

UTRECHT MICROPALEONTOLOGICAL BULLETINS

B.W.M. DRIEVER



Project no. 1

CALCAREOUS NANNOFOSSIL BIOSTRATIGRAPHY AND
PALEOENVIRONMENTAL INTERPRETATION OF THE
MEDITERRANEAN PLIOCENE

36

UTRECHT MICROPALAEONTOLOGICAL BULLETINS

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CALCAREOUS NANNOFOSSIL BIOSTRATIGRAPHY AND
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MEDITERRANEAN PLIOCENE

I.G.C.P. Project no. 1

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ABSTRACT

The accuracy of the traditional calcareous nannofossil biostratigraphy of the Mediterranean Pliocene is low, because most of the zonal boundaries are defined on the presence or absence of the very rare species of the Ceratolithids and the Discoasterids. Coccolith floras of the Noëlaerhabdaceae, the most common group of Neogene calcareous nannofossils, yield useful alternative markers for biostratigraphy and give a good framework for paleoenvironmental interpretation.

On the basis of biometrical analysis of samples from the Pliocene and Lower Pleistocene of sections on Crete and in southern Italy, five taxa of *Reticulofenestra*, two taxa of *Gephyrocapsa* and one taxon of *Emiliana* are distinguished. Their quantitative record shows 12 major changes (biohorizons) in our sequences. Quantitative analysis of the Discoasterid associations resulted in distinguishing another 12 biohorizons, which are easily correlatable from Crete to South Italy; the Upper Pliocene ones are recognized in the record of deep-sea cores in the North Atlantic Ocean as well. A detailed zonal scheme of 13 Pliocene subzones is presented, based on selected Noëlaerhabdacean and Discoasterid biohorizons.

The composition of the calcareous nannofloras in the Mediterranean Pliocene is interpreted in terms of an alternating predominance of subtropical, transitional and subpolar floral assemblages. From the pattern of change, short-term fluctuations in surface water temperature and seasonal contrast are inferred, which were superimposed on the overall climatic deterioration in the course of the Pliocene.

Chapter 1

INTRODUCTION

The procedure of stratigraphic correlation is fundamental in the reconstruction of the earth's history. In a stratigraphic correlation, some kind of equivalence is assumed to exist between parts of the geological record in different localities. Equivalence can be demonstrated for certain descriptive properties, such as lithology or fossil content (lithostratigraphic and biostratigraphic correlation, respectively), and geophysical parameters such as seismic velocity or paleomagnetic signal (geophysical correlation). Correlation on the basis of descriptive rock properties is at the base of the interpretation of the temporal relation between rock sequences (chronostratigraphic correlation).

Because correlating surfaces seems to be much more precise than the correlation between three-dimensional bodies, the correlation efforts especially focus on the stratigraphic horizons. Such horizons correspond to changes or events in the defining properties of the stratigraphic unit, and they are often used for defining the unit-boundaries. The resolving power of the stratigraphic tool is a function of the number of horizons per stratigraphic interval. The accuracy of the correlation, and hence the quality of the geological reconstruction, depends on the resolution of the stratigraphic instrument (vertical component), and on the recognizability and isochronism of the individual horizons (horizontal component).

Biostratigraphic correlation is an important discipline in the analysis of marine sedimentary sequences. Nowadays, most such correlations are based on changes in the microfossil record. Westberg and Riedel (1978) gave a thorough discussion of the parameters, thought to be of influence on the accuracy of correlations, in their example based on radiolarian biostratigraphy. It is to be expected that the accuracy parameters, involved in correlations via other micropaleontological disciplines, are of a similar nature. The authors assumed the following series of factors to be of influence on biostratigraphic resolution:

- a) Lack of precision in defining the morphological limits of taxa
- b) Possibility of subdividing evolutionary lineages more finely
- c) Small percentage of the total radiolarian assemblage used
- d) Effort expended in searching
- e) Preservation
- f) Consistency or intermittence of occurrence of taxa' (in a broader sense : the

nature of the change(s) in a taxon's vertical frequency distribution, being gradual or abrupt, and single or repeated).

'g) Spacing of samples

h) Core recovery

i) Reworking and downworking'

The recognizability of the individual biohorizons in other sections is determined by the paleogeographical distribution (hence the set of paleoecological requirements) of the taxon (taxa) involved. Furthermore, if such horizons are introduced by different authors, their taxonomic concept and their working method play a role as well. It is clear that the synchronism of a certain biohorizon depends on the 'travel time' of the underlying change in the former biocoenosis.

The present study reports on aspects of the calcareous nannofossil biostratigraphy of the Pliocene in the Mediterranean area. Our investigation was initiated within the framework of IGCP-project nr.74/I/1, 'Accuracy in time'. The purpose of this multidisciplinary international project was to improve the insight into the principles of stratigraphic correlation and to improve procedures and techniques, by means of an evaluation of the various events, used for correlation, and their isochronism (see for instance C.W. Drooger, 1980).

The efforts of the team of stratigraphers concentrated on the biostratigraphic and magnetostratigraphic correlation of marine sequences. In the hilly landscape of the Neogene rocks in the countries around the Mediterranean Sea, several sections can be found which together span the entire Neogene and part of the Quaternary in fully marine facies. In the past decade, many such sections were subject to detailed sampling and subsequent multidisciplinary research. One of the benefits of investigating land-based sequences is the grip on the vertical stratigraphic continuity, which condition is essential for constructions of a biostratigraphic frame.

Considering the factors that influence the biostratigraphic resolution, listed by Westberg and Riedel, we thought that substantial improvement of the frame could be achieved from exploring the possibilities of a larger part of the flora (factor c), better taxonomic delimitation (factor a) and more detailed sampling (factor g). Our aim is to investigate the recognizability of the commonly used marker species in the calcareous nannofossil biostratigraphy of the Mediterranean Pliocene in terms of frequency change and taxonomy. For this purpose we made a quantitative inventory of the distribution of these taxa, and, if necessary, we tried to clarify the limits of their morphological variation through morphometrical analysis. We benefitted from preceding research in the project, especially from the studies dealing with quantitative methods and

from those concerning the lithostratigraphy, the biostratigraphy and the magnetostratigraphy of our sections.

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P. Hoonhout skilfully drew the greater part of the figures. The complex structures in figures 11 and 13 were drawn by T. van Hinte. A. van Doorn prepared the additional drawings. W.A. den Hartog carefully printed the photographs and arranged the plates. G.C. Ittmann prepared several slides. The technical assistance of G.J. van 't Veld, A.M. Pouw, H. In Thio and R. Hooft is gratefully acknowledged. C. Bakker and J. Pieters guided the operating of the Scanning Electron Microscope. H.E. Verwoerd and her staff are thanked for providing excellent library services.

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Chapter 2

CALCAREOUS NANNOFOSSIL BIOZONATIONS OF THE MEDITERRANEAN PLIOCENE

In this paper we will formally use the twofold subdivision of the Pliocene into a Lower/Early and an Upper/Late Pliocene (sensu Cita, 1973); the boundary is at the exit-level of the planktonic foraminifer *Globorotalia margaritae*.

The most widely applied general calcareous nannofossil zonations of the Pliocene are the so-called Standard Zonation of Martini and Worsley (1970), and the scheme of Bukry (1973b; 1975) which was encoded subsequently (Okada and Bukry, 1980). As is shown in the diagram of our figure 1, the former scheme distinguishes seven zones in the Pliocene. Of the eight zonal boundaries, five are biohorizons defined by changes in the *Eu-discoaster* associations, two boundaries are based on events in the Ceratolithaceae and one is based on the exit of a coccolithophore species (*Reticulofenestra pseudoumbilicus*). With the exception of the lowest occurrence horizon of *Eu-discoaster asymmetricus* (base NN14), Bukry used these biohorizons again in his scheme. Adding another seven bioevents, some of which are used in combination, his zonation of the stratigraphic interval under consideration consists of three zones with a total of nine subzones. Here, five of the floral events refer to the Ceratolithaceae and six to *Eu-discoaster*; the other three events are the exit of *Triquetrorhabdulus rugosus*, the exit of *Sphenolithus abies* and, again, the exit of *R. pseudoumbilicus*.

Many biostratigraphers of the Pliocene in the Mediterranean directly refer to the Martini and Worsley zonation. Some authors presented their own zonal schemes. To a greater or lesser extent, such schemes are variations on the zonation of Martini and Worsley and the one of Bukry (see figure 1), which means that the emphasis is laid again on the *Eu-discoasteraceae* and the Ceratolithaceae.

A serious drawback of the use of these nannofossil taxa in the biostratigraphy of the Mediterranean Pliocene is their scantiness. In our samples, the proportion of the discoasters in the entire calcareous nannofossil taphocoenoses rarely exceeds 1%, which means that the frequency of the individual species is usually far below that 1% level. The average frequency of *Triquetrorhabdulus* and of the Ceratolithids is of a still lower order of magnitude (see for example Schmidt, 1978; Schmidt et al., 1979; Driever, 1984). In their evaluations of the calcareous nannofossil biohorizons, used in the biostratigraphy of the Mediter-

ranean Pliocene, Raffi and Rio (1979) and Rio et al. (1984b) concluded that, for this reason, horizons based on events in the distribution of *Triquetrorhabdulus* and *Amaurolithus/Ceratolithus* are of low correlative value. As a consequence, the biostratigraphic framework for the lower part of the Pliocene in terms of the classical marker species is of poor quality, whereas a sound alternative subdivision has as yet not been put forward.

We thought it practical to concentrate in this study on the quantitative distribution of the species of *Eu-discoaster*. Furthermore, we made an effort to distract stratigraphically useful information from the distribution of the coccoliths of the Noëlaerhabdaceae (= Prinsiaceae), which hitherto have been largely neglected in the biostratigraphy of the Pliocene. The Noëlaerhabdaceae are numerically frequent, but their taxonomy is difficult ; in the case of *Eu-discoaster* the situation is just the reverse. As each group requires its own approach, they are dealt with in separate chapters.

Chapter 3

MATERIAL AND METHODS

THE SECTIONS AND STRATIGRAPHIC CONTROL

From the many sections in the Mediterranean area which show marine Pliocene sediments, we selected sections on Crete and on Sicily which had already been thoroughly investigated from a stratigraphical point of view by other Utrecht team members. For all these sections the planktonic foraminiferal biostratigraphy has been established (Spaak, 1983; Zijderveld et al., 1986; Zijderveld et al., in prep.), and a detailed magnetostratigraphic survey has been carried out in the Pliocene and Pleistocene of one of the Italian sequences (Zijderveld et al., *ibid.*). In earlier publications, we presented quantitative data concerning the *Eu-discoster* associations in some of the sections on Crete and Sicily (Driever, 1981, 1984).

Furthermore, it has been demonstrated for the sections on Crete (Jonkers, 1984), and for the sections in Italy (Hilgen, 1987; Verhallen, 1987), that the pattern in the alternation of thickness and lithology of the successive strata is continuous in a horizontal sense. The ensuing bed-by-bed correlations seem to be extremely accurate, as the correlated horizons appear to be parallel to the biostratigraphic and magnetostratigraphic horizons. We constructed composite sample sequences on the basis of such correlation schemes.

The four sections on Crete represent the lower and middle part of the Pliocene (up to Interval 8 of the *Globorotalia crassaformis* Zone of Spaak, 1983). The sedimentary sequence in southern Italy covers the entire Pliocene and the lower part of the Pleistocene.

Crete

The Cretan sections Kalithea I, Aghios Vlassios and Finikia are situated in the Heraklion Basin in central Crete (fig.2). In his study of the benthonic foraminifera from these sections, Jonkers (1984) presented photographs and detailed location maps. Section Francocastello is located on the southern coast of West Crete. Spaak (1983) established a planktonic foraminiferal biostratigraphy of the sections on Crete. For lithological columns and the location of the biozones the reader is referred to figure 3.

As there are several publications dealing with the lithostratigraphy of the Pliocene of Crete (see for example Meulenkamp, 1979; Jonkers, *op. cit.*), we

will give here only a summary. The lowermost unit of the local Pliocene sequence, overlying sediments of Messinian Age, is the so-called marl-breccia, a mixture of predominantly white marl and limestone. This unit is overlain by the white and homogeneous, trubi-like marls of the Kourtes facies. Higher up, brownish sapropelic layers are intercalated in the marls; the marls gradually change from white to greyish and the bed thickness increases (Finikia facies). Next higher in stratigraphy is the Stavromenos facies unit, showing an alternation of homogeneous yellowish marls and grey or white, usually diatomaceous, laminites. The youngest marine Pliocene rocks of Crete are found in an isolated occurrence of Upper Pliocene sediments in the Francocastello area.

Kalithea I

The section lies SW of the Kalithea village. The sampled interval measures about 40 stratigraphic metres and shows, from base to top, some 6 metres of Kourtes marls, followed by an alternation of whitish homogeneous marls and brown laminites. There are two unexposed intervals of a few meters each. The sediments are assigned to the lowermost three Pliocene foraminiferal zones, i.e. the *Sphaeroidinellopsis* Acme-zone, the *Globorotalia margaritae* Zone, and the *G. margaritae*-*G. puncticulata* Concurrent-range Zone (Spaak, 1983).

Aghios Vlassios

In the section, situated NW of the village of Aghios Vlassios, an about 100 metres thick and continuously exposed sequence of Pliocene sediments is found. The sequence shows sediments of the Finikia and Stavromenos facies, and ranges from the *G. margaritae* Zone up into the *G. crassaformis* Zone (Inter-

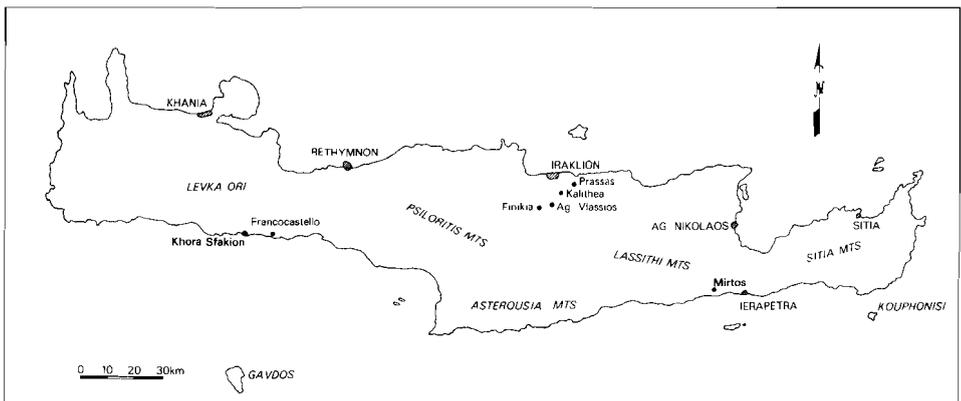


Fig.2 Location map of Crete.

val 6). We investigated a set of samples, taken from the lower half of the section (CP2351-CP2362 and CP2205-CP2280). We previously published about the quantitative composition of the associations of *Eu-discoaster* in this part of the section (Driever, 1981). The stratigraphic interval of the top part of the sequence is covered by the samples from the Finikia section.

Finikia

In the main exposure of the Finikia section, SW of Finikia village, stratigraphically about 128 metres of sediment of the Finikia and Stavromenos facies were sampled (samples CP2001-CP2176). The sequence corresponds with the upper part of the *G. puncticulata* Zone up to the middle of Interval 6 of the *G. crassaformis* Zone. We presented details of the frequency distribution of the *Eu-discoaster*-species in an earlier publication (Driever, 1981).

In the basal part of the uppermost diatomite, a volcanic ash-layer is intercalated. The horizontal distribution of this bed in the Heraklion Basin supports Jonkers' scheme of bed-to-bed correlations, as the ash was found in its proper position both in the top part of the Aghios Vlassios section and in the nearby Prassas section. The biotite from the ash bed yielded K/Ar dates between 3.20 Ma and 3.25 Ma (Bianchi et al., 1975).

Francocastello

The section is situated in the coastal cliffs east of the ancient castle of Francocastello, some 7.5 kilometers E of Khora Sfakion on the southern coast of the province of Khania. The outcrop was originally described as Francocastello II, exposure 817 by Meulenkamp (1969). The 35 metres thick sedimentary sequence consists of an alternation of greyish homogeneous clays and brownish sapropelic beds. There are a few intercalations of relatively coarse clastic sediment. The section covers the upper part of Interval 6, probably the entire Interval 7 and maybe the lowermost part of Interval 8 of the *G. crassaformis* Zone. We previously established that the section ranges from the *Eu-discoaster surculus* Zone (NN16) probably into the *E. brouweri* Zone (Driever, 1984). The total number of discoasters and the discoaster-diversity were seen to show a marked decrease from sample GR1218 upwards.

Italy

We studied material from the well-known sections Punta di Maiata, Punta Piccola and Monte San Nicola in the Caltanissetta Basin on Sicily (for locations see figure 4). Detailed location maps and data on the planktonic foraminiferal biostratigraphy can be found in a.o. Broolsma (1978) and Spaak (1983). Furthermore, we selected a series of samples from the Pliocene-Pleistocene of the Singa

section in South Calabria (Zijderveld et al., 1986). Except for a hiatus representing a fairly large mid-Pliocene interval, Monte Singa offers a seemingly continuous record of the Pliocene. As the preservation of the calcareous nanofossils from the Lower Pliocene of Monte Singa is quite good, and as there is a detailed paleomagnetic record of this section, we preferred studying the Singa section, rather than investigating the Miocene-Pliocene boundary stratotype section in the Trubi facies of Capo Rossello.

For an account of the lithostratigraphic development of the Pliocene-Pleistocene in South Italy, the reader is referred to Meulenkamp et al. (1986) and Hilgen (1987). In summary, the lithostratigraphic sequence is as follows. On Sicily, the lowermost facies unit of the Pliocene, overlying with a sharp contact various rocks of older age, is the Trubi facies. The Trubi shows an alternation of white, indurated, carbonate-rich and sometimes diatomaceous beds and greyish, less indurated relatively carbonate-poor beds. Along the southern coast of Sicily, the entire Lower Pliocene may consist of Trubi sediments. In more northern parts of the Caltanissetta Basin, and in Calabria, the sediments of the Lower Pliocene contain on average less carbonate. Here, a typical Trubi-



Fig.4 Location map of southern Italy.

aspect is not or only poorly developed, but again an alternation of more and less indurated beds is shown in the weathering profile.

In the terminology of Hilgen (1987), a doublet of a carbonate-poor and a carbonate-rich layer is a basic rhythmite. Careful observations and measurements on Pliocene sequences on Sicily and in Calabria yielded a consistent pattern in the succession of the Lower Pliocene basic rhythmites. Hereupon the individual doublets were numbered, starting with the lowermost Pliocene one. Because our samples from the Trubi of the sections Punta di Maiata and Monte San Nicola were taken before such a rhythmite scheme was constructed, the proper rhythmite number can be assigned to only part of them on the basis of the sampling list descriptions. If samples are from the carbonate-poor layer of a doublet, the corresponding rhythmite number is coded with the suffix 'a' (fig.6).

The Trubi marls of Sicily become less calcareous in upward sense. From some mid-Pliocene level onwards, it is increasingly difficult to distinguish between carbonate-rich and carbonate-poor beds. The lithology gradually changes towards an alternation of homogeneous greyish marls or marly clays and brownish, usually laminated sapropelitic beds (Monte Narbone facies). This facies is overlain by coarse clastic sediments of the Pleistocene Agrigento Formation. A similar facies development is found in the Upper Pliocene and Lower Pleistocene of Calabria. The vertical variation in the thickness of the individual homogeneous and sapropelitic beds shows a characteristic pattern, which can be recognized to a greater or less extent in many sections on Sicily and in Calabria. As the sapropels in the Singa sequence cluster in three stratigraphic intervals, they were subdivided into an A-group, a B-group and a C-group (Verhallen, 1987). Our Pliocene sections on Sicily show a sapropel cluster (here called the O-group), which is slightly below the aforementioned A-group.

Monte Singa

The Singa sequence consists of some 230 metres of Pliocene sediments, which were sampled in a number of subsections called Singa Varda, Singa Riace, Singa I, IA, II, III and IV. The exposures are in the northern flank of Monte Singa, a few kilometres W of Riace Marina in South Calabria (for a detailed location map see Zijdeveld et al., 1986). Because the original set of samples was in some intervals insufficient, Hilgen sampled the subsections Singa Riace and Singa IA in addition. As Singa II has a not-exposed interval, we preferred to study the corresponding part of Singa IA. All subsections are correlatable on the basis of the pattern in the rhythmite succession. Lithological columns, the position of the samples and the correspondence to the planktonic foraminiferal zones and

about 83 metres from the base of the sequence, situated in the middle of Singa II and immediately above Singa IA.

In terms of planktonic foraminiferal biostratigraphy, the sediments below the hiatus belong to the *Sphaeroidinellopsis* Acme-zone, the *Globorotalia margaritae* Zone and the *G. margaritae*/*G. puncticulata* Concurrent-range Zone. Four intervals with normal magnetic polarity were found in this part of the sequence, interpreted to represent the Thvera, Sidufjall, Nunivak and Cochiti (p.p.) sub-zones of the Gilbert reversed polarity zone. The age of the base of the section (Miocene-Pliocene boundary) was extrapolated to be 4.83 or 4.84 Ma (Zijderveld et al., 1986).

The sedimentary sequence above the hiatus was sampled in the subsections Singa II (top part), III and IV. The hiatus is not marked by a distinct lithological change. It is increasingly difficult to distinguish between carbonate-rich and carbonate-poor beds in the interval above the hiatus (change in legend in figure 5). The sapropels of the A-group are situated between about 11 and 23 metres above the hiatus; those of the B-group are between about 60 and 88 metres, and those of the C-group from about 109 metres onwards to the top of the section. In Singa III, an about 10 centimetres thick pteropod-rich layer was observed. Many of the laminites in Singa IV are underlain by a thin sandy layer, which predominantly consists of foraminiferal shells. In the top part of Singa IV, a few yellow sandy layers with mainly terrigenous particles are intercalated.

The sedimentary sequence above the hiatus almost entirely belongs to the upper part of the *Globorotalia crassaformis* Zone and the *G. inflata* Zone. Samples immediately above the hiatus yielded *G. crassaformis* faunas with predominantly dextral coiling, fitting in the upper (second) dextral *G. crassaformis* interval (lower part of Interval VI of Spaak, 1983). The *Neogloboquadrina atlantica* Interval (VII) is in the lower half of the Singa III subsection, but the nominative species was found to be present discontinuously and in low numbers. The base of the *G. inflata* Zone was positioned at or near the top of Singa III, but there is a short interval with *G. inflata* some ten metres lower down in the section ('*G. inflata* influx'). Similarly, *Globorotalia truncatulinoides* was found in a few samples in Singa IV (JT9553 up to JT9556), some 50 metres below the actual *G. truncatulinoides* Zone; the base of the latter zone is in the topmost part of the Singa IV subsection, not covered by our set of samples. Rio et al. (1984a) observed such a '*G. truncatulinoides* influx' in the same stratigraphic position in several South Italian sections. Spaak (1983) used the entry of the benthic foraminifer *Hyalinea balthica* as the top of his *G. inflata* Zone. In Singa IV, this biohorizon is in sapropel C13 (Verhallen, 1987).

The magnetostratigraphic subdivision of the sequence above the hiatus has

not yet been published (Zijderveld et al., in prep.). In chapter 13, the preliminary magnetostratigraphic data will be used as a framework for our biochronology.

The Pliocene-Pleistocene boundary in the sense of the Vrica boundary stratotype (Selli et al., 1977; Aguirre and Pasini, 1985) is to be positioned at the top of the C6 sapropel in the Singa IV subsection (Verhallen, 1987).

Punta di Maiata

The cliffs of Punta di Maiata are located on the South coast of Sicily, W of the city of Agrigento and some hundreds of metres SE of the Miocene/Pliocene boundary stratotype locality of Capo Rossello (Cita, 1975). The section shows a nearly 100 metres thick sequence of Pliocene sediments (fig.6). Up to about sample CP4092, the sedimentary facies is an alternation of white, greyish and beige calcareous marls (Trubi). On the basis of the sampling list and biostratigraphic data, many of the beds from this interval can be related to the standard rhythmite sequence (Hilgen, 1987). Higher up in the section, the sediment gradually becomes more clayey and the relatively carbonate-rich, indurated beds become fewer and thinner. The top of the section shows an alternation of greyish marly clays and brown, usually laminated sapropelitic layers of the O-group. Following Broolsma's (1978) lithostratigraphic concept, the lower part of the section up to the first brownish bed is assigned to the Trubi, while the higher part with the sapropels is considered to belong to the Monte Narbone Formation.

The section ranges from the higher part of the *G. margaritae* Zone up to the middle of Interval 6 of the *G. crassaformis* Zone, including the two intervals with predominantly dextrally coiled *G. crassaformis*. It therefore is likely that the mid-Pliocene hiatus of the Singa sequence is completely covered in Punta di Maiata. Quantitative data concerning the composition of the *Eu-discoaster* floras were presented in a previous publication (Driever, 1981).

Punta Piccola

Punta Piccola is situated roughly 2 kilometres E of Punta di Maiata. The section comprises about 45 metres of Upper Pliocene sediments of the Trubi and Monte Narbone facies (fig.6). The brownish beds of the Monte Narbone facies-interval are of the O-group and the A-group. As the average thickness of both the homogeneous and the brownish layers increases in upward sense, one may assume an increase of the sedimentation rate for the higher part of the section.

Our samples from Punta Piccola cover the upper part of Interval 5 and the greater part of Interval 6 of Spaak's *G. crassaformis* Zone. In their study of the Punta Piccola section, Rio et al. (1984b) included a longer Trubi interval at the base of the section. They assigned their sample sequence to the *Eu-discoaster*

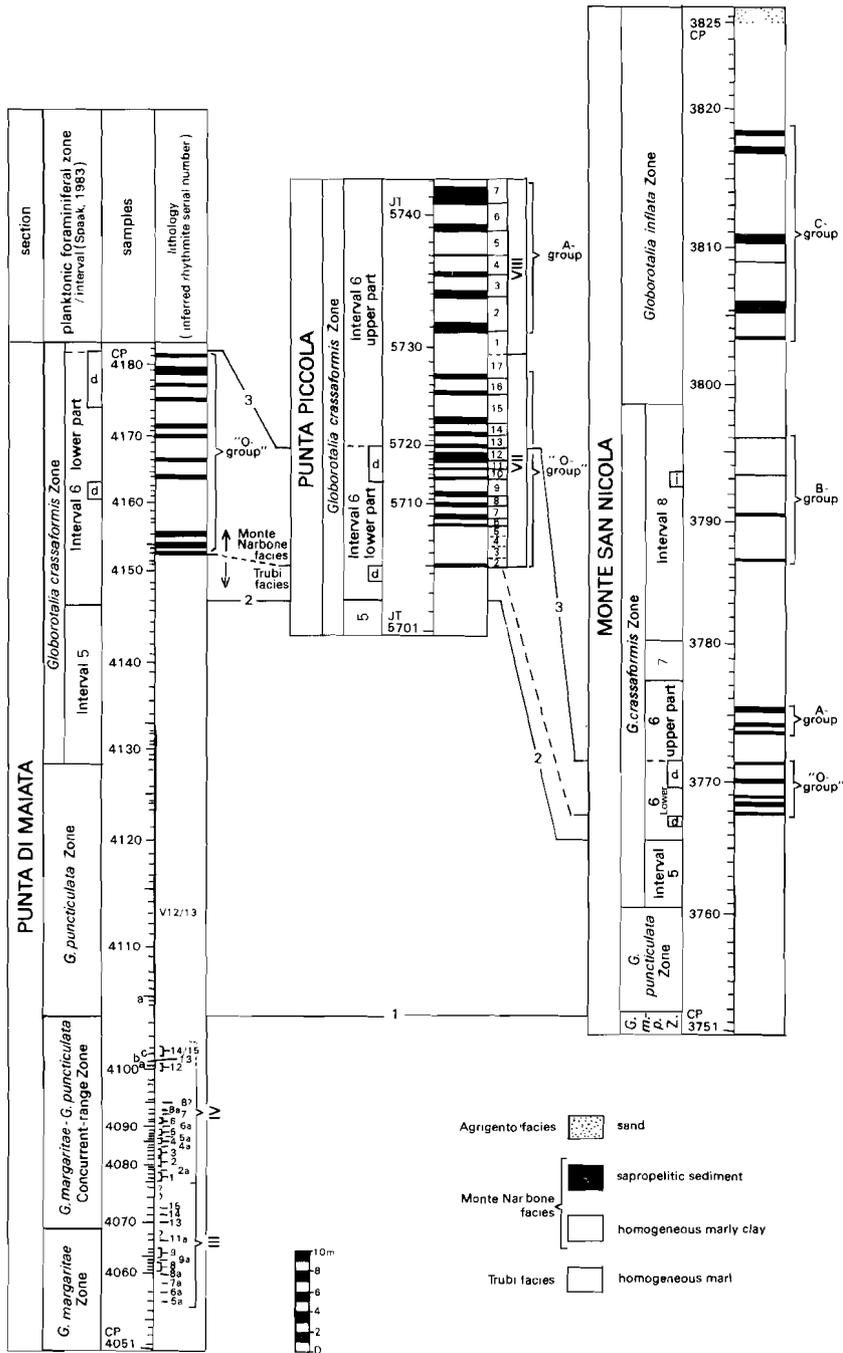


Fig.6 Lithostratigraphy, planktonic foraminiferal biostratigraphy and position of the samples in the sections on Sicily. Correlation horizon 1 is the exit-level of *G. margaritae* ; horizon 2 is the exit-level of *G. puncticulata* ; 3 is the top of the second interval with predominantly dextrally coiled *G. crassaformis* (indicated with the symbol d). The dashed correlation line shows the boundary between the Trubi facies and the Monte Narbone facies. See also explanation of figure 5.

tamalis and *E. pentaradiatus* Subzones of the *E. surculus* Zone (Raffi and Rio, 1979), and to the *Sphaeroidinellopsis subdehiscens* (MPL4) and *Globigerinoides elongatus* (MPL5) Zones of Cita (1973).

A magneto- and biostratigraphic survey of the sections Punta Grande and Punta Piccola was carried out in 1987 (Zijderveld et al., in prep.). The stratigraphic interval of the Punta Grande section approximately corresponds with the nearby Punta di Maiata sequence. In comparison with our sample sequence, the new set of samples from Punta Piccola includes a lower stratigraphic interval. Correlation via the rhythmite pattern (Hilgen, 1987) enables to use the magnetostratigraphic data for calculating the numerical ages of our biohorizons (chapter 13).

Monte San Nicola

The section is located in the southern flanks of the Monte San Nicola, about 9 kilometres N of Gela along the road from Gela to Butera. The lower 22 metres show Trubi-like marls, which are overlain by an about 77 metres of (marly) clays with sapropelic intercalations of the Monte Narbone Formation (fig.6). The brownish beds are of the groups O, A, B and C, but the number of such beds in each group is less than normal. The top of the sequence shows sands of the Agrigento Formation. There are some hiatuses in the section, due to small scale normal faults which especially affect the lower part of the Monte Narbone interval. On the other hand, Spaak (1983) recorded a seemingly undisturbed sequence of bioevents.

The section ranges from the *G. margaritae*-*G. puncticulata* Concurrent-range Zone up into the *G. inflata* Zone. As in the Singa section, there is an influx of *G. inflata* below the proper *G. inflata* Zone, but a *G. truncatulinoides* influx is not found in our set of samples (Verhallen, pers. com.). In a previous paper (Driever, 1984), we preliminarily assigned the interval from the base of the section up to sample CP3803 to the calcareous nannofossil zones NN13 (*E. asymmetricus* Zone) up to NN18 (*E. brouweri* Zone). It was observed that the total *Eu-discoaster* number is low from about sample CP3776 (top part of the *E. surculus* Zone) upwards, while the *Eu-discoaster* diversity decreases from sample CP3782 (in the alleged *E. pentaradiatus* Zone) upwards. Details of the numerical distribution of the species, used in the above paper, are presented in chapter 11.

Rio et al. (1984a) studied the planktonic foraminifera and the calcareous nannofossils from the higher part of the Monte San Nicola section, ranging from their *E. pentaradiatus* Zone up into the Pleistocene *C. macintyreii* Subzone of the *P. lacunosa* Zone. It is not easy to establish the exact position of their samples relative to ours, as there are differences in the lithological columns. Furthermore, it is not clear whether their entry of *G. inflata* corresponds with

our *G. inflata* influx or with the base of our *G. inflata* Zone. The Italian team managed to trace the influx of *G. truncatulinoides* in the Monte San Nicola section (a few metres above their *G. inflata* entry), which influx was not detected in our set of samples. Sprovieri et al. (1986) made geochemical and foraminiferal analyses of samples taken in or close to three of the brownish beds in the Monte San Nicola section. Their G1 laminite is one of our B-group laminites. The laminites G2 and G3 are in our C-group ; their very thick G2 bed may correspond with our CP3806 laminite.

Individual samples

For SEM-study of the configuration of coccoliths of the Noëlaerhabdaceae, the following samples were used in addition :

- Lido Rossello CP4220 (Spaak, 1983) : from the *G. crassaformis* Zone (Interval 8) of section Lido Rossello, Sicily.
- Vrica JT6269, JT6332 (Spaak, 1983) : from the *G. inflata* Zone (Pleistocene part) of the Vrica section, Calabria.
- Bianco-sample : a single sample from the *E. ovata* Zone (Subzone NN19B, see chapter 13) of the Pleistocene of Bianco, Calabria (sampled by R.R. Schmidt, 1979).
- Levkos GR3139, GR3140 : from the *E. ovata* Zone (Subzone NN19B) of the Pleistocene of section Levkos on the island of Karpathos, Greece (Barrier et al., 1979).
- Adria 404-4 : from the *E. huxleyi* Zone of Core IN68-38 in the Adriatic Sea (Colantoni and Gallignani, 1977).
- A-92 : a laboratory culture of *Emiliania huxleyi*, provided by the Department of Biochemistry of the State University of Leiden (courtesy of P. Westbroek).

TECHNICAL METHODS

All data concerning the quantitative distribution of the calcareous nanofossils were gained by light-microscope (LM) study of smear slides. For *Eudiscoaster* counts we used a magnification of 1250 X, and for the study of the Noëlaerhabdaceae the calculated magnification was 1562.5 X.

Electron microscopy has the obvious advantage of a higher morphological resolution power. However, quantitative data are obtained and repeated far more easily with the LM, and the classifying of specimens is less dependent on the preservation of the nannoliths. Further, in our method of preparing slides there is no fractionation of material involved, so our slides are supposed to yield representative samples from the taphocoenoses (Schmidt, 1978).

We prepared our slides from raw sediment. A small quantity of sediment was taken (about 1 mm³) from a fresh surface of the rock-sample. The material was smeared over a cover glass in a tiny drop of water until the suspended matter was evenly distributed. For permanent mounts, the cover glass was dried and mounted on an object slide with canada balsam. Preparations on the cover glass instead of the object slide are practical in case microscope lenses are used with a low depth of focus.

In order to investigate the optical configuration of the coccoliths of the Noëlaerhabdaceae, we made mobile mounts prepared with castor oil. For structural details of these coccoliths, we made observations at a Cambridge Mark II SEM (Amsterdam University) and at a Cambridge Stereoscan 600 M (Utrecht University). The SEM mounts were prepared from slightly fractionated sediment suspensions (settling method), and sputtered with gold. In order to investigate the relation between the physical (SEM images) and the optical (LM images) properties, we studied some coccolith associations of the Noëlaerhabdaceae both with the LM and with the SEM. For this purpose, copper location grids were glued on small glass plates. After the sediment suspension was applied onto the grid and dried, LM observation was made by using M.I.B.K. or water as the agent between objects and cover glass. In about half of the experiments we successfully relocated the specimens with the SEM.

Chapter 4

THE ROLE OF THE NOËLAERHABDACEAE IN BIOSTRATIGRAPHY

The coccoliths of the family Noëlaerhabdaceae are the dominant components in the calcareous nannofossil taphocoenoses of the Neogene and the Quaternary. Research on the distribution of calcareous nannoplankton in oceans and marginal basins has shown that the Recent representatives of the family are quantitatively important members of the live assemblages. In some areas, especially in subpolar waters and in marginal seas, the assemblages are monopolized by the Noëlaerhabdaceae (see for instance Okada, 1983). *Emiliania huxleyi* (Lohmann) is the most ubiquitous taxon (see for instance Lohmann, 1912; Borsetti and Cati, 1972; Gaarder and Hasle, 1972; Okada and Honjo, 1973, 1975; Kling, 1975; Okada and McIntyre, 1977; Conley, 1979; Winter et al., 1979; Reid, 1980).

Despite the abundance of the Noëlaerhabdaceae in the fossil record, only few zonal boundaries in the nannofossil biostratigraphy of the Neogene have been based on events in the family's history. In the commonly used zonal schemes there is no (Martini, 1971) or only one zonal boundary (Bukry, 1973; Okada and Bukry, 1980) in the Miocene which is based on a taxon of the Noëlaerhabdaceae. In the Pliocene, one such a zonal boundary is usually distinguished (NN15 - NN16 boundary). The group, however, plays a predominant role in biostratigraphic schemes of the Quaternary (in Martini's standard zonation 2 out of 3 zonal boundaries, in Gartner's (1977a) revised zonation of the Pleistocene 4 out of 7). In Nishida's zonation (1978) of the Upper Pliocene and Quaternary of sections in Japan, all zones are defined on events in the Noëlaerhabdaceae.

Zonations of the Miocene and Lower Pliocene, if based solely on events in the Noëlaerhabdaceae, have a low resolution. This was illustrated by Perch-Nielsen (1972), Müller (1976) and Martini (1979), who presented biostratigraphical studies of high latitude northern Atlantic DSDP cores. In these sedimentary records, many of the usual Neogene zones are hard to recognize because of the extreme scarcity of the Discoasterids and the Ceratolithids. The biostratigraphic subdivision of the cores, which by necessity was based mainly on Noëlaerhabdaceae, resulted in only two zones for the entire Pliocene, as contrasted with e.g. the six standard zones of Martini and the ten (sub)zones of Bukry (1981) for lower latitude successions.

In the literature on Neogene calcareous nannofossils the Noëlaerhabdaceae

seem to become of interest especially in the higher intervals of the Pliocene and in the Quaternary. This increase of importance is not merely due to an increase of the number of events in the family. In the course of the Pliocene, important nannofossil groups vanish from the record (discoasters, amaurooliths, sphenoliths); thus the pool from which marker species are to be chosen becomes restricted. So far, the usually abundant coccoliths of the Noëlaerhabdaceae from the lower part of the record have gained relatively little attention in the literature, and the major part of the Noëlaerhabdacean taxa have unknown (paleo)environmental affinities or are extremely eurytopic (Backman, 1980). The difficulty to systematically subdivide the Noëlaerhabdacean variation, ergo to select (marker) species from the variation seems to be at the base of these phenomena.

BIOHORIZONS IN THE PLIOCENE

In the interval of the Pliocene we focused our attention on, three events in the family's history are usually mentioned in the literature : the disappearance of *Reticulofenestra pseudoumbilicus*, the appearance of *Pseudoemiliana* (i.e. our *Emiliana*) species and the appearance of *Gephyrocapsa* species. The level of last occurrence of *R. pseudoumbilicus* is used in almost all biostratigraphic studies. Some authors apply the appearance of *Pseudoemiliana* in their zonation as well (Gartner, 1977b; Raffi and Rio, 1979). The distribution pattern of *Gephyrocapsa* taxa has not been used so far in zonations of the Pliocene.

THE RETICULOFENESTRA PSEUDOUMBILICUS EXIT

In 1967, Gartner introduced the species *Coccolithus pseudoumbilicus*, found in a core from the Sigsbee knolls in the Gulf of Mexico. He defined subsequently (1969) the *Reticulofenestra pseudoumbilica* Zone in the Pliocene of a deep-sea core in the subtropical western Atlantic. This zone was defined as the interval from the last occurrence of *Ceratolithus tricorniculatus* to the last occurrence of his *Reticulofenestra pseudoumbilica*. Amongst many of Gartner's (1969) zones for the Pliocene, his *Reticulofenestra pseudoumbilica* Zone was incorporated in the standard zonation for calcareous nannofossils as Zone NN15 (Martini and Worsley, 1970; Martini, 1971). Especially the zone's upper boundary is one of the most universally utilized horizons in Pliocene biostratigraphy, both in low and in high latitude sequences.

Likewise, the *R. pseudoumbilicus* exit has been discussed in all biostratigraphic studies of Pliocene sequences in the Mediterranean. Some authors characterized the horizon in their sections in terms of Gartner's definition, i.e. the extinction

level or the level of last occurrence of the species (Schmidt, 1973; Backman, 1979; Ellis and Lohman, 1979). Many authors commented on the horizon in remarks concerning the species' morphology and/or its frequency distribution. Occasionally, other markers were used in combination in order to improve the recognizability of the zonal boundary.

Differences in the concept of the marker species mainly concern the overall size of the coccoliths (see chapter 6). Usually, the taxon is thought to comprise all large size coccoliths of the Noëlaerhabdaceae in the Pliocene. Some authors (e.g. Müller, 1978) also included relatively small-sized specimens in their concept of the species. Such small specimens range further upwards in the Pliocene than do the larger ones. The stratigraphic position of the *Reticulofenestra pseudumbilicus* exit is therefore determined by the operator's concept of the size range of the species. For example, Meulenkamp et al. (1978) considered the diatomite bearing interval of the Prassas section on Crete to belong to the *Reticulofenestra pseudumbilicus* Zone (NN15) on the basis of the presence of small-sized specimens of the nominative species. By contrast, Bianchi et al. (1985) placed a stratigraphically lower interval of the same Prassas sequence in the *Eu-discoaster surculus* Zone (NN16) because of the absence of large size coccoliths of *R. pseudumbilicus*.

In some sections in the Mediterranean area, the upper boundary of the zone was reported to be badly recognizable due to the continuity of the nominal species. In studies on the calcareous nannofossils from the Piacenzian (Castell'Arquato and Crostolo sections, western Emily, N. Italy), the zonal boundary was defined on another marker, *Eu-discoaster tamalis*, because *R. pseudumbilicus* was found to range throughout the Upper Pliocene into the Pleistocene. This distribution pattern was attributed to reworking (Barbieri and Rio, 1974; Barbieri et al., 1975). Likewise, Gartner (1977b) considered the familiar zonal boundaries for the Pliocene, which are mainly based on highest occurrences, to be not applicable in the Capo Rossello section on Sicily because of reworking. He coined an *R. pseudumbilicus* exit through correlation with the appearance of *Pseudoemiliana lacunosa*. In the Upper Pliocene of sections on Crete and Sicily, *R. pseudumbilicus* was observed to remain present discontinuously and in low numbers (Meulenkamp et al., 1979a; Driever, 1981).

THE PSEUDOEMILIANA LACUNOSA ENTRY

Since Gartner (1969) introduced the genus *Pseudoemiliana*, typified by *Ellipsoplacolithus lacunosus* Kamptner (1963), genus and species have become a source of taxonomic dispute (Loeblich and Tappan, 1970; Hay, 1970; Gartner, 1977a). Furthermore, some authors distinguished two species based on elliptical

or circular morphotypes (Bukry, 1973c, after Hay, 1970). For the sake of convenience, we will adhere in the following section to Gartner's combination (i.e. the wider concept) since the discussion does not concern so much morphology and stratigraphic range of the taxon (taxa) as nomenclatorial validity.

The highest level of occurrence of *Pseudoemiliana lacunosa*, which Gartner (1969) used for defining the top of his *Pseudoemiliana* Zone, has become a familiar zonal boundary in Pleistocene biostratigraphy. It was adopted in Martini and Worsley's standard zonation as the top of the equivalent *P. lacunosa* Zone (NN19), and Gartner (1977a) used it again in his refined zonation of the Pleistocene.

The level of the species' lowest occurrence, however, is applied less frequently as a marker level. In the original description of the taxon, Kamptner (1963) only referred to the type level, in the Middle Quaternary of a Mid-Pacific core of the Swedish Deep Sea Expedition. According to Gartner (1969), *P. lacunosa* enters the record in the middle part of the Pliocene, at a level that would correspond approximately to the exit-level of *R. pseudoumbilicus*. While referring to the West Atlantic core which Gartner (ibid.) used for his zonation, Martini (1971) reported the first occurrence of the species in the lower part of Zone NN16, slightly above the exit of *R. pseudoumbilicus*. Several authors found the first *P. lacunosa* slightly below the exit of *R. pseudoumbilicus* (see Backman, 1979). Hay (1970) observed elliptical and circular morphotypes in the taxon, which types had different acmes and ranges. The acme of the oval form was reported to be in the lower part of the species' range. In some later studies (Bukry, 1975; Ellis, 1979), mainly the distribution of these morphotypes in the highest part of the range gained attention.

In biostratigraphic studies of the Mediterranean Pliocene, the entry of *P. lacunosa* was usually treated as a subordinate event (Bukry, 1973a; Schmidt, 1973; Pirini Radrizzani and Valleri, 1977; Müller, 1978; Ellis, 1979; Moshkovitz and Ehrlich, 1980). In the Italian stratotype sections of Pliocene stages, where reworking was found to obscure the exit of *R. pseudoumbilicus*, the entry of *P. lacunosa* was considered as an alternative marker horizon in the interval under consideration (Cita and Gartner, 1973; Barbieri and Rio, 1974), although in subsequent reports on the same suites of samples the authors localized the event at slightly different levels (Gartner, 1977b; Barbieri et al., 1975). In addition to the disappearance of (large) *R. pseudoumbilicus* and of *Sphenolithus* spp., the entry of *P. lacunosa* was used to define the top of the *R. pseudoumbilicus* Zone by Raffi and Rio (1979). Dermitzakis and Theodoridis (1978), however, reported specimens of *P. lacunosa* from as low as Zone NN13 on Koufonisi island (Greece), far below the exit of *R. pseudoumbilicus*. Discrepancies with respect to the entry of *P. lacunosa* relate to the delimitation of the taxon's morphology and to the resolving power of the microscope (see chapter 6).

Coccoliths of *Gephyrocapsa* are important constituents of Quaternary nanofossil associations. The distribution of some selected morphotypes was used in zonations (for instance Hay et al., 1967; Bukry, 1978), and as a correlation tool for the Pliocene - Pleistocene boundary (a.o. Sachs and Skinner, 1973; Cati and Borsetti, 1981; Raffi and Rio, 1980a,b,c; Rio, 1982).

Less attention has been paid to the genus in the lower part of its range. The group, often referred to as 'small *Gephyrocapsa*', was considered to appear close to the base of the Pleistocene (Gartner, 1969, 1977a; Geitzenauer, 1972; Sachs and Skinner, 1973) or somewhere in the Upper Pliocene (Gartner, 1977b; Haq et al., 1977; Hay, 1977). More recently, *Gephyrocapsa* was reported from Lower Pliocene sediments. Chen, T.C. Huang et al. (1977) mentioned *Gephyrocapsa* occurring in the lowermost Pliocene of Taiwan. In his monograph of *Gephyrocapsa* from the Atlantic, Samtleben (1980) stated that the oldest representatives of the genus are found in the Lower Pliocene *R. pseudoumbilicus* Zone. Jiang and Gartner (1984), however, reported small-sized species of *Gephyrocapsa* to be quite consistently present from the Middle Miocene Zone NN6 upwards in DSDP site 526 in the South Atlantic. Pujos (1985d) observed Gephyrocapsids in DSDP material from the lower Middle Miocene of the central equatorial Pacific.

In the literature on the Mediterranean Pliocene, *Gephyrocapsa* was reported from Zone NN13 by Dermitzakis and Theodoridis (1978) and by Müller (1978). Pirini Radrizzani and Valleri (1977) and Lohman and Ellis (1981) introduced two new species of *Gephyrocapsa* from DSDP cores in the Tyrrhenian Sea and in the eastern Mediterranean. These species were observed to occur in the *Eu-discoaster asymmetricus* Zone (NN14) and upward. Raffi and Rio (1979) noticed the first specimens of the genus in the Tyrrhenian DSDP site 132 at the level of the *P. lacunosa* entry.

It was usually considered that Gephyrocapsids were hardly of significance for Pliocene biostratigraphy because, due to their minute size, the recognizability of the taxa was thought to be too low. Rio (1982) pointed out that the distribution of *Gephyrocapsa* in the Pliocene can be of stratigraphic value. By studying the distribution of 'small *Gephyrocapsa*' in oceanic deep-sea cores and in Mediterranean sections, he observed that the first representatives appear near the top of the *R. pseudoumbilicus* Zone (NN15). The group is quite frequent up to some level in the *E. surculus* Zone (NN16), above which there is a low-frequency interval up to about the base of the *E. brouweri* Zone (NN18).

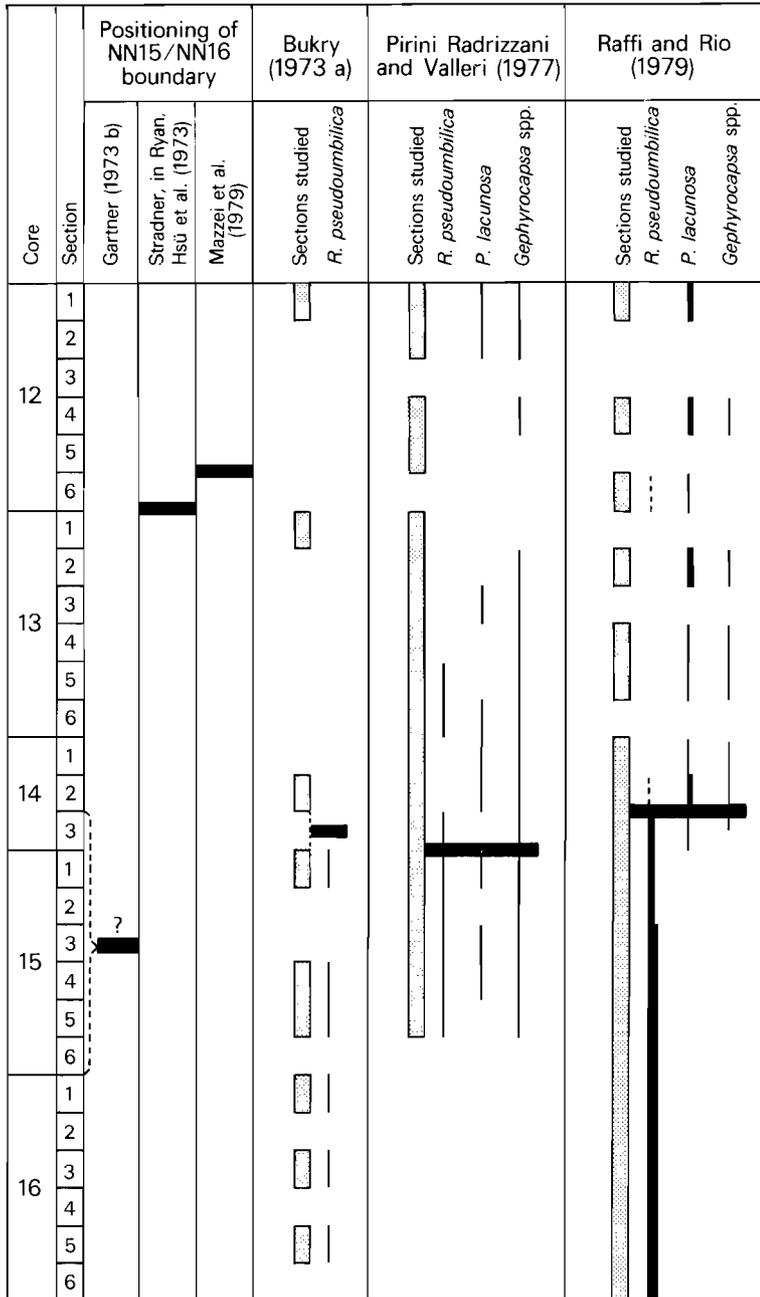


Fig.7 The position of the upper boundary of the *Reticulofenestra pseudumbilica* - NN15 Zone (indicated with horizontal bars) and the ranges of selected Noëlaerhabdacean taxa, as shown in various biostratigraphic studies of the Pliocene of DSDP Site 132 in the Tyrrhenian Sea.

It might be inferred from the previous paragraphs that Pliocene biohorizons, defined by members of the Noëlaerhabdaceae, are diachronous and that the events are controlled by local (paleoenvironmental; syn- or post-depositional) conditions. On the other hand, the difference in relative stratigraphic position might as well have been the result of the application of different taxonomic concepts, of different frequency standards, and/or of differences in sample-spacing.

Because independent criteria for pure-time-correlation are often not available, it is hard to prove whether biohorizons are real time-planes. But the subjective factor in biostratigraphy can be checked by comparing the ranges of species and the position of zonal boundaries, as obtained by different authors for the same sedimentary sequence. The Pliocene of DSDP site 132 in the Tyrrhenian Sea offers a good example. The cores from this site have been studied by several authors, with apparently quite divergent scopes and facilities (Bukry, 1973a; Gartner, 1973; Stradner, in Ryan, Hsü et al., 1973; Pirini Radrizzani and Valleri, 1977; Mazzei et al., 1979; Raffi and Rio, 1979). As shown in our figure 7, their positioning of the exit of *R. pseudoumbilicus* (= top *R. pseudoumbilicus* Zone) and of the entry of *P. lacunosa*, if investigated, in this sequence shows marked differences. These differences seem to be a consequence of a different appreciation of the morphology and the frequency pattern of the marker species, and of differences in sample spacing.

Chapter 5

THE MORPHOLOGY OF COCCOLITHS OF THE NOËLAERHABDACEAE

As follows from the above case history, from our own microscope practice, and from the taxonomic dispute in the literature, it is not easy to separate clear-cut taxonomic units from the pool of the Noëlaerhabdaceae. In the literature, marker species of the Noëlaerhabdaceae are often commented upon in terms of morphology (shape and size). We have the feeling that such marker taxa can only be adequately described against the background of the composition of the entire Noëlaerhabdaceae association in the samples. Thus we touch on the taxonomy of the entire variation. Before going into Noëlaerhabdaceae taxonomy, an idea is needed of the variables in coccolith morphology and of the basic construction of the coccoliths.

