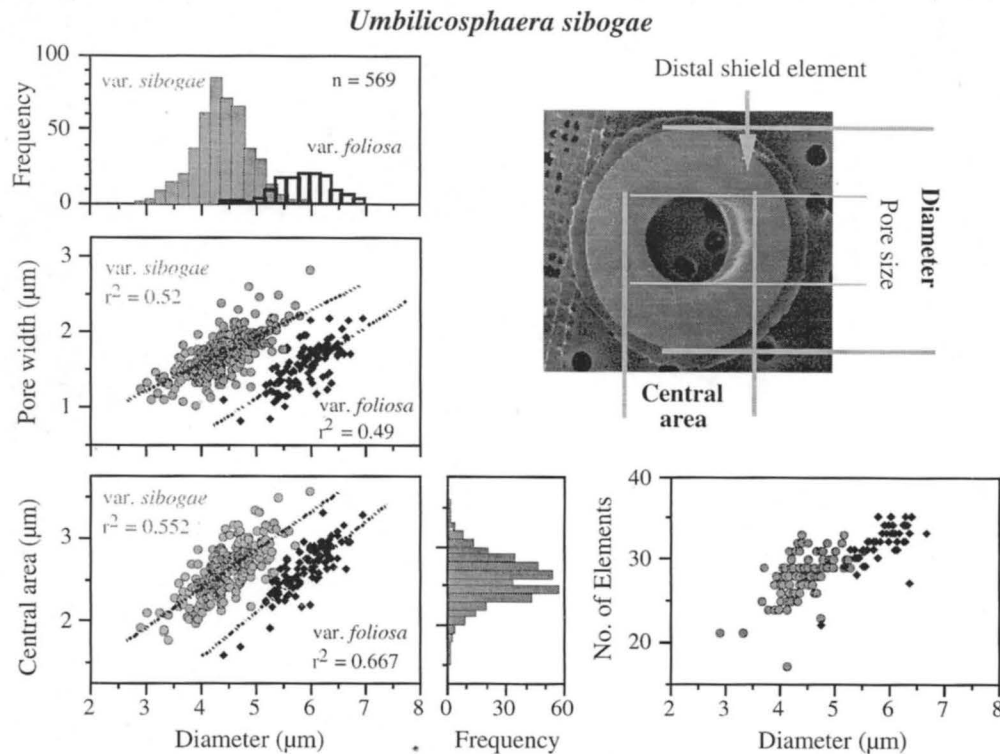
Figure 8: Scatter plots and frequency distribution (at 0.2µm intervals for the coccolith diameter; at 0.1µm intervals for the central area) of all *U. sibogae* coccoliths measured. Measured parameters are indicated in the SEM picture (representing *U. sibogae* var. *sibogae*).

the total genotypic heterogeneity of the investigated species. Thus, the total variation in coccolith morphology of a distinct species can only be identified on a global distribution. Different morphotypes of a species, however, may have distinct ecological adaptations, as is indicated by both varieties of *U. sibogae*. In fact, there is increasing evidence that morphological varieties reflect genotypic rather than ecophenotypic variation (*e.g.* Young & Westbroek, 1991; Knappertsbusch *et al.*, 1997; J. Young, pers. comm., 2000), of which the distributions are environmentally controlled.

relative abundances of the deep-dwelling *F. profunda* in pre- and post-bloom phase and clearly dominating *E. huxleyi* during bloom-phase (Sprengel *et al.*, 2000). *U. sibogae* also shows only little variation in placolith morphology with increasing total coccolith flux and decreasing temperatures. However, only results of *U. sibogae* var. *sibogae* are shown here due to the fact that increased numbers of var. *foliosa* only occur in 'bloom' samples, whereas this variety is very sparsely present in the pre- and post-bloom samples. This finding corresponds well with the observations of Broerse *et al.* (2000), who showed that var. *foliosa* becomes more abundant in nutrient-enriched (upwelling) regions, whereas var. *sibogae* is thought to be associated with oligotrophic conditions. Nevertheless, very slight morphological variations of both varieties are less than the standard deviation (Table 1) and do not display any seasonal trend.

The only noteworthy exceptions seem to be the size variations in *C. leptoporus*. However, although the absolute variation in the diameter of *C. leptoporus* is 1.5µm (6.68µm to 8.18µm), which is 20% of the size, a clear seasonal pattern is not revealed (Figure 9). Highest and lowest mean diameters are found in winter samples (November/December 1995 and December 1996, respectively). Whether this is due to the low number of measurements in some of the samples or to a real trend remains rather unclear. However, as shown before, three different morphotypes of *C. leptoporus* occur, and their appearance may be environmentally controlled (Knappertsbusch *et al.*,1997). In total, the results of this study suggest that oceanic populations from distinct regions, such as the Canary Islands, are relatively homogeneous with respect to coccolith morphology, probably representing only part of

Conclusions

In summary, all investigated coccolith species generally are characterised by a relatively strong correlation of the various parameters measured. They all exhibit a unimodal distribution of lengths/diameters and show only slight morphological variation throughout the year. This is rather surprising, since strong seasonal coccolith fluxes, coinciding with variation in SST, are well illustrated at the trap position north of Gran Canaria. Thus, it is suggested that these populations represent a local part of the total genotypic morphovariability of the species.

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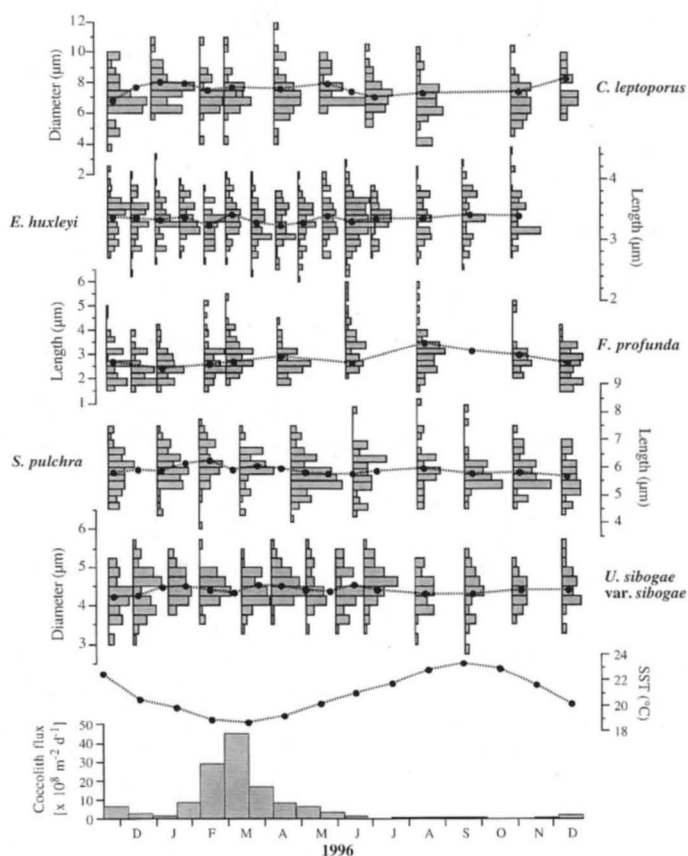
Figure 9: Comparison of the seasonal size-variation data of distinct species together with monthly sea-surface temperature (SST) for the sediment trap mooring location (29.1°N, 15.5°W) for the period November 1995 to December 1996, and the total coccolith flux (from Sprengel *et al.*, 2000).

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