Most features have been described from electron microscope (SEM) images. However, many of such physical characters are not recognizable with the light-microscope (LM), due to its lower resolution power. For instance, a number of characters of supposed genus-level are only visible with the SEM. On the other hand, badly preserved specimens may not be determinable at all with the SEM, whereas they usually can be classified with the LM on the basis of their optical characteristics. Descriptions of the optical images of Noëlaerhabdaceae are strikingly vague, and there is no satisfactory classification of such images. This is probably due to the ill-understood relation between the physical and the optical properties of these coccoliths.

PHYSICAL PROPERTIES

The Pliocene/Quaternary coccoliths of the Noëlaerhabdaceae are elliptical to circular placoliths which are tightly interlocking on coccospheres (Pl.1, figs.1,2). The coccoliths are concavo-convex. They consist of usually identical, subradially oriented and roughly U-shaped segments or units, which consist of a distal portion (distal shield element), a tube portion (distal and proximal tube elements) and a proximal portion (proximal shield element). The segments open outward and are arranged in such a way that an elliptical to circular tube is formed in the centre of the coccolith. In the tube area, there are a collar cycle (centro-distal cycle, rim, wall cycle), a central plate (sieve plate, reticulum, membrane, grill, grid) and occasionally a bridge (cross-bar). For terminology, the reader is referred to figure 8.

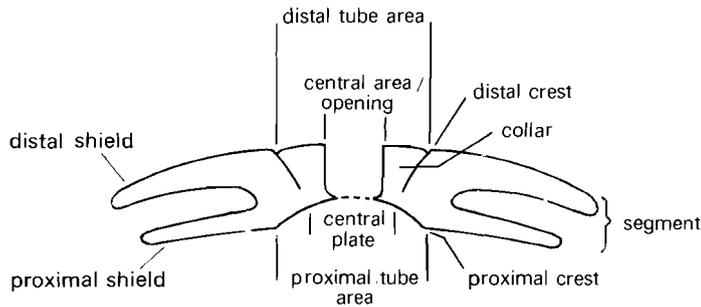


Fig.8 Schematic cross-section and descriptive terminology of a coccolith of the Noëlaerhabdaceae.

Segments

Many of the structural details of Noëlaerhabdacean coccoliths were described by Watabe (1967) in his account of the morphology of *Emiliana huxleyi* coccoliths. Watabe observed that each element of the distal shield is continuous with an element of the proximal shield, these elements being connected along the tube. The proximal element has a continuation into the central area. It was noticed that the distal tube elements have a dextral imbrication (see also Pl.1, figs. 3-6), from which it was concluded that in plan views the distal element has an offset from the corresponding proximal element. Watabe did not mention a collar cycle to be present in the tube, presumably because this cycle was not present in the material he studied (op. cit., fig.1). Parker et al. (1983) noticed that the bonds between the tube elements and the proximal shield elements are relatively weak. The latter elements were often found isolated. Bonds between the individual tube elements seem to be relatively strong, since it is not uncommon to find a coccolith's central core intact, without its shield elements.

The shield elements usually taper inwards. Often, the elements can be seen to merge into one another, leaving indistinct sutures. Such specimens commonly have smooth outer peripheries (Pl.1, figs.7,8). It is hard to estimate to what extent diagenetic processes play a role here. When sutures are clearly visible, the elements are flatly juxtaposed or seem to be slightly imbricated. Imbrication is especially suggested in specimens with crenulate shield peripheries. Like in many other placolith taxa, such imbrication is dextral (Pl.1, figs.9,10). In distal views, the sutures of the shield element are slightly rotated in anti-clockwise direction (Pl.1, fig.3); in proximal views the pattern is opposite.

As Watabe observed in *E. huxleyi*, the distal shield elements of Noëlaerhabdacean coccoliths typically turn to the right when they pass from the shield

over the distal crest into the tube. In most Neogene and Quaternary forms, the sutures bend at crest-level. In some Paleogene Noëlaerhabdaceae the bend to the right is situated in a somewhat lower position, down the tube. Also the angle of bending seems to be smaller in these coccoliths (see for instance Perch-Nielsen, 1972, pl.6, fig.4; Roth, 1973, pl.7, figs.2-4; Steinmetz, 1984, pl.28, fig.9). Steinmetz (1984, pl.3, figs.1-3) pictured some specimens of Pliocene *Reticulofenestra* showing distal shield elements which rise steeply upwards just before reaching the distal crest. We do not know whether this is a common feature in the Noëlaerhabdaceae of the Neogene.

Although usually less pronounced, the pattern of directions, followed by the elements in the proximal shield is comparable to the pattern we described for the distal elements. In proximal view, the elements follow a subradial direction in the peripheral part. Inwards, there is a less sharp crest where the elements bend sinistrally into the often shallower proximal 'tube' (Pl.2, figs.1-4). At the inner margin of this tube, (most of) the elements continue into the elements of the central plate. Comparison of proximal and distal views learns that, in plan view, the proximal and distal element of a segment virtually lie above each other, which is contradictory to Watabe's observation. He did not take into account that the elements in the proximal tube also bend, in a direction opposite to the direction in the distal tube.

Collar and bridge

The distal tube is coated with the collar cycle. If this cycle leaves a central opening and preservation is favourable, a central plate is shown underneath. The collar extends from the margin of the tube inwards, and occasionally slightly outwards over the crest. The portion of the tube area, occupied by the collar, varies. The cycle may completely fill the tube area in a plug-like manner, or leave a median slit, or occupy the area only marginally, thereby leaving a central area which in well-preserved specimens is covered with the thin central plate (Pl.2, figs.5-9). The degree of infilling may vary even in coccoliths of one coccosphere (Okada and McIntyre, 1977, pl.2, figs.3-5). Sometimes a collar is hardly developed.

If not merged into a seemingly amorphous structure, the collar elements vary in shape from rhombic to blade-like, depending on their centreward extension. The sutures between the elements point to the centre of the coccolith. Typically for the Noëlaerhabdaceae, the collar elements imbricate sinistrally (Pl.2, figs.10-13,15). This means that the elements of collar and tube have opposite imbrication in the distal part of the tube. The number of elements in the collar seems to be basically equal to the number of segments, but the former are often seen to merge and to show irregular shapes.

The central area at the distal side may be spanned by a bridge (cross-bar) of variable length, width and height. Such a bridge connects diagonally opposed collar elements (Pl.2, figs.14-18). In distal views, these collar elements are always situated somewhere in the northeastern and southwestern sector, if the longer axis of the coccolith is considered to be N-S. In some specimens, there is only a beginning of a true cross-bar (Pujos, 1985b). There may be more than two centreward projections from the collar cycle (Okada and McIntyre, *ibid.*, pl.3, figs.7-9). Usually, the inner margin of the collar is quite smooth, so that the outline of the central area is regularly (sub)elliptical to (sub)circular.

Central plate

On the proximal side, the tube area of well-preserved coccoliths of the Noëlaerhabdaceae is covered with a thin central plate. This plate consists of essentially subradial elements which are continuous with the proximal shield elements (Pl.2, figs.3,4). Its morphology varies from a solid plate to an intricate mesh work (Pl.3, figs.1-6). We have the impression that in Pliocene Noëlaerhabdaceae, the latter type is mainly formed in relatively large coccoliths, whereas subradially arranged laths occur throughout the size range. The arrangement of elements and perforations in the central plate can be quite variable, even in a single coccolith (Pl.3, fig.1). In coccoliths with a very small reticulum or a longitudinal furrow, the margin of the central plate is often solid.

In well-preserved specimens, the proximal tube is covered with the central plate, and the distal tube is partly or completely filled with the collar cycle. It seems, therefore, that there is a double layer in (part of) the tube. In some coccoliths the collar elements are continuous with elements of the central plate (Pl.3, figs.7,8), which suggests the double layer to be present in the central area as well. However, such element continuations may be of secondary origin. Possibly, the collar cycle merges with the underlying central plate.

THE OPTICAL IMAGE

For light microscope observation, we preferably oriented the specimens with their longer axis parallel to the polarizer's direction (i.e. the vertical cross-hair).

The elements of Noëlaerhabdacean coccoliths are usually too small to be discernible with a standard light-microscope. With increasing overall size, the size of the shield elements may increase subradially. Element width seems to be fairly constant; there is a significant positive correlation ($r = .99$) between the number of elements and overall size (Backman, 1980; Samtleben, 1980).

Noëlaerhabdaceae are easily recognizable in cross-polarized light. One can distinguish the quite closely appressed birefringent shields, a central opening (if

present) with a very weakly birefringent central plate (if preserved), and in between a strongly birefringent rim surrounding the central opening. Damaged specimens show that the proximal shield is more birefringent than the distal shield. When the central opening is smaller, the inner margin of the bright rim is situated closer to the centre of the coccolith; in specimens without a central opening, the 'rim' occupies the whole central area (fig.8; e.g. Pl.4, figs.1a,2a). In small specimens, it is hard to distinguish between a dim peripheral zone and a bright rim. In such specimens the peripheral zone is usually narrow.

The pattern of the extinction lines is characteristic (fig.9). It is most distinct in larger specimens with a relatively narrow central opening. They show, from periphery to centre, a subradial component, a tangential component and again a subradial component, which means that there is an offset in the extinction lines. The tangential portion is found in all Noëlaerhabdaceae, regardless of size. In the dim peripheral zone, the lines are relatively broad and vaguely outlined, and they follow the subradial direction. At about the outer margin of the bright rim, the lines bend and they get a sharper and more narrow outline. In the bright rim, the lines proceed subradially again towards the centre or towards the margin of the central opening. In distal view, the lines are dextrogyre. Proximal images yield laevogyre curves.

The relative length of the inner subradial component of the extinction lines corresponds to the width of the bright rim. The lines end abruptly and are set

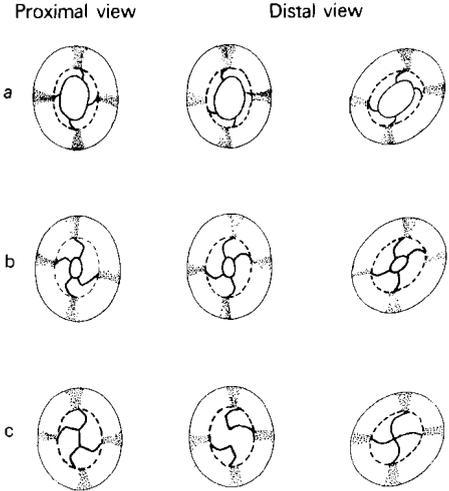


Fig.9 Cross-polarized light images of Noëlaerhabdacean coccoliths with decreasing central opening diameter (a - c). The diameter of segments and tube area is kept constant.

apart when a relatively large central opening is present. With a narrow central opening or slit, the lines are seen to almost join in pairs. When the centre of the coccolith is fully occupied by the bright rim, and the specimen is oriented with its longer axis parallel to the polarizer's direction, the lines join in pairs, leaving a bright field in between. When oriented with their longer axis diagonally, such specimens show 'swastika'-like patterns.

CRYSTALLOGRAPHY

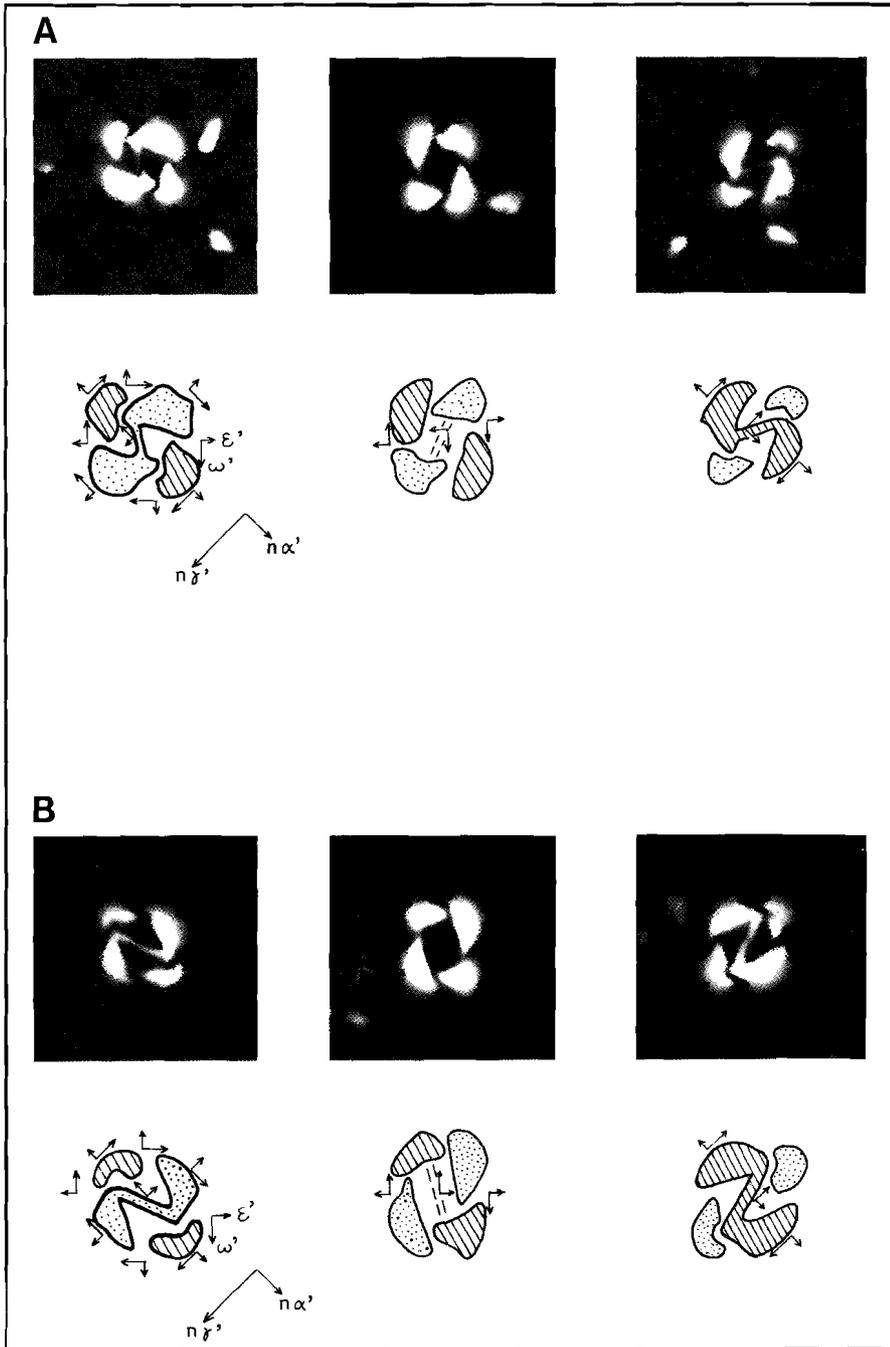
Coccoliths are aggregates of polymorphs of calcite crystals. Calcite has uniaxial negative properties.

From electron diffraction patterns of *E. huxleyi* Watabe (1967) inferred that the direction of the crystallographic axis is constant throughout each segment. Each segment was thought to behave as a separate, hollow crystal, although it might actually be a mozaïc of three individual crystallites (proximal, distal, and tube elements). The c-axis was found to be parallel to the elongation of the segment, the a-axes perpendicular to the shield surfaces.

Parker et al. (1983) arrived at a partly different conclusion. On the basis of transmission electron microscopy and of electron diffraction analysis with an ultra-high resolution electron microscope, they observed that a segment of *E. huxleyi* is probably a composite crystal. The ordered electron diffraction pattern, derived from proximal elements, suggested that these elements can be considered to be single crystals. The pattern derived from the distal elements indicated that these elements consist of a series of microcrystals ('microdomain structures' of 300-500 Å) which are only roughly oriented in the direction of elongation of the elements. It was considered likely that the proximal and distal elements are formed by different mechanisms of mineralization. However, in subsequent electron diffraction analyses of distal elements of *E. huxleyi*, similar diffraction patterns were found in both proximal and distal shield elements, confirming the results of Watabe (op. cit.). As a consequence, the pattern found in the previous analyses of distal elements, had to be discarded as an instrumental artefact (P. Westbroek, pers. comm.). The authors did not mention collar elements, and they did not succeed in separating single tube elements for analysis since these elements appeared to be tightly connected.

Pattern of birefringence

LM observations indicate that the above crystallographic construction is true for all Neogene/Quaternary Noëlaerhabdaceae. In side views with crossed nicols, a portion in the middle of the coccoliths remains dark when the stage is rotated. This means that the elements have isotropic properties (their optical axis) in longitudinal, i.e. in subradial, direction.



Text-figs. A, B Two specimens of *Gephyrocapsa caribbeanica* from the Vrica section in southern Italy (sample JT6332, Subzone NN19B). The coccoliths are viewed in cross-polarized light from the distal (specimen A) and the proximal (specimen B) side, in alternating positions of highest and lowest birefringence (rotation of 45 degrees). Addition of the gypsum plate yields yellow (dots) and blue (hatched) interference colours. The inferred orientation of the refractive indices in the coccolith's segments is shown (Magnification X 3000).

With the aid of the gypsum plate, one can reconstruct the orientation of the refractive indices n_e (for the optical axes) and n_w in the coccoliths (see Romein, 1979). From the images we can conclude again that the optical axis follows the elongation of the shield elements (text-figs.A,B). In plan views, the refractive indices in the peripheral zone probably do not reach maximum values, because the elements are not situated in the plane of the slide. There is the same interference colour throughout opposite sectors and in the bridge, connecting them. This means that the optical axis in the bright rim (and bridge) is more or less in the same plane as that of the adjoining peripheral elements. Depending on its orientation, the bridge shows oblique extinction to a greater or lesser extent.

In plan view, the shields show relatively weak birefringence. This may be due to the segments being hollow and to the inclination of the shield elements. The birefringence of the distal shield is weaker than that of the proximal shield.

Because the elements fuse in the tube, the segment is thickest and most solid between its crests (Pl.3, figs.9,10). One could argue that this increased segment thickness causes the rim of higher birefringence in cross-polarized light. However, the width of the bright rim is variable. In specimens without a central opening, the rim extends to the very centre of the coccolith, ergo beyond the crests of the segments. The width of the area, occupied by the distal tube elements, is fairly constant since the 'slope' of the distal tube seems to have a fixed inclination. Apparently, the width of the bright rim of light-microscope images is related to the width of the collar cycle. This assumption is corroborated by comparison of LM and SEM photographs of the same specimen (Pl.4, figs.1-8). Probably, the collar attributes most to the birefringence in the bright rim. The proximal tube elements, underlying the collar, may add to the birefringence. The vertical thickness of a collar element usually does not exceed that of a segment. Therefore, the optical axis in the collar cycle may be less in-

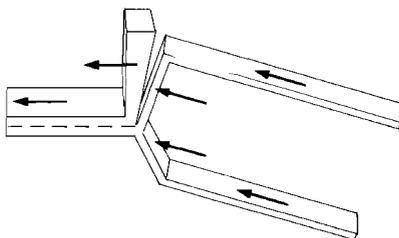


Fig.10 A model of a coccolith segment and its adjoining collar element and central plate element. The arrows indicate the inferred orientation of the optical axes.

clined, compared to that in the segment cycle; it may be parallel to the central plate (fig.10). Electron diffraction analysis of collar elements and proximal tube elements is needed to confirm this assumption.

In specimens with a small tube area (generally small sized specimens), the central area has such a small size that there is hardly any space to be recognized between a bridge and the surrounding collar. The presence of a bridge is sometimes strongly suggested by a highly birefringent zone across the coccolith (see for instance Raffi and Rio, 1979, pl.2, figs.1-4). This may be due to the increased thickness of the crystals which form the bridge in some small specimens (Pl.3, figs.11-13). Further, very small species like *Gephyrocapsa mediterranea* Pirini Radrizzani and Valleri (1977) and *G. florenzia* Lohman and Ellis (1981), which were found in the middle of the Mediterranean Pliocene, have a bridge which rises upwards almost perpendicular to the coccolith surface. If the optical axis of the bridge elements is indeed parallel to the central plate, such a bridge position would considerably add to its birefringence.

Extinction lines

We observed in an earlier paragraph that there is an offset in each extinction line. The outer subradial portion, corresponding to the shield elements, is relatively wide and vaguely outlined. This may be due to the space between the shield elements, to the weak crystallographic organization of the distal elements, to the fan-shape of the shield elements, and to a minor offset between a segment's shield elements. The innermost subradial portion, situated in the bright rim, is caused by the extinction of collar elements; the direction of this part of the lines fits in with the elongation of the collar elements. Occasional specimens show a dimly birefringent central plate with very faint extinction lines. These lines are in subradial continuation with the lines in the collar cycle. A collar element is probably optically continuous with the central plate element. The central plates are usually invisible with the LM because they are too thin or absent.

It is likely that the tangential portion of the extinction lines is caused by the tube elements. Both in proximal and in distal view, the curved portion of the lines agrees with the position and orientation of tube elements. Watabe (1967) derived only few electron diffraction spots from distal tube elements of coccoliths of *Emiliana huxleyi*. These spots suggested a direction of the optical axis in the distal tube element which was the same as that of the corresponding shield elements. It would follow that, in the proper position, the entire segment is extinguished in cross-polarized light. Schmidt (1979) remarked that the gyre pattern does not change in specimens without a collar. Further, the inclination

of the collar elements down the tube is not in accordance with the direction of the tangential portion of the extinction lines.

We conclude that the extinction lines probably follow the entire segments, which means that the optical axis has a constant direction throughout the segment. At the median level of the coccoliths, which is at the bottom of the distal tube, the optical axis of the terminal part of a segment is in the same plane as that of the collar element, attached there (see fig.11). This assumption is confirmed by our observation that both the elements of the collar cycle and those of the proximal tube continue into the elements of the central plate. Furthermore, the number of segments is essentially the same as the number of elements in collar and central plate.

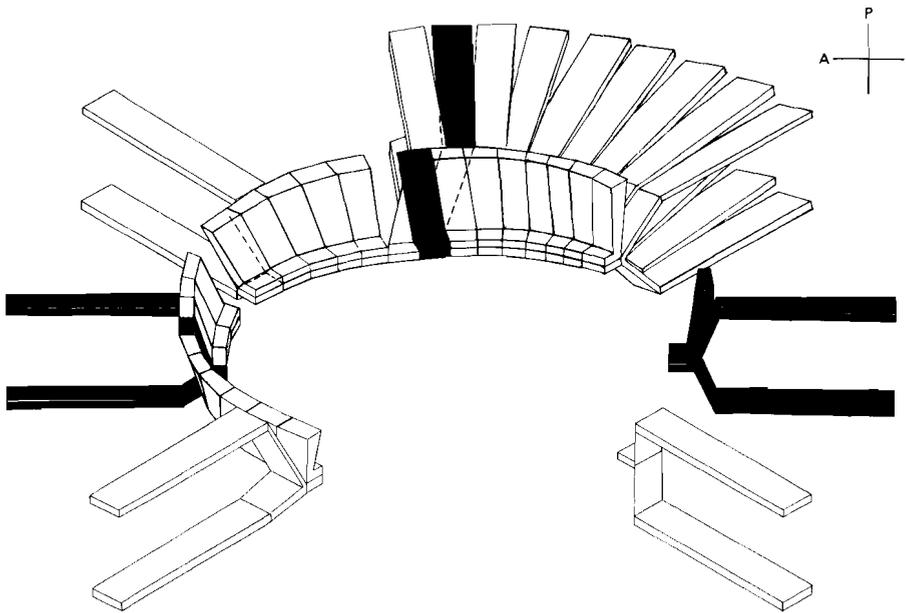


Fig.11 Schematic drawing of a coccolith of the Noëlaerhabdaceae, showing our interpretation of the elements in the segments, collar and central plate which extinguish between crossed polarizers.

Summarizing, the coccoliths of the Noëlaerhabdaceae consist of peripheral segments, a collar cycle and, if present, a central plate. In cross-polarized light, these units can be recognized as the dim peripheral cycle, the rim of higher birefringence, and the hardly birefringent central area, respectively. The optical axis of a segment is in the direction of elongation of the segment, and it has a constant direction throughout the segment. In plan view, the shield elements are weakly birefringent. They pass into the tube elements at the position

where, in cross-polarized light, the extinction lines show a curvature. Consequently, the extinction lines are dextrogyre in distal view and laevogyre in proximal view. The optical axes of a collar element and of the adjoining central plate element are situated in subradial direction, probably parallel to the median plate. The optical axes in the collar cycle and central plate are offset with respect to those in the segment cycle.

Variation in the morphology of the coccoliths is largely determined by variation in the relative width of the three structural units : segments (s), collar (c) and central opening (o). In the literature, morphology is usually dealt with in terms of two components, i.e. in terms of the relative size of the central opening. Little or no attention is paid to the relative width of the segments versus that of the collar. A differential diagnosis of, for example, *Cyclicargolithus* in terms of our three components would facilitate the recognition of the coccoliths under consideration. Apart from its subcircular outline, *Cyclicargolithus* typically shows relatively large shields, whereas its collar cycle and central opening are small. This morphology could be described as $s > c + o$; $c \approx o$. In the majority of Noëlaerhabdaceean associations of the Neogene and Quaternary, such a combination is very rare. A small central area, a subcircular outline or a combination of both are not uncommon, but such coccoliths usually have relatively wide collars.

Chapter 6

THE PRESENT STATE OF THE TAXONOMY OF THE NOËLAERHABDACEAE

Until the nineteenfifties, coccolith taxonomy was based on light-microscope observations, and holotypes were depicted by means of drawings. Cross-polarized light was used from the sixties onwards. Some of the Noëlaerhabdacean taxa from this early period were described as coccolithophore cells. *Pontosphaera huxleyi* Lohmann (1902) and *P. sessilis* Lohmann (1912) are such species. The technical equipment of the time allowed descriptions of the cells and their mode of life rather than handling the morphology of the individual coccoliths on the cells. Even with the present-day optics, the coccoliths of Lohmann's species are hard to differentiate. A new dimension in systematics was added by the application of electron microscopy. Meanwhile, the appreciation of calcareous nanofossils for practical use in biostratigraphy increased. In

<i>Light-microscopy</i>	<i>Scanning electron microscopy</i>
size - overall - central area/opening - proximal/distal shield	size - overall - central area/opening - proximal/distal shield
outline - overall - central area/opening	outline - overall - central area/opening
shields - (slits) - (no slits)	shields - number of elements - imbrication of elements - morphology of elements
bridge - angle - width	- presence/morphology of slits - periphery - smooth - crenulate
(cross-polarized light image)	tube area - median plate - morphology - size
(collar width)	- centrodistal cycle - morphology - width
(shape/composition of coccosphere)	- bridge - angle - height - width - morphology
stratigraphic range	shape/composition of coccospheres stratigraphic range

Table 1: Parameters used in the taxonomy of the Noëlaerhabdaceae.

GENUS, AUTHOR(S)	TYPE SPECIES	EMENDATIONS, SUBSEQUENT DESCRIPTIONS	TAXONOMICAL/ NOMENCLATORAL COMMENTS
<i>Coccolithus</i> Schwarz, 1894	<i>Coccolithus oceanicus</i> Schwarz, 1894 Type level : Lias Lectotype (Braarud et al., 1964) : <i>Coccosphaera pelagica</i> Wallich, 1877	Hay, 1977	-- Schwarz did not designate a type specimen for <i>Coccolithus oceanicus</i> ; Braarud et al. (1964) designated a lectotype. -- Romein (1979): <i>Coccolithus</i> is to be avoided because its type species <i>Coccolithus oceanicus</i> was meant to be a collective epithet.
<i>Crenalithus</i> Roth, 1973	<i>Coccolithus doronicoides</i> Black & Barnes, 1961	Hay, 1977	-- Backman (1980): synonym of <i>Reticulofenestra</i> Hay, Mohler & Wade
<i>Dictyococcites</i> Black, 1967	<i>Dictyococcites danicus</i> Black, 1967	Black, 1973 Hay, 1977 Backman, 1980	-- Edwards (1973): synonym of <i>Reticulofenestra</i> Hay, Mohler & Wade
<i>Ellipsoplacolithus</i> Kamptner, 1963	<i>Ellipsoplacolithus lacunosus</i> Kamptner, 1963		-- Kamptner (1963): provisional taxon; most specimens of <i>Ellipsoplacolithus</i> may belong to <i>Coccolithus</i> . -- Loeblich and Tappan (1966): invalid
<i>Emiliana</i> Hay & Mohler, in Hay et al., 1967	<i>Pontosphaera huxleyi</i> Lohmann, 1902	Hay, 1977	
<i>Gephyrocapsa</i> Kamptner, 1943	<i>Gephyrocapsa oceanica</i> Kamptner, 1943	Bukry, 1973 (c) Hay, 1977	
<i>Pseudoemiliana</i> Gartner, 1969	<i>Ellipsoplacolithus lacunosus</i> Kamptner, 1963	Hay, 1977	-- Loeblich and Tappan (1970): invalid -- Gartner (1977a): valid and legitimate -- Bukry (1973c): synonym of <i>Emiliana</i> Hay & Mohler
<i>Reticulofenestra</i> Hay, Mohler & Wade, 1966	<i>Reticulofenestra caucastica</i> Hay, Mohler & Wade, 1966	Stradner, in Stradner and Edwards, 1968 Edwards, 1973 Hay, 1977	

Table II: Genera, commonly used in the taxonomy of the Late Neogene and Quaternary Noëlaerhabdaceae.

the past decades, numerous taxa have been added, usually on the basis of either SEM or LM. Their classification is based on several parameters, most of which are listed in Table I.

In over a century of calcareous nannofossil and nannoplankton study, a considerable number of taxa has been created for the Noëlaerhabdaceae. A lot of these taxa are probably superfluous. One of the problems of nannofossil taxonomy is evaluating the combination of LM- and SEM-based taxa. In addition, SEM-based definitions have their own drawbacks, since only one side of the holotype can be viewed and photographed. Most parameters used are to be seen in distal views. A taxon like *Crenalithus* Roth is open to discussion because the holotype of its type species, *Coccolithus doronicoides* Black & Barnes, was viewed from the proximal side (see Backman, 1980). The same problem applies to *Dictyococcites danicus* Black, the type species of *Dictyococcites* Black (see below).

FAMILY NAMES

On all taxonomic levels, opinions vary as to the label to be used. Structurally, the coccoliths of the Noëlaerhabdaceae are a homogeneous group. Rather than lumping them in the highly heterogeneous Coccolithaceae Poche (1913), we prefer using a separate family name. Three names are available : Prinsiaceae Hay and Mohler (1967), Noëlaerhabdaceae Jerković (1970) and Gephyrocapsaceae Black (1971). Gephyrocapsaceae Hay (1977) is obviously a homonym of Gephyrocapsaceae Black. The first validly published family name is Noëlaerhabdaceae, as Hay and Mohler did not explicitly mention a type genus for their family name Prinsiaceae.

GENERA

The Paleogene representatives of the Noëlaerhabdaceae (sensu Romein, 1979) are recorded under various generic names, such as *Prinsius*, *Toweius*, *Cribrocentrum*, *Cyclicargolithus*, *Reticulofenestra* and *Dictyococcites*. The associations from the Upper Miocene and the lower part of the Lower Pliocene are characterized by a low taxonomic diversity. Usually, only *Reticulofenestra* and *Dictyococcites* are distinguished. Upwards, the morphological (and taxonomic) diversity increases again with the appearance of new coccolith characters like a cross-bar (*Gephyrocapsa*) and slits between the shield elements (*Pseudoemiliana*, *Emiliana*).

Generic names, which are frequently applied for Late Miocene to Recent Noëlaerhabdaceae, are listed in Table II. In defining these taxa, different parameters have been used, most of which are not exclusive. Furthermore,

these characters were usually not weighed in differential diagnoses. The synonymy column of Table II shows that opinions among the taxonomists vary as to the names to be used. Following Backman (1980), we consider *Crenalithus* to be a junior synonym of *Reticulofenestra*. *Coccolithus* is a collective name which we prefer not to use for the structurally distinct Noëlaerhabdaceae.

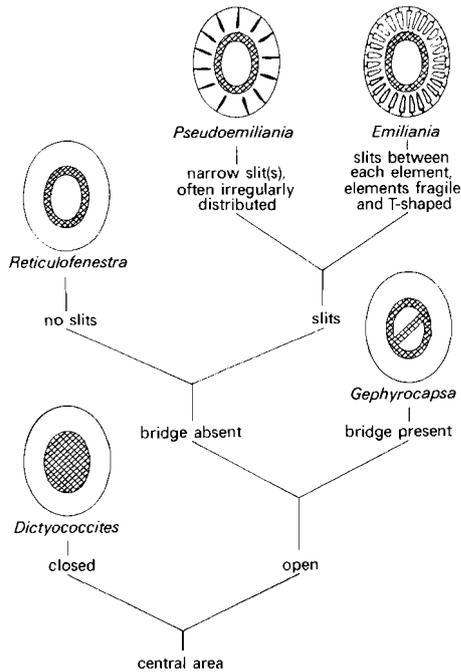


Fig.12 Distribution of distal side characters in genera, commonly used in the taxonomy of the Pliocene/Quaternary Noëlaerhabdaceae. Size of segments and tube area is kept constant ; cross-hatched areas represent the collar cycle (cross-bar) ; central plates are not shown.

Gephyrocapsa and *Pseudoemiliana* appeared in the course of the Pliocene. *Emiliana* is usually treated as a monospecific genus, the species being *E. huxleyi* which appeared in the Late Pleistocene. Some authors regard *Pseudoemiliana* as an illegitimate taxon and use instead *Emiliana* also for species from the Pliocene (after Bukry, 1973c). Of the listed genera, only *Pseudoemiliana* is mentioned to become extinct ; its exit marks the top of the Pleistocene Zone NN19. The literature leaves a possible exit of *Reticulofenestra* and *Dictyococcites* undecided, although these taxa are usually not applied for describing Quaternary coccolith associations and Recent coccolithophores. However, the

Quaternary coccoliths, treated as *Crenolithus* or *Coccolithus*, are not or hardly different from their Neogene predecessors.

Backman (1980) and Perch-Nielsen (1985) presented useful overviews of the taxonomy and morphology of the Noëlaerhabdaceae. Shortly, the characteristics of the genera they used for the Pliocene to Recent coccoliths can be described as follows (fig.12) :

Reticulofenestra has a central opening without a bridge ; its segments form solid shields. *Dictyococcites* sensu Backman (1980) is similar but has a collar cycle which fills the tube area completely. *Gephyrocapsa* has a bridge crossing the central area. *Pseudoemiliana* has a central opening and one or more slits between the segments. In *Emiliana*, there are slits between all segments, and the slits have a width to the extent that the (distal) shield elements are fragile and T- or I - shaped.

It is questionable whether the building plan of *Reticulofenestra* remains the same throughout its range. As we mentioned above, in some Eocene *Reticulofenestra* the dextral bend in the distal sutures is not at the level of the distal crest but lower down in the distal tube.

Inter-generic variation

Bridge, collar and central opening

The characters, emphasized in the above generic concepts, are not mutually exclusive, which means that a combination of them may be found in one coccolith. For generic identification such characters have to be weighed. For instance, the presence of a bridge is usually considered to outweigh the particular composition of the distal shield. Consequently, coccoliths assigned to *Gephyrocapsa* show a wide range of distal shield morphologies ; if not for the bridge, they would be classified as *Reticulofenestra* or *Emiliana* (see Samtleben, 1980). A classical example is *Gephyrocapsa protohuxleyi* McIntyre (1970), which shows both a bridge and I - shaped distal shield elements. McIntyre suggested that the species was the evolutionary stage between *Gephyrocapsa* and *Emiliana*. Subsequently the species was observed in the life assemblages of the Gulf of Elat (Winter et al., 1978) and in the central North Pacific (Reid, 1980).

Further, there are gradational series of coccolith morphotypes in which particular genus characters are not clearly developed. We already observed that the central area in some coccoliths is reduced due to centreward projections from the collar. The bridge of *Gephyrocapsa* is a regular form of such projections. Pujos (1985a) remarked that there is a gradational evolutionary series of coccolith morphotypes without a cross-bar to morphotypes with a cross-bar. For this reason she used only one genus (*Gephyrocapsa*) for the coccoliths in question.

Collar and bridge may have a width to the extent that the central area is almost completely filled. In some specimens it is hard to distinguish between a cross-bar and the collar cycle (Pl.3, figs.14,15), especially when the observations pertain to small specimens under the light-microscope. In specimens with a small tube area (generally in small specimens), the central area may have such a small size that there is hardly space left between a bridge and the collar cycle (see for instance Rio, 1982, pl.1, fig.2). With the light-microscope, such specimens are hard to distinguish from *Dictyococcites* sensu Backman.

Reticulofenestra shows a central opening of variable size. There seems to be a continuous variation between coccoliths with a large central opening and specimens with a completely filled tube area. The latter morphotypes would be referable to *Dictyococcites* sensu Backman.

Slits between the segments

Winter et al. (1978) pointed out that, in the coccoliths of *Gephyrocapsa protobuxleyi*, the shape of the slits between the elements varies from very narrow to relatively wide. Only the latter type of slits produces clearly I - shaped elements. Such a variation may be proven to be present in coccoliths without a bar (*Emiliana*) as well. Coccoliths of *Pseudoemiliana* have slits between (some of) the distal shield elements, which per se is a presence/absence character. One may wonder whether the presence of one or very few slits on a coccolith justifies separating the specimen taxonomically from *Reticulofenestra*. In such terms Samtleben (1978) questioned the systematic boundary between *Pseudoemiliana* and *Crenalithus* (= *Reticulofenestra*). He postulated an 'uncertain triangular relationship' between *Crenalithus*, *Gephyrocapsa* and *Pseudoemiliana*. In the Pleistocene of section Kolimpia on Rhodes, we found coccoliths with slits and an almost closed central area (Pl.2, fig.6). Such coccoliths could be assigned to *Pseudoemiliana*, *Reticulofenestra*, or even to *Dictyococcites*.

The number and the outline of the slits between the shield elements can be ascertained only by means of electron microscopy. In specimens smaller than about 4 μ , details like slits and the element make-up are beyond the resolution capacity of the light-microscope. Therefore, the coccoliths of *Emiliana*, being usually smaller than 4 μ , are indistinguishable from those of *Reticulofenestra* or *Pseudoemiliana* with the light-microscope. Specimens of *Pseudoemiliana*, if large enough and with abundant slits, can be recognized by their serrate periphery between crossed polarizers. Perch-Nielsen (1985) remarked that phase contrast illumination can be of help. Because the stratigraphic ranges of *Pseudoemiliana* and *Emiliana* are different, specimens from the Pliocene or Lower Pleistocene with a serrate periphery are referred to *Pseudoemiliana*.

When dealing with Holocene associations, it proves to be difficult to classify such specimens because they may be either large specimens of *Emiliania* or reworked *Pseudoemiliania*.

Variation on coccospheres

In the majority of Noëlaerhabdacean associations from the Pliocene/Quaternary, a generic classification as outlined above can be used for systematically subdividing the coccolith morphotypes. Some of the genus characters are SEM-parameters, which is not incorrect but unpractical. Especially in the case of the Noëlaerhabdaceae, a strict form-classification is not by necessity a 'natural' classification. The presence of 'generic' intergrades, and observations of coccoliths of supposedly differing generic affiliation on one coccosphere are relevant. Coccospheres have been described bearing coccoliths of both the *Gephyrocapsa* and the *Emiliania* types (Clocchiatti, 1971; Samtleben, 1978; Winter et al., 1979). Such 'hybrid' cells do suggest that certain *Gephyrocapsa* and *Emiliania* coccoliths belong to one biologic species. A similar relation may exist between *Crenalithus* (= *Reticulofenestra*) and *Gephyrocapsa* coccoliths (Winter, 1982). Okada and McIntyre (1977; pl.3, figs.1,2) pictured coccospheres of *Gephyrocapsa ornata* Heimdal (1973), showing coccoliths with and others without a cross-bar, and with a varying number of slits between the distal shield elements. The individual coccoliths of such spheres can be assigned to *Gephyrocapsa*, to *Emiliania* (*Pseudoemiliania*) and to *Reticulofenestra*.

Although coccospheres usually show a constant-shape coccolith cover, the occasional coccolith polymorphism on spheres suggests that the 'natural' coccosphere species have the genetic potential to produce highly variable coccolith morphotypes. Such species would overstep the existing coccolith-systematic boundaries. If true, the type of coccolith to be formed on the cell may be the result of environmental factors like nutrients, temperature, salinity (see also chapter 7), and/or depend on the particular stage in a possibly pleomorphic life cycle of the cell. The latter phenomenon made Paasche (1968) remark that the 'classification of coccolithophorid species by coccolith morphology alone is unsatisfactory'. Although perfectly acceptable, we will primarily adhere to the 'classical' approach of coccolith classification because the coccolithophores are of no use for fossil associations.

The taxonomic status of Dictyococcites Black

Dictyococcites danicus Black (1967), originally described from the Oligocene of Denmark, is the type species of *Dictyococcites* Black (ibid.). In the species' protologue, the proximal side of the holotype was portrayed. Black emphasized the construction of the central plate but did not mention the mode of infilling of the tube area on the distal side. In later publications, Black (1968, pl.145,

fig.4) pictured a proximal view of a similar coccolith as the newly combined *Tremalithus danicus*, and thereupon (1971) considered *Dictyococcites* and *Reticulofenestra* to be synonyms of *Tremalithus* Kamptner (1948). According to Loeblich and Tappan (1970a), *Tremalithus danicus* is an invalid combination. Roth (1970) placed Black's species in *Reticulofenestra*. Hay (1977) remarked that, because *Dictyococcites danicus* belongs to *Reticulofenestra*, *Dictyococcites* is a subjective synonym of *Reticulofenestra*, but he retained *Dictyococcites* and its type species. Hay's diagnosis of the genus differs from Black's diagnosis only in details. Again the distal side morphology of the coccoliths was not mentioned.

Backman (1980) redefined *Dictyococcites* to encompass 'elliptic placoliths with a closed central area in line with the distal shield'. In our terms, Backman refers to placoliths in which the collar cycle either completely fills the tube area or leaves only 'a median slit or furrow, or a minute pore'. This emendation meets the current concept of the *Dictyococcites* morphology, but by defining the genus on the basis of distal side properties, Backman may have created a homonym (ICBN, article 48). It is questionable whether the morphology of the genotype fits his circumscription, because the holotype of *D. danicus* was portrayed from the proximal side.

SPECIES

By far the greater number of calcareous nannofossil and coccolithophore species has been introduced on the basis of a typological approach. In the systematics of the Noëlaerhabdaceae, such a concept is not easily applicable because its narrow delimitation interferes with the highly variable morphology of the coccoliths.

In the literature it is often remarked that the morphological variation in the Noëlaerhabdacean associations is large, that many gradational or intermediate morphotypes are present between specimens referable to different species, and that only the end-members of the variation are easily distinguishable. Such statements often refer to the *Gephyrocapsa* variation (Chen, C.Y. Huang et al., 1977; Gartner, 1977a; Haq et al., 1977; Samtleben, 1980; Roth and Coulbourn, 1982), but a variation range covering several 'species' has also been extended to Noëlaerhabdaceae without a cross-bar. For example, Winter et al. (1978) suggested that *Gephyrocapsa protobuxleyi*, *G. ericsonii* and *Emiliania huxleyi* may be morphotypes of the same taxon. Winter (1982) proposed such a relation to exist between his *Gephyrocapsa* cf. *ornata*, *G. ericsonii* and *Crenalithus* spp.

Species names

There are many species names available for coccoliths belonging to the Noëlaerhabdaceae. Light-microscope workers easily get the impression that some Reticulofenestrid morphotypes range from Middle Eocene to Recent. However, the species names, used for Eocene to Middle Miocene specimens differ from those used for the Upper Miocene and Lower Pliocene ones, and again from those used for the Upper Pliocene and Quaternary Noëlaerhabdaceae. It is beyond our scope to investigate the relation between the Late Neogene/Quaternary taxa and the many Eocene/Early Miocene species (for an overview see Perch-Nielsen, 1985). Differences, if any, mainly concern central area characters. We have the feeling that the array of available names comprises several (subjective) synonyms. Evidently, tradition seems to play such a role in systematics that the age of the sample determines the labels to be used.

In Table III we listed several species names which are used for the Late Neogene Noëlaerhabdaceae.

Specific characters

The main characters used for distinguishing species in the coccoliths of the Noëlaerhabdaceae are overall size, outline, the relative size of the central opening, the number of elements and the composition of the central plate. In the taxonomy of the Gephyrocapsids, the angle, width and height of the bridge are used in addition. Element number, central plate configuration and bridge height can only be established by means of electron microscopy. Although the variation of central plates on one coccosphere seems to be limited, it is hard to find two coccoliths in a sediment sample with exactly the same central plate morphology. For LM systematics, element number, central plate configuration and bridge height are not of practical use.

Outline and slits

A circular coccolith outline is an recurrent feature in the record of the Noëlaerhabdaceae, usually applying to a minor portion of the coccolith associations. It has been used as a generic character (in the Early Neogene *Cyclicargolithus* Bukry) and as a species character (e.g. in the Late Miocene *Reticulofenestra rotaria* Theodoridis, and in the Late Pliocene/Early Pleistocene *Emiliania annula* (Cohen) Bukry). In most samples the variation in coccolith outline is such that there is no clear break between oval and circular forms. Such a distribution suggests that Noëlaerhabdaceae coccospheres are capable to produce both forms, which means that the coccolith outline is of subordinate weight. Roth, Mullin and Berger (1975) reported on the presence of both

SPECIES, GENUS OF BASIONYM, AUTHOR(S)	LM - TYPE (FIG.13)	COCCOLITH LENGTH OF HOLOTYPE, SYNTYPES, AND SIZE-RANGE	OTHER COMBINATIONS
<i>aequiscutum</i> , <i>Cyclocoocolithus</i> Gartner, 1967b	18	4.8 μ (3.7-4.9 μ)	
<i>annulus</i> , <i>Coccolithites</i> Cohen, 1964	??	\pm 9 μ (5-9 μ)	<i>Cyclolithella</i> McIntyre & BÉ, 1967 <i>Emiliania</i> Bukry, 1971c
<i>antarcticus</i> , <i>Dietyococites</i> Haq, 1976	2	\pm 6 μ (4-8 μ)	
<i>aperta</i> , <i>Gephyrocapsa</i> Kamptner, 1963	20	?? (1.5-2.2 μ)	
<i>bukryi</i> , <i>Cylioargolithus</i> Wise, 1973	6	6.2 μ (6-8 μ)	
<i>caribbeanica</i> , <i>Gephyrocapsa</i> Boudreaux & Hay, in Hay et al, 1967	14 (8,9)	4 μ (4-4.5 μ)	
<i>cricotus</i> , <i>Cyclocoocolithus</i> Gartner, 1967b	18 (subcircular)	?? (\pm 4.5-5.5 μ)	<i>Umbilicosphaera</i> Reinhardt, in Cohen and Reinhardt, 1968 <i>Coccolithus</i> Cita et al., 1970 <i>Cyclocoocolithina</i> Wilcoxon, 1970
<i>doronicoides</i> , <i>Coccolithus</i> Black & Barnes, 1961	12 ?	3.4 μ (2.5-5 μ)	<i>Ellipsoplacolithus</i> Black, 1971 <i>Gephyrocapsa</i> Bukry, 1973c <i>Crenolithus</i> Roth, 1973 <i>Cylioargolithus</i> Wise, 1973 <i>Reticulofenestra</i> Pujos, 1985c
<i>ericsonii</i> , <i>Gephyrocapsa</i> McIntyre & BÉ, 1967	21	1.9-2.2 μ	
<i>florenzia</i> , <i>Gephyrocapsa</i> Lohman & Ellis, 1981	14 ?	\pm 2.25 μ (1.3-2.6 μ)	
<i>gelidus</i> , <i>Coccolithus</i> Geitzenauer, in Geitzenauer and Huddleston, 1972	5	\pm 10 μ (6-12 μ)	<i>Reticulofenestra</i> Backman, 1978 <i>R. pseudumbilica</i> subsp. <i>gelida</i> Wise, 1983
<i>haqi</i> , <i>Reticulofenestra</i> Backman, 1978	5	\pm 4.7 μ (3-5 μ)	
<i>hesslandii</i> , <i>Ericsonia</i> Haq, 1966	5	4.7 μ (3.5-9.1 μ)	<i>Reticulofenestra</i> Roth, 1970 <i>Prinsius</i> Haq, 1971 <i>Dietyococites</i> Haq & Lohmann, 1976
<i>japonica</i> , <i>Reticulofenestra</i> Nishida, 1979	6	10 μ ? (5-6 μ)	

Table III: Species names, used for the Pliocene Noëlaerhabdaceae.

<i>lacunosus</i> , <i>Ellipsoplacolithus</i> Kamptner, 1963	18 ¹	4.6 μ	<i>Pseudoemiliana</i> Gartner, 1969
<i>margeneli</i> , <i>Gephyrocapsa</i> Breheret, 1978	21 (15)	3.5 μ (2.7-4.8 μ)	
<i>mediterranea</i> , <i>Gephyrocapsa</i> Pirini Radrizzani & Valeri, 1977	14 ?	\pm 2.5 μ (? - 4 μ)	
<i>minuta</i> , <i>Reticulofenestra</i> Roth, 1970	11	1.5 μ (2 μ)	
<i>minutus</i> , <i>Prinsius</i> Haq, 1971	4 (11)	3 μ (2.5-3 μ)	<i>Dietyococites</i> Haq, Lohmann & Wise, 1976
<i>minutulus</i> , <i>Coccolithus</i> Gartner, 1967b	17	?? (\pm 3.6- \pm 4.5 μ)	<i>Reticulofenestra</i> Haq & Berggren, 1978
<i>oceanica</i> , <i>Gephyrocapsa</i> Kamptner, 1943	15	2.9-5.7 μ	
<i>ovata</i> , <i>Emiliana</i> Bukry, 1973c	17 ¹ ?	\pm 5 μ (4-8 μ)	
<i>pacifica</i> , <i>Reticulofenestra</i> Nishida, 1979	18 ¹	9.7 μ ? (5-6 μ)	
<i>perplexa</i> , <i>Dietyococites</i> Burns, 1975	2	\pm 20 μ (18-20 μ)	<i>Reticulofenestra</i> Wise, 1983
<i>productellus</i> , <i>Crenalithus</i> Bukry, 1975	2	\pm 3.2 μ (3-8 μ)	
<i>productus</i> , <i>Ellipsoplacolithus</i> Kamptner, 1963	2 ?	2.7-2.9 μ	<i>Actinoephaera</i> Noël, 1965 <i>Gephyrocapsa</i> Bukry, 1971b <i>Coccolithus</i> Sachs & Skinner, 1973 <i>Dietyococites</i> Backman, 1980 <i>Crenalithus</i> Pujos, 1985a
<i>pseudoumbilicus</i> , <i>Coccolithus</i> Gartner, 1967	12	\pm 8.5 μ (\pm 6.8-9.5 μ)	<i>Reticulofenestra</i> Gartner, 1969
<i>reticulata</i> , <i>Gephyrocapsa</i> Nishida, 1971	6	10 μ ? (5-6 μ)	<i>Reticulofenestra</i> Nishida, 1973
<i>rotaria</i> , <i>Reticulofenestra</i> Theodoridis, 1984	17 ? (circular)	\pm 6.7 μ (5-7 μ)	
<i>scrippsae</i> , <i>Dietyococites</i> Bukry & Percival, 1971	1	\pm 9.5 μ (6-12 μ)	<i>Reticulofenestra</i> Roth, 1973
<i>taganus</i> , <i>Coccolithus</i> Fonseca, 1976	4	1.9 μ (1.75-2.5 μ)	<i>Crenalithus</i> Bukry, 1981a "Reticulofenestra" Pujos, 1985b

elliptical and circular coccoliths on coccospheres of *Emiliana huxleyi* from laboratory cultures. The authors remarked that the circular forms probably do not occur in life assemblages of *E. huxleyi*. Still, their observation may corroborate our above assumption.

In the coccoliths of the Pliocene/Early Pleistocene *Pseudoemiliana* (= *Emiliana* auct.), there seems to be a trend with time towards an increasing number of slits, a larger overall size, a larger size of the central opening, and a circular outline. Elliptical forms appeared earlier than the circular forms; they disappeared earlier (according to Hay, 1970) or later (according to Bukry, 1975; Ellis, 1979). To our knowledge, such a distribution with time has as yet not been verified by means of biometrics. Relatively large ($> 5 \mu$) circular forms with abundant slits and a large central opening are found in the higher intervals of the Pliocene and in the Lower Pleistocene.

There is a controversy in the literature about the taxonomy of *Pseudoemiliana*-like coccoliths. As we mentioned in a previous paragraph, it is questionable whether it is realistic to assign Noëlaerhabdacean coccoliths without slits and those with one or only a few slits to different genera. We wonder whether the number of slits is homogeneously distributed over the coccoliths of a coccosphere. The boundary between a *Pseudoemiliana* coccolith with abundant slits and coccoliths of *Emiliana* s.s. is equally hard to define. A difference in overall size (*Pseudoemiliana* is thought to be larger) and the supposed gap between the ranges of the genera are used to differentiate between the two genera. Müller (1972) found relatively large (6.5 - 8 μ) coccoliths with abundant slits ('*Pseudoemiliana lacunosa*') to be present throughout the Quaternary of deep-sea cores from the Ionian Sea, and she raised the question whether this stratigraphic distribution is due to reworking.

Several authors distinguished between a circular and an oval coccolith morphotype, either as forms (varieties) of the species *Pseudoemiliana lacunosa* (Kamptner) Gartner or, when *Pseudoemiliana* was not used, as two separate species *Emiliana annula* (Cohen) Bukry and *Emiliana ovata* Bukry. Gartner (1977a) argued that making a distinction on the species level between an elliptical and a circular form is not useful. Bukry, by using Cohen's *Coccolithites annulus* as the basionym for his circular species, had made an unfortunate choice because the coccoliths of Cohen's species are structurally different from those of the Noëlaerhabdaceae (see also Backman, 1980). For reasons given above, it is not surprising that Bukry included *Pseudoemiliana* Gartner in his concept of *Emiliana* s.l. Besides, there are reasons of a nomenclatorial nature to discard *Pseudoemiliana*. According to Loeblich and Tappan (1970b), *Pseudoemiliana* Gartner is invalid because the type species, *lacunosus* Kamptner, is invalid; in the basionym, this species had been combined with the provisional, hence in-

valid, genus *Ellipsoplacolithus* Kamptner (see Loeblich and Tappan, 1966).

Nishida (1979) created a species *Reticulofenestra pacifica* which was characterized by an elliptical outline and few slits between the distal elements. *Pseudoemiliania lacunosa* was thought to have a larger overall size, a larger central area, and more than 10 slits in the distal shield. In addition to an elliptical and a round type of *Pseudoemiliania lacunosa*, Pujos (1985a,b) distinguished a slit-bearing variety of '*Gephyrocapsa doronicoides*', called *G. doronicoides* var. '*lacunosa*' or *G. doronicoides* var. (lacunoid). This variety was recognized on the basis of a relatively low number of slits.

No matter which taxonomic label is chosen for the coccoliths under consideration, the systematic boundaries are hard to delineate. Furthermore, SEM workers will end up with a longer stratigraphic range of slit-bearing coccoliths because the instrument allows for the recognition of any number of slits. For these reasons, biostratigraphic discrepancies, as outlined in chapter 4, are only to be expected.

Numerical parameters

Overall size, size of the central opening, the number of elements (segments), bridge angle, bridge width and bridge height are the other features, used in the descriptions of the species of the Noëlaerhabdaceae. Such parameters allow for a biometrical approach through which the variation width per sample can be defined numerically. However, for most of the species introduced, the variation range of these parameters has not been given, and several of the species are in the same size order.

In our samples the *Gephyrocapsids* are often so small that applying the characteristics of the cross-bar, used for distinguishing *Gephyrocapsa* species, is beyond the limits of light-microscopy. For an overview of *Gephyrocapsa* taxonomy, the reader is referred to Samtleben's (1980) extensive monograph. Samtleben gave a biometrical definition of his *Gephyrocapsa* species, using the following parameters : coccolith length, bridge angle, roundness and pore width. He considered bridge height to be of systematic importance as well, but it is hard to measure this parameter consistently.

The segments can be counted only with the aid of the electron microscope, but as we observed earlier, the number of segments is a function of overall size (Backman, 1980; Samtleben, 1980).

Overall size (coccolith length) is one of the parameters used most frequently for distinguishing between species. Characterizing species on the basis of coccolith diameter would be very practical if the distribution of coccolith sizes in Noëlaerhabdacean associations would be constant in all samples. However, this distribution seems to be unstable both in time and in space, as can be il-

lustrated by the discussion in the literature about the morphology of *Reticulofenestra pseudoumbilicus*.

This species is often commented upon because it is used as a zonal marker. Very often, it is the only specific epithet used for large-size Noëlaerhabdacean coccoliths in the Upper Miocene and Pliocene. Remarks on the morphology of the Mediterranean *R. pseudoumbilicus* mainly concern its size. Bukry (1973a) and Gartner (1977b) mentioned the taxon in question to consist of 'large (specimens of) *R. pseudoumbilicus*'. Müller (1978) and Meulenkamp et al. (1978) reported 'small specimens' of the species to be present in the higher part of the *R. pseudoumbilicus* Zone. Others were more specific about the size range of the taxon (Raffi and Rio, 1979 : about 12 μ ; Schmidt, 1979 : > 5.5 μ - \pm 9 μ ; Moshkovitz and Ehrlich, 1980 : 8 - 10 μ). These authors mentioned the co-occurrence of smaller sized morphotypes of the species (about 6 μ , 2 - 5 μ , and 4 - 5 μ , respectively), that persist into higher levels of the Pliocene. From such concepts one could infer that the actual event in the middle of the Pliocene has been the disappearance of part of the size variation of the Mediterranean *R. pseudoumbilicus*. Since most of the papers mentioned, focused on such a 'large size species', the remaining part of the variation was paid little or no attention to. Often, the small-sized coccoliths are listed as *Coccolithus daronicoides* or as *Reticulofenestra* spp. From many range charts it would appear that the genus *Reticulofenestra* vanished from the record at the top of the *R. pseudoumbilicus* Zone, which is certainly not correct if one follows the generic concept outlined in the section on generic names (see above).

BIOMETRICAL DATA FROM THE LITERATURE

In a previous paragraph we already referred to Samtleben's (1980) biometrical study of *Gephyrocapsa*.

A major study on the intra- and interspecific variation in the Neogene *Reticulofenestra* and *Dictyococcites* was presented by Backman in his thesis (1980). The author studied the Miocene-Pliocene from DSDP site 116 in the Hatton - Rockall basin (NE North Atlantic), and used additional material from several sedimentary sequences in the Atlantic Ocean and in the western Mediterranean. Most of his data are based on light-microscope observation. Backman discriminated a priori between *Dictyococcites* (emend.) and *Reticulofenestra*. Because of the difficulty to distinguish between small to medium sized *Pseudoemiliana* and *Reticulofenestra* with the LM, he refrained from analyzing the Noëlaerhabdaceae from the stratigraphic interval above the entry of *P. lacunosa*.

Dictyococcites

On the basis of the extinction line pattern, Backman distinguished two groups of *Dictyococcites* morphotypes. One, *D. hesslandii*, is characterized by extinction lines radiating from the centre or central pore. In site 116, this species was found to vanish from the associations in the Middle Miocene. In the Lower Miocene, the coccolith size varies between 3 and 5 μ ; the variation range is 3 - 8 μ in the lower Middle Miocene.

The other group of *Dictyococcites* coccoliths shows a straight extinction line along part of the major coccolith axis. This group ranges from the Miocene up to Recent. For investigating the variation in shape within this group, the author measured length and width of 50 specimens in 13 samples from several localities, covering the entire stratigraphic range of the group. The mean values of the samples proved to be on an almost straight line ($r=0.997$), which means that there is no significant shape variation in the samples. Upon measuring the length of 100 specimens per sample in an extended sample set, he found that the Pliocene associations consistently have a smaller size than the Miocene ones, although the variation ranges show overlap. The size variation in the Miocene associations is considerable, but the mean coccolith length is always larger than 4 μ . In the Pliocene samples, the variation is less and the mean length is smaller than 4 μ , with the exception of a sample from the lowermost Pliocene of DSDP site 132 in the Tyrrhenian Sea (mean length about 4.5 μ). The difference in mean length was used to discriminate between a Miocene species *D. antarcticus* Haq, and the Pliocene - Recent species *D. productus* (Kamptner) Backman n. comb. The former species was considered to be the evolutionary ancestor of the latter. The change in size, being quite abrupt, was thought to fit in with the punctuated equilibrium model (after Eldridge and Gould, 1972), and could be a useful tool for approximating the position of the Miocene/Pliocene boundary in the northern Atlantic. Later, Backman (INA Newsletter, 1981, vol.3(1), p.40) considered *D. antarcticus* to be a junior synonym of *Dictyococcites perplexa* Burns (1975). The latter species' overall size (18 - 20 μ), however, is considerably larger than that in Backman's *D. antarcticus* concept.

Reticulofenestra

Backman (1980) ascribed the open-centred Noëlaerhabdaceae from his material to *Reticulofenestra*. He argued that several of his specimens could be assigned to particular species, but in the associations there were many morphotypes, intermediate between such species. A biometrical study was performed to investigate whether, and on the basis of which variables, 'natural mor-

phospecies' could be distinguished. Using phase contrast microscopy, the author measured the following variables : coccolith length and width, central opening length and width, and collar width. In total, 900 specimens were measured from 5 Miocene and Pliocene samples from site 116 and from the Rio Grande Rise (SW Atlantic Ocean).

In a principle component analysis of the resulting data, the five variables attributed with fairly similar loadings to the first principle component which described 82.5 % of the total variation. This was explained in terms of an isometric relation between the variables (generally, large size coccoliths have a large central area and a wide collar). However, it was found that in almost all small-sized specimens (about 500 ; $< 5 \mu$), measuring the collar width was below the resolution of the microscope (0.5μ). A plot of the scores for the first two principle components (together 95.4 % of the total variation) showed two clusters of specimens, one characterized by sizes smaller than 5μ , and the other by sizes larger than 5μ . Separate analysis of the large sized coccoliths revealed that the parameter collar width attributed insignificantly to the first component. From the opposite values of the loadings in the second component, Backman inferred a negative correlation between the collar width and the central opening size, which in our opinion is not necessarily a correct conclusion. It was concluded that the variation could be described on the basis of overall size and central opening size. A plot of the scores for the two components showed a homogeneous distribution, however, which means that on the basis of principle component analysis there is no clear morphometric subdivision to be made in the associations studied. It was suggested that this homogeneity was due to the mixing of associations differing in age and geographic location.

The author subsequently measured overall size and central opening size in Reticulofenestrads from 15 samples from the Miocene and Pliocene of Atlantic and Mediterranean deep-sea cores. The results indicate that, in terms of the parameters overall size and central opening size, the composition of the associations varied markedly in space and time. In some samples, clusters of smaller and larger specimens are clear, but in others there is no bimodal distribution. For biostratigraphic reasons, the author proposed that it would be useful to distinguish a small-sized species *Reticulofenestra minuta* (all Reticulofenestrads smaller than 3μ). In the size range between 3 and 5 microns, he distinguished another two species : *R. minutula* (relatively large central opening) and *R. haqii* (small central opening). It appeared to be impossible to consistently distinguish in the larger fraction ($> 5 \mu$) between the species *R. pseudoumbilicus* (relatively small overall size, relatively large central opening) and *R. gelidus* (large overall size, small central opening). It was proposed that the latter species is a synonym of *R. pseudoumbilicus*. According to this *R. pseudoumbilicus* concept, the overall

size and the central opening size of the species have a very wide range. By restricting the species to specimens larger than about 5 microns, the author thought to give a useful morphometric and taxonomic circumscription of that part of the size range of the Reticulofenestrids that disappeared in the middle of the Pliocene.

We conclude that overall size, collar width and central opening size are the most important variables in the Noëlaerhabdaceae. It is clear from Backman's data that the distribution pattern of overall size and central opening size is not constant in a succession of Noëlaerhabdacean associations. We met with this problem when trying to quantify the calcareous nannofossil taphocoenoses from the lowermost Mediterranean Pliocene. Using a fixed lower size limit of *R. pseudoumbilicus* (5.5μ ; after Schmidt et al., 1979) appeared not to be practical in a lot of samples (see also Schmidt, 1979). It is hard to classify the coccoliths of the Noëlaerhabdaceae into clear-cut taxonomic units. The variation pattern hampers quantification of fossil associations.

We thought to gain information concerning taxonomy and biostratigraphy of the coccoliths of the Noëlaerhabdaceae by treating them as a coherent group of coccolith morphotypes. Stepping aside from a priori genus and species assignments, we tried to make a quantitative description of the variation in the composition of the entire association in a series of samples. In such an exercise all specimens encountered should be classified in terms of the above three variables. Since our attention focused on Pliocene biostratigraphy, we selected a number of samples from sections covering the lower and middle parts of the Pliocene. In this sample sequence we expected to record in addition qualitative changes in the associations like the appearance of coccoliths with a cross-bar (*Gephyrocapsa*) and coccoliths with slits between the segments (*Pseudoemiliana*). The section should contain also the disappearance of the larger sized Reticulofenestrids (*R. pseudoumbilicus*). Thus we aimed not only at describing the distribution of morphotypes with time, but also at getting an insight into the distribution of the variables in the entire association. Our selection of samples covers only a small part of the family's record, but investigating the complex relations within the whole scala of Noëlaerhabdacean morphotypes is beyond the scope of this study.

Chapter 7

THE QUANTITATIVE COMPOSITION OF ASSOCIATIONS OF THE NOËLAERHABDACEAE IN THE PLIOCENE OF CRETE

MATERIAL

For a detailed study of the composition of Noëlaerhabdacean floras, a good coccolith preservation and a negligible amount of reworked nannofossils are prerequisites. The calcareous nannofloras from the Pliocene of Crete meet our requirements. Even in the Trubi-like marls of the lowermost Pliocene (Kourtes facies) the coccoliths are well-preserved. We selected a set of 40 samples from the sections Kalithea I, Aghios Vlassios and Finikia (see chapter 3). These sections correspond with the lower and middle part of the Pliocene, and they range from the calcareous nannofossil Zone NN 12 up to the middle of Zone NN 16. The exit of large specimens of *Reticulofenestra pseudoumbilicus* (top NN 15) is at about sample CP2245 in the Aghios Vlassios section (Driever, 1981). We studied some widely spaced samples from section Finikia in order to get an impression of the composition of stratigraphically higher associations as well. In terms of planktonic foraminiferal biostratigraphy, the sections on Crete cover the interval from the *Sphaeroidinellopsis* Acme-zone up to the middle of the *Globorotalia crassaformis* Zone (Spaak, 1983). Following Jonkers' (1984) correlation table (op. cit., fig.20), there is some stratigraphic overlap between our sections.

Samples from sapropelic layers were not studied, since the preservational state of the nannofossils from this lithofacies often suggests that post-depositional processes (especially dissolution) have altered the original composition of the taphocoenoses.

METHOD

Equipment and counting procedure

For quantifying the composition of the associations, we used the light-microscope, working with crossed nicols at a magnification of 1562.5 X, and with a high light intensity. We prepared slides with a relatively low particle density for accurate observation of each separate specimen.

Counts of 200 Noëlaerhabdacean coccoliths per sample are supposed to document the quantitative composition of the associations sufficiently well. Schmidt (1978) showed that the variation in frequencies, resulting from repeated 200-counts in the same slide, is well within what is to be expected for random samples from a single population. We made observations on the first 200 coccoliths belonging to the Noëlaerhabdaceae, encountered along a traverse in a series of successive fields. These fields are defined by an ocular template which is used for delineating a photographic field. When there are many specimens in a field, one risks to lose track of specimens already recorded and specimens still to be recorded, the more so because the object table is often rotated (for measurements, for establishing the presence/absence of a cross-bar). In order to concentrate on the field, we did not write down individual observations, but we spoke them into a microphone/cassette recorder combination, meanwhile scoring the number of recorded specimens with a foot counter.

Morphotypes distinguished

As was observed in an earlier chapter, the structural characteristics of the coccoliths of the Noëlaerhabdaceae can be described in terms of the proportions of the variables central opening diameter, collar width and shield width. Using these parameters, Schmidt (1979) presented a key for LM workers to subdivide the larger fraction ($> 5.5 \mu$) of Late Miocene Noëlaerhabdaceae. In this scheme, five morphotypes were distinguished which were all assigned to the variation of *Reticulofenestra pseudoumbilicus* (op. cit., fig.6). The holotype of *R. pseudoumbilicus* conform his type E. The morphotype with the closed centre (his type A) shows the characteristics of *Dictyococcites* sensu Backman (1980).

We amplified this key in order to cover the entire variation in associations of Pliocene Noëlaerhabdaceae. Coccoliths with a bridge ('*Gephyrocapsa*') and those with slits between the shield elements ('*Emiliana*') were included as well. We paid no attention to the position of the cross-bar relative to the longer axis of the coccoliths, nor to the parameter 'roundness'. Because it proved to be unsatisfactory to classify only in terms of 'larger than' and 'smaller than', we added an intermediate category ('more or less equal'). The system in our key is such that the criteria are increasingly difficult to establish with the light-microscope (see figure 13).

Determination steps I and II in the key classify according to the configuration of the central area. Step I distinguishes between a small, an intermediate and a large central opening size relative to the total coccolith width. In step IIa, these three 'types' are subdivided on the basis of the presence or absence of a cross-bar, yielding our six 'groups' a through f. In specimens with a relatively

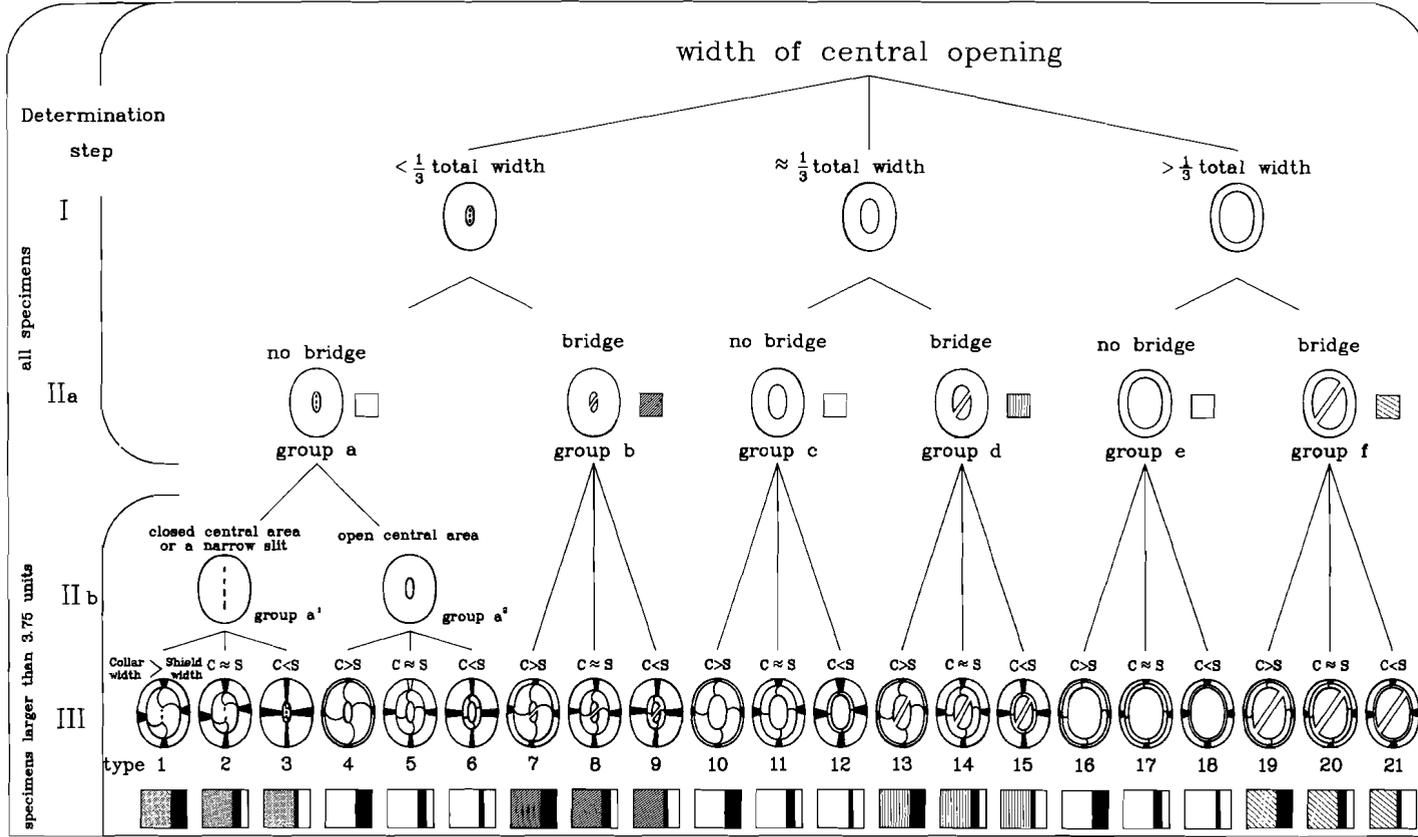


Fig.13 Key for distinguishing morphotypes in Pliocene coccoliths of the Noëlaerhabdaceae. Variables are the relative width of the central opening, of the collar (c) and of the shields (s). All are distal views ; overall diameter and outline of the coccoliths is kept constant. The presence of slits in the peripheral area of the coccoliths is indicated by the suffix 'l'.

small central area, one can distinguish between those with a closed central area or a narrow slit, and those with a clear opening (step IIb, yielding groups a¹ and a²). Step III subdivides each group according to the width of the collar cycle relative to the width of the shields (=segment cycle); it yields 21 hypothetical parameter combinations or morphotypes. Finally, it is determined whether the coccoliths have crenulate outer peripheries, suggesting that there are slits between the shield elements (step IV). If so, the suffix 'l' (after the species *lacunosus* Kamptner) is added to the morphotype serial number.

There are 42 hypothetical parameter combinations (21 morphotypes plus 21 'l'-morphotypes) in our key. In the Pliocene of Crete, not all of these coccolith configurations are present.

During trial counts it became apparent that the low resolution power of the light-microscope interferes with classifying small specimens (smaller than about 3.5 μ) at the higher splitting levels. Usually, small specimens are weakly birefringent, so the collar and the shields are hard to differentiate (step III); recognizing slits in the shield peripheries is equally difficult (step IV). Furthermore, it is very difficult to distinguish consistently between small specimens with a small central opening and those which have a (nearly) closed central area (step IIb). As a consequence, we classified the small coccoliths up to determination level IIa, which means that we distinguished only 6 coccolith morphologies (groups a-f) in the smallest size fraction (fig.13).

Observations on coccolith dimensions

For measuring the length of the coccoliths, we used an ocular scale with units of .9 μ and a reading accuracy of a half unit. So the measuring error is plus and minus a quarter unit. Evidently there is a relatively large error involved in the measurements of specimens of only few units in size. Considering, moreover, that small specimens are hard to classify accurately, we decided to limit the effort spent on the small specimens, by estimating their diameter. During the 200-counts, only the specimens of an estimated 4 units ($\pm 3.5 \mu$) or more were measured.

In some slides we made a repeated 200-count along a different traverse. The results of these repeated counts tell about the consistency of our size estimates. The data on size, found in the sets of counts, match surprisingly well (fig.14). We used the median test corrected for ties (see M.M. Drooger et al., 1979) for numerically testing the degree of similarity between the data sets. The median test is distribution-free or non-parametric. In our case it was used to test the hypothesis that the distributions of coccolith diameters in repeated 200-counts in the same slide have the same probability distribution. The statistic of the test

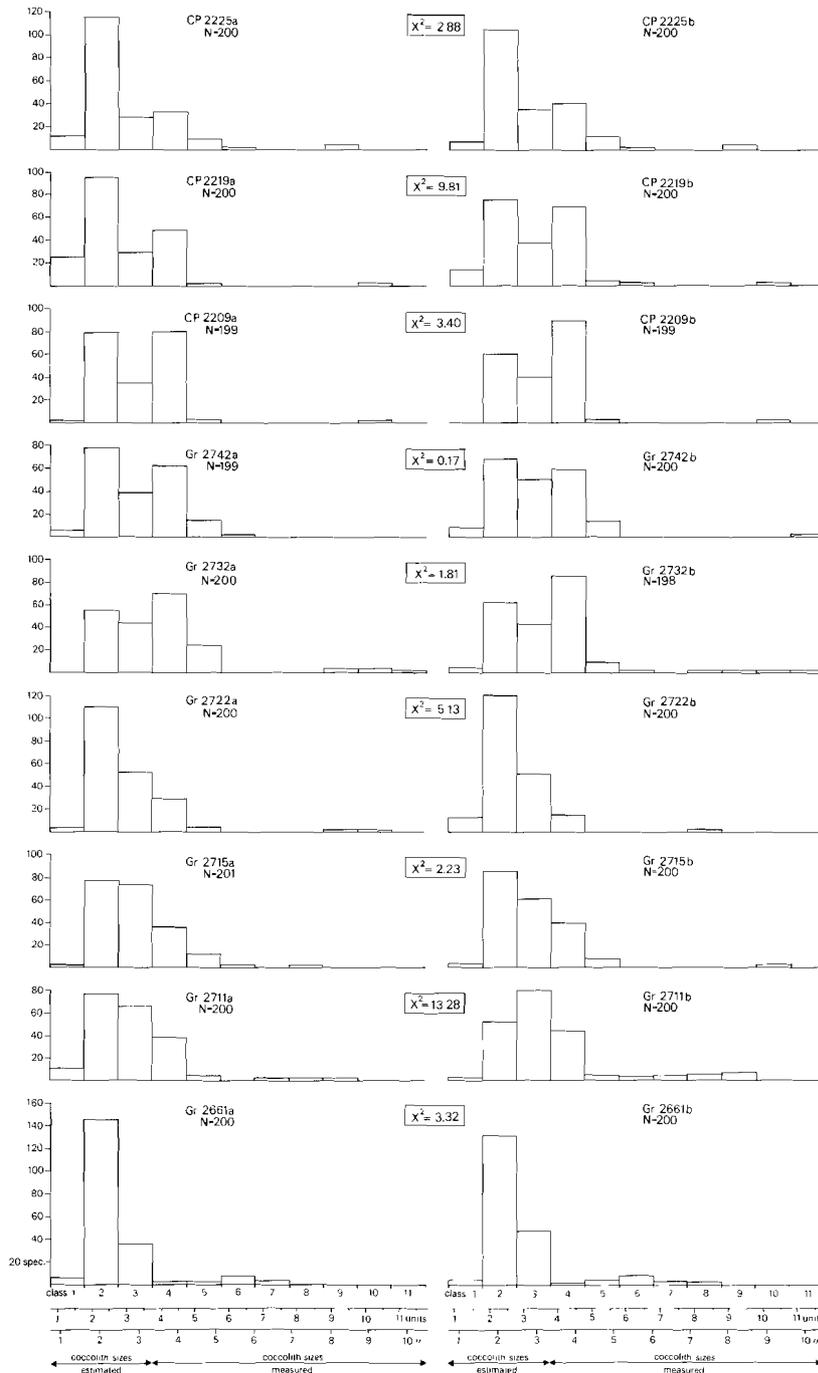


Fig.14 Histograms of the size (diameter) distribution of coccoliths of the Noëlaerhabdaceae in two 200-counts (a and b) in 9 samples along different traverses. Coccoliths larger than 4 units (about 3.6μ) were measured. χ^2 values refer to the results of the median test, corrected for ties ($P_{0.01} = 6.33$, one degree of freedom).

has a chi square distribution with one degree of freedom. When using the 99 percentile ($\chi^2 = 6.63$) as the criterion, the hypothesis is rejected in only two of our nine pairs. We conclude that we can quite consistently reproduce our data on coccolith size.

Size distribution in the large fraction ('*R. pseudumbilicus*')

As we mentioned in chapter 4, one's size concept of *Reticulofenestra pseudumbilicus* plays a part in situating the top of Zone NN15. Usually the species is considered to consist of the relatively large specimens in the associations of the Noëlaerhabdaceae. In our view, observations and measurements on 30 large specimens per sample give a reliable impression of configuration and size in this size fraction. It became apparent that applying a fixed lower size limit for the category of 'large specimens', as was suggested by Schmidt et al. (1979), was not realistic because of shifts in the distribution pattern of coccolith size throughout the sequence. We determined the size limit between smaller and larger specimens in each sample on the basis of the (supposed) dent in the frequency polygon of the 200-count. Thereupon, the number of already registered specimens in the 200-count from the thus established large-size fraction was supplemented up to 30.

Coccoliths of the large fraction of the Noëlaerhabdaceae become increasingly scarce near the middle of the Pliocene ('exit of *R. pseudumbilicus*'). We stopped the 30-counts at the stratigraphic level where searching large specimens became too time consuming.

Presentation of data

The scores in the counts relate to both the configuration and the size of the coccoliths. In order to evaluate the results more easily, we subdivided the total variation spectrum into morphotype/size units, using size classes of one measuring unit each. Coccolith size appeared to vary between 1 and 13 measuring units. In case all 21 morphotypes would have been present in the 13 size classes, we would have to consider 273 morphotype/size units. If all these combinations would have slit-bearing equivalents, the number would be even double. Fortunately this number is largely reduced in practice. We distinguished only 6 coccolith morphologies (groups a-f) in the three smallest size classes, and furthermore, only part of the remaining possible combinations was met with during the counting sessions. We labelled the scoring combinations with two characters for shape and size, successively. An 'l' was added for coccoliths showing slits in the shield periphery. For example, a/3 is a coccolith of group 'a' (see fig.13) with a length of 3 or 3.5 measuring units ; 12l/6 refers to a 'type

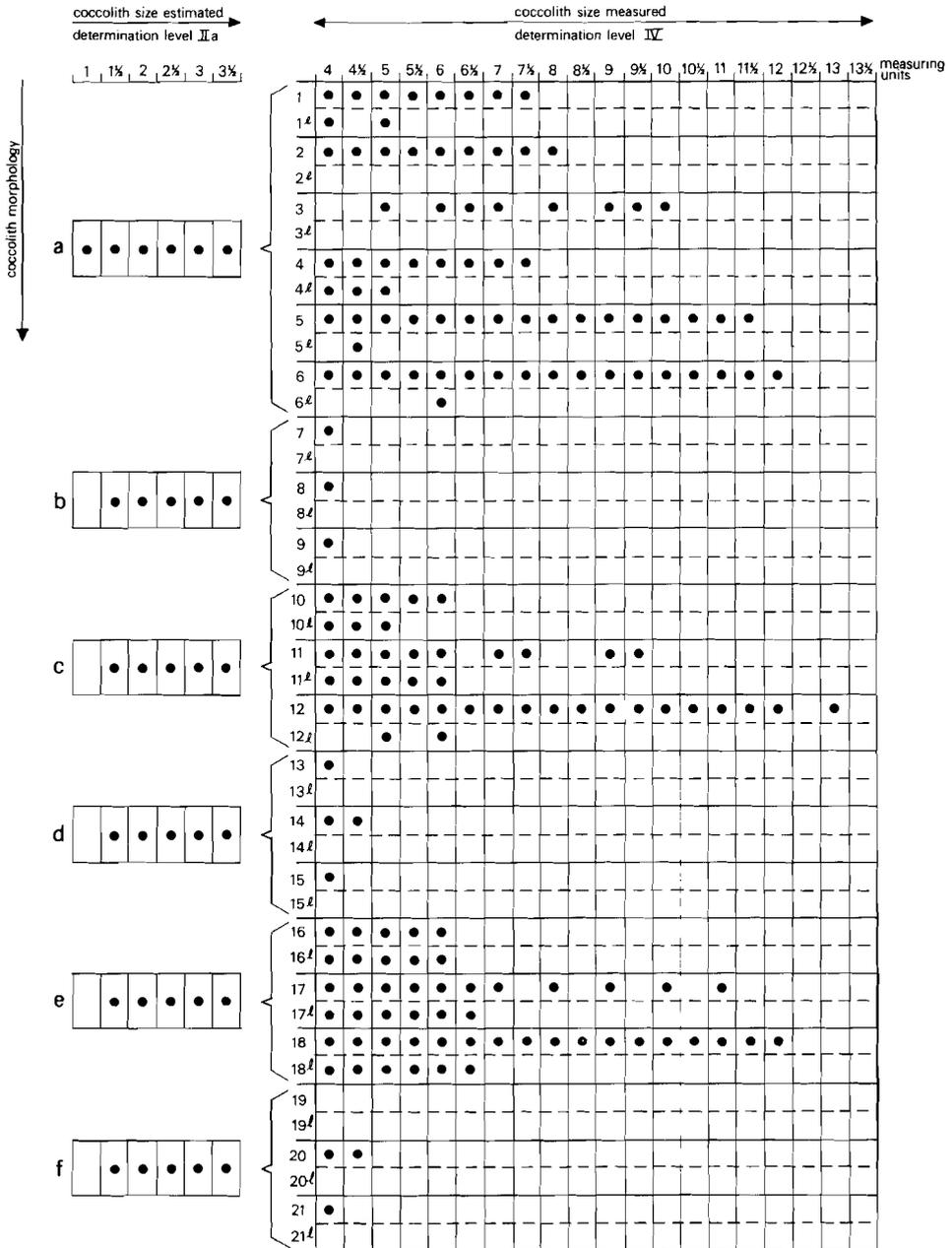


Fig.15 The size (diameter) range of coccolith morphotypes of the Noëlaerhabdaceae in the Pliocene of Crete. Morphotype indices refer to the subdivision of figure 13 ; one measuring unit equals 0.9μ .

12' coccolith with slits, having a length of 6 or 6.5 units. The combinations of morphology and size, found in the 200- and in the 30-counts, are shown in the diagram of figure 15. The labelling of these combinations is shown in figure 16.

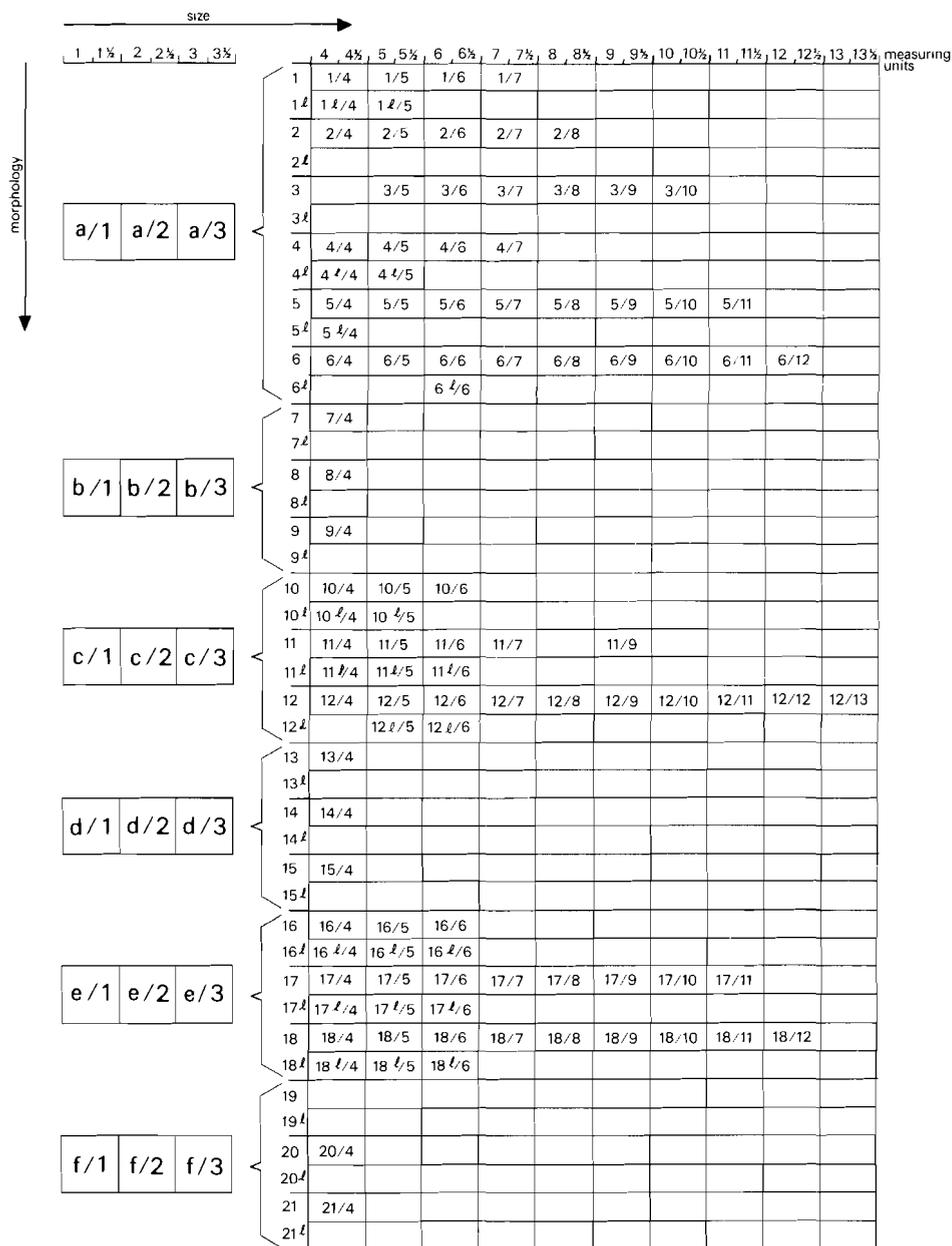


Fig.16 Labelling of the morphotype/size combinations observed.

Morphotypes and their size range

The matrix of figure 15 gives a good impression of the variation in the configuration and the size of the Noëlaerhabdaceae in the Pliocene of Crete.

In the size fraction smaller than 4 units, representatives of all six groups (a-f) were observed. The coccoliths have a size range of 1.5 to 3.5 units; only specimens of group a are occasionally smaller than 1.5 units. Considering that there are minimal measures for the width of shields and collar, this is hardly surprising.

In the size fraction larger than 3.5 units, all morphotypes from our hypothetical series were observed except type 19.

There are some interesting aspects in the size ranges of the individual morphotypes, and in the distribution of slits ('l-forms') in the total spectrum.

In our samples, the size of coccoliths with a bridge does not exceed 4.5 units. In comparison with the sizes other types occasionally reach, such coccoliths are relatively small. We did not observe the combination of a cross-bar and peripheral slits in one coccolith. This is in accordance with the literature, in which the first appearance of such coccolith morphotypes (cf *Gephyrocapsa protobuxleyi* McIntyre) is reported from the Pleistocene (McIntyre, 1970). In the practice of the counts, the cross-bars were readily discernible. Only in very small coccoliths with a small central opening bridges were sometimes hard to recognize as such. In the three groups with bridges (b, d, f), the size range of the coccoliths is comparable. This particular size range emphasizes the separate status of the group of Noëlaerhabdaceae with a cross-bar.

Slits in the shields were found to be present in all three groups of coccoliths without a cross-bar (groups a, c, e). It seems, though, that the slits are preferably developed in coccoliths with a central opening of some size (groups c and e). The widest size range of the slit-bearing coccoliths was found in specimens with a large central opening (group e). In our material, coccoliths with slits are of small to medium size, the maximum size observed being 6.5 units ($\pm 5.8 \mu$).

The pattern in the size distribution of the morphotypes without slits or bridges is remarkably regular. In the categories we distinguished on the basis of the relative central opening size (a, c, e), the range of the coccolith length increases with decreasing relative collar width. In other words, the maximum coccolith size and the widest size range are found in specimens with narrow collars. There is some consistency in the size range, displayed by morphotypes of the same 'collar/shield ratio' (compare 1,4,10,16 vs 2,5,11,17 vs 3,6,12,18).

It can be concluded from the patterns in the morphotype/size combinations that, if the size range of the coccoliths is used for discriminating taxa, the group of coccoliths with a bridge is quite distinct. In the group of coccoliths without a bridge or slits, there seems to be a relation between the size range and the collar/shield ratio. One could speculate on the basis of these phenomena that the relative size of the central opening is a parameter of subordinate taxonomic weight. On the other hand, slits in the shields seem to have developed preferably in coccoliths with an intermediate or a large central opening.

The 200-counts

Printing the data-matrices of the 200-counts and the 30-counts would be too space-consuming. All data are stored at the Institute of Earth Sciences, Utrecht. For frequency diagrams and histograms the reader is referred to figures 17-26

In terms of our 'taxa' there are considerable changes in the composition of the associations in a vertical sense. 'Exits' and 'entries' are manifold. In order to describe the developments in the associations as systematically as possible, we will adhere to the order in which the parameters are used in the determination key (fig.13).

The central opening

As we could determine all coccoliths, regardless of their size, up to the second determination step (IIa), we have a good record of the distribution of the relative central opening sizes in the associations (cumulative curves of figure 17).

It appears that we set a narrow range to the intermediate size category. These coccoliths score relatively low and fairly constant numbers of some 15-20 % throughout the composite set. Hence, the frequencies of the other two categories are mutually complementary. In the lowermost samples, specimens with a small central opening dominate the associations. Upwards, their proportion decreases and we observed a minimum value in sample GR2727; this sample shows a maximum number of specimens with a large central opening. Between samples GR2732 and CP2107, frequencies are relatively stable, being higher in the coccoliths with a small central opening. In the topmost two samples, specimens with a large central opening are again relatively frequent.

Central opening and bridge

When distinguishing between specimens with and without a cross-bar, the pattern becomes more intricate (see figure 17, frequency patterns of groups a-f). In our counts specimens with a bridge first appear in sample GR2727 of section Kalithea I. They show a small central opening size (group b). In the three

categories distinguished on the basis of the central opening size, numbers of specimens with a cross-bar are usually lower than bridge-less coccoliths. Throughout the sample sequence, specimens with a bridge show no apparent preference for a particular central opening size. Coccoliths with a cross-bar, and especially those with a small central opening, are relatively frequent in most of the Aghios Vlassios samples. The acme of this group enables a subdivision of this section and especially its part characterized by high frequencies of coccoliths with a small central opening.

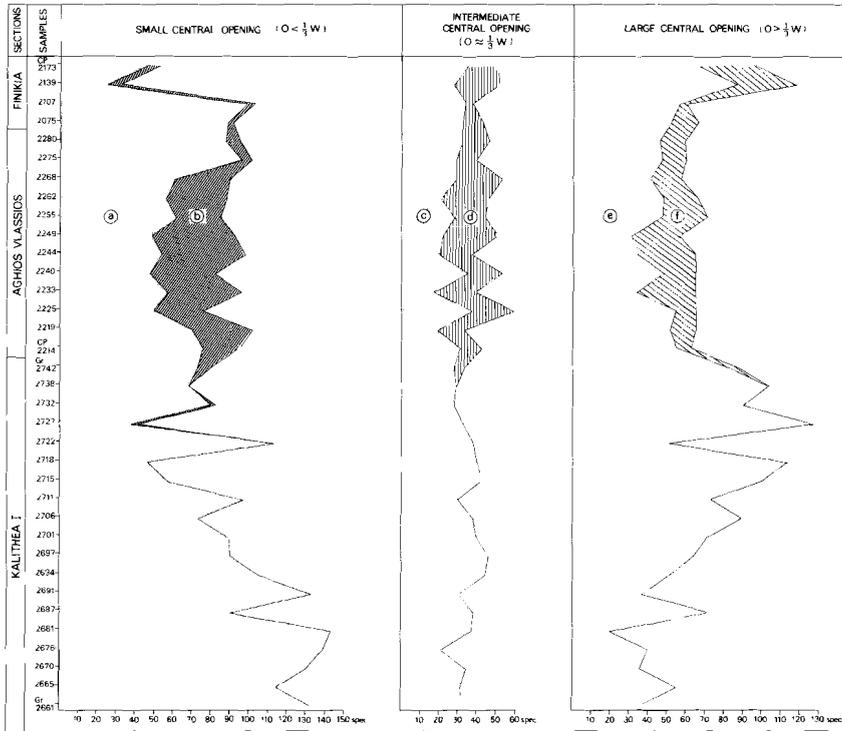


Fig. 17 Frequencies of coccolith morphotypes, distinguished on the basis of the relative size of the central opening (determination step I; cumulative curves) and the presence/absence of a cross-bar (step IIa; groups a-f) in the Cretan composite section (N=200). Overall coccolith size is not considered here.

Central opening, bridge and collar

We set a minimum length of 4 units as the criterion for observations on the relative width of the collar (determination level III). One should realize that our quantitative record of the morphotypes and their 'l'-equivalents (for fre-

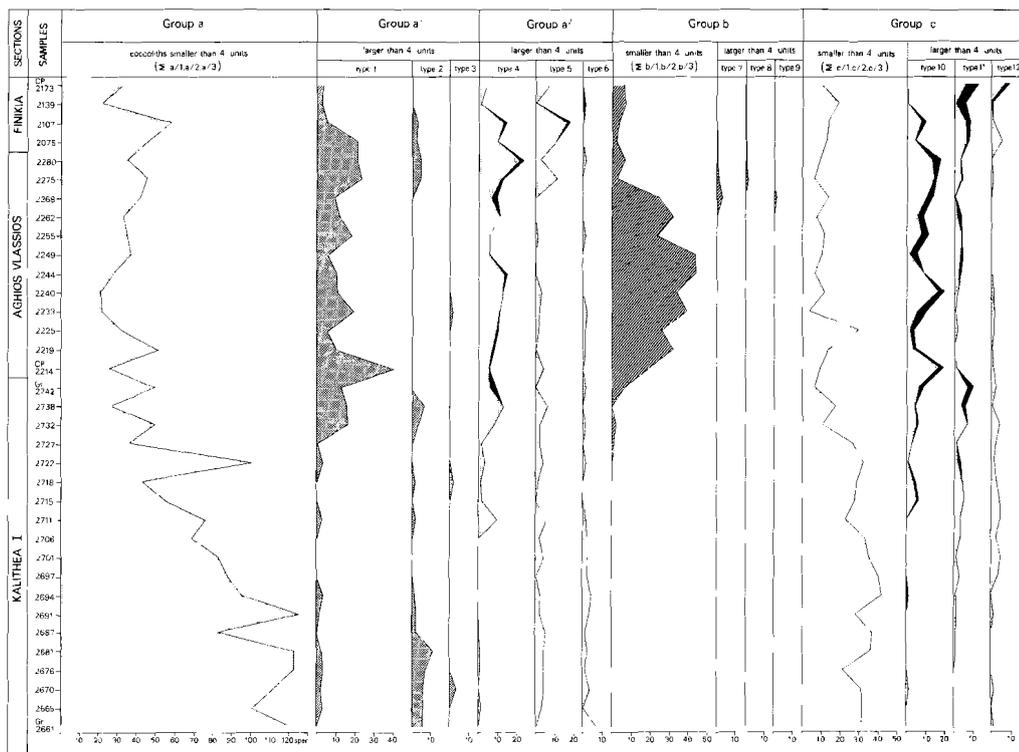


Fig.18a Frequency of coccolith morphotypes in the Cretan composite section (N=200). The specimens are determined on the highest possible determination level (groups a-f for specimens smaller than 4 units ; types 1-21 for larger specimens). Black areas refer to specimens with peripheral slits ('l-types').

quency diagrams see figure 18) give a size-restricted impression of the overall frequency distribution of the types in question. We will discuss the distribution of the morphotypes in more detail in the context of the size distribution, and in the context of the '30-counts'. Some general remarks can be made here.

On the basis of the frequency pattern, the size range and the vertical distribution, the coccoliths with a bridge (groups b, d, f) can be treated separately. They appear halfway our column and are predominantly represented by small specimens. Only few specimens, found in the upper part of the Aghios Vlassios sequence, were large enough to be classified according to their collar/shield ratio. In these few specimens no particular type is predominant. There is an acme of small specimens with a small central opening (group b) in section Aghios Vlassios.

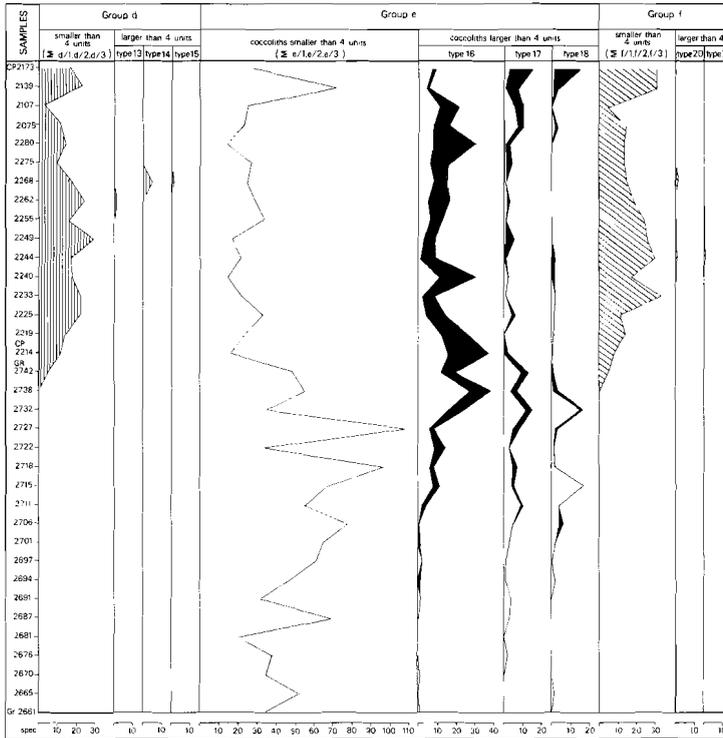


Fig.18b (continued)

In the distribution pattern of coccoliths without a bridge (groups a, c, e) some aspects deserve mentioning. In the lower part of the composite section up to about sample GR2727, small sized specimens are predominant. In this interval there is a gradual change from predominantly small central opening sizes to a greater proportion of individuals with a large central opening. Upwards, the coccoliths in the fraction larger than 4 units are dominated by types with a relatively wide collar (types 1, 4, 10, 16), except in the uppermost two samples. The frequency curves of these types are comparable. There is less similarity between the curves of the types with an intermediate collar (types 2, 5, 11, 17), just as between the curves representing the narrow collar types (3, 6, 12, 18), but these types have relatively low scores.

Slits

With the light-microscope, the presence of slits in the shield periphery can be well observed in relatively large specimens with many slits, distributed equally along the outer coccolith periphery. We recorded the presence of slits only in specimens of dimensions of 4 units, or more, as in the case of the collar/shield ratio. It is likely that the scores of the 'l'-forms in the 200-counts underrate the actual frequencies. Still, there is some consistency in the distribution pattern found (figure 18).

Specimens with slits appear in the counts in sample GR2694 of section Kalithea I. These specimens have an intermediate or a large central opening and a relatively wide collar (types 10l and 16l). From the topmost sample of section Kalithea upwards, slits are also present in specimens with a small central opening. In the counts there was only one slit-bearing specimen with a closed central area. It seems that slits are preferably developed in coccoliths with a large or intermediate central opening. The record of type 16 shows 'l'-forms most frequently. In many samples in the sections Aghios Vlassios and Finikia, there are more specimens of types 16, 17 and 18 with slits than without slits. We noticed the first (sub)circular specimens with slits in sample CP2244. These specimens usually have a relatively large central opening (group e).

It may be concluded that most of our morphotypes have variants with slits in the shield periphery. By stressing the presence of the slits, however, it may be stated that coccoliths with slits are very variable in terms of the relative size of the central opening, collar and shields. Some phenomena justify treating the coccoliths with slits as a distinct unit. The presence of slits is the common character in otherwise variable coccoliths with a (sub)circular outline. Furthermore, coccoliths with slits have a limited size range. We will treat these coccoliths again in our discussion of coccolith size.

Concluding, we can distinguish three major morphological units on the basis of our counting data. First, there is the category of specimens with a bridge (groups b,d,f), which is set apart by the limited size range of the coccoliths and by its stratigraphic distribution. The second category is characterized by the presence of slits. This category is distinguished because specimens with slits have a limited size range. Further, the presence of slits is a consistent feature in (sub)circular coccoliths. In our material, the characters 'bridge' and 'slits' are mutually exclusive. The third category is the 'rest-category', consisting of coccoliths without a cross-bar and without slits (types 1-6, 10-12, 16-18).

Thus, the characters 'bridge' and 'slits' are of primary systematic importance, while the relative sizes of central opening and collar are of lower systematic weight; in terms of the latter characteristics, the three first-order categories are extremely variable. We use the distribution of coccolith size as a tool to verify such a ranking.

KALITHEA I

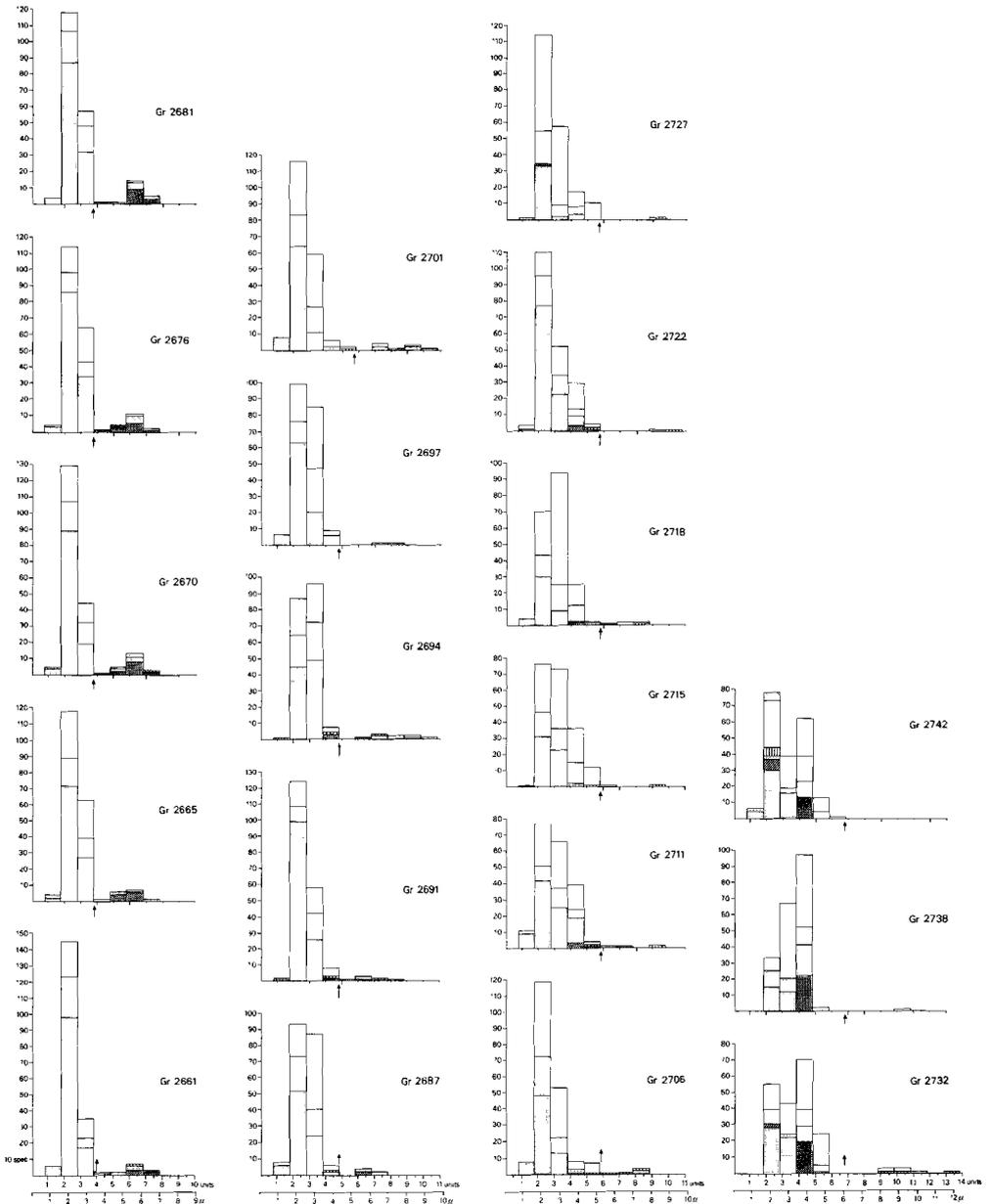


Fig.20a Histograms showing diameter and morphology (key step II, see fig.13) in coccolith associations of the Noëlaerhabdaceae (N=200) from the sections Kalithea I, Aghios Vlassios and Finikia on Crete. Each size (diameter) class has a width of 0.9 μ . The arrows mark the truncation limit, used in additional counts (N=30) of large-size specimens.

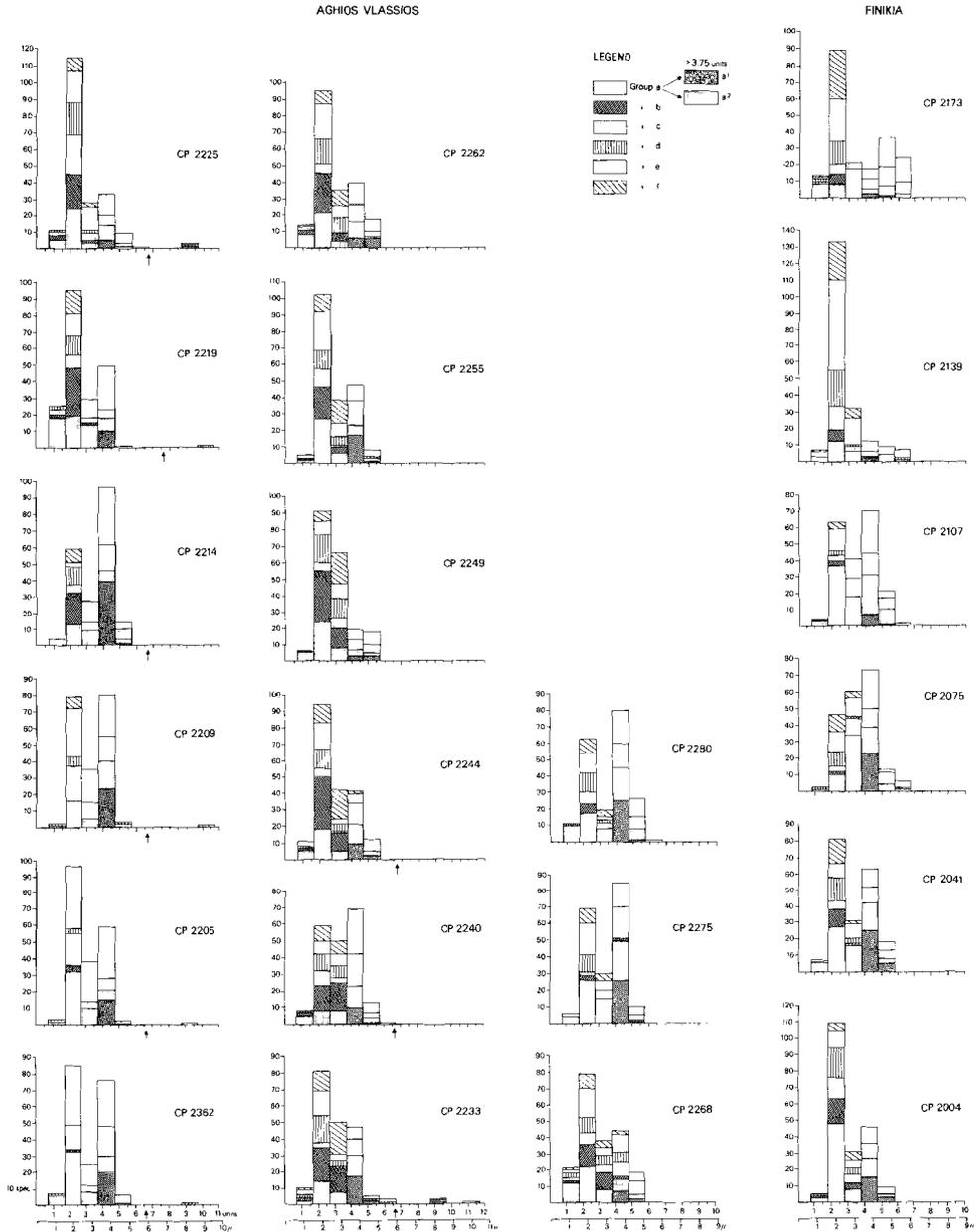


Fig.20b

Distribution of coccolith size in the 200-counts

The distribution of the diameter of the coccoliths on the basis of the 200-counts is presented in the frequency diagram of figure 19, and in the histograms of figures 20a and 20b. A class width of one measuring unit was chosen.

The histograms often show bimodal or even more complex distribution patterns. In many of the histograms, the 'sub-populations' seem to be normally distributed. We calculated means only for the large fraction (30-counts).

Five successive patterns (A-E) can be recognized in the size-frequency distribution (fig.21). Pattern E is based on only two samples.

- PATTERN A : Bimodal distribution with modes in class 2 and in class 6; smaller fraction is predominant; low numbers in intermediate classes 4 and 5; maximum size observed is 8 units (GR2661 to GR2691).
- PATTERN B : Less distinct bimodal distribution; accent in the smaller fraction is on classes 2 and 3; compared with pattern A, the size range in the smaller fraction is larger (ranging up to up to 6 units); coccoliths in the large fraction are between 6 and 12 units, rather evenly distributed with very low frequencies (GR2694 to GR2727).
- PATTERN C : Trimodal (?) distribution; two clusters in the coccoliths up to 6 units, with modes in class 2 and in class 4; large fraction is between 7 and 13 units, represented by very low numbers (GR2732 to CP2244).
- PATTERN D : Bimodal distribution with modes in class 2 and in class 4; maximum coccolith size is 6.5 units ; larger coccoliths are absent (CP2248 to CP2107).
- PATTERN E : Bimodal distribution with modes in class 2 and in class 5; maximum coccolith size is 6.5 units (CP2139, CP2173).

We thus recognized five successive patterns in the distribution of coccolith size in the samples. It is clear that the distribution of the coccolith size in the successive associations of the Noëlaerhabdaceae does not fit in with a regularly changing pattern. Instead, we found that the size distribution is stable throughout short intervals, each time changing rather abruptly and without a distinct trend.

Morphology and size in the three categories

In the following paragraphs, the distribution of the coccolith length within each of the three categories is used as a control on their homogeneity. Further, their composition in terms of central opening size and relative collar width (in terms of the 21 morphotypes) will be discussed.

Coccoliths with cross-bars

Figure 22 shows histograms of size and configuration of the coccoliths with

a bridge. Only few specimens were large enough to be measured and typified precisely. The first specimens with a cross-bar to appear in our record (top of the Kalithea I section) are of small size (class 2). The specimens gradually increase both in relative number and in size in section Aghios Vlassios. In the top part of this section, the largest specimens in our Cretan samples (class 4) were observed. The samples from Finikia show relatively small-sized specimens.

There is no indication for heterogeneity in the distribution of the coccolith

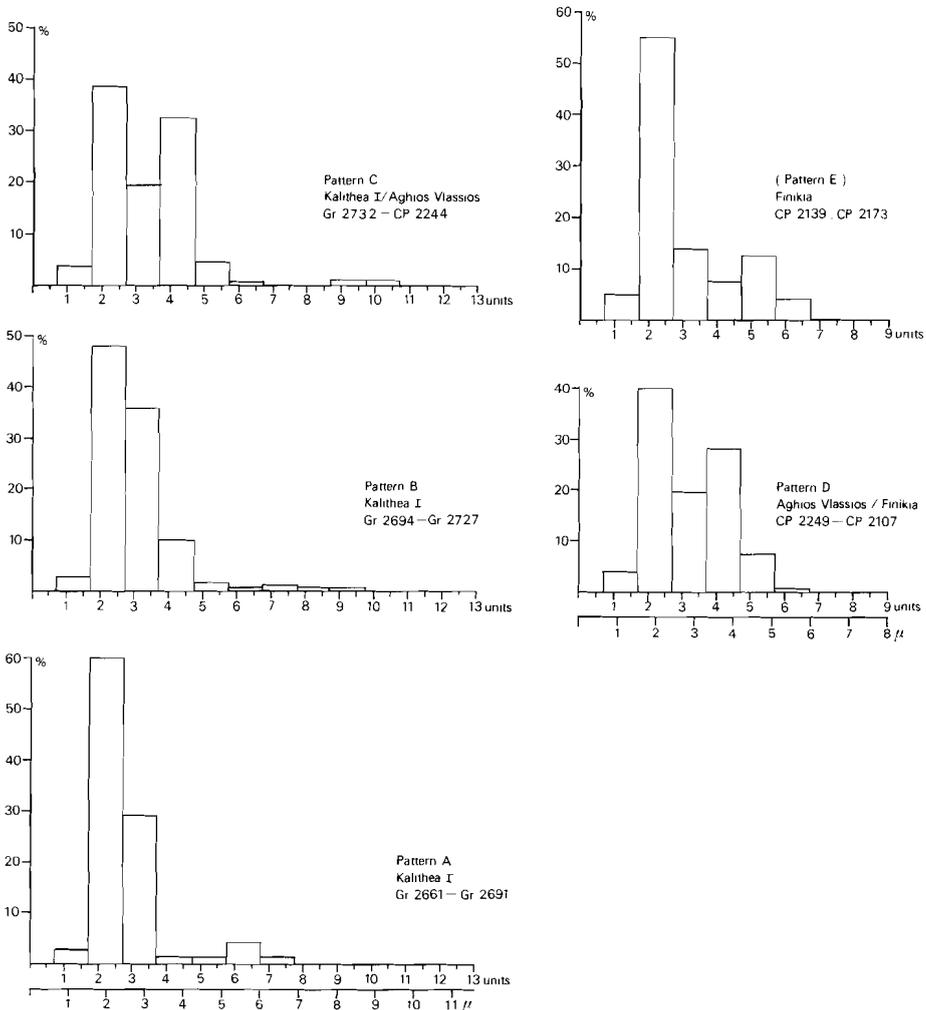


Fig.21 Class averages in five successive distribution patterns of coccolith size of the Noëlaerhabdaceae in the Pliocene of Crete. Averages less than 0.5 % are not shown.

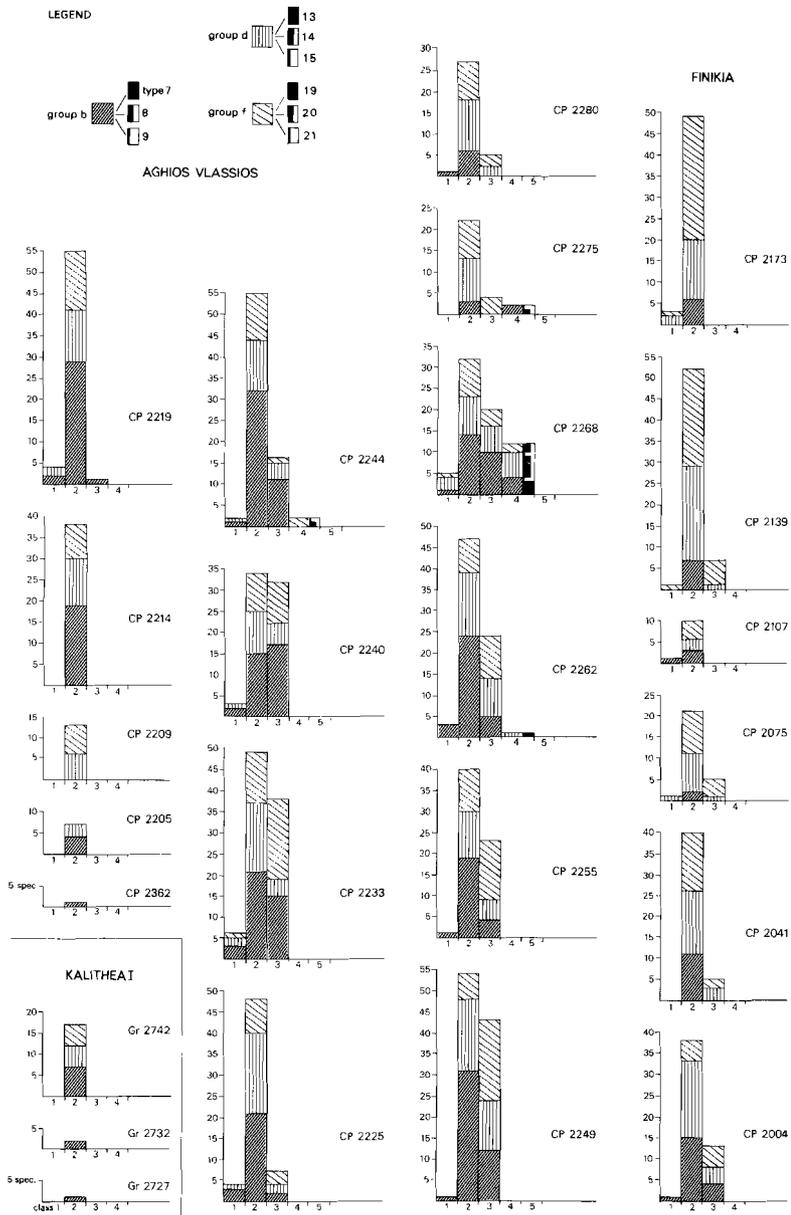


Fig.22 Histograms showing frequency, morphology and length of coccoliths with a cross-bar, observed in the 200-counts. Only specimens larger than 3.5 measuring units were determined on morphotype level. The length of specimens smaller than 4 units (nearly all specimens) was estimated.

size in this category. In most associations, small, intermediate and large central opening sizes are well represented. There is a preference for an intermediate or a large central opening in the topmost samples of Aghios Vlassios, and in the Finikia samples, but there is no regular pattern of change (see GR2209). The central opening size seems to have no relation to the coccolith diameter. Likewise, there is no evident relation between the relative collar width and the central opening size in the few specimens that could be studied in detail.

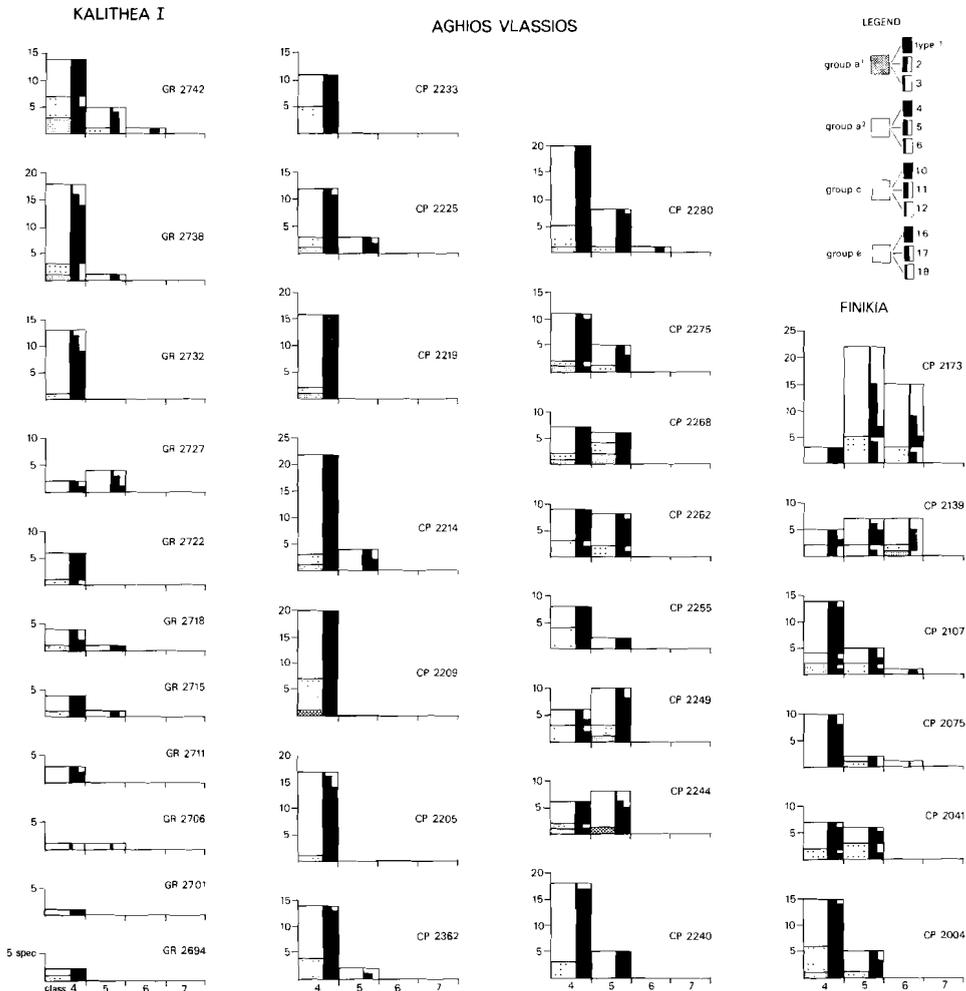


Fig.23 Histograms showing frequency ($N=200$), overall size (diameter) and morphology of the coccolith specimens with peripheral slits ('l-types') in the samples from Crete. Specimens smaller than 4 measuring units (about 3.6μ) were not qualified. One measuring unit equals 0.9μ .

Specimens with slits

A minimum coccolith length of 4 units was used while recording the presence of slits in the periphery of the shields. In figure 23, histograms are presented showing the distribution of morphology and diameter of the slit-bearing specimens in the 200-counts; the samples without such specimens are omitted. The stratigraphically lowest specimens, entering the counts in sample GR2694, are of small size (class 4). Higherup, their number increases up to an average of some 10 percent of the coccoliths, and the size range is widened up to and including class 6. Our electron microscope practice supports the suggestion that in our material the peripheral slits predominantly develop in 'mid-size' coccoliths; in other words, they range from about 3 to 6.5 units ($2.5 \mu - 6 \mu$), and the mode in most samples is around 4 units (3.5μ), in the uppermost two

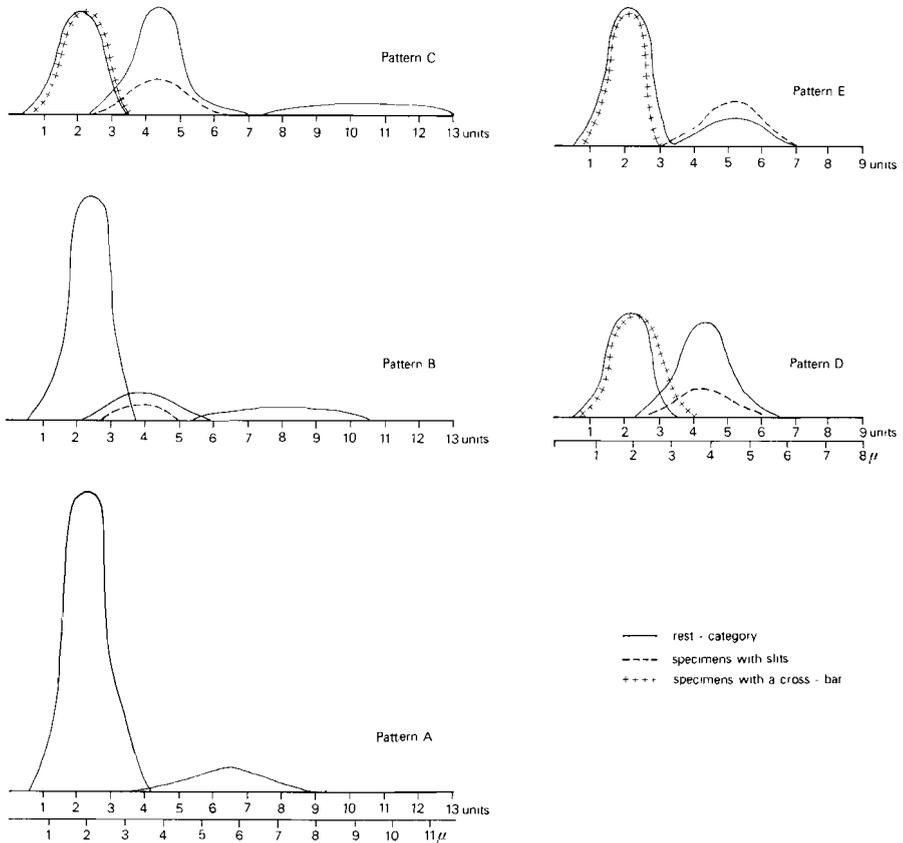


Fig.24 Approximate non-cumulative size/frequency distribution of the three main categories of coccoliths of the Noëlaerhabdaceae in the Pliocene of Crete.

samples from Finikia it is around 5 units (4.5 μ). So, if it is assumed that the coccolith length is normally distributed, our application of a lower size limit resulted in the truncation of only a small portion of the association.

Intermediate and large central opening sizes are predominant. There is no clear relation between the relative size of the central opening and the length of the coccoliths. Wide collars are predominant. It seems that the proportion of coccoliths with a narrow collar increases with coccolith diameter.

Morphology and size of the 'rest-category'

In this section we will pay attention to specimens of the 'rest-category' of small and intermediate size (up to 6 units). The 'rest-category' remains after stripping the coccoliths with cross-bars and the slit-bearing specimens (fig.24). The largest specimens of the Noëlaerhabdaceae in our samples, ranging up to 13 units in diameter, belong to the 'rest' category as well, but their morphology and size will be discussed in the paragraphs on the '30-counts'. The coccolith morphology in the intermediate size classes in terms of the relative size of central opening and collar is shown in the histograms of figure 25.

PATTERN A (GR2661-2691) : In the interval characterized by size distribution pattern A, all coccoliths belong to the 'rest-category'. Coccoliths of intermediate size are few, and their morphology in terms of the relative central opening size and collar size is variable.

PATTERN B (GR2694-GR2727) : Apart from a few coccoliths, belonging to the category of slit-bearing specimens, the associations are made up of coccoliths of the 'rest-category'. The distribution of size in the classes up to 6 units seems to be unimodal. In classes 4 and 5 the central opening size and the relative collar width are variable. In some samples, there are relatively few specimens with a small or a closed central opening in these classes.

PATTERNS C, D (GR2732-CP2107) : In the populations of the smallest coccoliths, a variable portion of the specimens shows a cross-bar. The number of specimens with slits increases slightly in the middle fraction. In most samples, the distribution of the diameter of the coccoliths of the 'rest-category' is bimodal. In the mid-size populations no clear preference for a particular central opening size is shown. Compared with the distribution in pattern B, the closed central area type is relatively common. Most coccoliths have a wide collar. It is to be noted that the proportions of the three collar types are more or less stable throughout the central opening groups. Hence, it seems that relative collar width is not directly related to relative central opening size.

PATTERN E (CP2139, CP2173) : Possibly a bimodal pattern with peak frequencies in the smallest population (around 2 units). The relative dimensions

KALITHEA I

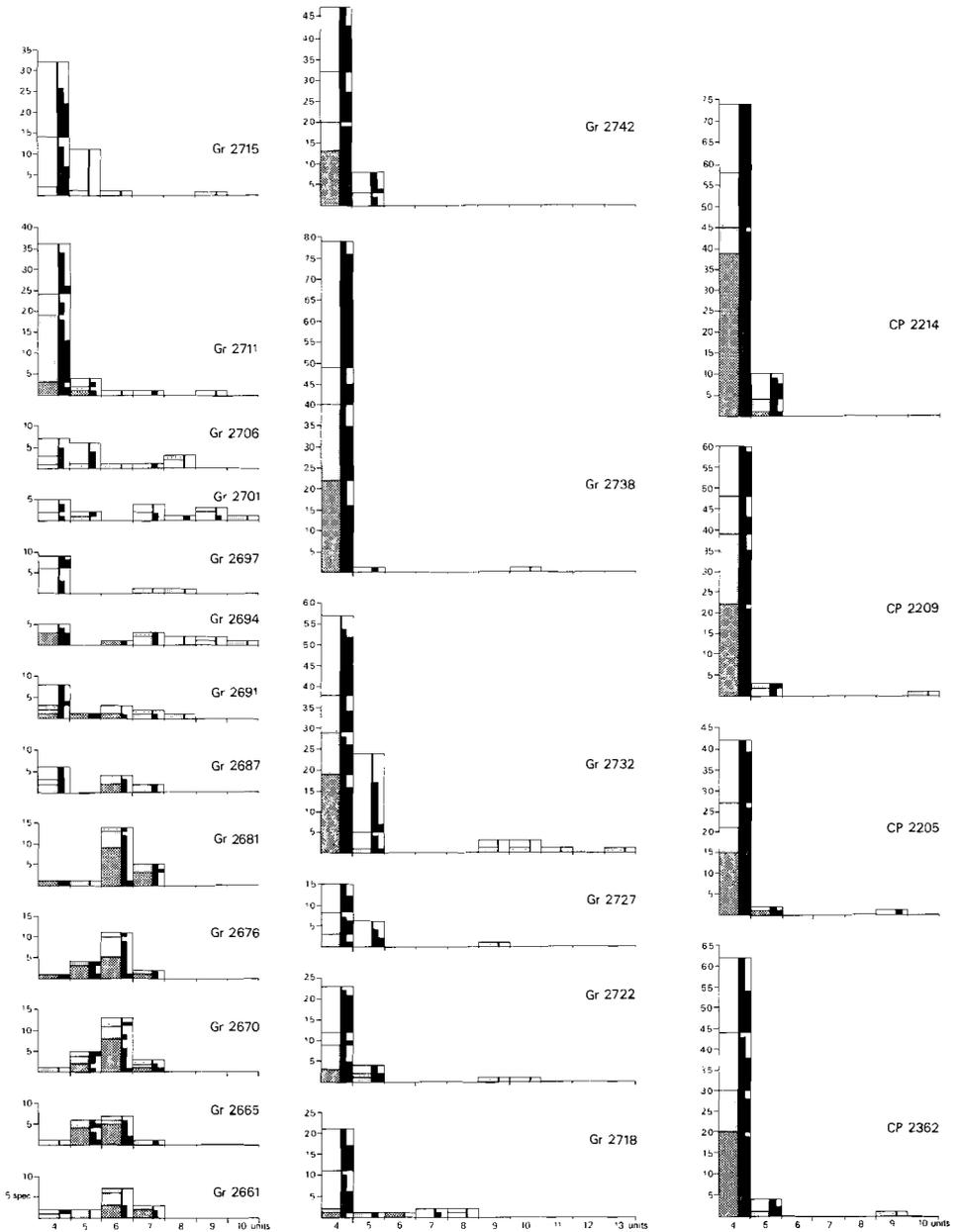


Fig.25a Histograms showing the distribution of overall size (diameter) and morphology of coccoliths without cross-bars and without peripheral slits ('rest-group') in the Cretan samples. Specimens smaller than 4 measuring units were not determined on the morphotype-level. One measuring unit equals 0.9 μ .

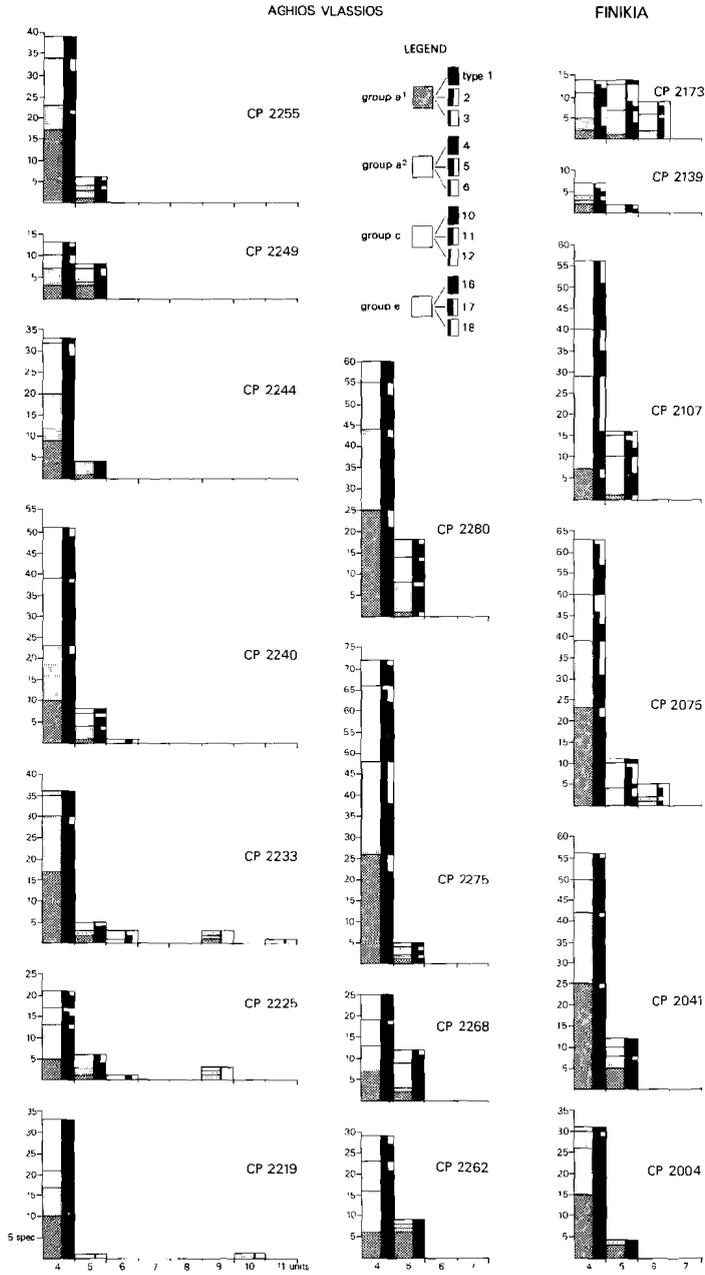


Fig.25b (continued)

of central opening and collar are variable in the specimens of intermediate size.

Summarizing, if it is assumed that there are few specimens with peripheral slits in the size classes 1, 2 and 3, the estimates and measurements in the 200-counts suggest two major patterns in the size distribution of the smaller coccoliths of the 'rest-category'. Pattern A suggests a unimodal population of the small specimens, with an average size of about 2 units. Patterns C, D and E show a bimodality with modes in class 2 and in classes 4 or 5. The size-frequency distribution of the mid-size populations seems to coincide with the distribution of the category of the slit-bearing specimens. As the latter category is present in associations of pattern B, it is quite likely that the broadly unimodal histograms of pattern B are the result of a mixture of a predominant population of the small-size specimens and a numerically unimportant mid-size population (fig.24).

Morphology and size in the larger coccoliths (30-counts)

Histograms of the distribution of the length and morphology of the large-size coccoliths, resulting from the 30-counts, are shown in figure 26.

Determining the lower size limit on the basis of the distribution in the 200-count proved to be difficult in only a few samples (e.g. sample GR2694). It seems that our setting of a size limit between the smaller and the larger specimens did not induce an unnatural truncation, since in most histograms the number of specimens in the smallest class of the larger forms is very low or zero. Because the frequencies were getting too low, we stopped recording the large specimens in samples above the Aghios Vlassios sample CP2244. In the slide of the latter sample, 5 traverses had to be scanned in order to obtain the required 30 specimens.

All large specimens belong to the 'rest-category'. Two successive associations can be distinguished, showing marked differences in the distribution of both size and morphology of the coccoliths.

The stratigraphically lower association corresponds with the larger coccolith fraction in distribution pattern A, which was found in the *Kalitheia* I samples GR2661 through GR2694 (fig.21). The histograms are unimodal, and a normal distribution is suggested. Coccolith diameter ranges from 4 to 8.5 units (3.5μ to 8μ), the mean diameter varies between about 5.9 and 6.5 units (5μ and 6μ ; see figure 27). The coccolith morphology varies widely, but there are some characteristic accents. The association consists for the greater part of coccoliths with a closed or small central opening ('group a'). Specimens with a (nearly)

closed central opening ('group a¹') predominate. Nearly all such a¹ specimens have an intermediate or a wide collar (Table IV). In the other groups, narrow collars are more common, but there is no continuous shift in the relation between the relative dimensions of the collar and the central opening. Both parameters seem to show no relation with coccolith length (fig.26).

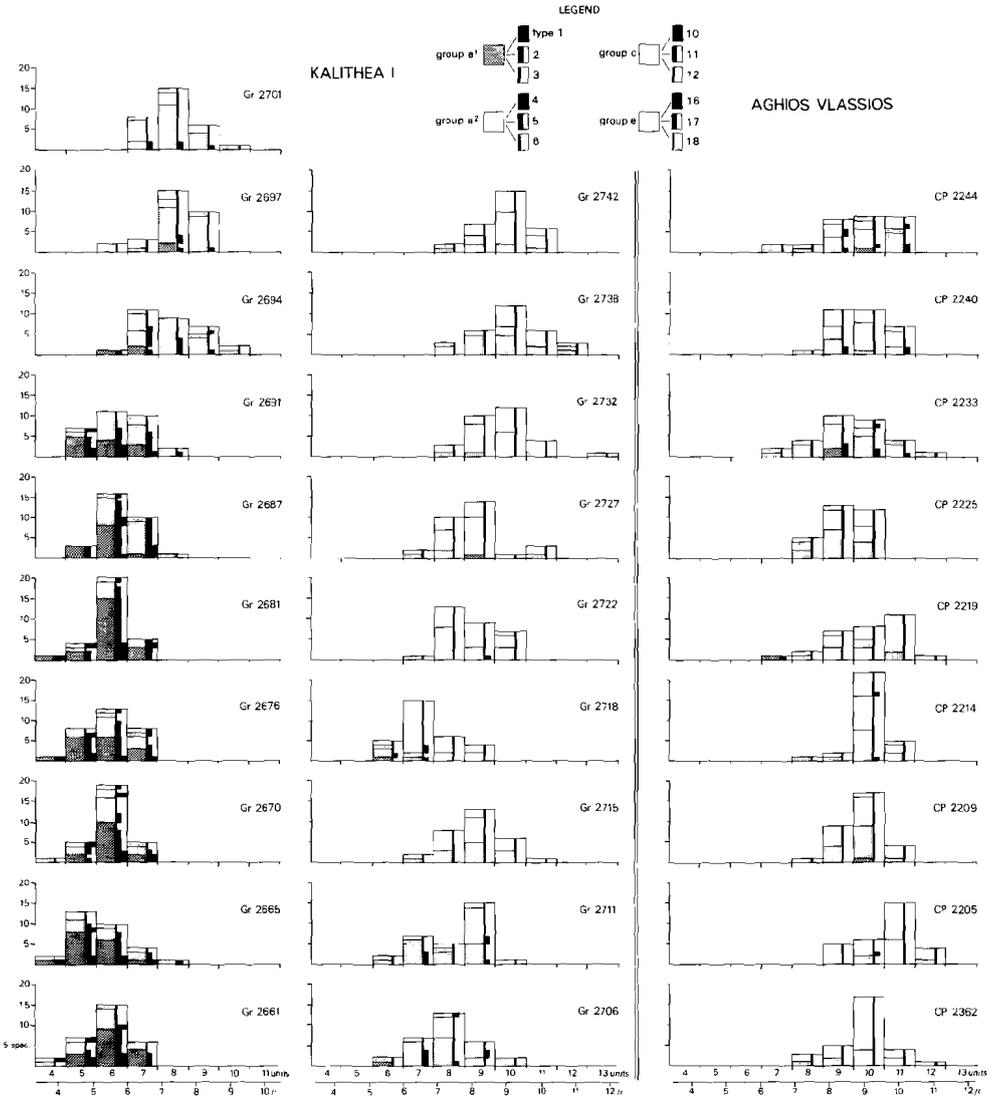


Fig.26 Histograms showing morphology and length in the large-size coccolith fraction (N=30) of the Noëlaerhabdaceae in the Lower Pliocene of Crete.

	COLLAR						sum	perc.
	wide		inter- mediate		narrow			
CENTRAL OPENING								
closed	(type 1)	34	(type 2)	69	(type 3)	4	107	51.0
small	(type 4)	8	(type 5)	38	(type 6)	32	78	37.1
intermediate	(type 10)	1	(type 11)	4	(type 12)	9	14	6.7
large	(type 16)	5	(type 17)	3	(type 18)	3	11	5.2
sum		48		114		48	210	
percentage		22.9		54.2		22.9		

Table IV: Frequencies for the combination of collar type and central opening type in the large coccoliths of pattern A (section Kalithea I, samples GR2661 up to GR2691).

The stratigraphically higher associations of large coccoliths correspond with size distribution patterns B and C. Compared with the lower associations, the average coccolith size is higher and there are very few specimens with a (nearly) closed central opening.

The diameter of the coccoliths ranges from 6 to 13 units (5.5μ to 12μ), the mean diameter varies between 7.5 and 10.8 units (about 6.5μ and 9.5μ ; see figure 27). From the interval of pattern B to the interval of pattern C there is a shift towards consistently higher mean values. In associations of pattern B, the average of the mean values is about 8.4 units (7.5μ), whereas in the associations of pattern C this average is around 10 units (about 9μ). This shift in coccolith size in the large fraction is not accompanied by a clear change in the distribution of other characters.

	COLLAR						sum	perc.
	wide		inter- mediate		narrow			
CENTRAL OPENING								
closed	(type 1)	0	(type 2)	4	(type 3)	9	13	2.1
small	(type 4)	0	(type 5)	42	(type 6)	182	224	35.6
intermediate	(type 10)	0	(type 11)	8	(type 12)	209	217	34.4
large	(type 16)	0	(type 17)	9	(type 18)	167	176	27.9
sum		0		63		576	630	
percentage		0		10		90		

Table V: Frequencies for the combination of collar type and central opening type in the large coccoliths of patterns B and C (section Kalithea I, samples GR2694 up to GR2741; section Aghios Vlassios, samples CP2362 up to CP2242).

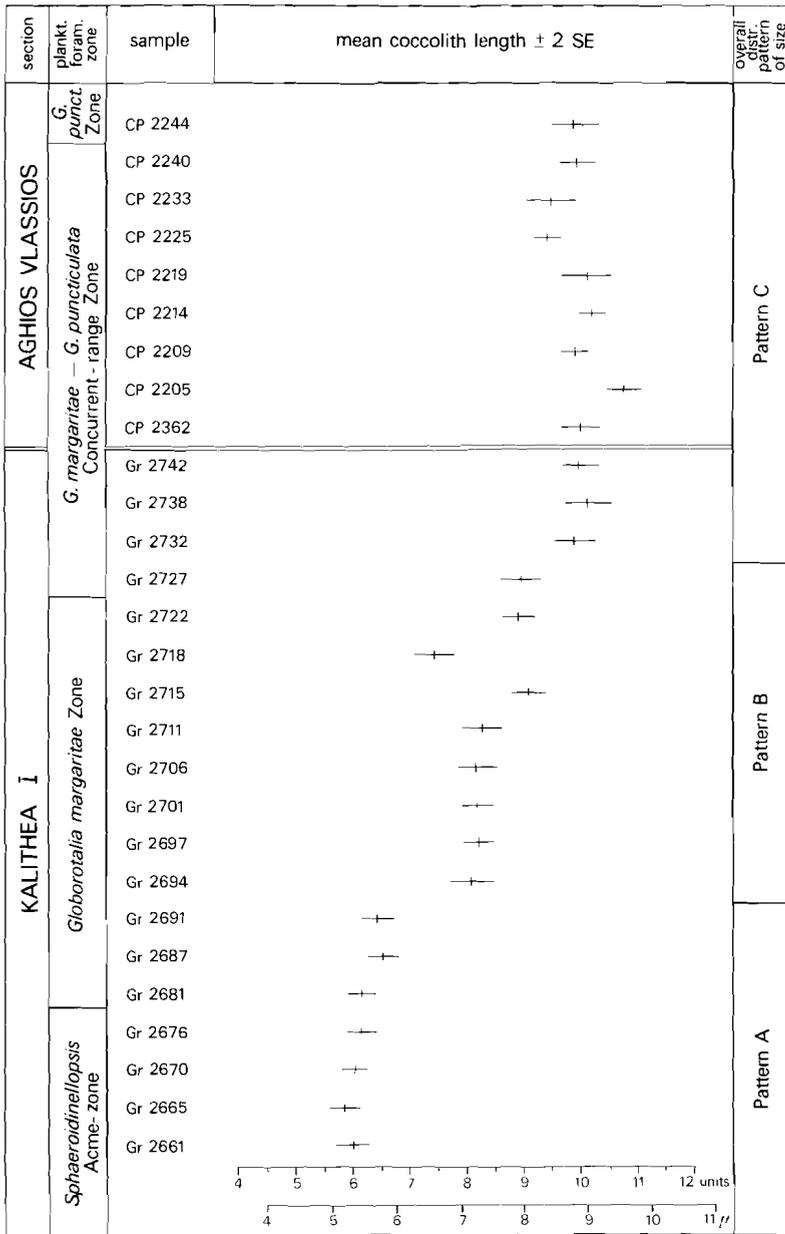


Fig.27

Means (\pm 2SE) of the length of the largest coccoliths (N=30) and the overall distribution pattern of size of the Noëlaerhabdaceae in the Pliocene of Crete. The stratigraphic interval, covered by the topmost three samples of Kalithea I, corresponds with the interval of the lowermost three samples in Aghios Vlassios.

There is no clear pattern of change in the distribution of the relative size of the central opening either. Coccoliths with a closed central area are very rare (Table V). Some samples show many coccoliths with a small central opening and only few with a large central opening, but in other samples the pattern is reversed. In two samples, the coccoliths only showed intermediate or large central openings (CP2362, CP2205). No clear relation is evident between the relative central opening size and the diameter of the coccoliths.

In the large coccoliths, associated with patterns B and C, the narrow collar type is predominant, and in a good many samples it is the only type observed. Specimens with large collars were not found at all.

Summarizing, one can distinguish two successive associations in the large coccolith fraction. The lower association (pattern A) consists of relatively small coccoliths (average diameter size about 5.5μ), many of which have a small or a closed central opening and a relatively wide collar. The coccoliths in the higher association (patterns B and C) are of larger size (averages between 6.5μ and 9.5μ); their central opening is variable but it is hardly ever closed, and their relative collar width is predominantly small. The average size of the coccoliths of the large fraction in pattern B is consistently smaller than the average in pattern C, but there is no conspicuous difference in the distribution of other variables.

THE NOËLAERHABDACEAE IN THE PLIOCENE OF ITALY

MATERIAL AND METHOD

In order to arrive at a more comprehensive view of the composition of the associations of the Noëlaerhabdaceae in the Mediterranean Pliocene, we investigated material from land-based sections in Italy. The stratigraphic sequence includes the upper part of the Upper Pliocene, which is not present in our Cretan sequence. The reader is referred to chapter 3 for a detailed account of location, lithology and biostratigraphy of the sections.

The Italian material consists of samples from section Monte Singa in southern Calabria and from the sections Punta di Maiata and Punta Piccola on the southern coast of Sicily.

Our 55 samples of section Singa I/IA are from a more or less regular alternation of indurated white calcareous marls and greyish clayey marls. The missing stratigraphic interval in the Singa section is covered in Punta di Maiata. We studied 31 samples from the lower part of the latter section which shows large-sized Reticulofenestrids, and we selected another 26 samples from the higher part. From the nearby section Punta Piccola, which partly overlaps with the topmost part of the Punta di Maiata section, 22 samples were analyzed. Finally, we investigated 49 samples from the Singa II, III and IV subsections, together covering the major part of the upper Pliocene and the lowermost Pleistocene. For reasons, mentioned in chapter 7, we did not study the Noëlaerhabdaceae in samples from sapropelic layers.

Instead of performing elaborate 200-counts, as was done with the material from Crete, we tried to recognize the Cretan patterns of the distribution of coccolith size A through E in a qualitative manner. In this procedure, it appeared to be difficult to distinguish clear distribution patterns of the B-type and the D-type without actual quantification of the size distribution (hence our symbols B/C and D/E, respectively). Many samples showed discrete clusters of very small and intermediate coccolith sizes, a distribution which was assigned to pattern E. Additional symbols were needed for characteristic deviations from the Cretan patterns. Associations of the D- or E-type with relatively few or hardly any small-size specimens were given the symbol 'D/E'. In some samples, stratigraphically above the exit of the large Reticulofenestrids, we found a few Noëlaerhabdacean coccoliths of relatively large size ('small mor-

phototype of the large-sized group'). In the distribution charts (figures 31, 34, 35), the presence of such specimens is indicated with an asterisk (*). The symbol *? is used to indicate that there is no clear size break between such specimens and the coccoliths of the intermediate-size group.

If present in the sample, 30 specimens of the large Reticulofenestrads were measured and qualified, and the presence of specimens with slits in the shield periphery was recorded. Furthermore, we were interested in the overall frequency pattern of the specimens with a cross-bar throughout the Pliocene. For ease of comparison with the data from Crete, we continued to establish their frequencies per 200 coccoliths of the Noëlaerhabdaceae. In the next chapter, the resulting frequency distributions will be discussed in more detail.

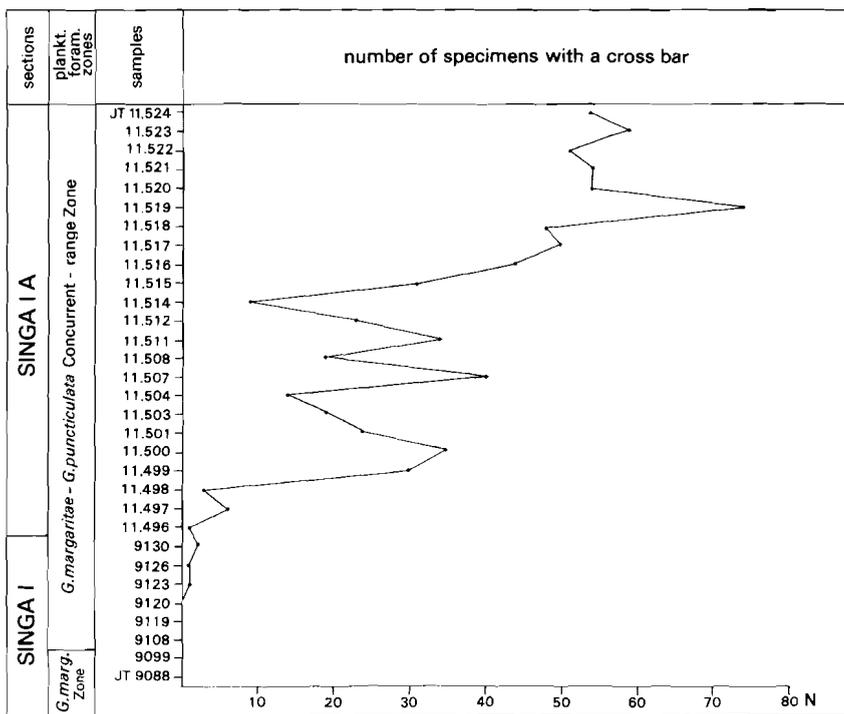


Fig.29 Frequency of specimens with a cross-bar (N=200) in the sections Singa I and IA.

Singa I

The results of our observations on the Noëlaerhabdaceae of the Singa I section are shown in the diagrams of figures 28 and 29, and in the histograms of figure 30. There is a good correspondence with the data from Crete, but there are some interesting differences as well.

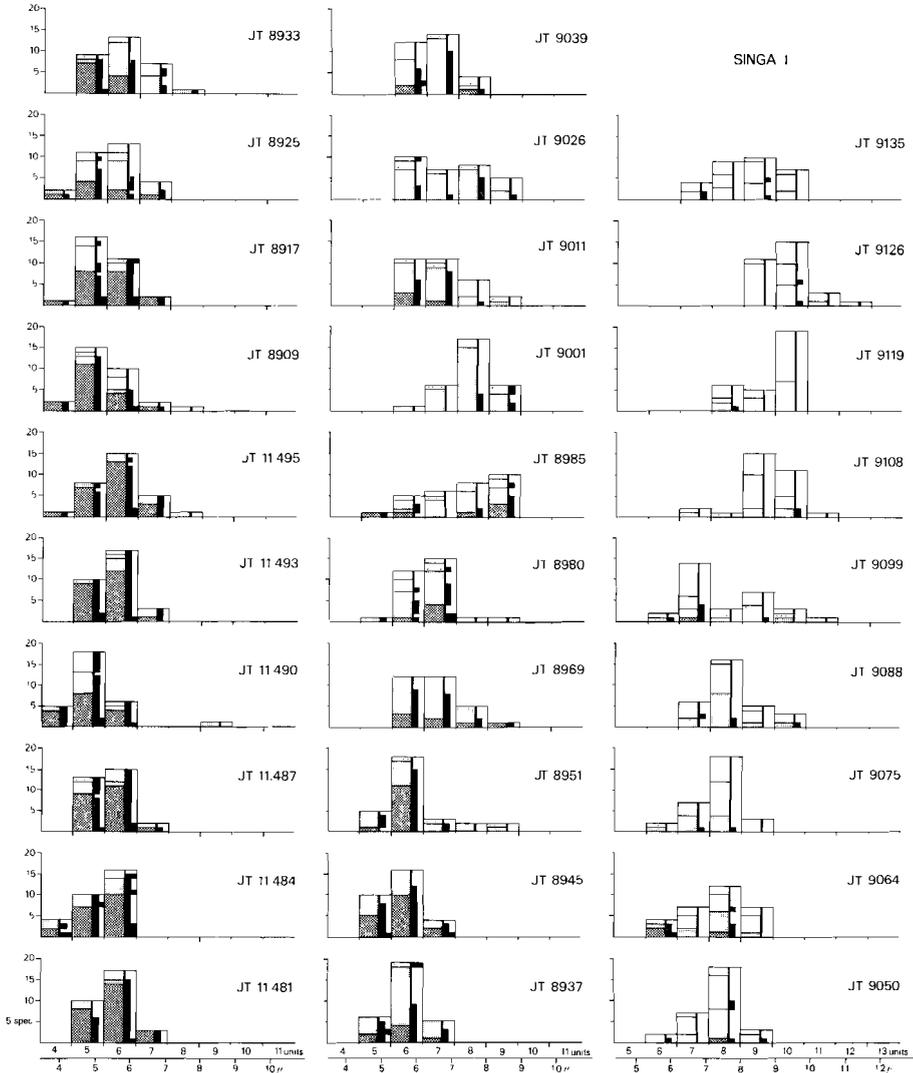


Fig.30 Histograms showing morphology and length of the large-size fraction of coccoliths (N=30) of the Noëlaerhabdaceae from the Lower Pliocene of section Singa I. For legend see figure 27.

Distribution pattern of coccolith size

As each of the size distribution patterns A through E of Crete is an average of the frequency distribution in a series of samples, it is to be expected that recognizing the pattern in an individual sample may be quite difficult. The difference between the patterns A and B is especially based on the frequency of mid-sized coccoliths (4 or 5 units) and on the size range and average size of the larger fraction. Because there was no clear break between smaller and larger sized specimens, and because it is hard to estimate the frequency of specimens in class 4, some samples could not be assigned to either pattern A or B; hence the symbol A/B (fig.28). The difference between the patterns B and C, based especially on the frequency of the mid-sized specimens, was often equally hard to establish in our qualitative exercise. Still, the development of the Noëlaerhabdacean associations in Singa I compares well with the development in Kalithea I.

Slits and cross-bars

With the light-microscope, we thought to detect peripheral slits in small specimens from sample JT11.493 upwards (fig.28). In specimens from sample JT8917 slits are clearly visible.

The first specimens with a clear cross-bar were seen in sample JT9108 (fig.29), although in lower samples some coccoliths show a thickening of opposite parts of the collar, reminiscent of a nearly complete bridge. Up to sample JT11.498, the frequencies are very low. Higher up there is an interval with relatively common *Gephyrocapsa*, followed by an acme-interval.

Morphology and dimensions of the large specimens

The observations on the large specimens (fig.30) show again that the main trend is similar to the one of Crete, but that there are differences in the details. In the basal part of the section up to sample JT8951 (distribution patterns A and A/B), the coccoliths in the large fraction are relatively small. There may be a few exceptionally large specimens (e.g. in sample JT11.490) but their state of preservation usually suggests that they are reworked. The coccolith diameter in the main group of the larger specimens ranges from 4 to 8.5 units ($\pm 3.6 \mu$ to 7.7μ), and the mean diameter varies between 5.3 and 6.3 units ($\pm 4.8 \mu$ and 5.7μ). The histograms are unimodal and suggest a normal distribution for most samples. The associations are dominated by coccoliths with a closed central area, while specimens with a small central opening are next frequent. Collars of the intermediate type predominate (Table VI).

	COLLAR						sum	perc.
	wide		inter- mediate		narrow			
CENTRAL OPENING								
closed	(type 1)	24	(type 2)	186	(type 3)	9	219	56.2
small	(type 4)	3	(type 5)	71	(type 6)	51	125	32.0
intermediate	(type 10)	3	(type 11)	12	(type 12)	19	34	8.7
large	(type 16)	0	(type 17)	7	(type 18)	5	12	3.1
sum		30		276		84	390	
percentage		7.7		70.8		21.5		

Table VI: Frequencies for the combination of collar type and central opening type in the large coccoliths of patterns A and A/B (samples JT11.481 up to JT8951) in section Singa I.

In the samples above JT8951 (patterns B and B/C), the mean length of the coccoliths is more than 6μ . The change towards the higher values is not as abrupt as in Kalithea I. In sample JT8951, the mode is in class 6, and there are still many coccoliths with a closed central area. However, the presence of coccoliths of 8 and 9 units in diameter points to heterogeneity; the composition of the association seems to be intermediate between the small-size population of the interval below and the large-size population above. Such a heterogeneity may be present in other samples from the higher interval as well, as some of the histograms are quite irregular or even bimodal.

The size of the coccoliths above sample JT8951 ranges from 5.5 to 12 units (5μ to 11μ), and the average length varies between about 7.0 and 9.9 units (6.4μ and 9.1μ). As in Kalithea I, there is a sudden increase in the average diameter, situated between samples JT9099 and JT9108. The average of the diameter means up to JT9099 is about 7.7 u ($\pm 7 \mu$), while in samples above it is 9.4 u ($\pm 8.6 \mu$).

Compared with the lower interval, specimens with a closed central area are few, whereas there are more specimens with a large central opening (Table VII). From sample JT8969 up to sample JT9039, small central openings and intermediate collars are relatively frequent, but higher up in the section the intermediate and large central openings and the narrow collars predominate.

Punta di Maiata

As the calcareous nannofossil associations in many of the samples from the lower part of the Punta di Maiata section are more or less seriously affected by dissolution, the record of the specimens with slits and the record of the size distribution pattern in this part are poor.

	COLLAR						sum	perc.
	wide		inter- mediate		narrow			
CENTRAL OPENING								
closed	(type 1)	3	(type 2)	24	(type 3)	3	30	6.3
small	(type 4)	2	(type 5)	80	(type 6)	134	216	45.0
intermediate	(type 10)	0	(type 11)	16	(type 12)	132	148	30.8
large	(type 16)	0	(type 17)	2	(type 18)	84	86	17.9
sum		5		122		353	480	
percentage		1.0		25.4		73.6		

TABLE VII: Frequencies for the combination of collar type and central opening type in the large coccoliths of patterns B and B/C (samples JT8969 up to JT9135) in the Singa I section.

It is quite complicated to locate the exit of the large specimens of the Noëlaerhabdaceae ('exit of *Reticulofenestra pseudoumbilicus*'). There is an overall frequency decrease above sample CP4109 (see chapter 9), but in higher samples large specimens are still present, though discontinuously and in low numbers. Furthermore, some samples yielded two discrete clusters of the large-sized specimens. Hence, our concept of 'large specimens' needed revision. We stopped the 30-counts above sample CP4110.

Distribution pattern of coccolith size

Below sample CP4110 the associations show coccoliths of small, intermediate and large sizes. Depending on the estimated relative frequencies of the intermediate specimens, the associations belong to patterns B, C or B/C (see figure 31). In accordance with the sequence from Crete, samples from higher stratigraphic levels mainly show a seemingly bimodal size distribution with coccoliths of small and intermediate size (patterns D, E, or D/E).

Slits and cross-bars

Due to the bad coccolith preservation in the lower part of the section, the lower part of the range of specimens with slits is not clear. With the light-microscope, we observed specimens with clear slits from sample CP4070 upwards (fig.31). The subcircular morphotype with its large central opening and its narrow collar and shields appears again close to the exit of the very large specimens of the Noëlaerhabdaceae.

As in the Lower Pliocene of Singa I/IA and the Cretan sequence, most samples from a certain level onwards contain specimens with a cross-bar (fig.31). In many samples, the specimens with cross-bars contribute considerably to the Noëlaerhabdaceae. There is an interval with relatively large specimens (diameters up to 4 μ) in the lower part of the range.

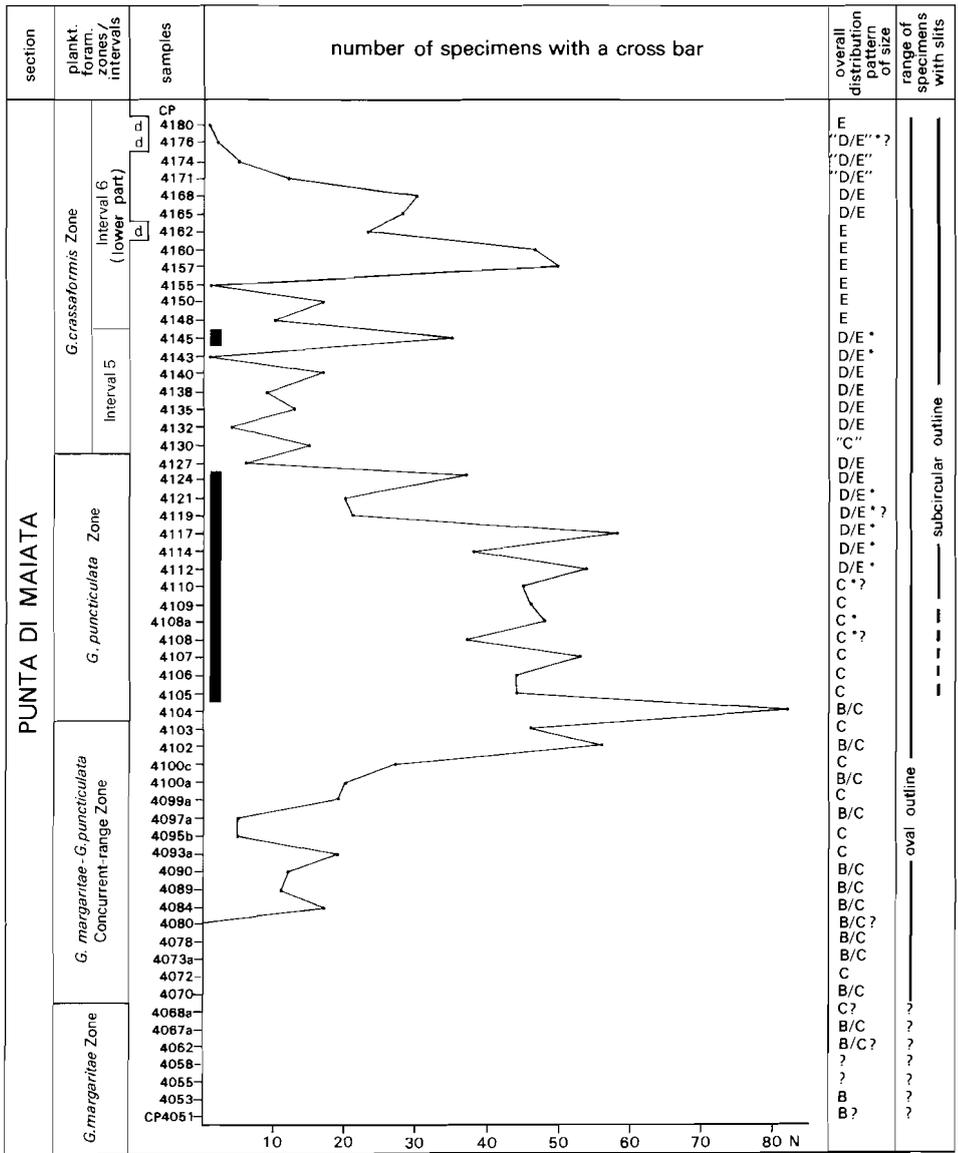


Fig.31 Frequency of specimens with a cross-bar (N=200), overall distribution pattern of size and range of specimens with slits in the Punta di Maiata section. Vertical bars on the left-hand side of the graph indicate the presence of relatively large-size specimens ($> 3.5 \mu$).

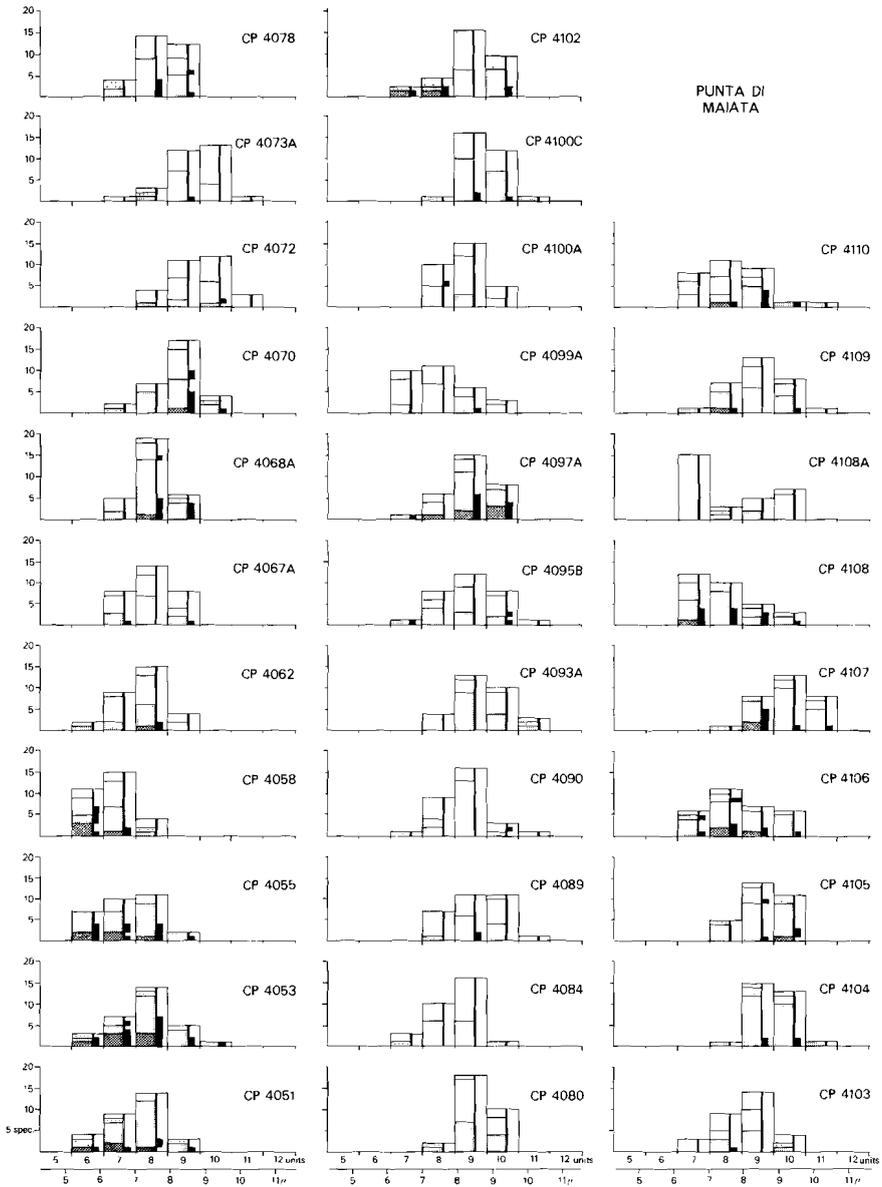


Fig.32 Histograms showing the distribution of morphology and length in the large-size coccoliths (N=30) of the Noëlaerhabdaceae from the Lower Pliocene of the Punta di Maiata section. For legend see figure 27.

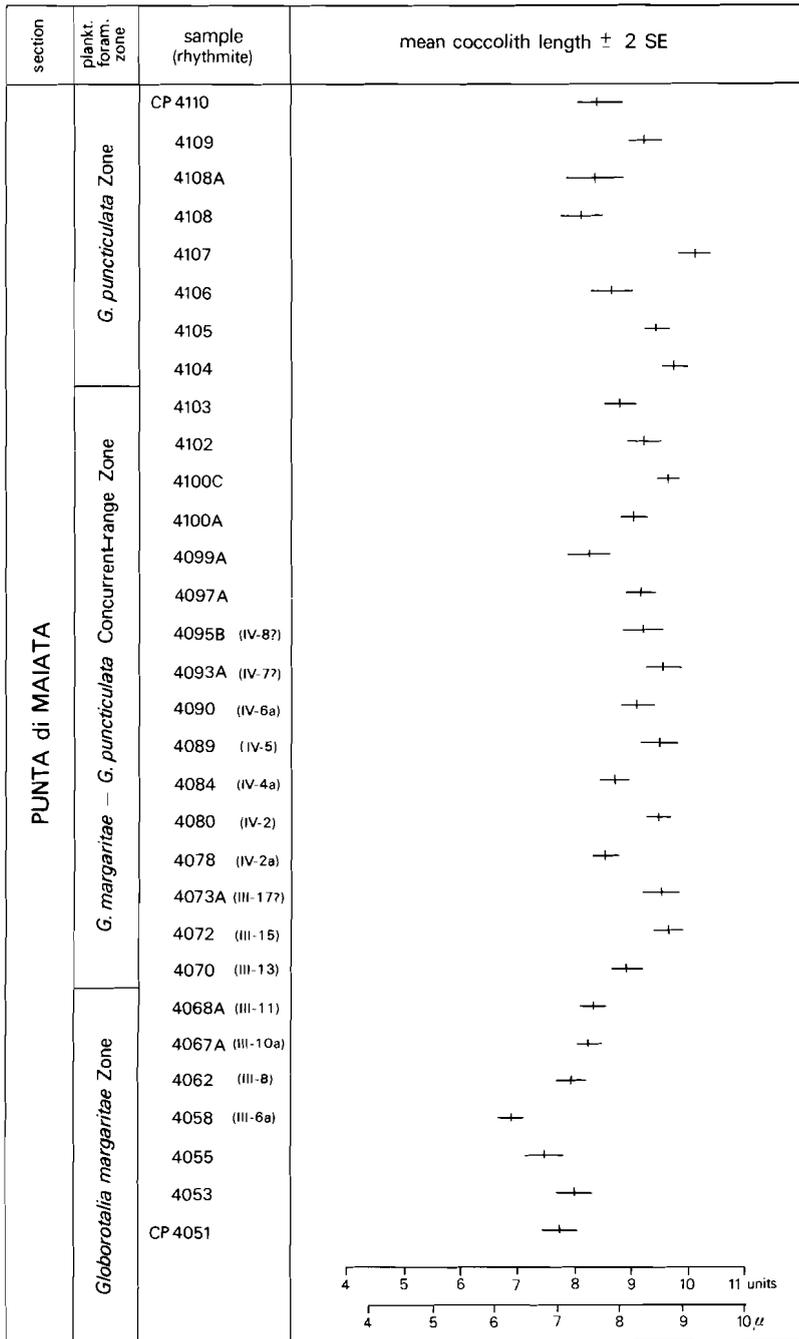


Fig.33 Means (\pm 2SE) of the length of the (N = 30) large coccoliths of the Noëlaerhabdaceae in the Punta di Maiata section.

Morphology and dimensions of the large specimens

Histograms of the shape and diameter of the large coccolith fraction in the Punta di Maiata samples are presented in figure 32, while the diameter means are shown in figure 33. The diameter of the large specimens, recorded in the 30-counts, ranges from 6 to 11 units ($\pm 5.5 \mu$ and 10μ), while the diameter means vary between 6.9 and 10.1 units (about 6.3μ and 9.1μ). There is an increase in the diameter means (around sample CP4070). The average of the diameter means below this sample is about 7.8 u (7.1μ), while above the average is about 9.1 u (8.3μ). The pattern in the succession of the diameter means in the interval between the rhythmites III-6a up to IV-2a in Punta di Maiata is strikingly similar to the pattern in the correlative interval of Singa I.

The diameter means fluctuate considerably. This may be partly due to the heterogeneity of some of the assemblages (see below). Furthermore, a relation is suggested between lithofacies and the coccolith diameter. The assemblages with the larger diameter means are predominantly found in the indurated marly beds, while the clayey beds show relatively small-sized specimens.

The histograms are unimodal, except the ones from the uppermost samples. In most samples the coccolith diameter seems to be normally distributed. The samples CP4108 and CP4108A yielded a skewed and a bimodal distribution, respectively.

No relation is evident between the relative size of central opening/collar and coccolith diameter, stratigraphic position or lithofacies. The lowermost samples show relatively many specimens with a small or closed central opening and with an intermediate collar, but such a morphological spectrum is repeated higher up (e.g. CP4097A, CP4107).

Small and intermediate central openings predominate in the Punta di Maiata assemblages, and there are very few specimens with a closed central area (Table VIII). By far the most specimens show a narrow collar, while wide collars were hardly found. All specimens with a large central opening had a narrow collar.

	COLLAR				sum	perc.
	wide	inter- mediate	narrow			
CENTRAL OPENING						
closed	(type 1) 0	(type 2) 34	(type 3) 7		41	4.4
small	(type 4) 0	(type 5) 92	(type 6) 305		397	42.7
intermediate	(type 10) 1	(type 11) 18	(type 12) 311		330	35.5
large	(type 16) 0	(type 17) 0	(type 18) 162		162	17.4
sum	1	144	785		930	
percentage	0.1	15.5	84.4			

Table VIII: Frequencies for the combination of collar type and central opening type in the large coccoliths of the Punta di Maiata section (samples CP4051 up to CP4110).

On the basis of the distribution of coccolith diameter and central opening in the histogram, we conclude that the association in CP4108A consists of two subpopulations. A large central opening size is characteristic for the smaller morphotype (average diameter about 6.5μ). The larger morphotype has an average diameter of some 9μ and a varying central opening size. The histograms of the samples CP4108 and CP4110 may be interpreted in terms of such a mixed association as well. In the inbetween sample CP4109 the smaller morphotype was not represented in the 30-count.

Punta Piccola

The coccolith associations of the Noëlaerhabdaceae from the homogeneous beds in the Punta Piccola section on Sicily predominantly show small and medium sized specimens (distribution patterns D, E, D/E or 'D/E'; see figure 34). The samples with relatively few small sized specimens are especially concentrated in the uppermost part of the section. The good state of preservation of the larger specimens refutes the suggestion that small specimens are few because of partial dissolution of the nannoflora. In many samples we found a few specimens belonging to the 'smaller morphotype ($\pm 6.5 \mu$) of the large-size group (* or *?)'.

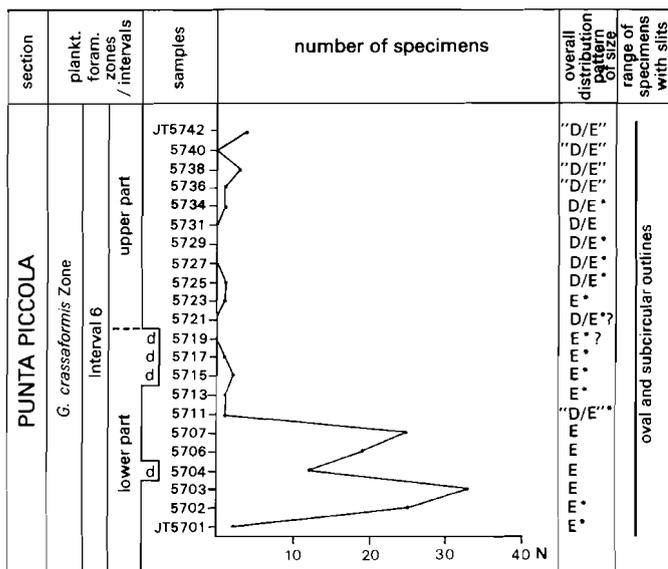


Fig.34 Frequency of specimens with a cross-bar (N=200), the distribution pattern of size and the range of specimens with slits in the Punta Piccola section.

Throughout the section, both elliptical and subcircular specimens with slits in the shield periphery were found. In the lower part of the section, coccoliths with a cross-bar are frequent, but higher up they are present in very low numbers. The coccolith diameter of the specimens is small ($< 2.5 \mu$).

Singa II, III, IV

Like the Noëlaerhabdacean associations from the upper part of section Punta di Maiata and from Punta Piccola, the coccoliths of the Noëlaerhabdaceae in the Upper Pliocene and Lower Pleistocene of the Singa sequence are of small or medium size (distribution patterns D, E, D/E or 'D/E'; see figure 35). Especially in the higher part of the sequence, the associations show discrete

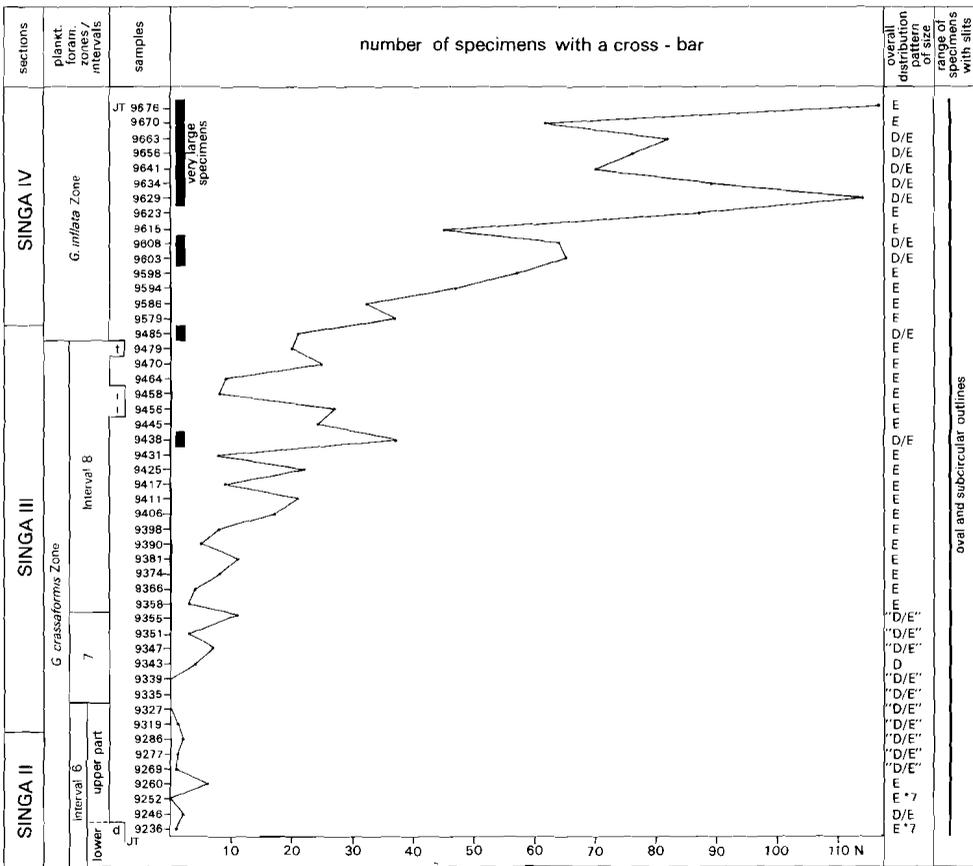


Fig.35 Frequency of specimens with a cross-bar (N=200), the distribution pattern of size, and the range of specimens with slits in the sections Singa II (upper part), III and IV. A vertical bar on the left hand side of the graph indicates samples with relatively large ($> 3.5 \mu$) specimens with a cross-bar.

clusters of very small and of medium-size specimens (pattern E). In many samples from the lower part, the small sized group is relatively low frequent (pattern 'D/E'). In some of those samples (JT9343 up to and including JT9355) a long traverse was needed for the 200-count, pointing to dilution of the nanofloras. Again, the coccolith preservation is quite good in the 'D/E'-associations. Throughout the sequence of samples, specimens with slits are found, with both oval and subcircular outlines.

There are only few coccoliths with a cross-bar in the lower part of our sequence. Higher up, their number increases until in samples of section Singa IV they constitute more than half of the Noëlaerhabdacean coccoliths. In the lower part, the specimens with a cross-bar are small-sized ($< 2.5 \mu$). In the interval between samples JT9425 and JT9629, the specimens are occasionally up to 4μ in diameter, and some associations seem to yield a bimodal distribution of their diameter (e.g. JT9438). From sample JT9623 upwards, the maximum diameter of the specimens with a cross-bar is seen to increase gradually from about 3μ up to 5.5μ . In sample JT9641 and above, the coccolith sizes cluster into a small sized group (average diameter some 2μ) and a larger sized group.

In order to make a quantitative inventory of the changes in the composition

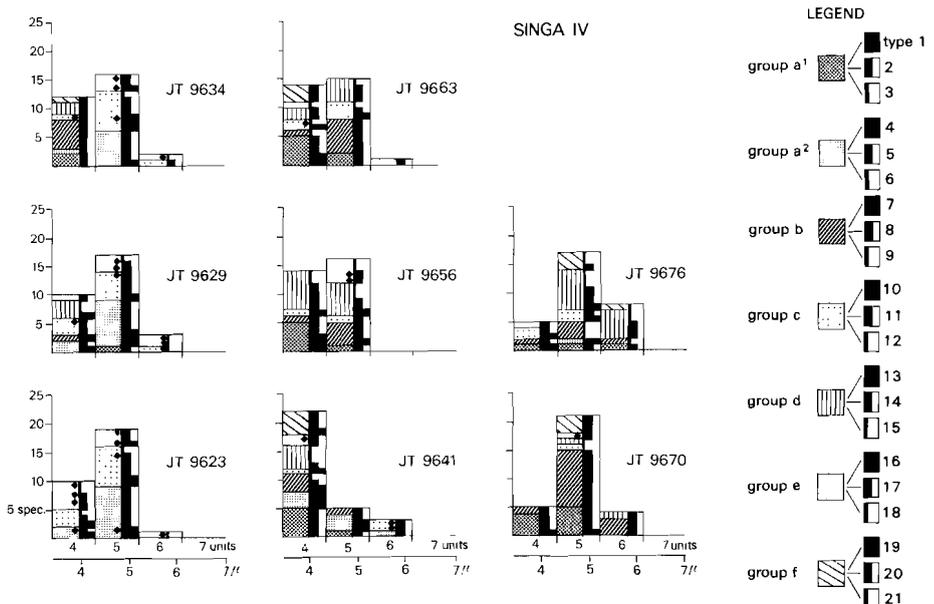


Fig.36 Morphology and size (diameter) in the larger coccoliths (≥ 4 units, i.e. $\geq 3.6 \mu$) of the Noëlaerhabdaceae (N=30) in the Pliocene-Pleistocene of section Singa IV. Specimens with peripheral slits are indicated with \blacklozenge .

of the intermediate-size category in the topmost part of the sequence, we measured and typified at random 30 specimens with a diameter of 4 units ($\pm 3.5 \mu$) or more in eight samples. The results are shown in the histograms of figure 36. The 30-count of sample JT9623 yielded no intermediate-size specimens with a cross-bar. In the higher samples, the maximum diameter of the coccoliths with a cross-bar gradually increases, while the overall frequency of specimens with a cross-bar increases as well. In the uppermost two samples, they predominate the coccoliths of intermediate size and they reach their maximum diameters. The central openings are predominantly of intermediate and small size. In many specimens there is hardly an opening on either side of the cross-bar. The collars are mostly of the intermediate type. The relative frequencies of the coccoliths without a cross-bar decrease upwards, but within this group the number of specimens with a closed central area shows a considerable increase.

RECAPITULATION

We may conclude that the pattern in the development of the Noëlaerhabdacean associations in the Pliocene of Crete is repeated in the Pliocene of the Italian sections. It is often difficult to distinguish the individual patterns A through E of the distribution of coccolith size on the basis of qualitative observations. The three major patterns are A and the combinations B/C and D/E. Some assemblages from the Upper Pliocene of the Monte Singa sequence are characterized by relatively low numbers of the smallest specimens of the Noëlaerhabdaceae (pattern 'D/E').

In our Italian record of the large-size group, we recognized the Cretan sequence of the relatively small sized coccoliths with predominantly closed centres in the lowermost Pliocene, stratigraphically followed by larger sized assemblages which usually show a central opening. Both in Italy and in Crete, the very large specimens disappear in the middle of the Pliocene. In comparison, the diameter means fluctuate considerably more in the Italian sequence. This may be due to the variation of the lithofacies we sampled in Italy; from the Cretan sections we studied only one lithofacies, i.e. the marly beds. Furthermore, the diameter means of some of the Italian assemblages are influenced by the presence of a relatively small morphotype. This morphotype continues to be present in very low numbers in the Upper Pliocene of Italy.

With the LM, we observed the first specimens with slits in the Singa I section in assemblages with an A-type distribution pattern, whereas in the material from Crete they were found in the lowermost assemblage of the B-type.

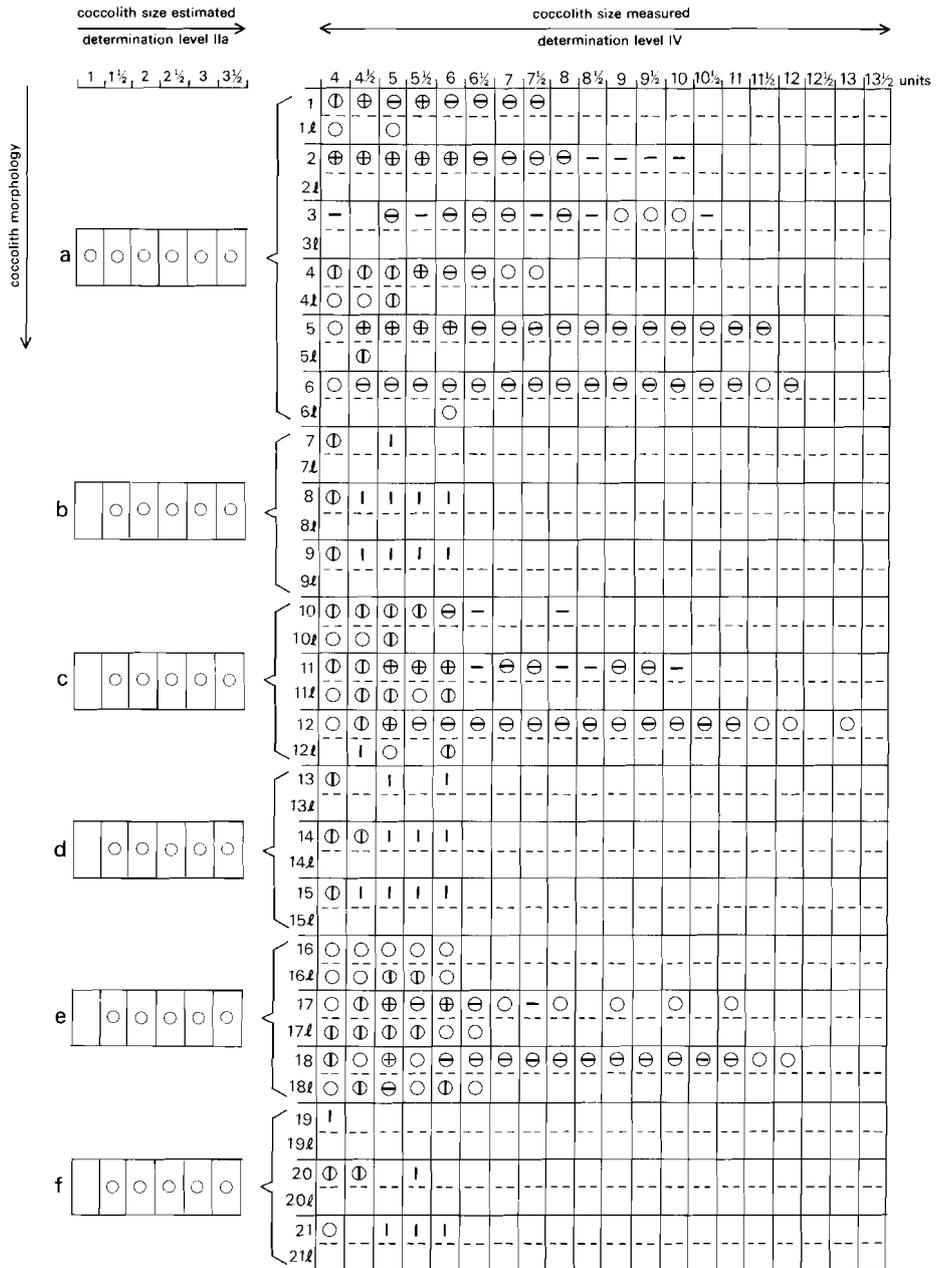


Fig.37 Size (diameter) range of coccolith morphotypes of the Noëlaerhabdaceae, observed in the counts. One measuring unit equals 0.9 μ .
 ○ : 200-counts and 30-counts, 40 samples from Crete.
 - : 30-counts on large specimens, 60 samples from Monte Singa and Punta di Maiata.
 | : 30-counts on specimens of intermediate size, 8 samples from the Pliocene-Pleistocene of Monte Singa.

In Crete, the first specimen with a cross-bar was seen to occur in the 200-counts at the base of the C-interval. In the sections Singa I/IA and Punta di Maiata, the boundary between the B- and C-distributions was not very distinct; here, the first specimens with a cross-bar were observed to occur above assemblages with a B/C characteristic. Both the Cretan and the Italian sequence shows a mid-Pliocene interval with relatively large specimens with a cross-bar. Our stratigraphically highest samples from the Pleistocene of section Singa IV show a bimodal distribution of coccolith size in the category of specimens with a cross-bar. The population of the large-size coccoliths in these samples shows diameters up to 5.5μ .

The configuration and diameter ranges of the coccoliths of the Noëlaerhabdaceae from the Italian Pliocene compare well with the coccolith spectrum, found in the Pliocene of Crete (see figure 37). Due to the associations from the topmost samples of Singa IV, the size range of the specimens with a cross-bar (morphotypes 7,8,9,13,14,15,19,20,21) increased up to 6 units ($\pm 5.5 \mu$). We found no addition to the size range of the specimens with slits in the shield periphery.

The diameter ranges, found for the Italian specimens without cross-bar and peripheral slits, show a good correspondence with the Cretan ranges. Differences are only minor. For example, type 16 (large central opening, wide collar) with a diameter of 4 units or more was only found in the Cretan samples. However, its main occurrences are in the intermediate-size category (compare figures 25 and 26), which we hardly quantified in the Italian samples. For types 12, 17 and 18 we found larger diameters in the Cretan samples, but for type 2 the range was widest in the samples from Italy. We conclude that our Italian data confirm the characteristic pattern, found in the diameter ranges of the morphotypes in the samples from Crete, i.e. the maximum range and the largest coccolith diameter are found in specimens with a narrow collar ; specimens with a wide collar show a relatively narrow size range and their maximum diameter is relatively small.

Chapter 9

TAXONOMY AND BIOSTRATIGRAPHY OF THE NOËLAERHABDACEAE IN THE SECTIONS STUDIED

HIERARCHY OF THE PARAMETERS

In the previous chapters, we depicted the morphological composition in series of successive coccolith associations of the Noëlaerhabdaceae from the Pliocene of Crete, Calabria and Sicily. The relative dimensions of central opening and collar, the presence/absence of a cross-bar and of peripheral slits, and the longest diameter of the coccoliths were used as descriptive parameters. For the sake of pure taxonomy, as well as for purposes of biostratigraphy and paleoecology, ranking of these variables is needed. In other words, the parameters need to be arranged from most common to most individual.

The stable and unifying character in the coccoliths of the Noëlaerhabdaceae is their basic crystallographic structure, which determines the characteristic dextrogyre pattern of the extinction lines in distal views. In the Neogene and Quaternary coccoliths of the Noëlaerhabdaceae, the bend in the gyres presumably results from the offset of the optical axes in the collar cycle / central plate with respect to the optical axes in the segment cycle (chapter 5). These associations are further characterized by the relatively strong birefringence of the shield elements, due to the position of the optical axis in the direction of the elongation of these elements.

Cross-bars, slits, and coccolith size

On the basis of a particular combination of additional characters (size range, stratigraphic distribution, coccolith outline, mutual exclusiveness), we consider two of our morphological parameters to be of major importance for the systematics of the Noëlaerhabdaceae in our samples : the presence/absence of a cross-bar, and the presence/absence of slits. Distinguishing two main categories on the basis of the parameters 'cross-bar' and 'slits' leaves a third category which can be circumscribed as the coccoliths with smooth shield surfaces and with smooth outer peripheries, and without a cross-bar (see chapter 7).

In the literature there is little detailed information about the variability of coccolith size in life assemblages of the Noëlaerhabdaceae. The size of the coccoliths on an individual coccosphere seems to be quite stable. There may be a

relation between the overall size of the cell and the size of the coccoliths (Gartner et al., 1983), but it is uncertain whether the cell size varies significantly within a species. One may safely assume that in a biocoenosis of a species of the Noëlaerhabdaceae the size of the coccoliths has a narrow variation range. Hence, we consider the size of the coccoliths to be a reliable parameter for distinguishing between species.

In nearly all our taphocoenoses, the coccoliths in all three categories appear to be arranged in a number of unimodal distributions with a narrow variation range of size (fig.21). As we did not go into the specific details of specimens with a cross-bar, there may be more than one species in this category per sample. Further, the broadly unimodal size-frequency distribution in pattern B may be the result of an overlap in the size-range of two populations (fig.24). For each of the remaining unimodal populations it is assumed that they represent the coccoliths of a separate species.

We treat our three categories as genera. One may argue that the genus is too high a rank for such categories. Throughout the stratigraphic record, there seems to be a continuous morphological variation between the coccoliths with slits, those with a cross-bar, those with an open centre and those with a closed centre ('*Pseudoemiliana*', '*Emiliana* s.s.', '*Gephyrocapsa*', '*Reticulofenestra*' and '*Dictyococcites*'). Furthermore, Recent coccospheres have been found to show coccoliths assignable to more than one of the above genera (chapter 6). If so, the classical genus characteristics are of species rank at most, and one would have only one genus left (*Gephyrocapsa* has the priority) for the entire spectrum of variation of the Late Neogene and Quaternary Noëlaerhabdaceae. On the other hand, it seems to be a quite common feature in the record of the calcareous nannofossils and the calcareous nannoplankton that a coccolith morphospectrum is continuous and that it covers more than one taxon. For example, the variation width of a species may be such that the species shows the characteristics of two genera (e.g. the *Cruciplacolithus primus* - *Chiasmolithus consuetus* lineage of Romein, 1979). For such cases, Sigal (1966) thought of his 'spectrum taxonomy', but this system seems to offer only a modification of the classical hierarchy of the Linnean taxa. Apparently, it is hard to establish a Linnean hierarchy in the coccolith characteristics. We feel that a comprehensive electron-microscopic study of the coccolith configurations on coccospheres from life assemblages is the only means of successfully evaluating the morphological variation in taxonomical terms. In our light-microscopic study of the Noëlaerhabdaceae from the Pliocene, difficulties of assigning specimens to one of our three categories were few. For practical reasons, we assign our categories to currently used genera.

Two of our categories comply with current views on the genera *Gephyrocapsa* and *Emiliana*. As we do not use the parameter 'closed centre' for the genus level, our rest-category is somewhat broader than the modern use of *Reticulofenestra*.

In some samples, the size-ranges of species of *Reticulofenestra* show an overlap. A coccolith of 'inbetween size' in such associations is treated as an intercentral specimen.

The relative dimensions of central opening, collar and shields

Treating the size-populations as species, we allow within some of the species for a considerable variability of the relative dimensions of the three structural components (shields, collar, central opening). Because these dimensions were recorded in relative terms, it is hard to figure out how exactly the parameters are mutually related, and how they are related to coccolith size.

We found no clear relation between the relative width of the central opening and the coccolith length. The specimens with a (nearly) closed central area (group a1, morphotypes 1,2,3) show a relatively short diameter range, and their number decreases with increasing coccolith length. Specimens with a small central opening (group a2, types 4,5,6), however, are quite frequent up to the largest size class. In some samples there is a marked difference in the predominant central opening type between the smaller and the larger sized species (for example, CP2362 and CP2205; figures 20b and 26). Apparently, there is no overall control on the relative central opening size throughout an individual association.

Some of our species, such as the single species of *Emiliana*, show a preference for a particular central opening size. In other species, however, all central opening types are fairly equally distributed. We assume that the variability of the relative central opening size is a specific character.

On the basis of the size range of the individual Reticulofenestrid morphotypes (figs.15,37), it was concluded that there is a positive correlation between the relative collar width and the coccolith diameter. Furthermore, in *Emiliana* the proportion of coccoliths with a narrow collar was seen to increase with coccolith length. Because the relative central opening size is not clearly related to coccolith size, one could assume that the collar/shield ratio is negatively correlated with coccolith length. In other words, in very large coccoliths one would expect to find only narrow collars. The species *Dictyococcites perplexa* Burns (1975) from the Middle Miocene of the Southeast Indian Ocean, however, contradicts the above assumption, as it shows very large coccoliths (18-20 μ) with a closed centre and an intermediate collar (our type 2).

Summarizing, we use the parameters 'presence/absence of a cross-bar' and 'presence/absence of slits' as generic characteristics. The variable coccolith length is of species level, and the parameters 'relative size of the central opening' and 'coccolith outline' are infra-specific variables. Collar width may not be an independent variable as it seems to be correlated with coccolith length in our material.

TAXONOMY

Family NOËLAERHABDACEAE Jerković, 1970

Type genus : *Noëlaerhabdus* Jerković, 1970

Description : Oval to circular, concavo-convex placolith-like coccoliths showing various modifications of an outer (proximal and distal shield) cycle and a centro-distal cycle. The shield elements are for the greater part subradially arranged, but their distal tube portion typically shows a dextral imbrication; the proximal tube portion usually shows a slight sinistral imbrication. Between crossed nicols the extinction lines are dextrogyre in distal view. The centro-distal cycle is strongly birefringent; the birefringence of the proximal and distal shields is variable.

From the Late Eocene onwards, the Noëlaerhabdaceae are represented only by *Reticulofenestra*-like coccoliths. Such coccoliths show a single distal shield, and a single centro-distal cycle which, especially when narrow, is sinistrally imbricate. Both distal and proximal shield are birefringent.

Remarks : Because of similarity in coccolith configuration and optical image, the Noëlaerhabdaceae may have evolved from the predominantly Mesozoic Ellipsagelosphaeraceae (Noël, 1965).

Genera and species

For an overview of the genera, used in combination with the species or synonyms of species, other than those used in the basionyms, the reader is referred to p. 56-57.

The second column of Table III shows the results of our attempts to fit the holotypes of frequently used species within our morphotype scheme. Some of the species are hard to classify because their morphology is not sufficiently clear (for example Lohmann's species). Each of our species covers several key morphotypes. We therefore selected names from the list of species especially on the basis of the size of the holotypes.

Genus **Reticulofenestra** Hay, Mohler & Wade, 1966, emend. Stradner
(in : Stradner and Edwards, 1968)

Type species : *Reticulofenestra caucasica* Hay, Mohler & Wade, 1966.
Stradner (ibid.) proposed the invalid *Tremalithus placomorphus* Kamptner (1948) as the type species of *Reticulofenestra*.

Synonyms: *Dictyococcites* Black, 1967
Cribrocentrum Perch-Nielsen, 1971
Cyclicargolithus Bukry, 1971a
Crenalithus Roth, 1973

Remarks : The genus is meant to include the entire variation between coccoliths with an open central area and those with a (distally) closed central area (closed collar cycle). In the Noëlaerhabdaceae, characteristics of the coccolith outline ('*Cyclicargolithus*'), the periphery ('*Crenalithus*'), the central plate ('*Cribrocentrum*') and the relative width of the central opening or central area ('*Dictyococcites*') are considered to be taxonomic parameters of lower than generic rank.

Reticulofenestra antarctica (Haq) nov. comb.
(Pl.4, figs.9-13)

Dictyococcites antarcticus Haq, 1976, p.561, pl.3, figs.1-5, 7,8

Remarks : The populations of large-sized coccoliths of *Reticulofenestra* in our size distribution pattern A or A/B (figs.21,24) are assigned to this species. Coccolith length varies between 3.5 μ and 7.7 μ (figs.26,30), the mean length is between 4.8 μ and 5.8 μ (figs.27,28). A predominantly closed or small central opening further characterizes the coccoliths in the assemblages; intermediate collars are predominant (Tables VI, VIII).

Reticulofenestra minutula (Gartner) Haq & Berggren, emend.
(Pl.1, figs.1,3-5,7,8,10; Pl.2, figs.4,11-13; Pl.3, figs.4,10(?); Pl.4, figs.2,3,7,8;
Pl.5, figs.2-7; Pl.6, figs.1,3; Pl.7, fig.28; Pl.9, figs.2,3)

? *Coccolithus doronicoides* Black & Barnes, 1961, p.142, pl.25, fig.3

Coccolithus minutulus Gartner, 1967, p.3, pl.5, figs.3-5

? *Cyclococcolithus aequiscutum* Gartner, 1967, p.4, pl.7, figs.1-4

Gephyrocapsa reticulata Nishida, 1971, p.150, pl.17, figs.1-3, text-fig.1 (fide Nishida, 1979)

Reticulofenestra haqii Backman, 1978, p.110, pl.1, figs.1-4; pl.2, fig.10

Reticulofenestra japonica Nishida, 1979, p.105, pl.1, figs.1-3

Remarks : Gartner (1967) did not indicate one particular coccolith specimen as the holotype of his species. We herewith designate the larger coccolith

specimen in Gartner's figures 5a,b,c as the holotype of *Reticulofenestra minutula* (Gartner) Haq & Berggren.

We assign the mid-size Reticulofenestrid coccoliths of the size distribution patterns B, C, D and E to this species (figs.21,24). The ranges of the coccolith length of our *R. minutula* and *R. minuta* show some overlap, especially in associations with a B, C or D pattern. The minimum length of the coccoliths of *R. minutula* in our samples is estimated to be around 2 μ , the maximum length is about 6.5 μ . The mean coccolith length in the assemblages is between about 4 and 5 μ . The relative central opening size is variable, and wide collars are common (fig.25). In Upper Pliocene and Lower Pleistocene samples, *R. minutula* often shows relatively large coccoliths with a small or (nearly) closed central opening. Such coccolith assemblages resemble those of *R. antarctica*, but usually the average coccolith diameter in the latter species is slightly larger.

Backman (1980) rightly rejected the species *Coccolithus doronicoides* because he considered the documentation of its holotype (a SEM photograph of a proximal view) in the protologue to be too poor.

Reticulofenestra minuta Roth

(Pl.2, figs.4,11-13; Pl.3, fig.8; Pl.4, figs.10,13; Pl.5, figs.1,7; Pl.6, figs.1,3; Pl.7, figs.11,12,28; Pl.8, fig.4; Pl.9, fig.3)

Ellipsoplacolithus productus Kamptner, 1963, p.172, pl.8, figs.42,44 (genus invalid; Loeblich and Tappan, 1966)

Reticulofenestra minuta Roth, 1970, p.850, pl.5, figs.3,4

Prinsius minutus Haq, 1971, p.78, pl.6, figs.4,5

Crenolithus productellus Bukry, 1975, p.688 (holotype : pl.2, fig.2 in Bukry, 1971b)

Coccolithus taganus Fonseca, 1976, p.29, pl.1, figs.1-8

Crenolithus sessilis (Lohmann) Okada & McIntyre, 1977, p.8, pl.5, figs.1-3

Remarks : The populations with the smallest-size coccoliths in the distribution patterns A through E belong to this species (fig.24). Coccolith length ranges from less than 1 μ to about 3.5 μ , and the mean length in the assemblages is around 2 μ . In many samples there is an overlap with the size-range of *R. minutula*. The relative central opening size is variable, but in some assemblages a particular central opening type is predominant (fig.19). The relative collar size is variable; intermediate and wide collars seem to predominate.

Reticulofenestra pseudoumbilicus (Gartner) Gartner

(Pl.1, fig.6; Pl.2, figs.5,7,8; Pl.3, figs.2,3,5-7; Pl.4, figs.1,5,6; Pl.5, fig.7; Pl.6, figs.1-5)

Coccolithus pseudoumbilicus Gartner, 1967, p.4, pl.6, figs.1-4

Coccolithus gelidus Geitzenauer, in : Geitzenauer and Huddlestun, 1972, p.407, pl.1, figs.1,2,5,6

Cyclicargolithus bukryi Wise, 1973, p.594, pl.9, figs.1-4

Remarks : The populations of the largest coccoliths of the Noëlaerhabdaceae in associations with a distribution pattern B, C or B/C are assigned to this species (figs.24,26,30,32). Coccolith length ranges from about 5 μ up to 12 μ . The mean coccolith length in our *R. pseudoumbilicus* assemblages varies between about 6.3 μ and 9.5 μ (figs.27,28,33). In the lower part of the range, the coccolith diameters are relatively small. The average of the diameter means in the Kalithea/Vlassios sequence is 7.5 μ , in Singa I it is 7 μ , and in Punta di Maiata it is 7.1 μ . The higher part of the range of *R. pseudoumbilicus* is characterized by relatively large coccolith diameters (9 μ , 8.6 μ and 8.3 μ , respectively). Only few specimens in the assemblages have a closed central area. Narrow collars predominate. Types 12, 6 and 18, in order of decreasing frequency, are most important (Tables VII, IX, X).

Reticulofenestra sp.

(Pl.9, figs.1-3)

Remarks : This taxon includes the smaller morphotype, figuring in some of the histograms of the large-size specimens with a bimodal size-distribution (pattern C), and the largest coccoliths, found in some samples with patterns D, E, D/E or 'D/E'. In the range-charts, these specimens were indicated with the symbol *. The species is markedly present in the histogram of sample CP4108A from Punta di Maiata (fig.32), where it mainly shows open-centre coccoliths with a narrow collar (type 18). In other samples, we found specimens with small and intermediate central openings and with intermediate collars as well. The coccolith diameter seems to range from about 6.5 μ to 7.5 μ , and we estimate the average diameter to be about 7 μ . Some associations show an overlap in the size-ranges between *R. minutula* and *Reticulofenestra* sp. Specimens assignable to *Reticulofenestra* sp. are present in the corresponding stratigraphic intervals on Crete as well.

Genus **Emiliana** Hay & Mohler, 1967

Type species : *Pontosphaera huxleyi* Lohmann, 1902

Synonym : *Pseudoemiliana* Gartner, 1969 (invalid; Loeblich and Tappan, 1970b)

Emiliana ovata Bukry

(Pl.1, fig.2; Pl.2, figs.6,10; Pl.6, figs.6-11; Pl.7, figs.1-8)

Ellipsoplacolithus lacunosus Kamptner, 1963, p.172, pl.9, fig.50 (invalid; Loeblich and Tappan, 1966)

? *Cyclococcolithus cricotus* Gartner, 1967, p.5, pl.7, figs.5-7

Emiliana annula, non *Coccolithites annulus* Cohen, 1964; Bukry, 1971c, p.1514 ; Bukry, 1973c, p.678
Emiliana ovata Bukry, 1973c, p.678, pl.2, figs.10-12
Reticulofenestra pacifica Nishida, 1979, p.106, pl.1, figs.4-6

Remarks : All Reticulofenestrid specimens with peripheral slits are assigned to this genus and species. The minimum coccolith length is estimated to be about 2.5 μ , the maximum length in our material is about 6 μ . In most samples from the lower part of the range, the diameter mode is probably around 3.5 μ . In the uppermost samples from Finikia, and in the sections Punta Piccola and Singa II, III and IV, the mode is usually higher (about 4.5 μ). Intermediate and large central openings are predominant, and so are wide collars (fig.23). In size distribution patterns D, E, D/E and 'D/E', part of the specimens has a (sub)circular outline.

Genus **Gephyrocapsa** Kamptner, 1943

Type species : *Gephyrocapsa oceanica* Kamptner, 1943

Remarks : As most Gephyrocapsids in our material are smaller than 3.5 μ , the major part of our data of these coccoliths pertain only to estimates of their diameter and to observations of the relative size of the central opening. We made observations on the collar/shield ratio only in few of the specimens from Crete, and in the large Gephyrocapsids from the Pleistocene of Singa IV. Furthermore, we refrained from measuring the angle between the cross-bar and one of either axes of the coccoliths, due to the small size of the majority of the specimens. Because our documentation of the morphological variation of the Gephyrocapsids is rather poor, we will present a very concise taxonomical concept.

Some samples from the Pleistocene of section Singa IV yielded a bimodal distribution of the coccolith diameter of the Gephyrocapsids. As the population with the large-size coccoliths in these samples (treated in figure 36) seems to be morphologically homogeneous, this population is considered to represent one species. The Gephyrocapsid associations from the Pliocene and the populations of the small sized Gephyrocapsids of Singa IV seem to yield only unimodal populations. However, as there seems to be a wide variation in collar width and in the position and configuration of the cross-bars, including these variables in our analysis would probably result in more than one cluster.

Gephyrocapsa spp.

(Pl.2, figs.15-17; Pl.3, figs.11-13; Pl.7, figs.9-29; Pl.8, figs.1-19, 22,25;
Pl.9, fig.2)

Remarks : The diameter of the small *Gephyrocapsids* in our material ranges from about 1 μ up to about 4 μ . There are fluctuations in the range and the average of the diameter. Especially in many samples with an E-pattern of the size-distribution, the diameter range is very narrow (diameters smaller than 2 μ). There is variation in the relative central opening size and in the relative collar width (see figure 22). In some samples, intermediate and large central openings predominate.

The position and configuration of the cross-bars vary as well. The bridges vary from very broad to very narrow. They are weakly to very brightly birefringent, probably depending on the angle of inclination of the cross-bar with respect to the overall coccolith surface. Between crossed nicols, some small *Gephyrocapsids* in our material show a very bright and relatively wide bridge, reminiscent of the species *Gephyrocapsa mediterranea* Pirini Radrizzani & Valeri (1977) and *G. florenzia* Lohman & Ellis (1981). It seems that in our samples, the angle of the cross-bar with respect to the longer axis of the coccolith is predominantly small ($< 45^\circ$). Most of our specimens seem to belong to the species-group *Gephyrocapsa* sp.1, *G. aperta*, *G. margereli* and *G. ericsonii* in the sense of Samtleben (1980).

Gephyrocapsa caribbeanica Boudreaux & Hay

(Pl.1, fig.9; Pl.2, figs.1(?),14,18; Pl.3, figs.14,15(?); Pl.4, fig.4; Pl.8, figs.20-25;
Text-figs.A,B, p.41)

Gephyrocapsa caribbeanica Boudreaux & Hay, 1967, in: Hay et al., 1967, p.447, pl.12, figs.1-4

Gephyrocapsa caribbeanica Boudreaux & Hay - Samtleben, 1980, p.110, pl.14, figs.9-14

Gephyrocapsa lumina Bukry, 1973c, p.678, pl.3, figs.1-4

Gephyrocapsa oceanica Kamptner subsp.1 - Rio, 1982, p.329, pl.2, figs.11,12

Gephyrocapsa oceanica Kamptner subsp.2 - Rio, 1982, p.330, pl.2, figs.4,5,7,9,10

Remarks : The populations of the large-size coccoliths in the associations with a bimodal distribution of size in the Singa IV section are assigned to this species. The morphological variation in the assemblages fits in well with Samtleben's (1980) biometrical description of *G. caribbeanica*. The diameter of the coccoliths varies between about 3 and 5.5 μ . The central opening size is variable; (very) small and intermediate openings are most common (see figure 36). There is no preference for a particular relative collar size. The angle between the cross-bar and the longer axis of the coccolith is less than 45° . Between samples JT9629 and JT9676 the average diameter is seen to increase gradually from

about 3.5 μ up to about 5 μ . Rio (1982) reported the same trend in the *Gephyrocapsa*-associations from the Lower Pleistocene of other Mediterranean sequences and of extra-Mediterranean deep-sea cores.

In some samples from lower stratigraphic levels (Aghios Vlassios, Punta di Maiata, Singa III, basal part of Singa IV), the *Gephyrocapsids* show a wide diameter range and relatively large diameters as well. It is tempting to assign the largest specimens ($> 3.5 \mu$) in such associations to *G. caribbeanica*, but such specimens seem to show a continuous morphological variation with the smaller sized *Gephyrocapsids* in the samples. Samtleben (op. cit.) remarked that in many associations the species *G. caribbeanica* is hard to separate from *G. margereli*. The coccoliths of the latter taxon, which seem to be present in our *Gephyrocapsa* spp., show a similar morphology but their average diameter is smaller.

BIOSTRATIGRAPHY

The changes in the composition of the coccolith taphocoenoses of the Noëlaerhabdaceae yield a surprisingly refined biostratigraphic subdivision of our Pliocene sections. Such a stratigraphy offers the advantage that it is based on the most prolific of the Neogene nannofossil families. Once one has gained some practice in evaluating the distribution of coccolith size in the association, it is usually quite easy to establish the specific composition of the flora, and hence its biostratigraphic position. It should be borne in mind that most of our species of *Reticulofenestra* are coccolith assemblages with quite a wide morphological variation. A particular morphotype may belong to a certain species in sample x, whereas it occurs in the variation of another species in sample y.

We cannot show the exact frequency distribution of our species on the basis of 200-counts. The 200-counts pertain only to the Cretan samples. Furthermore, in our light-microscope study we did not make observations on the collar and peripheral slits in specimens smaller than 4 measuring units. However, we have a good qualitative and semi-quantitative record of the composition of the associations in all samples (distribution patterns of size), we have a quantitative record of *Reticulofenestra pseudoumbilicus* close to its disappearance (see below), and there is a detailed record of the numerical distribution of the *Gephyrocapsids*.

For the framework and the control on the correlative value of the changes in the associations, we use the planktonic foraminiferal zones and zonal intervals, described by Spaak (1983).

The exit of *Reticulofenestra pseudoumbilicus*

In order to have a detailed record of the distribution of *R. pseudoumbilicus* in the highest part of its range, we established the species' frequencies in 10,000 counts in two sets of closely spaced samples in the sections Aghios Vlassios on Crete and Punta di Maiata on Sicily (fig.38). The graphs show that it is impossible to indicate a particular horizon of highest occurrence, as from a certain level upwards the species was found intermittently and with very low numbers. Even in those samples which yielded no specimen in the 10,000 count, we observed one or a few specimens in an additional search.

On average, the frequencies in the Punta di Maiata samples are higher than those in the corresponding interval in the Aghios Vlassios section, but there is some similarity in the graphs. The lowermost samples show relatively high frequencies. Higherup, there is an interval with lower and variable frequencies, and in the uppermost samples the scores are very low or zero. The most easily recognizable horizon which can be used for the taxon's exit-level in such a numerical sequence seems to be the level of the stratigraphically highest frequency drop to near-zero ('highest common occurrence ; subtop'). In Aghios Vlassios, we locate this break between samples CP2248 and CP2249, and in Punta di Maiata between CP4109 and CP4110. The accuracy of the correlation

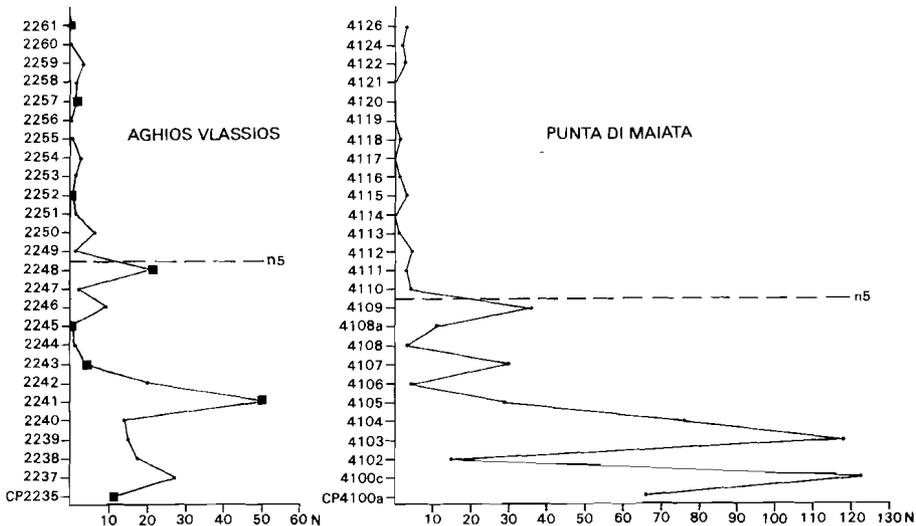


Fig.38 Frequency of *Reticulofenestra pseudoumbilicus* in the uppermost part of its range in the sections Aghios Vlassios and Punta di Maiata ($N = \pm 10,000$). Black squares (■) in the Aghios Vlassios curve indicate samples from sapropelic layers. Horizon n5 shows the subtop of the species.

between both sections on the basis of this biohorizon cannot be estimated, but for the time being we consider it to be relatively low.

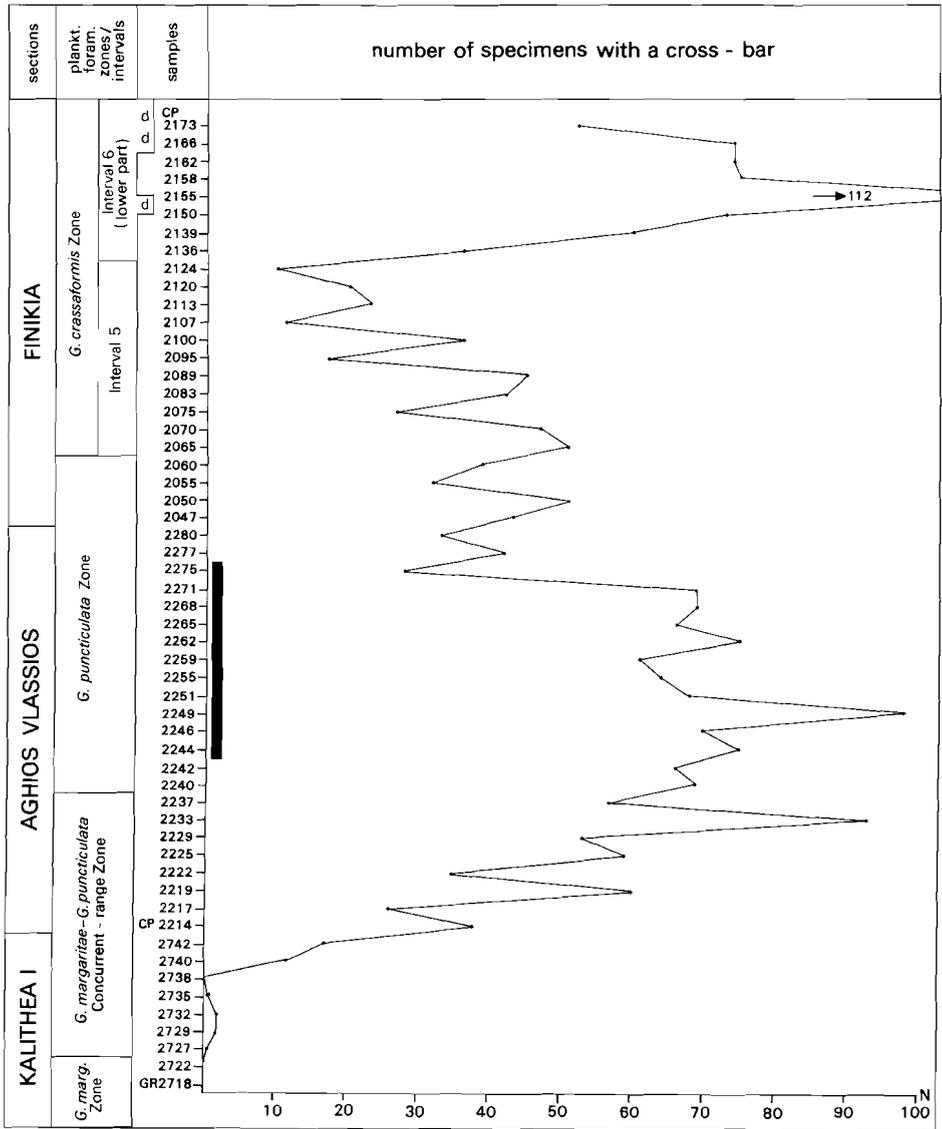


Fig.39 Frequency of specimens with a cross-bar in the Cretan composite section (N=200). The presence of relatively large specimens (> 3.5 μ) is indicated with a vertical bar on the left-hand side of the graph.

The frequency distribution of *Gephyrocapsa*

For a good comparison between the Italian and the Cretan record, we established the frequency of the *Gephyrocapsid* taxa in some more samples from the Cretan sections. The resulting frequency diagram for the Cretan composite sequence (fig.39) is remarkably similar to the diagram for the corresponding interval of the Italian sections Singa I/IA and Punta di Maiata (figs.29,31). Like in the Singa section, we found a few *Gephyrocapsids* in the lowermost part of the *G. margaritae* - *G. puncticulata* Concurrent-range Zone in Kalithea I. Higher up in this zone, the frequencies increase rapidly, leading to a series of samples in which 30 to 50 % of the Noëlaerhabdacean coccoliths are *Gephyrocapsids*. The upper part of the above mentioned foraminiferal concurrent-range zone and the major part of the next higher *G. puncticulata* Zone show this acme of *Gephyrocapsa*. There are large specimens present in samples from the higher part of this acme zone. In the upper part of the *G. puncticulata* Zone and the lower part of the *G. crassaformis* Zone, the frequencies show considerably lower relative values. There is another acme in the lower part of Interval 6 of the *G. crassaformis* Zone. In comparison with the associations in the samples from Italy, the *Gephyrocapsids* are on average far more frequent in the material from Crete.

The *Gephyrocapsa* record in the higher part of the Upper Pliocene was established in the Italian sections Punta Piccola and Monte Singa (figs.34,35). In the higher part of Interval 6 of the *G. crassaformis* Zone, which is above the second interval with predominant dextral coiling of *G. crassaformis*, the *Gephyrocapsids* are very low- frequent up to the *Neogloboquadrina atlantica* interval (Interval 7). Higher up, the frequencies are seen to increase again, leading to a third acme in the *G. inflata* Zone. As mentioned already in chapter 8, the frequency as well as the maximum diameter of *Gephyrocapsa* show an upwards increase in this interval. The uppermost samples of Singa IV show a combination of assemblages of small size and large size specimens (*Gephyrocapsa* spp. and *G. caribbeanica*).

Biostratigraphy on the basis of the distribution of the Noëlaerhabdaceae

The range chart of figure 40 gives a semi-quantitative picture of the frequency distribution of the species of the Noëlaerhabdaceae in the Pliocene/Lower Pleistocene of our sections. On the basis of various changes in the Noëlaerhabdacean association, we are able to recognize a series of biohorizons (coded with prefix 'n'), allowing some 13 biostratigraphic intervals to be distinguished. The corresponding sample-intervals in the sections are also shown in figure 40.

Generally, the intervals are readily recognizable but in some of them the composition of the Noëlaerhabdaceae is quite similar. Furthermore, not all biohorizons are very clear-cut as some of them are based on a gradual frequency change (e.g. the boundaries of the acmes of *Gephyrocapsa* spp.).

From the base of the Pliocene upwards, the biohorizons correspond with the following changes in the associations of the Noëlaerhabdaceae :

- n1) change in the large-size coccoliths from predominantly *R. antarctica* to predominantly *R. pseudoumbilicus* ; low-frequency entries of *R. minutula* and *E. ovata*
- n2) size-increase of the coccoliths of *R. pseudoumbilicus* ; increase of the frequencies of *R. minutula* and of *E. ovata* ; appearance of rare *Gephyrocapsa* spp. ; decrease of *R. minuta*
- n3) frequency increase of *Gephyrocapsa* spp. to common
- n4) *Gephyrocapsa* spp. increase to become abundant
- n5) (nearly complete) disappearance of *R. pseudoumbilicus*, preceded by the appearance of *Reticulofenestra* sp. and of subcircular specimens of *E. ovata*
- n6) first frequency decrease of *Gephyrocapsa* spp.
- n7) second frequency increase of *Gephyrocapsa* spp. ; most of the assemblages of *R. minuta* show small-size coccoliths, whereas the coccoliths of *R. minutula* become relatively large
- n8) second frequency decrease of *Gephyrocapsa* spp.
- n9) *R. minuta* becomes relatively low frequent, *R. minutula* becomes relatively abundant ; possibly the disappearance level of *Reticulofenestra* sp.
- n10) increase again of *R. minuta*, decrease of *R. minutula* ; third but gradual frequency increase of *Gephyrocapsa* spp.
- n11) *Gephyrocapsa* becomes abundant
- n12) appearance of a *Gephyrocapsa* association with a bimodal distribution of the coccolith diameter (appearance of *G. caribbeanica*)

In chapter 13, we will discuss these events and their timing in the context of a zonal scheme for the Pliocene in the Mediterranean. Their significance in terms of paleoenvironmental change will be dealt with in chapter 14.

THE ROLE OF EU-DISCOASTER IN BIOSTRATIGRAPHY

From the earliest days of calcareous nannofossil biostratigraphy, it has been recognized that the discoasters are valuable biostratigraphic instruments. In fact, it was on the basis of the limited stratigraphical range of some *Eu-discoaster* species that Bramlette and Riedel (1954) pointed out the possibility of developing a calcareous nannofossil biostratigraphy. Since then, numerous zones are distinguished in the Tertiary on the basis of events in the *Eu-discoaster* associations (see for example Hay et al., 1967; Gartner, 1969; Martini, 1971; Bukry, 1973b, 1975). The discoasters appear in the Upper Paleocene (Aubry, 1986). Discoasters are unimportant for the biostratigraphy of Oligocene/Lower Miocene sediments due to the very low diversity of the *Eu-discoaster* floras (Bukry, 1978a; Perch-Nielsen, 1985).

In chapter 2 it was observed that some 5 or 6 *Eu-discoaster* events figure in the biostratigraphic schemes of the Pliocene (see figure 1). In the following paragraphs, the appreciation of these biohorizons in the bio- and chronostratigraphy of the Mediterranean Pliocene will be discussed.

THE LOWER AND UPPER BOUNDARIES OF THE PLIOCENE

In the literature, opinions vary as to the position of the Miocene/Pliocene boundary in the calcareous nannofossil schemes. The selected levels range from the top of the *Eu-discoaster quinqueramus* Zone (NN11 of Martini and Worsley, 1970; CN9 of Okada and Bukry, 1980) to some level in the *Ceratolithus rugosus* Zone (NN13), or the *C. rugosus* Subzone (CN10c), respectively (for reviews see Berggren, 1973; Rio et al., 1984b). A Miocene/Pliocene boundary stratotype section has been chosen in the Capo Rossello section on Sicily, covering the boundary between the Arenazzolo facies and the Trubi facies (Cita, 1975). It appears to be difficult to translate this lithohorizon in terms of biostratigraphy, as the relevant marker species (*Eu-discoaster quinqueramus*, *Triquetrorhabdulus rugosus*, *Ceratolithus amplifiscus*, *C. rugosus*) are not or only very scarcely present in Mediterranean sediments. However, recent magnetostratigraphic data permit a chronostratigraphic correlation of the Mediterranean Miocene/Pliocene boundary. Zijdeveld et al. (1986) pinpointed the boundary in the Singa section in South Italy at a level slightly below the Thvera Subzone of the Gilbert Reversed Polarity Zone; its age was estimated to be 4.83 or 4.84 Ma (see fig.5). According to the correlation scheme of Berggren et al. (1985), this

magnetostratigraphic level corresponds with an horizon in the upper part of the *Ceratolithus tricorniculatus* Zone (NN12), i.e. in Bukry's *Ceratolithus acutus* Subzone (CN10b).

The Pliocene/Pleistocene boundary, in the sense of the new boundary stratotype section of Vrica in Calabria (Selli et al., 1977), is immediately above the Olduvai Subzone of the Matuyama Reversed Polarity Zone (age about 1.64 Ma ; Aguirre and Pasini, 1985). In terms of calcareous nannofossil zones, this horizon in the Vrica section is situated in the basal part of Martini and Worsley's (1970) *Pseudoemiliana lacunosa* Zone (NN19), above the exit of the last Discoasterid species, *E. brouweri* and below the exit of *Calcidiscus macintyrei* (Cati and Borsetti, 1981; Backman et al., 1983). The horizon is to be located in Bukry's *Crenolithus doronicoides* Zone (CN13). The application of Bukry's subzonal subdivision appears to be hampered by differences in the taxonomic subdivision of the Gephyrocapsids. Bukry defined a *Gephyrocapsa caribbeanica* Subzone (CN13b) as the interval between the successive entries of *Gephyrocapsa caribbeanica* and *G. oceanica*. Cati and Borsetti (1981) recorded both horizons in the above order in the Vrica section. The entry of *G. caribbeanica* was found to coincide approximately with the e-sapropel. According to Aguirre and Pasini (op. cit.), however, these species enter simultaneously in the Vrica section, some 25 metres above the proposed boundary level. Rio (1982) observed the entry of his *G. oceanica* s.l. some metres below the boundary horizon, while he did not specify the distribution of *G. caribbeanica*.

THE FIRST (COMMON) OCCURRENCES OF *E. ASYMMETRICUS* AND *E. TAMALIS*

In the current biostratigraphic subdivisions of the Pliocene, the lowest *Eu-discoaster* horizon is the base of the *E. asymmetricus* Zone (NN14), or the base of Bukry's homonymous Subzone (CN11b). Although the event is often referred to as the species' first appearance or the lowest occurrence datum (after Gartner, 1969), it has been observed since that *E. asymmetricus* is present in low numbers in Upper Miocene and lowermost Pliocene sediments as well. It is therefore appropriate to define the Pliocene biohorizon under consideration as the base of the acme-interval of *E. asymmetricus* (after Bukry, 1971c; 1973a,b).

A similar pattern is found for the distribution of *E. tamalis*. The species shows an acme in mid-Pliocene sediments as well. The base of this interval is mentioned to be only slightly above the base of the *E. asymmetricus* acme-interval. Through quantification of the *Eu-discoaster* associations from Lower and mid-Pliocene samples, we previously established both the presence and the relative stratigraphic position of the acme intervals of *E. asymmetricus* and *E.*

tamalis (Driever, 1981). By interpolation, Rio et al. (1984b) estimated the ages of the onset of the acmes of both species to be at about 3.80 Ma and 3.70 Ma, respectively.

THE EU-DISCOASTER EXITS IN THE UPPER PLIOCENE

In the course of the Late Pliocene, the number of *Eu-discoaster* species decreased until there were no species left in Pleistocene times. Accordingly, the frame of the Upper Pliocene biozonations consists of a sequence of exit-levels of *Eu-discoaster*. Martini and Worsley (1970) used the last occurrences of *E. surculus*, *E. pentaradiatus* and *E. brouweri* to define the tops of the *E. surculus* Zone (NN16), the *E. pentaradiatus* Zone (NN17) and the *E. brouweri* Zone (NN18), respectively. In the interval between the last occurrences of *R. pseudoumbilicus* and *E. pentaradiatus*, Bukry (1973b) distinguished in addition the exit-level of *E. tamalis*.

The biostratigraphy of the Upper Pliocene in the Mediterranean is often conformable to the classical schemes which focus on the *Eu-discoaster* exits (see for instance Stradner, 1973 ; Ellis, 1979). It has been observed, both in Mediterranean and extra-Mediterranean sequences, that the *E. pentaradiatus* Zone or Bukry's homonymous Subzone is very thin or even indistinguishable because the levels of highest occurrence of the critical species (*E. surculus* and *E. pentaradiatus*) were found to coincide or nearly so (Bukry, 1973a ; Müller, 1978; Raffi and Rio, 1979, 1980c). In Mediterranean sections, the total number of *Eu-discoaster* specimens shows a marked decrease in or at about the *E. pentaradiatus* Zone (Driever, 1984). In the next higher *E. brouweri* Zone, *E. brouweri* is seen to be low frequent and discontinuously present. Despite such a distribution characteristic, the highest occurrence level of the species in Mediterranean sections is considered to be of correlation value (Rio et al., 1984b). In the Vrica section, Backman et al. (1983) found a relative increase of the three-rayed variety *E. triradiatus* immediately below the highest occurrence level of *E. brouweri*. Backman and Shackleton (1983) observed such a *E. triradiatus* acme in the same biostratigraphic position in *Eu-discoaster* - rich sequences outside the Mediterranean as well.

THE STANDARD FOR QUANTIFICATION

In the literature, most data concerning the distribution of the species of *Eu-discoaster* are based on qualitative or semi-quantitative observation. Such data may be pure presence-absence accounts. Evidently, one's appreciation of the ac-

curacy of the biostratigraphic assignment of a sample increases markedly if there is some impression of the frequency of the key species in the sample. Such information is to be evaluated against the existing data pool of the vertical frequency distribution of the species. In its turn, each time the frequency of a particular species is established and published, the data pool is enlarged. The more precise and repeatable such abundance data, the higher is the quality of this standard of comparison.

The fastest, but also the most subjective method of gathering abundance data is the qualitative estimate of abundance (many, scarce). However, a numerical expression of the abundance, if based on counts according to a standardized procedure, is much more objective and repeatable.

Hay (1970) introduced the technique of the 'logarithmic estimates'. This method consists of grouping the taxon's scores in a few categories, defined on the basis of the number of fields of the slide which had to be scanned in order to find one specimen. Following this procedure, Raffi and Rio investigated several sedimentary sequences in the Mediterranean Pliocene. Backman and Shackleton (1983) used another standard for quantification. In the case of the discoasters (except *E. triradiatus*), they established the number of specimens of the critical taxon per standard slide area. In practice, for each species the number of fields to be searched was determined. For the sake of comparison, the scores of the various species were subsequently recalculated for a standard slide area (1 mm²). Compared with the Hay-method, this procedure yields more detailed numerical data sets and, in addition, a numerical evaluation of the relations between the counted taxa.

Because a number of view fields is used as the counting standard, Schmidt (1978) objected against such methods. In his view, the repeatability of the thus obtained scores is negatively influenced by fluctuations in the overall particle density of the slides (even if prepared by a single operator), as well as by fluctuations in the proportion of the calcareous nannofossil particles relative to all other particles in the rock sample. In other words, the scores do not relate to comparable total numbers of calcareous nannofossils. Such objections can be more or less overcome if for each slide a measure of the calcareous nannofossil density is given (cf. Raffi and Rio, 1979), or if one concentrates on preparing slides with a comparable particle concentration (Backman and Shackleton, op. cit.).

Schmidt (1978) concentrated on numerical estimates of the abundances of the calcareous nannofossil species, which procedure is supposed to yield reproducible results. As a measure for the abundance of rare species (Discoasterids, Ceratolithids), he chose to establish their frequency per 10,000 calcareous nan-

nofossils. The application of such a standard requires that in each slide the average nannofossil concentration per field is estimated, after which this number is extrapolated in terms of a traverse length belonging to a 10,000 count in that particular slide. Schmidt (1979) suggested that scores of marker species that are lower than 10 specimens per 50,000 nannofossils reflect pure chance occurrences. It was proposed by Schmidt et al. (1979) to restrict this 50,000 standard to all non-Noëlaerhabdacean nannofossils; such a restriction, however, seems to be an unnecessary complication of the standard. In the opinion of C.W. Drooger (1980), a relative frequency of 0.01 % is a practical limit for establishing the presence or absence of a marker species.

Another method of dealing with the frequencies of species is to concentrate on a fixed number of specimens from a group of potential candidates (Schmidt, 1979; Schmidt et al., 1979; Backman and Shackleton, 1983). In Pliocene sediments, such groups are, for example, the Discoasterids and the Ceratolithids. The counting results are no direct measure for the abundance of a taxon relative to the entire nannofossil association. On the other hand, such counts yield a very good and repeatable impression of the inter-specific frequency relations.

QUANTITATIVE DATA IN THE LITERATURE

To our knowledge, there are only a few studies dealing with quantification of Pliocene *Eu-discoaster* associations. Bukry (1975, 1978b) tried to gain an impression of the paleogeographical distribution of species of *Eu-discoaster* in the 'E. tamalis time-slice' on the basis of counts in some samples from different DSDP sites in the Atlantic and Pacific Oceans. The results were interpreted in terms of a preference for warm waters in the case of *E. pentaradiatus* and *E. brouweri*, and a preference for cooler waters for *E. surculus* and *E. intercalaris*.

Backman and Shackleton (1983) presented an extensive study of the numerical distribution of Pliocene index-species in deep-sea cores from the Atlantic, Pacific and Indian Oceans. As a standard for quantification of the discoasters they used a constant slide area (see above). Their taxonomic concept is virtually the same as ours. The counting data concerning the exits of the *Eu-discoaster* species show that in the case of nearly all species one cannot indicate a reliable extinction level from the highest or last observed occurrence. The frequencies commonly show an interval in which the species is regularly present in fair numbers, followed by an interval which shows a discontinuous presence of the species and very low frequencies. Most species-ranges show a conspicuous frequency drop which is the obvious level for drawing the true exit

boundary. On the basis of a comparison between the frequency distribution of *E. brouweri* and that of other, apparently reworked discoasters, it was investigated whether the low and intermittent scores in the uppermost part of the range of *E. brouweri* are due to reworking. In the samples below the conspicuous frequency decrease, *E. brouweri* is far more abundant than the total of reworked discoasters. From the level of the frequency decrease upwards, the *E. brouweri* abundances are in the order of magnitude of those of the reworked species and, moreover, both categories often show positive correlation. It is therefore assumed that the stratigraphically highest frequency decrease of importance reflects the extinction of the species, and that all stratigraphically higher occurrences are due to reworking. On the basis of similar frequency patterns, Doeven et al. (1982) distinguished between a species' first (lowest) occurrence and its first (lowest) common or stratigraphically regular occurrence (called the species' subbottom). Likewise, there is the last (highest) occurrence and the last common or stratigraphically regular occurrence (subtop). Subtops and subbottoms are the obvious horizons to be selected for correlation.

By means of magnetostratigraphic correlation, Backman and Shackleton (1983) gave numerical ages to many of the Pliocene/Lower Pleistocene calcareous nannofossil events, used in biostratigraphy. They showed that, according to the frequency patterns found, the subtop of the coccolithophore species *Calcidiscus macintyreii* (1.45 Ma) and those of *Eu-discoaster brouweri* (1.88 Ma) and *E. tamalis* (2.65 Ma) are reliable horizons in their sample sequences. They considered the usefulness of the disappearance levels of *E. asymmetricus*, *E. pentaradiatus* and *E. surculus* to be lower, either because of the absence of distinct frequency changes in series of low-frequency scores, or because the succession of events was not consistent throughout the cores.

COUNTING METHOD, MATERIAL AND TAXONOMY, USED IN
THE EU-DISCOASTER ANALYSES

METHOD AND MATERIAL

A count of 100 *Eu-discoaster* specimens per sample was thought to give a good impression of the quantitative composition of the *Eu-discoaster* floras. It should be realized that the sum of discoasters in our samples rarely exceeds 1 % of the total nannofossil association. If a species of *Eu-discoaster* does not score in the 100-counts, it can be safely assumed to be extremely low frequent or entirely absent. We counted the first 100 specimens of *Eu-discoaster* in successive fields along random traverses. If there were very few discoasters in a sample, we stopped the count. This was necessary only in the case of samples from the diatomites of the Finikia section, and in the case of samples from the uppermost Pliocene.

Because the discoasters become scarce in the Upper Pliocene of the Mediterranean, it is important to furnish the frequency data of the 100-counts with a measure of the overall abundance of the discoasters. In selected samples, we made estimates of the discoaster frequencies relative to a fixed total number of calcareous nannofossils. Following Schmidt (1978), we used a total number of 10,000 calcareous nannofossil specimens as a standard. In order to arrive at the corresponding area to be scanned in each particular slide, an estimate was made of the average concentration of calcareous nannofossil specimens per unit slide area (i.e. a photographic field, provided by an ocular template). We counted in each slide the first 2000 nannofossil specimens in successive fields along a random traverse. The average concentration, thus obtained for the particular slide, was subsequently extrapolated to a traverse length, supposedly corresponding with a number of 10,000 nannofossils. We concentrated our 10,000 estimates on Upper Pliocene sections in which we expected to find the exit of nearly all discoaster species, as well as the overall decrease in discoaster abundance.

In a previous paper, we presented the results of the 100-counts in samples from the sections Aghios Vlassios and Finikia on Crete, and from the Punta di Maiata section on Sicily (Driever, 1981). The counting data will be repeated in the present paper (figs.41,42,44). A closely spaced set of 148 samples was investigated from the two Cretan sections. These sections show a small stratigraphic overlap (see Chapter 3). As there is uncertainty about the vertical stratigraphic continuity in the basalmost part of the Aghios Vlassios outcrop,

the data from the sample interval CP2322 up to CP2341 are now omitted from the frequency chart. For a numerical age estimate of the base of the acme-interval of *E. asymmetricus*, we counted the discoasters in the critical interval of the Singa IA subsection.

In order to complete our picture of the composition of the *Eu-discoaster* floras in the Upper Pliocene, we made 100-counts in 75 samples, taken in the sections Punta Piccola and Monte San Nicola on Sicily. Punta Piccola gives a detailed stratigraphic record of the top part of Interval 5 and almost the entire Interval 6 of the *G. crassaformis* Zone (Chapter 3). The sediments of Monte San Nicola range from the Lower Pliocene into the Pleistocene, but in the upper part of the section the discoasters are too scarce for 100-counts.

We made estimates of the *Eu-discoaster* frequencies relative to the 10,000 standard in samples from the Upper Pliocene of the sections Francocastello, Monte San Nicola and Monte Singa. Part of the data from the former sections has already been published (Driever, 1984). We gathered new data from a few more samples from these sections. In addition, we studied 40 samples from the Singa II and Singa III subsections in order to have a direct link with the magnetostratigraphic record.

Summarizing, our *Eu-discoaster* data cover the entire Pliocene, with the exception of the lowermost part (*Sphaeroidinellopsis* Acme-zone and part of the *Globorotalia margaritae* Zone) and the uppermost part where the discoasters are too scanty (uppermost part of the *G. crassaformis* Zone, and the *G. inflata* Zone).

Contrary to our sample selection in the case of the Noëlaerhabdaceae, we also investigated the *Eu-discoaster* floras from laminated sediments. Due to selective dissolution, the sapropelitic facies often yields calcareous nannofossil associations in various states of etching, showing a relative increase of nicely preserved or slightly etched discoasters. In the relatively pure diatomites of the top part of the Finikia section, the calcareous nannofossils are an only minor component of the sediment particles. The discoasters from this facies are too scarce to be counted.

TAXONOMY OF EU-DISCOASTER

Theodoridis (1983, 1984) advocated to use Tan Sin Hok's genus name *Eu-discoaster* instead of the familiar *Discoaster*.

We used the following taxonomic subdivision for describing the quantitative composition of the *Eu-discoaster* associations in our sections :

Family EU-DISCOASTERACEAE Prins, 1971

Genus **Eu-discoaster** Tan Sin Hok, 1927, emend. Theodoridis, 1983

Eu-discoaster quintatus (Bukry & Bramlette) nov. comb.
(Pl.10, figs.1-6)

Discoaster quintatus Bukry & Bramlette, 1969, p.133, pl.1, figs.7,8 (non fig.6, see *D. berggrenii* Bukry, 1971d, p.45)

Discoaster stradneri Cati & Borsetti, 1970, p.629, pl.81, figs.2-4

Discoaster pentaradiatus Tan Sin Hok, Martini, 1971, pl.4, fig.14 ; Huang, 1980, pl.6, figs.4a-c ; Moshkovitz and Ehrlich, 1980, p.17, pl.6, fig.22 ; Driever, 1981, p.444, pl.2, figs.1-16, pl.3, figs.12-15

Discoaster pentaradiatus Tan Sin Hok emend. Bramlette & Riedel, Perch-Nielsen, 1985, p.478, figs.32.12, 33.5

Discoaster quadramus Bukry, 1973d, p.307, pl.9, figs.6-8 ; Perch-Nielsen, 1985, p.479, fig.32.5

Discoaster sp. cf. *D. pentaradiatus* Tan Sin Hok, Moshkovitz and Martinotti, 1979, p.111, pl.1, figs.8,9 ; Moshkovitz and Ehrlich, 1980, pl.6, figs.12,13,16

Eu-discoaster misconceptus Theodoridis, 1984, p.168, pl.37, figs.19,20, text-figs.A-D

Remarks : The species includes all Neogene discoasters that show birefringence in plan view. In many specimens the ray tips show the typical acute-angled bifurcation, but very often the bifurcation is missing. The five-rayed form is predominant, but occasionally the asteroliths show three, four or six rays. Like the typical five-rayed form, such specimens show optical discontinuity. Each arm behaves as a single crystal, and the direction of its optical axis, being normal to the arm, differs from the directions in the neighbouring arms. Between crossed nicols, the arms are separated by sutural extinction bands in the central area. Often, the specimen is situated in such a way that two (or three) arms are in the plane of view ; those arms do not show birefringence. Due to the umbrella-like shape of the asteroliths, the remaining arms of such specimens are not in the plane of view ; consequently, they will be bright between crossed nicols.

In the literature, the taxon in question is usually referred to as *Discoaster pentaradiatus* (also in Driever, 1981, 1984). However, Theodoridis (1984) correctly distinguished between a non-birefringent five-rayed discoaster species, showing an obtuse angle between the branches of the bifurcation (i.e. Tan's *Discoaster pentaradiatus*), and a more or less birefringent five-rayed species showing an acute angle between the branches of the bifurcation. By creating a new species name for the latter taxon (*Eu-discoaster misconceptus*), however, he neglected existing species names, such as *Discoaster quintatus* Bukry & Bramlette (1969) and *Discoaster quadramus* Bukry (1973d). According to the protologues, these species names fit the taxon in question as regards both its optical construction and its stratigraphic range. One of the paratypes of *E. quintatus* (loc. cit., fig.6) shows a relatively large knob on the concave side, the rays of which point to the inter-arm area. Bukry (1971d) subsequently transferred this atypical specimen to his *Discoaster berggrenii*.

Eu-discoaster brouweri (Tan Sin Hok) Theodoridis
(Pl.12, figs.1-5; Pl.13, fig.6)

- Discoaster brouweri* Tan Sin Hok, 1927, p.202, figs. 8a,b (invalid, ICBN art.43.1)
Discoaster brouweri Tan Sin Hok, 1931, p.93
Discoaster brouweri Tan Sin Hok emend. Bramlette & Riedel, 1954, p.402, pl.39, fig.12, text-fig.3a,b ; Perch-Nielsen, 1985, p.474, figs.32.11,33.3
Discoaster brouweri Tan Sin Hok, Martini, 1971, pl.4, fig.15 ; Bukry, 1971d, pl.1, figs.2,7 (non fig.1) ; Driever, 1981, p.445, pl.1, figs.7-9, pl.3, figs.2-5
Eu-discoaster brouweri (Tan Sin Hok) Theodoridis, 1983, p.17 ; Flores, 1986, p.231, pl.2, figs.1,3,5,7a?,7b,8,9 (non fig.4)
Eu-discoaster brouweri (Tan Sin Hok) Theodoridis subsp. *brouweri* Theodoridis, 1984, p.177, pl.36, fig.13

Remarks : The species is confined to the six-rayed specimens of the *Eu-discoaster brouweri* group. Often, the tips of the rays are bent downwards. Knobs are not or only poorly developed. In the first series of sample counts, some very rare three-rayed specimens (our *E. triradiatus*) were included in *E. brouweri* as well.

Eu-discoaster asymmetricus (Gartner) Theodoridis
(Pl.12, figs.6-10)

- Discoaster asymmetricus* Gartner, 1969, p.598, pl.1, figs.1-3 ; Martini, 1971, pl.4, fig.12 ; Bukry, 1971d, pl.1, figs.3,4 ; Driever, 1981, p.444, pl.1, figs.10-12, pl.3, figs.7-9 ; Perch-Nielsen, 1985, p.476, figs.32.3,33.2
Eu-discoaster asymmetricus (Gartner) Theodoridis, 1983, p.17 ; Flores, 1986, p.236, pl.3, figs.3,5,7, pl.4, fig.9

Remarks : *E. asymmetricus* is the asymmetrical, five-rayed species of the *E. brouweri* group. In Pliocene samples, the species is easily distinguished from the other five-rayed species *E. quintatus* on the basis of its optically homogeneous construction.

Eu-discoaster tamalis (Kamptner) Theodoridis
(Pl.12, fig.11; Pl.13, figs.1-3)

- Discoaster tamalis* Kamptner, 1967, p.166, text-fig.29 ; Bukry, 1973c, pl.5, fig.3 ; Raffi and Rio, 1979, pl.9, fig.3 ; Driever, 1981, p.444, pl.1, figs.13-15, pl.3, figs.10,11 ; Perch-Nielsen, 1985, p.479, figs.32.6,33.4
Eu-discoaster tamalis (Kamptner) Theodoridis, 1983, p.18

Remarks : With the exception of occasional mal-formed specimens of other species, the four-rayed discoasters of the Pliocene are *E. tamalis*. It is the four-rayed representative of the *E. brouweri* group.

Eu-discoaster triradiatus (Tan Sin Hok) nov. comb.
(Pl.13, figs.4-6)

- Discoaster triradiatus* Tan Sin Hok, 1927, p.204 ; Dermitzakis and Theodoridis, 1978, pl.37(2), fig.4 ; Perch-Nielsen, 1985, p.479, fig.32.7

Discoaster brouweri Tan Sin Hok, Bukry, 1971d, pl.1, fig.1 (non 2,7)
Discoaster brouweri Tan Sin Hok (3-rayed), Raffi and Rio, 1979, pl.9, figs.1,2

Remarks : *E. triradiatus* is the three-rayed species of the *E. brouweri* group.

Eu-discoaster surculus (Martini & Bramlette) Theodoridis (Pl.11, figs.5-9)

Discoaster surculus Martini & Bramlette, 1963, p.854, pl.104, figs.10-12 ; Martini, 1971, pl.4, fig.13 ; Raffi and Rio, 1979, pl.9, fig.6 ; Driever, 1981, p.445, pl.1, figs.1-3, pl.2, figs.17-19, pl.3, fig.1 ; Perch-Nielsen, 1985, p.478, figs.31.9,33.10
Eu-discoaster surculus (Martini & Bramlette) Theodoridis, 1983, p.18 ; Theodoridis, 1984, p.160

Remarks : The species is characterized by trifurcated ray-tips and (nearly) parallel-sided arms.

Eu-discoaster variabilis (Martini & Bramlette) Theodoridis (Pl.11, figs.1-4)

Discoaster variabilis Martini & Bramlette, 1963, p.854, pl.104, figs.4-8 ; Driever, 1981, p.445, pl.1, figs.4-6 ; Perch-Nielsen, 1985, p.474, fig.31.14
Discoaster variabilis group - Backman and Shackleton, 1983, p.144
Discoaster variabilis Martini & Bramlette subsp. *decorus* Bukry, 1971d, p.48, pl.3, figs.5,6
Discoaster decorus Bukry, 1973c, p.677, pl.2, figs.8,9, pl.4, fig.11 ; Perch-Nielsen, 1985, p.479, fig.32.9
Eu-discoaster variabilis (Martini & Bramlette) Theodoridis, 1983, p.19 ; Theodoridis, 1984, p.158, pl.32, fig.8

Remarks : Our *E. variabilis* includes the non-birefringent six-rayed discoasters with (nearly) parallel-sided arms and a more or less pronounced bifurcation. In badly preserved material, it is often difficult to distinguish between *E. surculus* and *E. variabilis*. Many such specimens had to be assigned to the indeterminable six-rayed discoasters.

Indeterminable six-rayed discoasters (Pl.11, figs.10,11)

Actually, this category should consist of heavily overgrown and/or partly dissolved specimens of *E. brouweri*, *E. surculus* and *E. variabilis*. However, we now recognize that, due to inexperience, we may have included quite a few reworked and badly preserved Eocene, Oligocene and Miocene discoasters as well.

It should be realized that, especially in the samples with many indeterminable six-rayed discoasters as a consequence of bad preservation, the frequencies shown for *E. brouweri*, *E. surculus* and *E. variabilis* are underrated. As we could identify virtually all discoasters with three, four and five rays, the frequencies of the species *E. triradiatus*, *E. tamalis*, *E. asymmetricus* and *E. quintatus* are representative.

Chapter 12

THE FREQUENCY DISTRIBUTION OF THE SPECIES OF *EU-DISCOASTER* IN THE MEDITERRANEAN PLIOCENE

RESULTS OF THE 100-COUNTS

Working with a magnification of 1250 X, our average traverse length for the 100-counts was about 65 mm (2.5 traverses). Only in rare cases did we spend more than one hour per sample.

The counting results are shown in the matrices of Tables 24-29 (see appendix). Frequency diagrams of the 100-counts are presented in figures 41 (Aghios Vlassios), 42 (Finikia), 43 (Singa IA), 44 (Punta di Maiata), 45 (Punta Piccola) and 46 (Monte San Nicola).

Unfortunately, the category of indeterminable six-rayed discoasters was found to be numerically large, especially in samples from the sections on Sicily. A large number of indeterminable six-rayed discoasters in a sample is indicative of bad preservation of the nannoflora. In such samples, the frequencies of *E. brouweri*, *E. surculus* and *E. variabilis* should be treated with care.

There are considerable, seemingly irregular fluctuations in the scores, but still some prominent changes in the records of the various *Eu-discoaster* species can be observed. Such changes are manifest in a persistent increase or decrease of a taxon's frequency, and they seem to refer to the (renewed) appearance or the (temporary) disappearance of a taxon. However, such appearances and disappearances are not simply to be understood as presence- and absence-intervals. In the case of the six-rayed species *E. brouweri*, *E. surculus* and *E. variabilis*, the low-frequency-ranges may be an artefact of bad nannofossil preservation. As, on the other hand, such ranges reflect primary signals in the case of the well-recognizable species *E. triradiatus*, *E. tamalis*, *E. asymmetricus* and *E. quintatus*, we will especially concentrate on the frequency distribution of the latter species. They show low-frequency-ranges in which the scores in the 100-counts are usually 0 % and never more than 5 %. Therefore, we use a 5.5 % frequency limit (100-counts) for delineating such low-frequency-ranges. Scores lower than 5.5 % are considered to be noise.

We recognized 11 major changes in the succession of the discoaster-floras (biohorizons d1 to d11). Except for the stratigraphically lowest one, we found these events to occur in more than one section and in a consistent order of occurrence. In the discussion of the species' ranges, given below, the planktonic

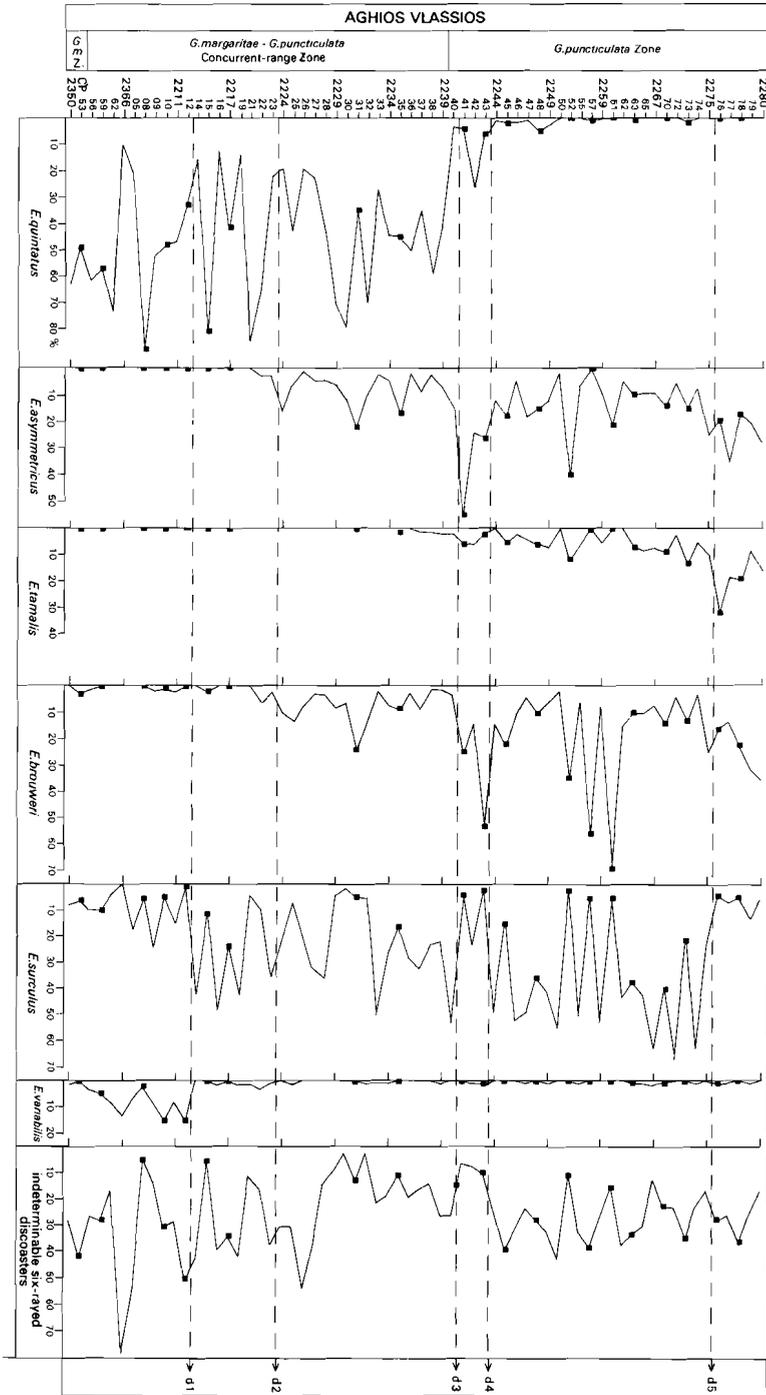


Fig.41 Equally spaced frequency chart of the species of *Eu-discoaster* in section Aghios Vlassios, based on counts of 100 discoaster specimens per sample. Samples from sapropelic layers are indicated with black squares (■), diatomites (in figure 42) are indicated with open circles (○); the remaining samples are from homogeneous marls.

foraminiferal zones will be used as the framework for comparison. A schematic presentation of the frequency patterns of the discoaster species and the arrangement of the various events in a biostratigraphic and chronostratigraphic scheme will be shown in figure 52 (Chapter 13).

Eu-discoaster quintatus

There are considerable fluctuations in the frequencies found for *E. quintatus* in the *G. margaritae* Zone and in the *G. margaritae* - *G. puncticulata* Concurrent-range Zone (sections Aghios Vlassios, Punta di Maiata, Singa IA, Monte San Nicola), but on average the scores are relatively high (average for all sections some 40 %). The frequencies vary between 0 % and 90 %. In the samples from the lower part of the Punta di Maiata section, the relative frequencies of *E. quintatus* seem to be influenced negatively by selective dissolution.

There is a conspicuous low-frequency interval in the range of *E. quintatus*, which approximately corresponds with the *G. puncticulata* Zone (Aghios Vlassios, Finikia, Punta di Maiata, Monte San Nicola). The frequencies in this interval are 0 in most samples, and they reach a maximum of 5 % only in one sample. The lower and upper boundary horizons are d4 and d5, respectively. In our 1981 paper, this interval was described as the *Discoaster pentaradiatus* paracme-interval.

The lower part of Interval 5 of the *G. crassaformis* Zone is characterized by relatively high values (Finikia, Punta di Maiata, Monte San Nicola). Above, the frequencies are relatively low up to the upper part of Interval 6 (same sections + Punta Piccola). The species shows an acme immediately below Interval 7 of the *G. crassaformis* Zone (Monte San Nicola, uppermost samples of Punta Piccola). The acme and its lower and upper boundary horizons (d10 and d11) are more easily recognizable in the 10,000-counts (see below). Horizon d11 coincides with the overall decrease in discoaster abundance. Above this level, *E. quintatus* is virtually absent.

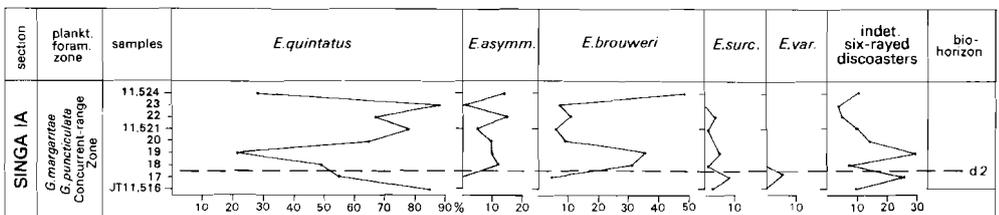


Fig. 43 Frequency of the species of *Eu-discoaster* in the top part of section Singa IA (N = 100 discoasters). *E. tamalis* was not observed.

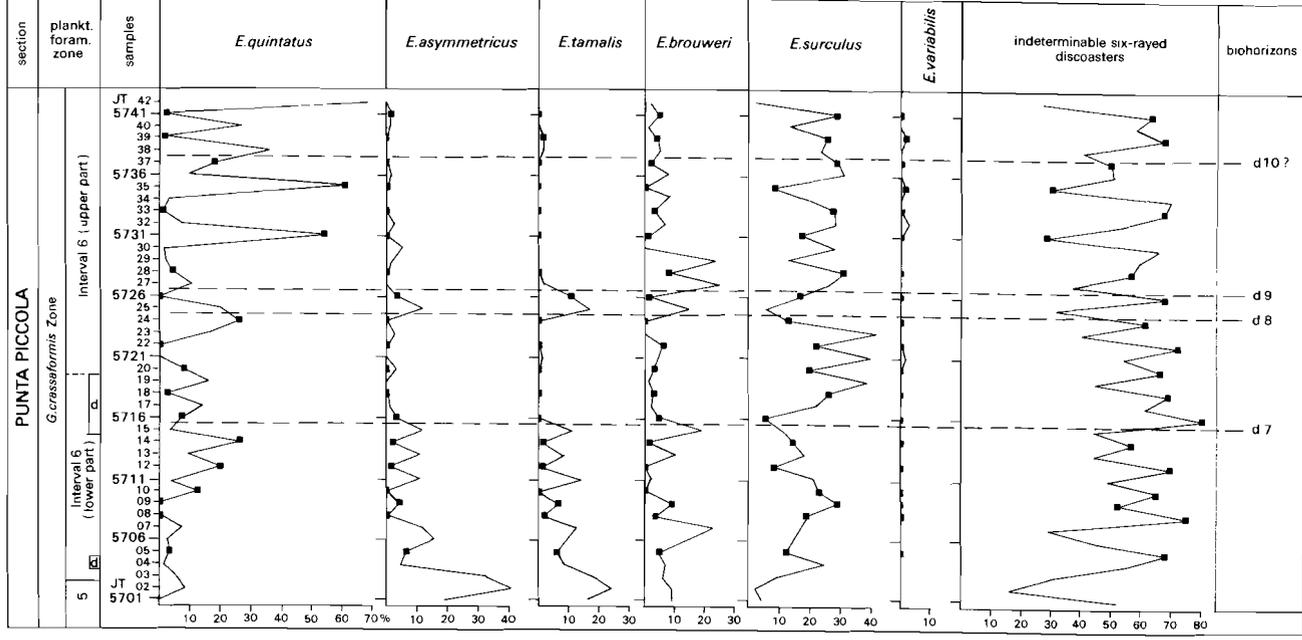
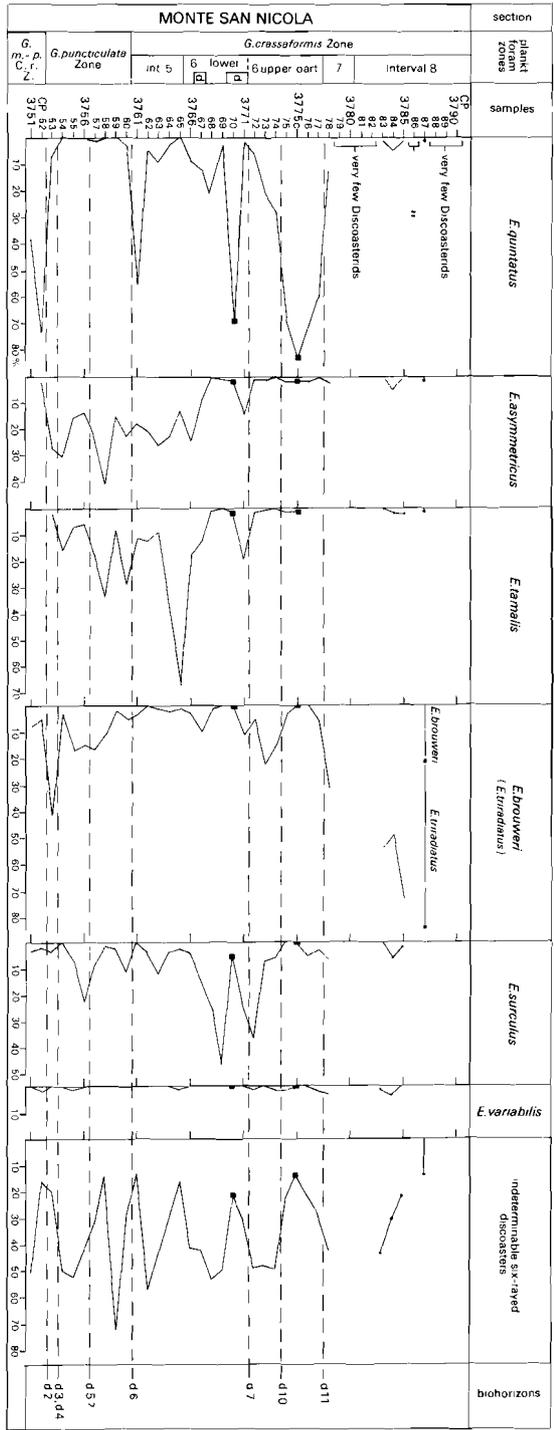


Fig.45 Frequency of the species of *Eu-discoaster* in the Punta Piccola section (N = 100 discoasters). For legend see figure 41.



Eu-discoaster triradiatus

In by far the greater part of our samples, *E. triradiatus* is very rare. However, there is one sample (CP3787) in Interval 8 of the *G. crassaformis* Zone in section Monte San Nicola with relatively many specimens of *E. triradiatus* (horizon d12). As we did not study the discoasters in samples from the overlying *G. inflata* Zone, we failed to record the acme interval of *E. triradiatus* immediately before the exit of *E. brouweri* (Backman et al., 1983).

Eu-discoaster asymmetricus

E. asymmetricus was found only sporadically in samples from the upper part of the *G. margaritae* Zone and the lower part of the *G. margaritae* - *G. puncticulata* Concurrent-range Zone. The species has an acme in the middle of the Pliocene, in which it is nearly continuously present (average in all sections is about 18 %) with frequencies varying between 0 % and 59 %. The base of the acme (horizon d2) was recorded in the sections Aghios Vlassios, Punta di Maiata and Singa IA, and probably in Monte San Nicola. The acme ranges from the upper part of the above mentioned concurrent-range zone up into the second interval with predominantly dextrally coiled specimens of *G. crassaformis* in Interval 6 of the *G. crassaformis* Zone. There is a pronounced frequency decrease slightly below the top of the acme, at a level between the first and the second interval with dextral *G. crassaformis*. Above the acme, *E. asymmetricus* is discontinuously present in low numbers ; it is more frequent again in one sample (JT5725) in Punta Piccola. The latter occurrence is delimited by the horizons d8 and d9 (see *E. tamalis*).

Eu-discoaster tamalis

Like *E. asymmetricus*, *E. tamalis* has a peak interval in mid-Pliocene sediments. The average frequency of *E. tamalis* in this interval is about 14 %, which is slightly lower than the average of *E. asymmetricus* in its acme ; the scores fluctuate between 0 % and 67 %. The base of the interval (horizon d3) is at about the base of the *G. puncticulata* Zone (i.e. the exit-level of *G. margaritae*). The top of the *E. tamalis* acme (d7) coincides with the top of the *E. asymmetricus* acme, which is close to the second interval with predominantly dextrally coiled *G. crassaformis* in Interval 6 of the *G. crassaformis* Zone. Like *E. asymmetricus*, *E. tamalis* shows a decrease in frequencies slightly below the top of its acme, at a level between the first and the second interval with dextrally coiled *G. crassaformis*. In the samples above the acme, *E. tamalis* is sporadically present, except for two samples in the upper part of Interval 6 of the *G. crassaformis* Zone in section Punta Piccola (bounded by horizons d8 and d9).

Eu-discoaster brouweri

Although accompanied by many indeterminable six-rayed specimens, *E. brouweri* seems to be very low frequent in the lower part of the *G. margaritae*-*G. puncticulata* Concurrent-range Zone. At the onset of the *E. asymmetricus* acme, *E. brouweri* shows a clear increase at horizon d2. Up to about the base of the *G. crassaformis* Zone, the species is relatively well represented. In higher stratigraphic levels, the frequencies seem to be lower. *E. brouweri* is the dominant species in the few samples yielding enough discoasters for a 100-count in Interval 8 of the *G. crassaformis* Zone (Monte San Nicola).

Eu-discoaster surculus

As in the case of *E. brouweri*, it is hard to evaluate the quantitative distribution of *E. surculus* in the presence of a considerable number of indeterminable six-rayed discoasters. The latter category is relatively unimportant in the Aghios Vlassios section. Here, the frequencies of *E. surculus* fluctuate between relatively low and high values up to a level with a marked frequency decrease in the upper part of the *G. puncticulata* Zone. The horizon (d5) is pronounced in the sections Aghios Vlassios and Finikia and its position confirms Jonkers' (1984) scheme of bed-to-bed correlations in the Pliocene of Crete. Probably as a result of bad preservation, the event is far less clear in our graphs from the sections Punta di Maiata and Monte San Nicola. In overlying samples, the scores of *E. surculus* appear to be relatively low up to about the base of Interval 6 of the *G. crassaformis* Zone. Higher up, the species seems to be quite frequent up to horizon d10 (base of *E. quintatus* acme). From the latter horizon upwards, *E. surculus* is present discontinuously and in low numbers.

Eu-discoaster variabilis

In our sections, *E. variabilis* seems to be an unimportant member of the discoaster floras, except for a small number of samples in the lower part of the *G. margaritae* - *G. puncticulata* Concurrent-range Zone. In this interval we found frequencies up to 16 %. Both in Aghios Vlassios and in Punta di Maiata there is a frequency decrease (horizon d1) at a comparable biostratigraphic level. Hence, this change seems to be more than a preservational artefact.

Indeterminable six-rayed discoasters

This category is of acceptable proportions in most samples from the Cretan sections Aghios Vlassios (average about 23 %) and Finikia (\pm 27 %). The number of indeterminable specimens is considerable in Punta di Maiata and

Monte San Nicola (average about 36 % and 35 %, respectively). The poor preservation of the discoasters in the Punta Piccola section is such (average about 53 %) that an evaluation of the frequency distribution of the six-rayed species is impossible.

RESULTS OF THE 10,000-COUNTS

The results of the 10,000-counts are shown in the data matrices of Tables 30,31,32 (see appendix). We needed 15 to 30 minutes for determining the average concentration of the slides and for the subsequent discoaster count. Between 4.75 mm and 170 mm of traverse had to be scanned to arrive at the estimated 10,000 specimen number. The average traverse length for the samples from Francocastello was about 30.7 mm ; for the Singa samples it was about 26.5 mm and for the samples from Monte San Nicola it was 20 mm. We dare not speculate on the background of the differences between these averages, as the slides were neither prepared in continuous runs, nor by a single operator. However, we may point out that there seems to be an increase of the dilution of the nannofloras in the upper part of Interval 6 of the *G. crassaformis* Zone both in section Monte San Nicola and in the Singa sequence. The long traverses, needed for several of the sapropelic samples, is caused at least partly by increased dissolution. Traverses are very long in the samples from Interval 7 of the *G. crassaformis* Zone as well. In the Singa sequence, the samples show a strong increase in the relative amount of the calcareous nannofossils at the base of Interval 8. In Monte San Nicola, the increased dilution appears to persist up into the *G. inflata* Zone.

The numbers of *Eu-discoaster* - specimens per 10,000 nannofossils vary between 0 and 169. In many of the sapropelic layers the discoasters show a relative increase, probably as a result of selective dissolution. If we compare the sections on the basis of the *Eu-discoaster* - frequencies in the same biostratigraphic interval (the upper part of the Interval 6 of the *G. crassaformis* Zone up to our horizon d11), it appears that the discoasters are more frequent in the Cretan section Francocastello (average is about 51 specimens ; see figure 47) than in the South Italian sections Monte San Nicola (average about 24 specimens ; figure 48) and Singa II/III (average about 23 specimens ; figure 49).

There is a sustained decrease in the discoaster-sum in the upper part of the *G. crassaformis* Zone. The horizon (d11) is coincident with the top of the uppermost *E. quintatus* acme. The frequency change is very pronounced in the sections Francocastello and Singa III/IV, where it is situated in the lower part of Interval 7 of the *G. crassaformis* Zone. The event is less pronounced in the

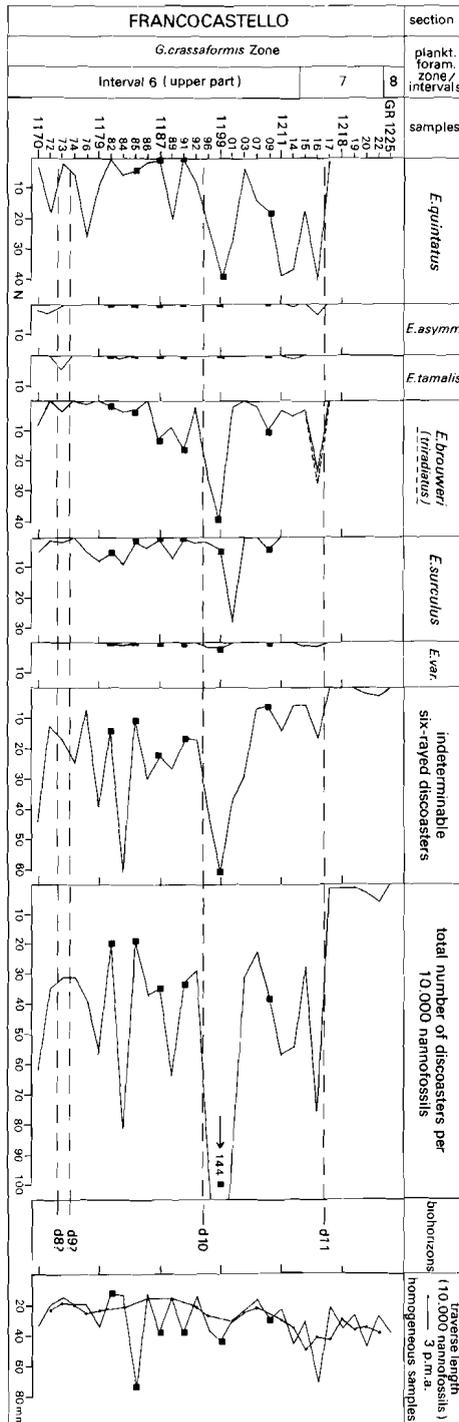
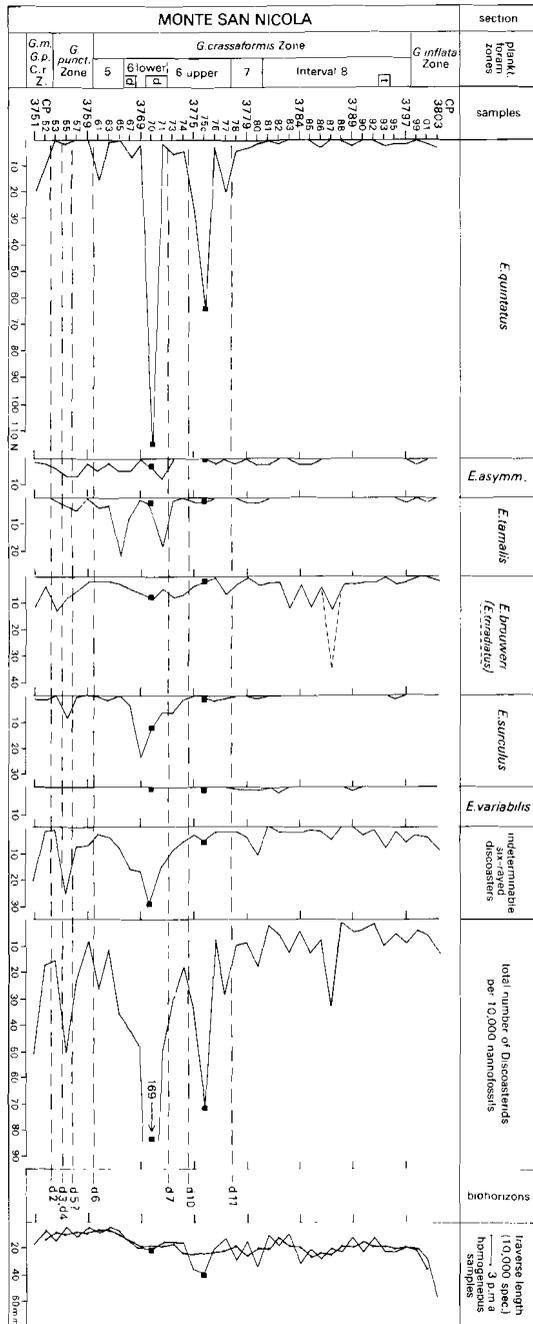


Fig.47

Equally spaced chart of the frequency of the species of *Eu-discoster* in section Francocastello, based on counts of approximately 10,000 calcareous nannofossil specimens. Samples from sapropelic layers are shown with black squares (■), the other samples are from homogeneous marls.



Monte San Nicola section, but it is in about the same biostratigraphic position. In the interval above d11, there are a few samples showing a relative increase of well preserved, seemingly autochthonous *E. brouweri* and *E. triradiatus*. Specimens of the other discoaster species occur only sporadically. Like most of the indeterminable six-rayed discoasters, they are probably reworked.

The frequency patterns of the individual species are similar to the patterns, found in the 100-counts, and the discoaster-horizons are quite easily recognized in the 10,000 counts. Hence, the horizons of the 100-counts reflect increases and decreases relative to the total calcareous nannoflora. Raising the standard in the 'total number counts' for samples in the Mediterranean Pliocene to at least 20,000 specimens seems to be advisable, in order to arrive at a pattern of change that is as easily recognized as that of the 100-counts.

THE ACME OF EU-DISCOASTER TRIRADIATUS IN THE UPPERMOST PLIOCENE

We did not inventory the discoasters from samples from the uppermost Pliocene in a quantitative manner, as *Eu-discoaster* is very rare in Mediterranean sections from Spaak's (1983) Interval 7 of the *G. crassaformis* Zone upwards. Backman et al. (1983) found a relative increase of *E. triradiatus* in an interval

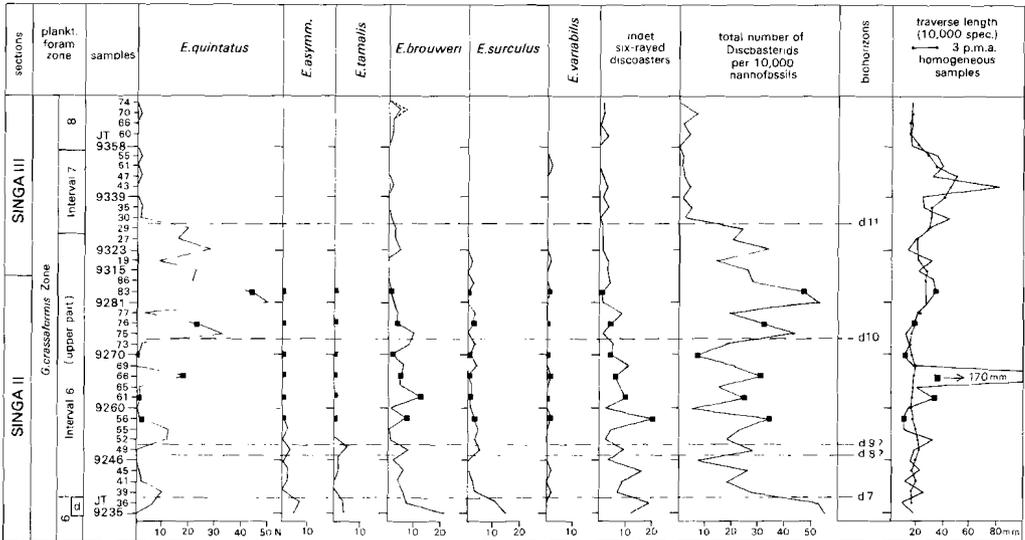


Fig.49 Frequency of the species of *Eu-discoaster* in 10,000-counts in samples from the sections Singa II and Singa III. For legend see figure 47.

covering the upper part of the section Stuni (= Semaforo auct.) and the lowermost part of the Vrica section. The base of this 'acme' is between their sapropels P8 and P9 in Stuni (our B2 and B3 sapropels ; Verhallen, 1987). The top of the acme coincides with the exit of the last *Eu-discoaster* species, *E. triradiatus* and *E. brouweri*, which is a few metres below the base of the Olduvai Subchron in the Vrica section. Actually, the acme pertains to very low specimen numbers (not exceeding two specimens per mm²). Nevertheless, the signal is correlatable with a clear acme of the species in the corresponding stratigraphic position in piston cores from the Atlantic and Pacific Oceans (Backman and Shackleton, 1983).

SUMMARY OF THE EU-DISCOASTER BIOHORIZONS

Recapitulating, we distinguish 13 events in the development of the *Eu-discoaster* floras from the upper part of the *G. margaritae* Zone upwards. In stratigraphic order, the horizons are defined by the following frequency changes :

- d1: decrease (subtop?) of *E. variabilis* ; probably increase of *E. surculus*
- d2: increase (subbottom) of *E. asymmetricus* ; probably increase of *E. brouweri*
- d3: increase (subbottom) of *E. tamalis*
- d4: first decrease of *E. quintatus*
- d5: temporary decrease of *E. surculus* ; further increase of *E. tamalis*
- d6: reappearance of *E. quintatus*
- d7: top of the acmes of *E. asymmetricus* and *E. tamalis*
- d8: base of the short-term reappearance interval of *E. asymmetricus* and *E. tamalis*
- d9: subtop of *E. asymmetricus* and *E. tamalis*
- d10: base of the stratigraphically highest acme of *E. quintatus*
- d11: decrease in total abundance of *Eu-discoaster* and subtop of *E. quintatus* and *E. surculus*
- d12: base of the acme of *E. triradiatus* (after Backman et al., 1983)
- d13: top of the acme and exit of *E. triradiatus* ; exit of *E. brouweri* (after Backman et al., 1983)

THE EXITS OF SPHENOLITHUS SPP. AND CALCIDISCUS MACINTYREI

For easier reference to current zonal schemes, we made in addition observations on the disappearance levels of *Sphenolithus* spp. and *Calcidiscus macintyreii*.

According to the zonal schemes of Bukry (1973a, 1973b) and Raffi and Rio (1979), the last occurrence of the sphenoliths is coincident with the exit of *R. pseudumbilicus* (fig.1). There is a nuance in Ellis' (1979) zonation of the Mediterranean Pliocene, which distinguishes between the top of the acme of *Sphenolithus* (coinciding with the base of the acme of *E. asymmetricus*) and its last occurrence level (coinciding with the exit of *R. pseudumbilicus*).

Sphenolithus spp. (encompassing *S. abies* Deflandre and *S. neoabies* Bukry & Bramlette ; see Pl.9, figs.6-10) occurs with fluctuating numbers in samples from the Lower Pliocene. In a composite of the Cretan sections Aghios Vlassios and Finikia, Meulenkamp et al. (1979a) observed the sphenoliths to be present in fairly large numbers especially in samples from sapropelic layers up to some level (between samples CP2027 and CP2032) in the higher part of the *G. puncticulata* Zone in the Upper Pliocene of the Finikia section. From this level (our horizon S1, i.e. the subtop of *Sphenolithus*) upwards, the sphenoliths are present discontinuously and in very low numbers. On the basis of 10,000-counts, we recorded this horizon between samples CP4117 and CP4118 in the corresponding part of the Punta di Maiata section as well (fig.50). Hence, in our sections the subtop of the sphenoliths is above the exit of *Reticulofenestra pseudumbilicus*.

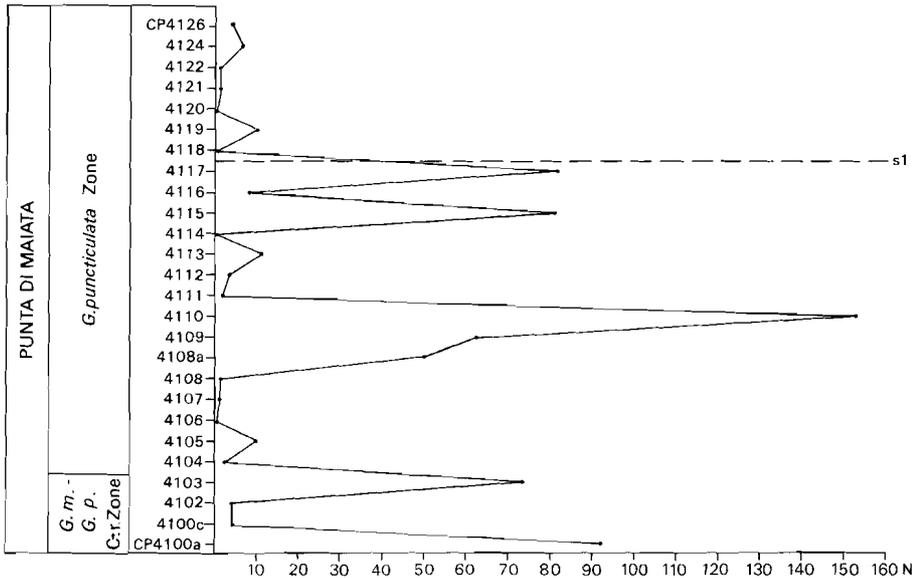


Fig.50 Frequency of *Sphenolithus* spp. in the uppermost part of its range in section Punta di Maiata (N = \pm 10,000 calcareous nannofossil specimens). Horizon s1 shows the location of the subtop of the Sphenolithids in the section.

Bizon and Müller (1977) proposed using the exit level of the coccolithophore species *Calcidiscus* (= *Cyclococcolithus*, = *Cyclococcolithina*) *macintyre*i (Bukry & Bramlette) Loeblich & Tappan as the approximate position of the Pliocene/Pleistocene boundary, especially in localities where the discoasters are rare. In the boundary stratotype section of Vrica, Backman et al. (1983) found the disappearance level of the species to be below their n-sapropel, about 50 metres stratigraphically above the Pliocene/Pleistocene boundary (sensu Aguirre and Pasini, 1985), and some 120 metres above the exits of *Eu-discoaster browneri* and *E. triradiatus*.

On the basis of 10,000-counts in samples from the Singa IV section, we observed that coccoliths of *C. macintyre*i (specimens larger than 10 μ ; see Pl.9, figs.4,5) are present regularly and in fair numbers up until sample JT9641 (fig.51). The disappearance level of the species (horizon m1) is between sapropels C9 and C10. As the latter sapropel correlates with the n-sapropel of the Vrica section (Verhallen, 1987), our result corresponds well with that of Backman et al. (op. cit.).

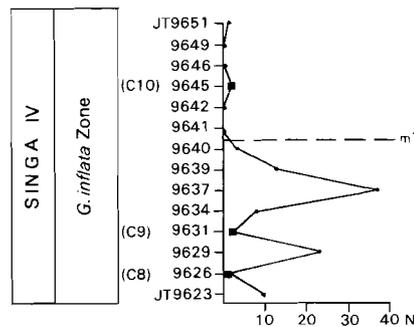


Fig.51 Frequency of *Calcidiscus macintyre*i in the uppermost part of its range in the Singa IV section (N = \pm 10,000 calcareous nannofossil specimens). Black quares indicate samples from sapropelic layers ; horizon m1 shows the position of the subtop of the species.

In the following chapters, our biohorizons will be discussed in the context of biostratigraphy, biochronology and paleoenvironmental change.

Chapter 13

CALCAREOUS NANNOFOSSIL BIOSTRATIGRAPHY AND CHRONOLOGY

NUMERICAL AGES OF THE BIOHORIZONS

Table IX shows the numerical ages calculated for our 27 biohorizons, together with the corresponding rhythmite numbers and the localities. The chronostratigraphy is based on the succession of geomagnetic reversals in the sections Singa and Punta Piccola/Punta Grande (Zijderveld et al., 1986, and in prep.) ; the geomagnetic time-scale of Berggren et al. (1985) was used. The biohorizons of the sections Monte Singa and Punta Piccola were dated by interpolating or extrapolating the average sedimentation rate, calculated for the interval between the nearest two geomagnetic reversals. The dates of the biohorizons, defined in the sections Aghios Vlassios, Finikia, Punta di Maiata and Monte San Nicola were obtained by dating the corresponding rhythmite (see Chapter 3) in the Punta Grande section.

It may be useful to emphasize here that the boundary between the Miocene and the Pliocene is younger than usually assumed. This boundary was defined in the Capo Rossello section of Sicily at the base of the Trubi, being the boundary between the Messinian and the Zanclean (Cita, 1975). Extrapolating the lithohorizon by means of biostratigraphic correlation, Berggren et al. (1985) located the chronohorizon at the base of the Gilbert Chron, dated at about 5.3 Ma. However, Zijderveld et al. (1986) found that in the Calabrian Singa section, the sedimentation of the Trubi started at about 4.83 or 4.84 Ma ago, corresponding with a level slightly below the base of the Thvera (or C2) Subchron.

In figure 52, a schematic representation is given of the frequency patterns of the species of the Noëlaerhabdaceae and the Eu-discoasteraceae, and of *Sphenolithus* spp. and *Calcidiscus macintyre*i (topmost part of their ranges) ; the ranges and the biohorizons are plotted against the numerical time scale.

BIOSTRATIGRAPHIC SUBDIVISION OF THE MEDITERRANEAN PLIOCENE

A good deal of the biohorizons, considered here, is defined on prominent changes in the frequency distribution of the species. Such biohorizons are ex-

cellent stratigraphic markers. For a new biostratigraphic scheme of the Pliocene and lowermost Pleistocene of Mediterranean sections, we selected four Noëlaerhabdacean horizons, eight discoaster horizons and further the exit-levels of *Sphenolithus* spp. and *Calcidiscus macintyreii*. Furthermore, we thought that making a refinement on the subzonal level within a zonal frame that is close to the 'Standard Zonation' (Martini and Worsley, 1970) would be most

<i>horizon</i>	<i>locality</i>	<i>sample interval</i>	<i>rhythmite</i>	<i>age (Ma)</i>
n1	Singa I	JT8945 - JT8951	II-12	4.51
n2	Singa I	JT9099 - JT9108	III-15	4.08
n3	Singa IA	JT11.498 - JT11.499	IV-2	3.98
n4	Singa IA	JT11.514 - JT11.515	IV-10	3.85
n5	Aghios Vlassios	CP2248 - CP2249	V-9	3.63
n6	Aghios Vlassios	CP2274 - CP2275	V-16	3.52
n7	Finikia	CP2128 - CP2131	VI-8	3.18
n8	Punta di Maiata	CP4171 - CP4172	VII-8	2.90
n9	Punta Piccola	JT5734 - JT5736	VIII-4	2.60
n10	Singa III	JT9355 - JT9358	VIII-16	2.31
n11	Singa IV	JT9586 - JT9594	? X-3	1.83
n12	Singa IV	JT9634 - JT9637	? X-12	1.45
d1	Punta di Maiata	CP4089 - CP4093A	IV-6	3.92
d2	Singa IA	JT11.517 - JT11.518	IV-11/IV-12	3.83
d3	Aghios Vlassios	CP2240 - CP2241	V-5	3.69
d4	Aghios Vlassios	CP2243 - CP2244	V-7	3.66
d5	Aghios Vlassios	CP2275 - CP2276	V-16	3.51
d6	Finikia	CP2054 - CP2055	V-22	3.42
d7	Punta Piccola	JT5715 - JT5716	VII-10	2.87
d8	Punta Piccola	JT5724 - JT5725	VII-15	2.79
d9	Punta Piccola	JT5726 - JT5727	VII-16	2.76
d10	Singa II	JT9273 - JT9274	VIII-4	2.58
d11	Singa III	JT9329 - JT9330	VIII-11	2.40
d12	Stuni (after Backman et al., 1983)		IX-4	2.14
d13	Vrica (after Backman et al., 1983)		? X-1	1.89
s1	Finikia	CP2027 - CP2032	V-17	3.50
m1	Singa IV	JT9640 - JT9641	X-14	1.40

Table IX: Stratigraphic position and numerical age estimates of the biohorizons.

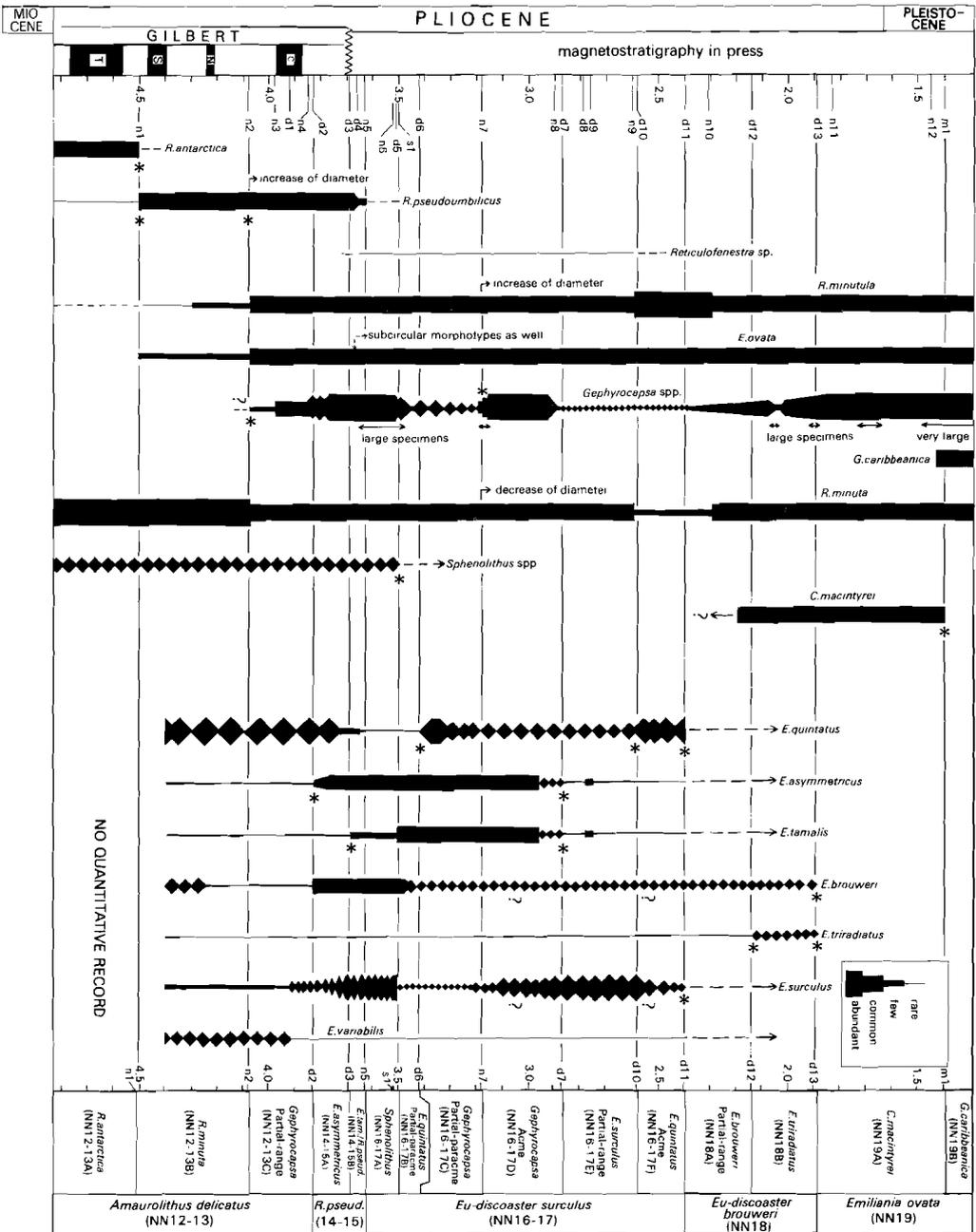


Fig.52 Schematic representation of the frequency of the calcareous nanofossil species of the Eu-discoasteraceae, the Noëlaerhabdaceae, *Sphenolithus* spp. and *Calcidiscus macintyreii* in the Pliocene/Lower Pleistocene of Greece and Italy. In addition, the position of the biohorizons and their timing (left-hand column) and our calcareous nanofossil zonation (right-hand column) are shown. Asterisks (*) indicate the events, used for zonal or subzonal boundaries.

practical. Our subzones are defined on entries, exits, acmes and paracmes of taxa. The term paracme-interval (Driever, 1981) is used to indicate an interval with relatively low frequencies of a certain species, in between two intervals with relatively high frequencies.

Because the recognizability of the biohorizons, defined on the ranges of *Amaurolithus* and *Ceratolithus* is low (see chapter 2), we combined the Standard Zones NN12 and NN13, as well as NN14 and NN15. Furthermore, as the exit of *E. surculus* proved not to be a clear-cut event, and as it approximately coincides with the exit of *E. quintatus*, we also combined Zones NN16 and NN17 (see figures 52 and 53).

In the below accounts of the subzones, all entries, except the one of *Gephyrocapsa* spp., and exits should be read as subbottoms and subtops, respectively. The descriptions of the floral contents emphasize the frequency distribution of the species of the Noëlaerhabdaceae and the discoasters. Obviously, the relative abundances, given for discoaster species, are of an altogether different order of magnitude than those given for the Noëlaerhabdaceae. In the statistics of the recognizability of the subzones, we used only those samples of which quantitative data on the critical species were available.

AMAUROLITHUS DELICATUS ZONE (NN12-13)

Definition : From the base of the Pliocene (provisionally thought to correspond with the exit of *Triquetrorhabdulus rugosus* outside the Mediterranean) up to the base of the acme of *Eu-discoaster asymmetricus*. The zone is equivalent with the similarly named zone of Raffi and Rio (1979). Three subzones are recognized.

Reticulofenestra antarctica Acme-subzone (NN12-13A)

Range : From the base of the Pliocene up to the change from the *R. antarctica*-dominated association to the *R. pseudoumbilicus* - dominated association (biohorizon n1).

Age : 4.83 - 4.51 Ma.

Association : *R. minuta* and *R. antarctica* are predominant ; large-size Reticulofenestrids are (nearly) absent ; varying numbers of *E. quintatus*, *E. brouweri*, *E. surculus* and *E. variabilis* (qualitative observations) ; specimens of *Amaurolithus delicatus* are found regularly, but typical specimens of *A. tricorniculatus* are rare.

Stratigraphic distribution : Kalithea I, GR2661 - GR2691 ; Singa I JT11.481 - JT8945.

Reference locality : Kalithea I.

Recognizability : On the basis of morphometrical analysis of 30 'large' specimens, the species *R. antarctica*, and hence its acme in the lowermost part of the Pliocene, is readily discernible from the larger *R. pseudoumbilicus* and the usually smaller *R. minutula*. In our Italian material, a few samples from close to the subzonal upper boundary seem to show a mixed association of *R. antarctica* and *R. pseudoumbilicus*.

<i>section</i>	<i>number of samples</i>	<i>positive</i>	<i>percentage</i>
Kalithea I	7	7	100
Singa I	12	12	100

Table X: Recognizability of Subzone NN12-13A for single samples. As the criterion for positive identification, a maximum average diameter of 5.8 μ in the 30-counts was chosen.

Remarks : If one accepts an age of 4.5 Ma for the entry of *Ceratolithus rugosus* (Berggren et al., 1985), the upper boundary of Subzone NN12-13A coincides with the boundary between NN12 and NN13. The lowest stratigraphic position we recorded for specimens of *C. rugosus* is sample CP4062 in the Punta di Maiata section, situated between horizons n1 and n2 (dated at about 4.3 Ma). *C. rugosus* is evidently not a practical marker species in the Mediterranean.

Reticulofenestra minuta Partial-range Subzone (NN12-13B)

Range : From the entry of *R. pseudoumbilicus* and the exit of *R. antarctica* (horizon n1) to the entry of *Gephyrocapsa* spp. (n2).

Age : 4.51 - 4.08 Ma.

Stratigraphic distribution : Kalithea I, GR2694 - GR2722 ; Aghios Vlassios, CP2350 - CP2363 ; Singa I JT8951 - JT9099 ; Punta di Maiata, CP4051 - \pm CP4068A.

Reference locality : Kalithea I.

Association : Common but relatively small-size *R. pseudoumbilicus* (averages in the 30-counts vary between 5.8 μ and 8.1 μ) ; many *R. minuta*, few *R. minutula* and few *Emiliania ovata* ; *E. brouweri* seems to be common only in the lower part of the subzone ; *E. quintatus* and *E. variabilis* are common throughout ; *E. surculus* seems to be low frequent ; *Amaurolithus delicatus* is regularly found.

Recognizability : Morphometrical analysis of 30 large-size specimens of the Noëlaerhabdaceae yields for nearly all samples a well recognizable association

of relatively small-size *R. pseudoumbilicus*. *Gephyrocapsa* spp. are not found in counts of 200 coccoliths of the Noëlaerhabdaceae. However, in the top part of the subzone, some very small specimens show a thickening of the collar which is reminiscent of the cross-bar of the *Gephyrocapsids*.

section	number of samples	positive	percentage
Kalitheia I	8	8	100
Singa I	13	12	92
Punta di Maiata	7	7	100

Table XI: Recognizability of Subzone NN12-13B for single samples ; the presence of the small-size morphotype of *R. pseudoumbilicus* (diameter averages between 5.8 μ and 8.1 μ) in combination with the absence of *Gephyrocapsa* spp. is the criterion for positive identification.

Remarks : Specimens of *Amaurolithus* can be found fairly regularly up to about the top of Subzone NN12-13B. They are very rare in the higher part of the Lower Pliocene (see also Raffi and Rio, 1979). *Ceratolithus rugosus* occurs only sporadically.

Gephyrocapsa Partial-range Subzone (NN12-13C)

Range : From the entry of *Gephyrocapsa* spp. (n2) to the base of the acme of *Eu-discoaster asymmetricus* (d2).

Age : 4.08 - 3.83 Ma.

Stratigraphic distribution : Kalitheia I, GR2727 - GR2743 ; Aghios Vlassios, CP2364 - CP2219 ; Singa I/IA, JT9108 - JT11.517 ; Punta di Maiata, \pm CP4070 - CP4100A ; Monte San Nicola, CP3751 ?, CP3752.

Reference locality : Singa I/IA.

Association : Common, usually large coccoliths of *R. pseudoumbilicus* (averages in the 30-counts vary between 7.5 μ and 9.6 μ) ; the *Gephyrocapsids* are few in the lower part of the subzone, but they become common (n3) to abundant (n4) in the upper part ; *R. minuta*, *R. minutula* and *E. ovata* are common ; few to abundant *E. quintatus*, *E. browneri* seems to be rare ; the top of the acme of *E. variabilis* seems to be at about the middle of the subzone (horizon d1), while from d1 upwards the frequencies of *E. surculus* seem to increase to common ; specimens of *Amaurolithus* and *Ceratolithus* are very rare.

Recognizability : As observed above, the *Gephyrocapsids* are few in the lowermost part of the subzone. In the samples from Punta di Maiata, dissolution seems to have removed the *Gephyrocapsids* from the lowermost part of the

range. Here, the increase in average diameter of *R. pseudoumbilicus* was used as an alternative for locating the lower zonal boundary. The lower boundary of the subzone was established in section Singa I on the basis of qualitative observations concerning the presence of *Gephyrocapsa*. In the 200-counts, the Gephyrocapsids scored in most samples. *R. pseudoumbilicus* is common throughout the subzone. The scores of *Eu-discoaster asymmetricus* in the discoaster counts are very low ($\leq 5\%$) and usually 0%.

section	number of samples	positive	percentage
Kalitheia I/ Aghios Vlassios	14	13	93
Singa I/IA	22	20	91
Punta di Maiata	13	8	62

Table XII: Recognizability of Subzone NN12-13C for single samples; the criteria for positive identification are the combined presence of the Gephyrocapsids in 200-counts and *R. pseudoumbilicus*, and very low ($\leq 5\%$, usually 0%) scores of *E. asymmetricus*.

RETICULOFENESTRA PSEUDOUMBILICUS ZONE (NN14-15)

Definition : From the base of the acme of *E. asymmetricus* to the exit of *R. pseudoumbilicus*. The zone comprises the same stratigraphic interval as the homonymous zones of Schmidt (1973) and Raffi and Rio (1979). Two subzones are recognized.

Eu-discoaster asymmetricus Partial-range Subzone (NN14-15A)

Range : From the base of the acme of *E. asymmetricus* (horizon d2) to the base of the acme of *E. tamalis* (d3).

Age : 3.83 - 3.69 Ma.

Stratigraphic distribution : Aghios Vlassios, CP2224 - CP2240 ; Singa IA, JT11.518 - JT11.524 ; Singa II, from about JT9221 up to JT9233 (qualitative observations ; horizon d3 is at about sample JT9233) ; Punta di Maiata, CP4100B - CP4102A ; Monte San Nicola, CP3753.

Reference locality : Aghios Vlassios.

Association : Common or abundant *Gephyrocapsa* spp. ; *R. minuta*, *R. minutula*, large-size *R. pseudoumbilicus* (average coccolith diameter between 8.3 μ and 8.9 μ) and *E. ovata* are common ; *E. quintatus* is common or abundant, *E. asymmetricus* and *E. brouweri* are common ; few to common *E. surculus* ; no or very few ($\leq 5\%$) *E. tamalis* ; specimens of *Amaurolithus* and *Ceratolithus* are rare.

Recognizability : The subzone is recognized on the basis of the nearly continuous presence of *E. asymmetricus* and *R. pseudoumbilicus* and the very low scores (usually 0%) of *E. tamalis*.

section	number of samples	positive	percentage
Aghios Vlassios	17	10	59
Singa IA	7	5	71
Punta di Maiata	5	5	100

Table XIII: Recognizability of Subzone NN14-15A for single samples ; the criteria for positive identification are the combined presence of *E. asymmetricus* (> 5%) and *R. pseudoumbilicus*, and very low (\leq 5%, usually 0%) scores of *E. tamalis*.

Eu-discoaster tamalis - Reticulofenestra pseudoumbilicus Concurrent-range Subzone (NN14-15B)

Range : From the base of the increase of *E. tamalis* (horizon d3) up to the exit of *R. pseudoumbilicus* (n5).

Age : 3.69 - 3.63 Ma.

Stratigraphic distribution : Aghios Vlassios, CP2241 - CP2248 ; Punta di Maiata, CP4102B - CP4109 ; Monte San Nicola, CP3754.

Reference locality : Aghios Vlassios.

Association : *Gephyrocapsa* spp. are common or abundant and specimens may be relatively large (coccolith diameter up to 4 μ) ; common *R. minuta* and *R. minutula* ; *E. ovata* is common and starts to show both oval and subcircular outlines ; few to common *Reticulofenestra* sp. ; *R. pseudoumbilicus* is common or abundant in the lower part of the subzone and low frequent in the upper part ; relatively few *E. tamalis* ; common *E. asymmetricus* and *E. brouweri* ; *E. quintatus* is common in the lower part but higher up (above horizon d4) it is rare ; few to abundant *E. surculus* ; one specimen of *Amaurolithus* was found in sample CP4107 (Punta di Maiata) ; *Ceratolithus rugosus* is rare.

Recognizability : The recognizability of individual samples from this subzone is relatively low, especially in section Aghios Vlassios. Many samples show only few *R. pseudoumbilicus* and few *E. tamalis*. In such cases, the presence of specimens of *Sphenolithus* spp., a relatively small diameter in the coccoliths of *R. minutula*, and very low frequencies of *E. quintatus* are additionally diagnostic for subzone NN14-15B.

section	number of samples	positive	percentage
Aghios Vlassios	8	2	25
Punta di Maiata	9	7	78

Table XIV: Recognizability of Subzone NN14-15B for single samples ; the criteria for positive identification are the combined presence of *E. tamalis* (> 5%) and *R. pseudoumbilicus* (N > 5 in 10,000-counts).

Remarks : Subzone NN14-15B covers the lowermost part of the *D. penta-radiatus* paracme-interval (Driever, 1981).

EU-DISCOASTER SURCULUS ZONE (NN16-17)

Definition : From the exit of *Reticulofenestra pseudoumbilicus* to the exit of *Eudiscoaster quintatus*. The zone is equivalent with the *Discoaster surculus* Zone of Raffi and Rio (1979). There are six subzones.

Sphenolithus Partial-range Subzone (NN16-17A)

Range : From the exit of *R. pseudoumbilicus* (horizon n5) to the exit of *Sphenolithus* spp. (s1).

Age : 3.63 - 3.50 Ma.

Stratigraphic distribution : Aghios Vlassios, CP2249 up to about CP2276 ; Finikia, CP2001 up to about CP2030 ; Punta di Maiata, CP4110 - CP4117 ; Monte San Nicola, CP3755 - CP3756(?)

Reference locality : Aghios Vlassios.

Association : Usually abundant coccoliths of *Gephyrocapsa* showing large diameters up to 4 μ ; *R. minuta* , *R. minutula* and *E. ovata* (oval and round) are common ; *E. quintatus* is (nearly) absent ; relatively few *E. tamalis* ; *E. asymmetricus*, *E. brouweri* and *E. surculus* are common ; near the top of the subzone *Gephyrocapsids* and *E. surculus* decrease in numbers (n6 and d5) ; *Sphenolithus* spp. is very frequent in the sapropelic beds of Aghios Vlassios and Finikia, and in dark-coloured clayey beds in Punta di Maiata ; *Ceratolithus rugosus* is found occasionally.

Recognizability : The flora in this subzone is characterized by the presence of *E. asymmetricus*, *E. tamalis* and *Sphenolithus* spp., and by the absence of *R. pseudoumbilicus* and *E. quintatus*. The presence of many and often large specimens of *Gephyrocapsa* spp., and the common presence of *E. surculus* are ad-

ditionally diagnostic. On the basis of a combination of all these parameters, the subzone is easily recognizable.

section	number of samples	positive	percentage
Finikia	8	5	62.5
Punta di Maiata	8	5	62.5

Table XV: Recognizability of Subzone NN16-17A for single samples. For the Punta di Maiata samples, the criteria for positive identification are the presence of *Sphenolithus* spp. ($N > 5$ in 10,000-counts) and the absence of *R. pseudoumbilicus* ($N \leq 5$) and *E. quintatus* ($\leq 5\%$). As we made only few 10,000-counts in the Cretan samples, we used as alternative criteria for the Finikia section the presence of *Sphenolithus* spp. ($> 2\%$ in counts of 200 'large' calcareous nannofossils; see Meulenkamp et al., 1979a), the presence of common or abundant *E. surculus* ($> 25\%$) and the absence of *E. quintatus* ($\leq 5\%$).

Remarks : Subzone 16-17A corresponds with the middle part of the *Discoaster pentaradiatus* paracme-interval (Driever, 1981).

Eu-discoaster quintatus Partial-paracme Subzone (NN16-17B)

Range : From the exit of *Sphenolithus* spp. (horizon s1) to the top of the paracme-interval of *E. quintatus* (d6).

Age : 3.50 - 3.42 Ma.

Stratigraphic distribution : Aghios Vlassios, from about CP2276 up to CP2280; Finikia, from about CP2030 up to CP2254; Punta di Maiata, CP4118 - CP4129; Monte San Nicola, CP3757 - CP3760.

Reference locality : Punta di Maiata.

Association : Common *Gephyrocapsa* spp. (specimens predominantly small-sized), common *R. minuta*, *R. minutula* and *E. ovata* (oval and subcircular), few *Reticulofenestra* sp.; common *E. asymmetricus* and *E. tamalis*, common or few *E. brouweri*, and few *E. surculus*; *E. quintatus* is (nearly) absent.

Recognizability : The calcareous nannofossil association in the subzone is characterized by the common presence of *E. asymmetricus* and *E. tamalis*, by the relatively low frequencies of the small Gephyrocapsids, by the low frequencies of *E. surculus* and the (near) absence of *E. quintatus* and *Sphenolithus* spp. However, samples from the next higher Subzone NN16-17C with few or no *E. quintatus* could be easily situated in the present subzone.

section	number of samples	positive	percentage
Aghios Vlassios	5	5	100
Finikia	10	10	100
Punta di Maiata	7	5	71
Monte San Nicola	4	4	100

Table XVI: Recognizability of Subzone NN16-17B for single samples. The criteria for positive identification in the Punta di Maiata section are the common presence of *E. asymmetricus* (> 5%) and *E. tamalis* (> 5%), relatively low frequencies for *E. surculus* (\leq 15%), and the absence of *E. quintatus* (\leq 5%) and *Sphenolithus* spp. ($N \leq 5$ in 10,000-counts; only samples from the lower part of the subzone were counted). In the Finikia section, the same discoaster-criteria are applied, but the absence of *Sphenolithus* spp. is based on scores less than 2% in the counts of Meulenkaamp et al., 1979a; in the sections Aghios Vlassios and Monte San Nicola, only the discoaster-criteria are used.

Remarks : The subzone corresponds with the upper part of the *Discoaster pentaradiatus* paracme-interval (Driever, 1981).

Gephyrocapsa Partial-paracme Subzone (NN16-17C)

Range : From the reappearance of *E. quintatus* (horizon d6) to the base of the second acme of *Gephyrocapsa* spp. (n7).

Age : 3.42 - 3.18 Ma.

Stratigraphic distribution : Finikia, CP2055 - CP2128 ; Punta di Maiata, CP4130 - CP4143 ; Punta Piccola, JT5701 ; Monte San Nicola, CP3761 - about CP3764.

Reference locality : Finikia.

Association : Relatively few and small-size *Gephyrocapsa* spp. (the differences between the frequency patterns of the Gephyrocapsids between the Cretan and the Italian sequences are such that it is not possible to indicate an overall frequency maximum) ; common *R. minuta*, *R. minutula* and *E. ovata* (oval and subcircular), few *Reticulofenestra* sp. ; *E. quintatus* is common or abundant in the lower half of the subzone, and rare to common in the upper half ; *E. asymmetricus* and *E. tamalis* are usually common, whereas there seem to be few *E. brouweri* and few to common *E. surculus*.

Recognizability : The subzone is recognized by the common presence of *E. asymmetricus* and *E. tamalis*, by the occurrence of *E. quintatus* and by the relatively low frequencies of the small Gephyrocapsids. The frequencies of *E. brouweri* seem to be low. The recognizability of the interval is relatively low due to the low frequencies of *E. quintatus* in many samples. Samples with very few *E. quintatus* occur also in Subzones NN16-17B and D.

section	number of samples	positive	percentage
Finikia	12	7	58
Punta di Maiata	6	3	50
Punta Piccola	1	0	0

Table XVII: Recognizability of Subzone NN16-17C for single samples. The criteria for positive identification are the presence of *E. asymmetricus* (> 5%), *E. tamalis* (> 5%) and *E. quintatus* (> 5%), and the relatively low frequency of the Gephyrocapsids (for the Cretan sequence a higher limiting value was chosen : for Finikia $N \leq 40$; for Punta di Maiata and Punta Piccola $N \leq 20$).

Gephyrocapsa Acme-subzone (NN16-17D)

Range : From the base of the second acme of *Gephyrocapsa* spp. (horizon n7) to the top of the acme of *E. asymmetricus* and *E. tamalis* (d7).

Age : 3.18 - 2.87 Ma.

Stratigraphic distribution : Finikia, CP2131 - CP2173 ; Punta di Maiata, CP4145 - CP4176; Punta Piccola, JT5702 - JT5715 ; Monte San Nicola, \pm CP3765 - CP3771 ; Singa II, JT9235 - JT9238.

Reference locality : Punta Piccola.

Association : Many or abundant Gephyrocapsids with small coccolith diameters to nearly the top of the subzone (n8) ; *E. ovata* (oval and round) is common; rare *Reticulofenestra* sp. ; *R. minuta* is common and of relatively small size, while *R. minutula* is common and of relatively large size ; *E. asymmetricus* and *E. tamalis* are common ; *E. quintatus* is few to common ; *E. brouweri* seems to be relatively low frequent, while *E. surculus* seems to be common.

Recognizability : The floral content of the subzone is characterized by the presence of *E. asymmetricus*, *E. tamalis* and *E. quintatus*, and by relatively high frequencies of the small Gephyrocapsids in the greater part of the range. The recognizability for individual samples is relatively low, as the Gephyrocapsids are low frequent in samples from the top part of the subzone, and as many samples show only few *E. quintatus*. Such samples are assignable to Subzones NN16-17B and C as well. The relatively large size of the coccoliths of *R. minutula* and the relatively small size of those of *R. minuta* and *Gephyrocapsa* are additionally indicative.

section	number of samples	positive	percentage
Finikia	7	5	71
Punta di Maiata	13	3	23
Punta Piccola	6	2	33

Table XVIII: Recognizability of Subzone NN16-17D for single samples. The criteria for positive identification are the presence of *E. asymmetricus* and/or *E. tamalis* (> 5%), the presence of *E. quintatus* (> 5%), and the relatively large numbers of *Gephyrocapsa* spp. (for Finikia N > 40; for Punta di Maiata and Punta Piccola N > 20).

Eu-discoaster surculus Partial-range Subzone (NN16-17E)

Range : From the top of the acme-interval of *E. asymmetricus* and *E. tamalis* (horizon d7) to the base of the uppermost acme-interval of *E. quintatus* (d10).

Age : 2.87 - 2.58 Ma.

Stratigraphic distribution : Punta di Maiata, CP4177 - CP4182 ; Punta Piccola, JT5716 - JT5737(?) ; Monte San Nicola, CP3772 - CP3774 ; Singa II, JT9239 - JT9273 ; Francocastello, GR1170 - ± GR1194.

Reference locality : Singa II.

Association : No or few *Gephyrocapsa* spp., *R. minuta* (usually small-sized), *R. minutula* (usually large) and *E. ovata* (oval and round) are common ; near the top of the subzone *R. minutula* becomes abundant, and *R. minuta* less common (n9) ; few *Reticulofenestra* sp. ; few *E. asymmetricus* and *E. tamalis*, except between the discoaster-horizons d8 and d9 ; *E. quintatus* is few to common ; *E. surculus* seems to be common or abundant ; *E. brouweri* seems to be few or common.

Recognizability : The flora of Subzone NN16-17E is characterized by very low scores of both *E. asymmetricus* and *E. tamalis*, by the very few small Gephyrocapsids, and by the relatively low frequencies of *E. quintatus*, as compared with the subzone above. The former three conditions apply to lowermost Pliocene associations (NN12-13A or B) as well, but there the absence of well-developed (subcircular) *E. ovata* and the presence of *Sphenolithus* spp. and *R. antarctica* or *R. pseudoumbilicus* are additional diagnostic characteristics. Subzone NN16-17E is not easily distinguished on the basis of single samples, as the scores of *E. quintatus* are below our limiting value in many samples. The increase of *E. quintatus* in the next higher subzone is relatively well recognizable in the scores of the 10,000-counts in Singa II/III and Monte San Nicola. The closed-sum discoaster counts (Punta Piccola, Monte San Nicola), however, yielded high scores (percentages) of *E. quintatus* in the present subzone as well, especially in samples from sapropelic sediment.

<i>section</i>	<i>number of samples</i>	<i>positive</i>	<i>percentage</i>
Punta di Maiata (100-counts)	6	3	50
Punta di Maiata (100-counts + <i>Geph.</i>)	1	1	100
Punta Piccola (100-counts)	22	12	55
Punta Piccola (100-counts + <i>Geph.</i>)	10	6	60
Monte San Nicola (100-counts)	3	3	100
Monte San Nicola (10,000-counts)	2	2	100
Singa II/III (10,000-counts)	15	5	33
Singa II/III (10,000-counts + <i>Geph.</i>)	4	1	25
Francocastello (100-counts)	14	6	43

Table XIX: Recognizability of Subzone NN16-17E for single samples. The criteria for positive identification are the presence in relatively low frequencies of *E. quintatus* (N between 3 and 15; between 5% and 30%) and the near absence of *E. asymmetricus* and *E. tamalis* (N < 3; ≤ 5%); for Punta di Maiata, Singa II/III and Punta Piccola, a frequency limit for the small Gephyrocapsids (N ≤ 5) is applied in addition (the counting data on the Gephyrocapsids were gathered mainly in samples from non-sapropelic sediment).

Eu-discoaster *quintatus* Acme-subzone (NN16-17F)

Range : From the base of the highest acme of *E. quintatus* (horizon d10) to the level of decrease of the total abundance of the discoasters (d11), i.e. to the exit of *E. quintatus*.

Age : 2.58 - 2.40 Ma.

Stratigraphic distribution : Punta Piccola, JT5738(?) - JT5741 ; Monte San Nicola, CP3775 - CP3777 ; Singa II/III, JT9274 - JT9329 ; Francocastello, ± GR1194 - GR1216.

Reference locality : Singa II/III.

Association : The Noëlaerhabdaceae show relatively many large-size coccoliths, with abundant *R. minutula* and common *E. ovata* (oval and round), and very few Gephyrocapsids and few *R. minuta* (distribution pattern 'D/E'); *E. quintatus* is common or abundant ; very few *E. asymmetricus* and *E. tamalis* ; in Singa II/III and Francocastello, *E. surculus* seems to show its subtop in this subzone, but in Monte San Nicola the species was found to range up into higher stratigraphic intervals ; *E. brouweri* seems to be few to common.

Recognizability : The floral content of this subzone is marked by relatively many *E. quintatus*, (virtually) no *D. asymmetricus* and *E. tamalis*, and very few Gephyrocapsids. It is distinguished from Lower Pliocene associations by the absence of *R. antarctica* or *R. pseudoumbilicus* and *Sphenolithus* spp. The very low frequencies of the small-size species of the Noëlaerhabdaceae are additionally characteristic.

<i>section</i>	<i>number of samples</i>	<i>positive</i>	<i>percentage</i>
Punta Piccola (100-counts)	5	2	40
Punta Piccola (100-counts + <i>Geph.</i>)	3	2	67
Monte San Nicola (100-counts)	4	4	100
Monte San Nicola (10,000-counts)	4	3	75
Singa II/III (10,000-counts)	11	9	82
Singa II/III (10,000-counts + <i>Geph.</i>)	4	2	50
Francocastello (100-counts)	10	7	70

Table XX: Recognizability of Subzone NN16-17F for single samples. The criteria for positive identification are relatively high frequencies of *E. quintatus* ($N \geq 15$; $\geq 30\%$) and the near absence of *E. asymmetricus* and *E. tamalis* ($N < 3$; $\leq 5\%$); for Singa II/III and Punta Piccola, a frequency limit for the small Gephyrocapsids ($N \leq 5$) is applied in addition (the counting data on the Gephyrocapsids were gathered mainly in samples from non-sapropelic sediment).

EU-DISCOASTER BROUWERI ZONE (NN18)

Definition : From the exit of *E. quintatus* to the exit of *E. brouweri*. The zone is equivalent with the *Discoaster brouweri* Zone (NN18) of Martini and Worsley (1970), the *Discoaster brouweri* Subzone of Raffi and Rio (1979), the *Cyclococcolithina macintyreii* Subzone of Bukry (1973b), i.e. the *Calcidiscus macintyreii* Subzone (CN12d) of Okada and Bukry (1980), and the *Cyclococcolithus macintyreii* Subzone of Ellis (1979). Two subzones are distinguished.

Eu-discoaster brouweri Partial-range Subzone (NN18A)

Range : From the level of decrease in the discoaster abundances and the exit of *E. quintatus* (horizon d11) to the base of the acme of *E. triradiatus* (d12).

Age : 2.40 - 2.14 Ma.

Stratigraphic distribution : Singa III, JT9330 - ± JT9410 (?) ; Monte San Nicola, CP3778 - ± CP3786 ; Francocastello, GR1217 - GR1225.

Reference locality : Singa III.

Association : In the lowermost part of the subzone (up to horizon n10), the associations of Singa III show predominantly large-size coccoliths of the Noëlaerhabdaceae (*R. minutula* and *E. ovata*), and few small-size Gephyrocapsids and *R. minuta*. This may be (partly ?) due to selective dissolution of the nannofloras, as the samples seem to show a lot of calcareous nannofossil fragments. Recognition of the corresponding interval in the sections Monte San Nicola and Francocastello on the basis of such a distribution pattern of coccolith size is hampered by the intermittent occurrence of associations with relatively many small specimens. In the higher part of the subzone, *R. minuta*, *R. minutula* and *E. ovata* are common or abundant, and there are relatively few and small-size Gephyrocapsids. *Calcidiscus macintyreii* is common. Horizon n10, based on relative frequencies of *R. minuta* and *R. minutula*, occurs near the middle of the subzone.

E. brouweri and *E. triradiatus* are the remaining indigenous species of *Eudiscoaster*. The former is present discontinuously and in very low numbers, while the latter is even more scarce in this subzone.

Recognizability : This subzone can be recognized by the scarcity of the discoasters and by the intermittent presence of *E. brouweri*. As this species is present only intermittently and in very low numbers, many of the samples from Subzone NN18A could be assigned to Subzone NN18B or NN19A as well. We made only qualitative observations on the distribution of the discoasters in the uppermost Pliocene. For the below statistic of the recognizability of the subzone in terms of discoaster abundance, we used the quantitative data of Backman et al. (1983) pertaining to the Stuni (Semaforo) section. Because of the very low numbers found, we lowered the standard for positive recognition of Subzone NN18A to the mere presence of the marker species. As we could check in samples from our section Semaforo (Spaak, 1983), their calcareous nannofloras satisfy the criterion of extremely low overall discoaster abundance. In a routine analysis of widely spaced samples in section Singa III, our first sample with relatively many *E. triradiatus* was JT9438. On the basis of bed-to-bed correlation from the base of the acme-interval of *E. triradiatus* in Stuni (after Backman et al.) to section Singa III, we tentatively draw the subzone's upper boundary (d12) at sample JT9410. If correct, the combination of very low total discoaster abundances and relatively low frequencies of the small Gephyrocapsids in the interval below can be used as additional

evidence for Subzone NN18A. The results shown for the entire interval in section Singa III (Table XXI) are based on the assumption that the former criterion is fulfilled.

<i>section</i>	<i>number of samples</i>	<i>positive</i>	<i>percentage</i>
Stuni	24	17	71
Singa III (<i>Geph.</i>)	13	10	77
Singa III (10,000-counts + <i>Geph.</i>)	9	8	89

Table XXI: Recognizability of Subzone NN18A for single samples. The criteria used for positive identification in section Stuni are the presence of *E. brouweri* and the absence of *E. triradiatus* (data after Backman et al., 1983). The criterion used for positively identifying NN18A in Singa III is a low number of *Gephyrocapsa* spp. ($N < 10$); for samples from the lower part of the subzone, our quantitative data (10,000-counts) allow applying the criterion of very low discoaster total abundances ($N \leq 5$) as well.

Eu-discoaster triradiatus Subzone (NN18B)

Range : From the base of the acme of *E. triradiatus* (horizon d12) to the exit of *E. brouweri* and *E. triradiatus* (d13).

Age : 2.14 - 1.89 Ma.

Stratigraphic distribution : Singa III/IV, JT9411 (?) - JT9580 ; Monte San Nicola, \pm CP3787 - \pm CP3804.

Reference locality : Stuni(Semaforo)/Vrica, southern Italy (see Backman et al., 1983).

Association : Common, occasionally large-size Gephyrocapsids ; *R. minuta*, *R. minutula* and *E. ovata* (oval and subcircular) are common ; very few *E. brouweri*, often in association with *E. triradiatus* ; common *C. macintyreii*.

Recognizability : The recognizability of the subzone is relatively low. Because of the intermittent occurrence and the very low numbers of the discoaster species, many of the samples are assignable to the lower NN18A or the higher NN19A as well. In a routine check (one traverse of 15 mm length) of 19 samples from the relevant interval in section Singa III/IV, we found between one and seven specimens of *E. brouweri* in each of 15 samples ; *E. triradiatus* was observed in four samples, including the topmost sample JT9580. It would seem that only very few samples would be positively recognized if we set a limiting value of $N = 5$ specimens of each of the two discoaster species per 10,000 calcareous nannofossils. We use again the data of Backman et al. (op. cit.)

for the recognizability of Subzone NN18B in the Stuni section (Table XXII). As a measure for the recognizability of NN18B in Singa III/IV, we set a maximum and a minimum value for the frequency of *Gephyrocapsa* spp. By using a score of 30 specimens as the upper frequency limit, the upper boundary of Subzone NN18B in Singa III/IV (horizon d13) nearly coincides with horizon n11 (base of the third acme of the Gephyrocapsids).

section	number of samples	positive	percentage
Stuni/Vrica	21	12	57
Singa III/IV (<i>Geph.</i>)	11	6	55

Table XXII: Recognizability of Subzone NN18B for single samples. The criterion for positive identification in section Stuni/Vrica is the combined presence of *E. browneri* and *E. triradiatus* (data after Backman et al., 1983). As the criterion for positively identifying NN18B in Singa III/IV, a common occurrence of *Gephyrocapsa* spp. (N between 10 and 30 specimens) was chosen.

EMILIANIA OVATA ZONE (NN19)

Definition : From the exit of *E. browneri* to the exit of *E. ovata*. The zone is equivalent with the *Pseudoemiliana lacunosa* Zone of Martini and Worsley (1970).

Calcidiscus macintyreii Partial-range Subzone (NN19A)

Range : From the exit of *E. browneri* and *E. triradiatus* (horizon d13) to the exit of *Calcidiscus macintyreii* (m1). The subzone is equivalent with the *Cyclococcolithina macintyreii* Zone of Gartner (1977a), the *Emiliana annula* Subzone of Ellis (1979), and with the combined *Crenalithus doronicoides* and *Cyclococcolithina macintyreii* Subzones of Raffi and Rio (1979).

Age : 1.89 - 1.40 Ma.

Stratigraphic distribution : Singa IV, ± JT9581 - JT9640 ; Monte San Nicola, ± CP3805 - CP3820.

Reference locality : Stuni(Semaforo)/Vrica (see Backman et al, 1983).

Association : Abundant and often relatively large-size Gephyrocapsids ; *G. caribbeanica* is present in the topmost samples of the subzone (above n12) ; common *E. ovata* (oval and subcircular) and *R. minutula* ; common or abundant *R. minuta* ; *C. macintyreii* is common.

Recognizability : The flora of this subzone is characterized by the absence of discoasters and by the presence of *C. macintyreii*. However, such an association is regularly found in samples with virtually no discoasters from the lower Sub-zones NN18A and NN18B as well. The scores of the recognizability of the subzone in the Vrica section (Table XXIII) are based on the data of Backman et al. (op. cit.). For a measure of positive recognition of the subzone in samples from section Singa IV, we used a minimum number of *Gephyrocapsa* spp. and the absence of *Gephyrocapsa caribbeanica*.

section	number of samples	positive	percentage
Vrica	22	18	82
Singa IV (<i>Geph.</i>)	11	10	91

Table XXIII: Recognizability of Subzone NN19A for single samples. The criteria for positive identification of samples from the Vrica section are the absence of *E. brouweri* and/or *E. triradiatus* and the presence ($N < 3$) of *C. macintyreii* (data after Backman et al., 1983). As the criteria for positively identifying NN19A in Singa IV, a high frequency of *Gephyrocapsa* spp. ($N > 30$) and the absence of *G. caribbeanica* was chosen.

Remarks : Subzone NN19A straddles the Pliocene/Pleistocene boundary in the sense of the boundary stratotype section of Vrica (Aguirre and Pasini, 1985).

***Gephyrocapsa caribbeanica* Partial-range Subzone (NN19B)**

Range : Interval from the exit of *C. macintyreii* (horizon m1 ; approximately the entry of *G. caribbeanica*, i.e. n12) upwards. It is suggested to use the top of the range of the very large-size *Gephyrocapsa* spp. (exit of *G. caribbeanica*) as subzonal upper boundary. Our sample record (Singa IV, Monte San Nicola) covers only the lower part of the stratigraphic interval under consideration.

Age : 1.40 - less than 1.30 Ma.

Stratigraphic distribution : Singa IV, JT9641 - top of section ; Monte San Nicola, CP3821 - CP3825.

Reference locality : Singa IV.

Association : *R. minuta* is common or abundant, *R. minutula* and *E. ovata* (oval and subcircular) are common ; in *Gephyrocapsa* a bimodal distribution of the coccolith diameter is observed (*Gephyrocapsa* spp. and *G. caribbeanica*) ; no *Calcidiscus macintyreii*.

Recognizability : Subzone NN19B is easily recognized on the basis of the presence of very large-size *Gephyrocapsa* spp. During routine analyses, we found

specimens of *Gephyrocapsa caribbeanica* to be common throughout the subzone. A further characteristic is the absence of *C. macintyreii*. As our data concerning the distribution of *G. caribbeanica* are mainly qualitative, we cannot give a numerical expression of the recognizability of the subzone.

Remarks : Subzone NN19 B corresponds approximately with the *Helicopontosphaera sellii* Zone of Gartner (1977a), with the homonymous subzone of Rafi and Rio (1979) and with Rio's (1982) *Helicosphaera selii* Zone. Our definition of the upper limit of Subzone NN19B leaves room for one or more subzones up to the exit of *E. ovata*.

CONCLUSIONS

The aim of this study was to improve our insight into the morphological variability of some biostratigraphically useful calcareous nannofossil taxa, and to establish a (semi-)quantitative record of these taxa. The investigation resulted in the zonal scheme, presented in the foregoing paragraphs. One of the most obvious conclusions is, that it is important to quantify the data on relevant calcareous nannofossil taxa. A considerable refinement of the classical presence/absence schemes can be attained by recognizing intervals with low and high frequencies within the ranges of the taxa. A numerical record of a species facilitates the evaluation of low-frequency ranges in terms of reworking. Furthermore, a quantitative data set is indispensable for establishing the specific responses to environmental changes, and for establishing the inter-specific paleoecological affinities. Finally, a quantitative record of the zonal markers yields a numerical yardstick for the probability that individual samples are assigned to the proper biozones.

Figure 54 shows the average recognizability of our subzones for individual samples. For positive identification of each of the subzones, a particular set of criteria was used, usually expressed in terms of frequency limits for the defining taxa. Therefore, if the quantitative composition of the nannoflora in a certain sample meets the criteria of one of the subzones (our average of positive samples per subzone is about 70 %), the probability of a correct biostratigraphic assignment is very high. Considering the high resolving power of the subzonal scheme (average duration of the subzones is about 245,000 years), the precision of the corresponding age estimates for such samples is very high. On the other hand, the fluctuations in the frequency pattern of the relevant taxa are such that on average 30 % of the samples scored negatively for assignment to a single subzone. Such samples individually qualify for longer stratigraphic intervals.

We set numerical limits for distinguishing between low- and high-frequency

	NN12-13A	NN12-13B	NN12-13C	NN14-15A	NN14-15B	NN16-17A	NN16-17B	NN16-17C	NN16-17D	NN16-17E	NN16-17F	NN18A	NN18B	NN19A	number of exercises
NN19A															33
NN18B															32
NN18A															46
NN16-17F															41
NN16-17E															77
NN16-17D															26
NN16-17C															19
NN16-17B															26
NN16-17A															16
NN14-15B															17
NN14-15A															29
NN12-13C															49
NN12-13B															28
NN12-13A															19

Fig.54 Recognizability of the Pliocene subzones for individual samples. The numbers in the squares indicate the averages (in percentages) of the positive designation scores, resulting from the application of the relevant criteria. The horizontal bars show the potential stratigraphic positioning of the samples without such positive scores ; the intervals of their most likely assignment are in black colour. The statistics of the zones NN18 and NN19 are partly based on data of Backman et al. (1983).

intervals, c.q. presence/absence intervals of a certain species, thus reducing the subjectivity in the drawing of boundary lines in the numerical sequences. It appeared to be quite easy to indicate such threshold values, which means that the frequency changes in question are quite obvious and that their recognizability is high. As the inter-sample distance around most of the biohorizons is less than the thickness of one rhythmite, we estimate that the precision of pinpointing these horizons is in most cases very high (maximum error some 20,000 years). The biohorizons are found in several sections in seemingly corresponding posi-

tions in the rhythmite succession, which indicates a virtual synchronism of the underlying bioevents throughout the eastern and central Mediterranean. We conclude that the accuracy of the correlations on the basis of our zonation is comparatively high.

Chapter 14

THE PALEOENVIRONMENTAL SIGNIFICANCE OF THE CALCAREOUS NANNOFOSSILS IN THE MEDITERRANEAN PLIOCENE

THE ACTUALISTIC APPROACH

There are very few well-documented studies on the relation between the areal distribution of calcareous nannoplankton species and their physical, chemical and biological environment. The same holds true for the depth distribution of calcareous nannofossil species, and for their seasonal variation. As a consequence, the life cycles of the species and the characteristics of their habitats are poorly understood.

For an overview of the areal extent and the depth distribution of the modern calcareous nannoplankton species in the Atlantic Ocean, reference is made to McIntyre and Bé (1967) and Okada and McIntyre (1979). The distribution of species from surface and near-surface sediments in the North Atlantic has been studied by McIntyre and Bé (1967), McIntyre et al. (1972) and by Geitzenauer et al. (1977). The living calcareous nannoplankton of the Pacific Ocean has been investigated by McIntyre et al. (1970), Okada and Honjo (1973), Honjo and Okada (1974), Okada and Honjo (1975) and Honjo (1977). Among others, Roth and Berger (1975), Geitzenauer et al. (1977) and Roth and Coulbourn (1982) published on the species distribution in Pacific surface sediments. Generally, the composition of the thanatocoenoses was found to be a fair reflection of the biocoenoses in the overlying waters, on the understanding that the number of species found in the sediment is markedly lower, due to selective preservation of resistant taxa.

Likewise, there are only very few papers dealing with the quantitative composition of biocoenoses and taphocoenoses of calcareous nannoplankton in the Mediterranean Sea. The few studies on the living calcareous nannoplankton relate to the summer distribution of the species (Bernard, 1959 ; Kimor and Wood, 1975 ; A. Kleijne, in prep.).

The insight into the relation between the distribution of calcareous nannofossils in the stratigraphic record and paleoenvironmental parameters is even more limited. Paleoenvironmental assessments by means of patterns in the calcareous nannofossil record are generally based on extrapolating modern biogeographic patterns, and they are usually specified in terms of seawater

temperature. Since most of the Recent species appeared in the course of the Pleistocene, and the coccoliths of many Recent species have a very low preservational potential, the applicability of such an actualistic approach is limited. Furthermore, the paradox in the distribution of modern and fossil *Coccolithus pelagicus* may show that coccolithophore species may have changed their habitats in the course of time. Recent *C. pelagicus* is found to be restricted to high latitude areas, whereas its pre-Holocene equivalents are frequently found in samples from low latitude localities.

Because of the poor understanding of modern calcareous nannoplankton ecology, and because of the restricted applicability of modern biogeography to pre-Quaternary levels, it is difficult to specify the calcareous nannoplankton record of the Mediterranean Pliocene in terms of paleoenvironmental conditions. In combination, however, with the wealth of information on Mediterranean Pliocene paleoenvironments provided by palynological, foraminiferal, stable isotope and micromammal studies, we gained a much better understanding of most of the major changes and trends in the calcareous nannofossil record of the Mediterranean Pliocene.

LITERATURE DATA ON THE (PALEO)HABITATS OF THE EU-DISCOASTERACEAE AND THE NOËLAERHABDACEAE

THE DISCOASTERS

As the extinct discoasters have been found to be abundant in low latitude localities, they are generally considered to be 'warm water taxa'. It should be taken into account that a relatively high number of discoasters in a sample may also result from enrichment by selective dissolution (for example, Lohmann and Carlson, 1981).

The habitat characteristics of individual species of *Eu-discoaster* are largely unknown. From differences in paleobiogeographic distribution patterns of *Eu-discoaster* species, Bukry (1971b, 1973c) inferred that *E. variabilis* is indicative for relatively cool and nutrient-rich water, while *E. brouweri*, *E. surculus* and *E. pentaradiatus* (= *E. quintatus*) are typical for warm and less fertile water. By counting the discoaster associations in 11 samples from one single time slice ('*E. tamalis*' Subzone) along North-South transects in the western Pacific and eastern Atlantic, Bukry (1975, 1978b) subsequently classified *E. brouweri* and *E. pentaradiatus* as warm-water species, and *E. surculus* as a species of temperate waters. Since the subzone in question spans some 900,000 years (after Berggren et al., 1985) and corresponds with a period of environmental instability (Zachariasse and Spaak, 1983), the number of samples is thought to be far too low for drawing such a conclusion.

Reticulofenestra

From the literature on Recent calcareous nannoplankton it seems that our Pliocene species of *Reticulofenestra* (*Reticulofenestra* sp., *R. antarctica*, *R. pseudoumbilicus*, *R. minutula* and *R. minuta*) have no living representatives. Possibly, the latter species name is applicable for a modern species with small-size coccoliths (for example, *Crenolithus sessilis* (Lohmann) Okada & McIntyre), but such a species seems to be quantitatively unimportant and its environmental affinities are unknown.

In a quantitative analysis of Miocene calcareous nannofossil assemblages in DSDP sites all over the Atlantic Ocean, Haq (1980) and Haq and Malmgren (1982) found that *R. antarctica* (*Dictyococcites antarcticus*) is very prominent in Middle and Late Miocene samples from the high latitudes of the southern hemisphere. The appearance of *R. antarctica* in the stratigraphic record was observed to coincide with the onset of a period of climatic deterioration which is related to the formation of the East Antarctic ice sheet at about 14 Ma (e.g. Shackleton and Kennett, 1975). Subsequent fluctuations in its frequency pattern were thought to be related to ice-volume changes.

Reticulofenestra pseudoumbilicus was a ubiquitous species, but its main distribution area seems to have been in mid-latitude waters (Haq, 1980 ; Takayama, 1980 ; Lohmann and Carlson, 1981).

On the basis of paleobiogeographic data, Haq et al. (1977) and Haq (1980) concluded that *Reticulofenestra minuta* (*Dictyococcites minutus*) has been an element of the tropical nannoflora, as the species first appeared in low-latitude localities in Middle Miocene time. Its appearances in calcareous nannofloras elsewhere were interpreted in terms of warming trends. Lohmann and Carlson (1981) distinguished a well-preserved tropical calcareous nannofossil assemblage in the Pacific Miocene, in which small elliptical placoliths (*Dictyococcites* and *Cyclococcolithus* affinities) are prominent. This assemblage was found to be typical for shallow water or for areas of relatively high primary productivity.

Emiliana

The species *Emiliana ovata* (*Pseudoemiliana lacunosa* auct. ; including *Emiliana annula* auct.) became extinct in mid-Pleistocene time (Berggren et al., 1975). Perch-Nielsen (1985) observed that the subcircular coccolith morphotype occurred in low latitudes during periods of temperature maxima, while the elliptical type was more frequent in high latitudes with temperature minimum spells.

Gephyrocapsa

The Pliocene Gephyrocapsids have as yet received relatively little attention. However, data on the modern distribution of extant species are valuable for our paleoenvironmental analysis of the Mediterranean Pliocene.

There are many species names available for the modern Gephyrocapsids. In quantitative studies of biocoenoses or thanatocoenoses, however, all or nearly all Gephyrocapsid specimens are assigned to two or three species, and there seems to be a consensus on a taxonomic concept which is more or less as follows: *Gephyrocapsa oceanica* is used for the species with relatively large-size coccoliths, having a cross-bar (nearly) aligned with the shorter axis of the coccolith and usually a relatively large central opening. *G. caribbeanica* is the name for the species with relatively large coccoliths which show a cross-bar forming an angle of some 45° with the coccolith's longer axis, and usually a relatively small central opening. Many authors seem to use *G. ericsonii* for all (specimens with) small-size coccoliths. Defined as such, the species probably covers a wide morphological range.

All three Gephyrocapsid species have been observed to occur throughout the Atlantic and Pacific Oceans, but each species seems to be especially frequent in certain areas (for an overview see Roth and Coulbourn, 1982). *G. oceanica* is found to be frequent in or under warm and moderately fertile waters. *G. caribbeanica* is considered to be the cold-water species, typical for subpolar and transitional floras. *G. ericsonii* seems to be a species of transitional associations. McIntyre and Bé (1967) and Okada and McIntyre (1979) reported that the Gephyrocapsids reach maximum frequencies in the Transitional Zone of the North Atlantic during spring and autumn blooms. Honjo and Okada (1974) found a large subsurface population of *G. ericsonii* in an area of upwelling cold and nutrient-rich water in the North Equatorial Divergence of the Pacific (see Honjo, 1977). Roth and Coulbourn (op. cit.) found a concentration of *E. ericsonii* in surface sediments from along the north-eastern periphery of the Pacific Ocean.

In the recent Atlantic, *G. ericsonii* and *G. caribbeanica* seem to be species characteristic for the transitional region between the subpolar and the subtropical water masses (McIntyre and Bé, 1967). In a year-round sampling campaign, both species were found to be unimportant in the subarctic stations Bravo and Charley, but the species bloomed at Gulf Stream station Delta in late autumn and spring (Okada and McIntyre, 1979). These peak frequencies seem to co-occur with increased levels of primary productivity.

COCCOLITH MORPHOLOGY AND (PALEO)ENVIRONMENT

In addition to interpretations of the habitat characteristics of individual species of the Noëlaerhabdaceae, there have been some speculations about the influence of environmental parameters on certain morphological characters of the coccoliths.

A relation has been proposed to exist between the infilling of the tube area and temperature. In life assemblages of *Emiliania huxleyi* in the Gulf of Elat, winter morphotypes have a small central area, a wide collar cycle and an imperforate central plate. In summer types, the central area is relatively wide and the central plate is reticulate (Winter et al., 1979 ; Winter, 1982). Similar observations were made by Okada and McIntyre (1977) on *E. huxleyi* from warm and cold waters in the Pacific and North Atlantic Ocean. They also mentioned that warm water forms have slits between the proximal elements, while in cold water forms the proximal shields are solid. In their species *Crenalithus parvulus*, both a reticulate and a solid central plate were commonly found in the same sample. It was interpreted that for this species, the variation cannot be solely environmentally controlled. Gartner (1977a) stated that the relative central opening size in Late Pleistocene to Recent Gephyrocapsids is indicative for (paleo)temperatures. Backman (1980) observed that high latitude specimens of the species *R. pseudoumbilicus* showed a distinct tendency to produce coccoliths with a small central opening.

The paleoenvironmental significance of the overall size of the coccoliths has been speculated upon as well. Gartner et al. (1983, 1987) remarked that a large coccolith size is likely to be associated with a slow rate of growth and reproduction, whereas small coccolith size relates to fast rates (e.g. in seasonal blooms). Shelf sediments, often below productive unstratified surface waters, usually show small-sized specimens of *Gephyrocapsa*, whereas the coccoliths from the low productive, warm and stratified surface waters of central oceanic gyres are generally large-sized. Likewise, relatively small-sized coccoliths of *R. pseudoumbilicus* seem to have predominated in shallow water environments, whereas the large-sized coccoliths were probably more characteristic for oceanic environments (B. Prins, pers. comm.).

FAUNAL AND FLORAL EXCHANGE BETWEEN THE MEDITERRANEAN AND THE ATLANTIC

Opinions vary as to the timing of the final closure of the Tethyan seaway (Drooger, 1979: Oligocene-Miocene boundary ; Adams et al., 1983: mid-Burdigalian ; Vergnaud-Grazzini, 1983: Late Burdigalian ; Rögl and Steininger, 1983, and Chamley et al., 1986: Late Serravallian). Whatever the timing, the

final closure of the seaway changed the Mediterranean into a semi-enclosed satellite basin of the Atlantic Ocean. The present-day negative water budget of the Mediterranean maintains a lagoonal type of circulation with a deep outflow and a surface inflow of Atlantic water (Lacombe and Tchernia, 1972). This inflowing water is derived from the Canary Current system, which transports relatively cool northern Atlantic water southwards along the Iberian and Northwest African coasts.

Along the Canary Current, northern faunal elements are displaced southwards into areas where they mix with subtropical and tropical elements (for example, Cifelli and Beniér, 1976). Mixed assemblages of northern and subtropical planktonic foraminifera west of Gibraltar are subsequently introduced into the Mediterranean. The northern elements dominate in the cooler and more productive western basin, while subtropical elements abound in the warm oligotrophic waters of the eastern basin (Cifelli, 1974). A similar picture might be true for the calcareous nannoplankton flora.

Since climate exerts a major control on the present-day circulation and, therefore, on the distribution of fauna and flora west and east of Gibraltar, it is to be expected that past changes in climate are reflected in the faunal and floral record of the Mediterranean. For example, Spaak (1981) showed that the discontinuous distribution of the *Globorotalia inflata* group in the Mediterranean Pliocene is closely linked with climatically controlled changes in the areal distribution of the species in the North Atlantic.

PLIOCENE - PLEISTOCENE PALEOENVIRONMENTS IN THE MEDITERRANEAN

Facies control

In the following paragraphs we will try to give a generalized impression of the paleoenvironmental history of the Mediterranean in Pliocene-Pleistocene times. Many Pliocene sections show alternating lithologies, such as sapropelic - non-sapropelic and carbonate-rich - carbonate-poor sequences, and occasionally a four-fold sedimentary rhythm (beige - whitish - greyish - whitish). Each of these facies-types seems to be associated with a specific set of paleoenvironmental conditions.

A major key for our paleoenvironmental interpretation is the frequency distribution of some of the taxa of the Noëlaerhabdaceae. As our observations on the Noëlaerhabdaceae are predominantly based on samples from the non-sapropelic, carbonate-rich facies, our inferences about the overall paleoenvironmental trends are biased towards the long-term episodes of more 'normal marine' conditions, associated with the deposition of the homogeneous,

carbonate-rich sedimentary facies. We have quantitative information about the composition of the *Eu-discoaster*-associations in the sapropelitic facies at our disposal, allowing some additional remarks to be made about the paleoenvironmental affinities of the Discoasterid species.

Major paleoenvironmental trends in the Mediterranean Pliocene

As in most of our samples the planktonic foraminifera have been studied (Spaak, 1983 ; Zijderfeld et al., 1986 ; Zijderfeld et al., in prep.), a direct comparison is possible with the paleoenvironmental interpretations on the basis of the planktonic foraminiferal record.

The Early Pliocene faunas in the Mediterranean point to tropical/subtropical surface water conditions (Ciaranfi and Cita, 1973; Thunell, 1979a,b; Spaak, 1983; Zachariasse and Spaak, 1983). This observation is consistent with the interpretation of the Early Pliocene palynological record in the Mediterranean in terms of an overall warm and humid climate (Suc, 1984). Likewise, the stable isotope records from samples of the Mediterranean Lower Pliocene (Thunell, 1983; Gudjonsson, 1987) suggest rather stable surface water temperatures in the Early Pliocene Mediterranean, possibly interrupted by some short-term relatively cool intervals between 4.83 and 4.72 Ma and between 4.62 and 4.30 Ma. In the Upper Pliocene, all planktonic foraminiferal taxa indicative of such tropical-subtropical conditions are seen to disappear or to diminish numerically, whereas taxa that are characteristic of more temperate conditions increase. In latest Pliocene times, the planktonic foraminiferal faunas in the Mediterranean were very similar to the Recent ones, i.e. the faunas had a mixed subtropical-temperate label (Spaak, 1983). According to the interpretation of palynological data (Suc, 1984), the modern type of Mediterranean climate with relatively dry summers and wet winters originated in earliest Late Pliocene time, corresponding with the base of the *Globorotalia crassaformis* Zone (Cravatte et al., 1974).

The pattern of change in the Late Pliocene foraminiferal faunas was not rectilinear. Especially in the time interval corresponding to the Upper Pliocene *G. crassaformis* Zone, the faunal changes show evidence of large-scale climatic oscillations in the North Atlantic, which have been interpreted in terms of warm (e.g. the 'lower absence interval of the *Globorotalia inflata* group' ; i.e. Interval 5 of Spaak, 1983) and cool climatic conditions (e.g. the 'upper absence interval', i.e. Intervals 7 and 8). Interval 7 seems to mark the onset of the Plio-Pleistocene glacial cycles in the northern hemisphere. The corresponding interval in the palynological record (Suc and Zagwijn, 1983) shows an increase of steppic elements, which has been interpreted in terms of drier climatic condi-

tions around the Mediterranean, possibly correlative with glacial climatic conditions in the more northern parts of Europe.

PALEOENVIRONMENTAL CHANGES AND THE PLIOCENE RECORD OF THE NOËLAE-RHABDACEAE AND THE DISCOASTERIDS

In figure 55, the frequency distributions of the Gephyrocapsids and of *Eudiscoaster quintatus* in the Mediterranean Pliocene are shown, together with the interpretation in terms of the average temperature and seasonality of sea surface water. The Pliocene calcareous nannofossil record is furthermore subdivided into a sequence of associations, each of which is characterized in terms of its best match in the modern coccolithophore assemblages of the North Atlantic (McIntyre and Bé, 1967; McIntyre et al., 1972).

R. antarctica Subzone (NN12-13A)
(4.87-4.51 Ma)

Our *R. antarctica* Subzone represents the lowermost Pliocene in the Mediterranean. The foraminiferal and palynological records bear evidence for a year-round warm and humid climate in the Mediterranean in earliest Pliocene times. The Noëlærhabdaceae show a characteristic association of the small-sized species *Reticulofenestra minuta* and *R. antarctica*. The dominance of small-size coccolith species in this interval may be indicative of relatively high productivity conditions in the surface waters. Most coccolith specimens of *R. antarctica* have a closed central opening. This is in clear contradiction with the view, proposed in the literature, that a small size of the central opening of coccoliths of Reticulofenestrid species would indicate low sea water temperatures. In summary, the earliest Pliocene Mediterranean calcareous nannoflora with *R. minuta* and *R. antarctica* dwelled most probably in warm and relatively productive waters in a humid climate with little seasonal contrasts.

R. minuta (NN12-13B) up to **E. quintatus** (NN16-17B) Subzones
(4.51-3.42 Ma)

R. pseudoumbilicus seems to have been most frequent in mid-latitude waters, which may indicate a preference for moderate surface water temperatures. However, in the lowermost part of its Pliocene range in the Mediterranean (*R. minuta* Subzone; 4.51-4.08 Ma), it is accompanied by relatively many specimens of the planktonic foraminifer *Globigerina nepenthes* and the calcareous nannofossil taxa *Scyphosphaera* and *Amaurolithus*; the latter association is thought to be indicative of subtropical/tropical waters (Rio and Sprovieri, 1986).

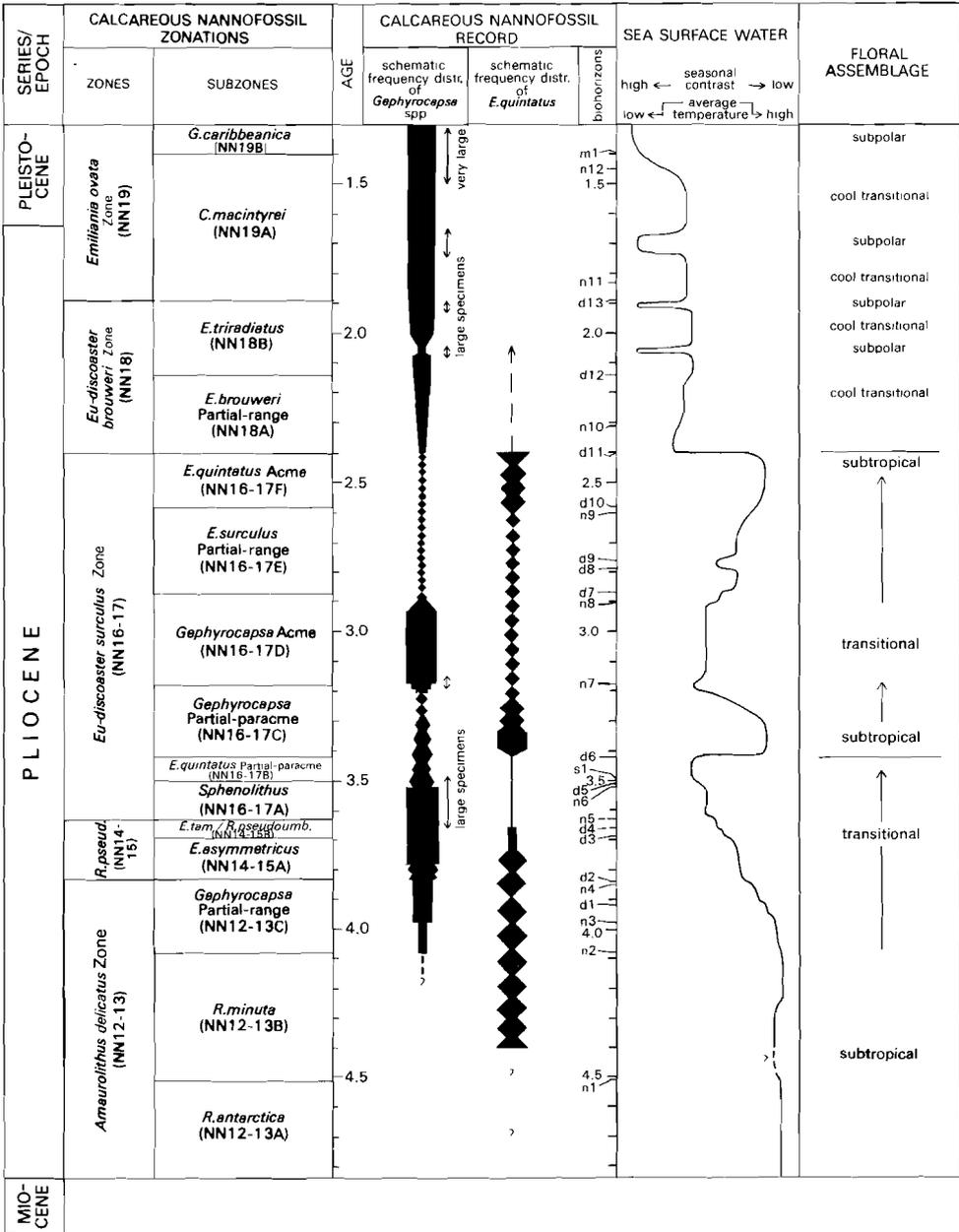


Fig.55 Schematic representation of the paleoenvironmental development in the Mediterranean and eastern North Atlantic during the Pliocene and Early Pleistocene.

In the time-lapse between about 4.08 and 3.42 Ma, which is represented by the Subzones NN12-13C up to and including NN16-17B, the associations of the Noëlaerhabdaceae and the Discoasterids underwent pronounced compositional changes. In our opinion, these changes bear witness to a gradual change-over from a (sub)tropical to a transitional floral association. This assumption is based on the combined appearance of the Gephyrocapsids and the planktonic foraminifer *Globorotalia puncticulata* in the Mediterranean record, and on the subsequent numerical increase of the former group.

The extinct species *G. puncticulata* is the precursor of the modern *Globorotalia inflata*. In the present day Atlantic, the latter species is a winter species in the waters of the Gulf Stream/Canaries Current System (Tolderlund and Bé, 1971). *G. inflata* seems to be also a winter species in the cooler water of the western Mediterranean (Glaçon et al., 1971; Duprat, 1983). It is assumed that the areal and seasonal distribution of its precursor species *G. puncticulata* has been similar (Berggren, 1981; Zachariasse and Spaak, 1983; Rio and Sprovieri, 1986).

Like *G. inflata*, the modern coccolithophore species *Gephyrocapsa ericsonii* seems to be a winter species of the temperate regions of the North Atlantic (McIntyre and Bé, 1967; Okada and McIntyre, 1979). By analogy, one expects this species to flourish in the Mediterranean Sea in the winter season as well. Many of the coccoliths of our Pliocene *Gephyrocapsa* spp. are referable to *G. ericsonii*; furthermore, the Gephyrocapsids show a stratigraphic distribution that is more or less similar to that of the *Globorotalia inflata* group (sensu Spaak, 1981). Hence, we assume that the distribution pattern of *Gephyrocapsa* spp. parallels the paleoenvironmental trends, deduced from the distribution of the *G. inflata* group.

The appearance and gradual predominance of species with a winter optimum indicates that, from about 4.08 until 3.42 Ma, the surface water temperatures lowered in winter, which may indicate that, at least during winter, cooler water flowed into the Mediterranean. This points to an increase of annual thermal contrasts (hence, seasonality) in the Atlantic and Mediterranean. Possibly, the winter blooms of the Gephyrocapsids in cool, well-mixed water alternated with blooms of *R. pseudoumbilicus* in the thermally well-stratified water of the summer seasons. Such conditions approach the modern annual cycle of surface water temperature and climate in the Mediterranean.

In the interval under consideration, the Gephyrocapsids not only show a numerical increase, their average coccolith size is also seen to increase, especially in the NN16-17A Subzone (lower part of the *G. puncticulata* Zone). Because these large-size Gephyrocapsid coccoliths are morphologically comparable with the modern subpolar species *Gephyrocapsa caribbeanica*, they may point

to even cooler surface water conditions between about 3.63 and 3.50 Ma. Associated herewith was the successive disappearance of *R. pseudoumbilicus* and *Sphenolithus* spp. We conclude that the first major Pliocene cooling culminated in the time lapse between about 3.63 and 3.42 Ma. *Reticulofenestra* sp., *R. minutula* and *Emiliania ovata* (oval and subcircular coccolith morphotypes) apparently were species favouring the progressive decrease of average temperature and the increase of seasonality.

Through a succession of bioevents, bracketed between the biohorizons d1 and d6, the Early Pliocene discoaster flora underwent a marked change from an association of *E. quintatus*, *E. variabilis*, *E. surculus* and *E. brouweri* (*R. minuta* Subzone) to an association of *E. asymmetricus*, *E. tamalis*, *E. brouweri* and few *E. surculus* (*E. quintatus* Partial-paracme Subzone). We interpret this floral change-over in terms of progressive cooling, by which a subtropical association of *Eu-discoaster* species is replaced by a temperate association. *E. quintatus* and *E. variabilis* are considered to be subtropical species, while *E. asymmetricus* and *E. tamalis* were elements of cooler waters. *E. brouweri* was more eurythermal, since this species is found both in supposedly subtropical intervals (NN12-13B) and in temperate intervals (NN16-17B). Furthermore, it was the only Discoasterid species to survive the first northern hemisphere glaciation (about 2.4 Ma).

The distribution of *E. surculus* is more difficult to fit in, especially since we see no clear relation between its frequency pattern and the distribution of *Gephyrocapsa* spp. Besides, our quantitative record of *E. surculus* is biased by preservational effects to an unknown extent. In the abundance plot of Pliocene discoasters from DSDP site 306 near the Azores (37° N), the ranges of *E. surculus* and *E. quintatus* (*'Discoaster pentaradiatus'*) are roughly similar (Backman and Pestiaux, 1987). A closer inspection of their frequency graphs suggests that the two species show a negative correlation in some intervals. Because in the Mediterranean Pliocene *E. surculus* shows an increase before the acmes of *E. asymmetricus* and *E. tamalis*, we speculate that the temperature optimum of *E. surculus* was in between that of the subtropical species *E. quintatus* and the temperate species *E. asymmetricus* and *E. tamalis*.

The changes in the Mediterranean discoaster floras between 4.08 and 3.42 Ma can be recognized easily in the discoaster frequency graphs of DSDP site 606 near the Azores, which location is towards the centre of the present-day North Atlantic subtropical gyre (Backman and Pestiaux, op. cit.). It seems, therefore, that the cooling of the Mediterranean surface waters in the time-span between 3.60 and 3.42 Ma affected areas in the Atlantic as far to the South as 37° N.

Gephyrocapsa Partial-paracme Subzone (NN16-17C) (3.42-3.18 Ma)

The Mediterranean planktonic foraminiferal faunas from this Subzone (Interval 5 of the *G. crassaformis* Zone of Spaak, 1983) show a temporary absence of the *G. inflata* group and increased frequencies of the warm water species *Globigerinoides trilobus*. From these faunal accents Zachariasse and Spaak (1983) inferred a northward shift of the *G. inflata* group in the North Atlantic due to climatic amelioration. On the other hand, Raymo et al. (1987) interpreted the planktonic foraminiferal faunas in the corresponding absence-interval of the *G. inflata* group in DSDP Site 609 (central North Atlantic) in terms of surface water cooling. The calcareous nannofloras from this interval (Backman and Pestiaux, 1987; this paper) are characterized by an acme of the supposedly subtropical species *E. quintatus* (lower part of the subzone) and by relatively low frequencies of *Gephyrocapsa* spp. Therefore, we surmise a northward shift of the isotherms in the North Atlantic, resulting in an increase of temperatures and possibly a lowering of seasonality in the surface waters of the Mediterranean, especially in the time-lapse corresponding with the lower part of the subzone.

Gephyrocapsa Acme-subzone (3.18-2.87 Ma)

In addition to the acme of *Gephyrocapsa* spp., the nannofloras show the regular presence of *E. asymmetricus*, *E. tamalis* and *E. surculus*, and fluctuating but usually low numbers of *E. quintatus*. The *G. inflata* group reappears at the base of this interval. We infer an increased seasonality and lowered average temperatures in the Mediterranean. The large average diameters of the coccoliths of *R. minutula* (increase at the base of the interval) may have been characteristic for cooler surface water, whereas the decrease of the average coccolith size of *R. minuta* may point to a concomitant increase of primary productivity (see Gartner et al., 1983; 1987). The relatively low frequencies of *E. asymmetricus* and *E. tamalis* in the top part of the subzone are interpreted in terms of climatic amelioration.

Substantial evidence for a cooling event in the North Atlantic at about 3.1 Ma ago was found in the deep-sea cores, taken during Leg 94 of the Deep Sea Drilling Project (see, for example, Keigwin, 1987; Ehrmann and Keigwin, 1987; Backman and Pestiaux, 1987).

E. surculus (NN16-17E) and **E. quintatus** Acme (NN16-17F) Subzones
(2.87-2.40 Ma)

The low frequencies of the Gephyrocapsids throughout this interval are interpreted to be indicative of a weakened seasonality in the Mediterranean. The combination of relatively high frequencies of *E. surculus* and the common presence of *E. quintatus* seem to point to, on average, moderately warm surface water. The low frequencies of the small-size *Gephyrocapsa* spp. and *R. minuta* may indicate a decrease of primary productivity. The acme of *E. quintatus* in the corresponding subzone NN16-17F may even indicate the return of subtropical conditions in the Mediterranean, just prior to the onset of the first major cooling phase. Relatively low oxygen isotope values in the correlative interval of the Punta Piccola section on Sicily (Van der Zwaan and Gudjonsson, 1986), and the presence of the tropical planktonic foraminiferal species *Globorotalia menardii* and *G. miocenica* in the corresponding interval of DSDP Site 397 off northwest Africa (see Driever, 1984) render support to the interpretation in terms of an overall increase of surface water paleotemperatures. The short-term reappearance of the species *E. asymmetricus* and *E. tamalis* between biohorizons d8 and d9 (2.76-2.79 Ma) may represent a short cooling event.

E. brouweri (NN18A) and **E. triradiatus** (NN18B) Subzones
(2.40-1.89 Ma)

At about 2.40 Ma ago, the discoaster abundances in the Mediterranean and in the North Atlantic suffered a drastic decrease. In the Mediterranean, this event (horizon d11) has been recorded in DSDP Site 132 in the Tyrrhenian Sea (Raffi and Rio, 1981) and in several land-based sections (Driever, 1984 ; this paper). In the North Atlantic, the reduction of the discoasters was observed in Site 397 off Northwest Africa and in DSDP Site 606 near the Azores (Driever, 1984; Backman and Pestiaux, 1987). Being concomitant with changes in the planktonic and benthonic assemblages, changes in the palynological record, and changes in the oxygen isotope composition of foraminiferal carbonate, the change in the discoaster floras is evidently related to the major cooling, associated with the onset of the first glaciation on the northern hemisphere (for an overview see Driever, 1984).

It is assumed that the subsequent interval of cool climatic conditions in the Mediterranean is stratigraphically represented by the lower part of the *E. brouweri* Partial-range Subzone, covering the time-span between 2.40 and 2.31 Ma ago. This part of the subzone roughly corresponds to the planktonic foraminiferal Interval-zone 7, which is characterized by an acme of the cool

North Atlantic species *Neogloboquadrina atlantica* (Spaak, 1983). The calcareous nannofloras show relatively low frequencies of *Gephyrocapsa* spp. and *R. minuta*. If not caused by dissolution, these low frequencies may indicate that the productivity of the surface waters was low. *R. minutula* and *E. ovata* are the dominant species. Apparently, these species have been eurytopic floral elements, as their Mediterranean record seems to cover a wide range of paleoenvironmental conditions.

In the upper part of the *E. brouweri* Subzone and in the next higher *E. triradiatus* Subzone (about 2.31 to 1.89 Ma ago), the frequencies of *Gephyrocapsa* spp. show a gradual increase, *R. minuta* is common, and the last discoaster species are present, though discontinuously. These phenomena point to a return of more productive and slightly warmer waters in the Mediterranean. There may have been an overall increase of temperate conditions throughout the interval under consideration. Climatic conditions seem to have fluctuated considerably, as is indicated by the intermittent occurrences of *E. brouweri* and *E. triradiatus*, by the rapid fluctuations in the planktonic foraminiferal faunas (Zachariasse and Spaak, 1983), and by the oscillations in the oxygen isotope records (Thunell and Williams, 1983; Gudjonsson and Van der Zwaan, 1985; Keigwin, 1987). At some levels, corresponding with numerical ages of about 2.06 and 1.91 Ma, we observed relatively large-size ($> 4 \mu$) *G. caribbeanica*-like coccoliths, which we consider to be associated with influxes of very cool Atlantic waters. Strong evidence for this interpretation is found in concomitant shifts towards heavier oxygen isotope values (Vergnaud-Grazzini, 1987; Gudjonsson, in prep.), and in the presence of 'cool' benthonic foraminiferal associations (Verhallen, in prep.).

C. macintyrei (NN19A) and **G. caribbeanica** (NN19B) Subzones (1.89-1.30 Ma)

The calcareous nannofloras in the subzones immediately above the exit of the last two discoaster species show a large number of *Gephyrocapsa* spp., while there are two intervals which also yielded many large-size *Gephyrocapsids* (called *G. caribbeanica* in the upper interval). We rely on the paleoenvironmental interpretations of McIntyre et al. (1972) and Roth and Coulbourn (1982), who consider *G. caribbeanica* to be a species of subpolar waters. Hence, the floral associations in our uppermost two subzones show alternating transitional and subpolar affinities. The disappearance of *E. brouweri* and *E. triradiatus* at the base of this interval is in line with such an explanation. However, we fail to understand the concomitant sharp decline in the frequencies of *Coccolithus*

pelagicus (Raffi and Rio, 1981), which species is nowadays restricted to the sub-polar waters of the North Atlantic. The entry of *G. caribbeanica* and the nearly concomitant exit of *Calcidiscus macintyreii* is thought to have been associated with a next cooling step, corresponding with the base of the *G. caribbeanica* Subzone (about 1.40 Ma). Apparently, the level of the Pliocene-Pleistocene boundary in the stratotype section of Vrica (1.64 Ma ; Aguirre and Pasini, 1985) is in a relatively warm interval in between two cool episodes.

THE COMPOSITION OF THE EU-DISCOASTER FLORAS IN PLIOCENE SAPROPELS

From analyses of foraminiferal faunas, calcareous nannofloras and stable isotopes of foraminiferal carbonate, it has become increasingly clear that the formation of the Pliocene sapropelic, usually laminated beds is related to relatively short-term episodes of increased run-off, which led to a lowering of surface water salinity and subsequently to anoxic conditions at greater depths (Meulenkamp et al., 1979b ; Spaak, 1983 ; Thunell and Williams, 1983 ; Jonkers, 1984 ; Gudjonsson and Van der Zwaan, 1985). Also the carbonate-rich - carbonate-poor rhythms are associated with variations in run-off. Carbonate-poor intervals were produced by higher input rates of terrigenous material as a result of increased river discharge (Gudjonsson, 1987; De Visser et al., in prep.).

Zijderveld et al. (1986) calculated a periodicity of some 20,000 years for the carbonate-rich - carbonate-poor cycles in the lowermost Pliocene of the Singa section. They suggested that this rhythmic pattern is connected with the astronomical cycle of precession, causing an alternation of relatively dry and relatively humid spells in the Mediterranean. A similar mechanism is thought to have generated the alternation of sapropelic and non-sapropelic sediments (Rossignol-Strick, 1983; Hilgen, 1987).

We infer a preference for or at least a tolerance to lowered surface water salinity and nutrient-rich conditions if a certain discoaster species shows increased frequencies in samples from laminites. Taking all our discoaster data into account (figs.41-49), no particular species predominates in the *Eu-discoaster* florals from such samples. In the lower part of the Aghios Vlassios/Finikia sequence on Crete, *E. quintatus* is frequent in many of the sapropels, whereas higher up the species of the *E. brouweri* group (*E. brouweri*, *E. asymmetricus* and *E. tamalis*) are predominant. *E. surculus* seems to show a negative correlation with sapropelic facies throughout the sequence. Unfortunately, the frequency distribution of *E. brouweri* and *E. surculus* in the laminites from Sicily (Punta di Maiata, Punta Piccola, Monte San Nicola) is obscured by the large numbers of indeterminable six-rayed discoasters. Analogous with the pattern of Crete,

we assume that the latter group consists predominantly of *E. brouweri*. Concluding, *E. quintatus* and the species of the *E. brouweri* group preferred or tolerated lowered salinities and increased nutrient levels. Surface water temperature may have been the main parameter in determining which of either groups predominated. *E. quintatus* probably was a euryhaline species; we speculate that it flourished in the relatively saline water of the central part of the subtropical gyre in the Atlantic as well. *E. surculus* probably was a species with a limited tolerance to salinity changes.

SUMMARY OF THE PLIOCENE PALEOENVIRONMENTAL TRENDS

The critical elements in our interpretation of the major paleoenvironmental trends in the Pliocene are the assumptions that the small Gephyrocapsids were floral elements of the transitional association of the Atlantic, and that the discoaster *E. quintatus* was a characteristic species of (sub)tropical waters. For the larger part of the Pliocene in the Mediterranean (4.84 up to 2.40 Ma), we recorded a pattern of alternating influences of (sub)tropical and transitional associations which is connected with a fluctuating pattern of surface water temperatures. From the beginning of the Pliocene up to about 4.08 Ma, conditions in the Mediterranean seem to have been subtropical. The first signs in the marine Mediterranean floral and faunal records of climatic cooling were found in sediments of about 4.1 Ma old. We gather that in the subsequent time interval unto 3.42 Ma, a gradual climatic deterioration took place from a subtropical to a temperate climate, which was associated with an increase of seasonal contrasts, and which culminated between 3.60 and 3.42 Ma.

For the time-span between 3.42 and 3.18 Ma, we infer a return of relatively warm conditions in the Mediterranean. A renewed installation of temperate conditions and increased seasonality are surmised for the interval between 3.18 and 2.87 Ma. In the subsequent period up to 2.40 Ma, the climate in the Mediterranean and adjacent parts of the Atlantic seems to have ameliorated again towards warm, and in the later part of the interval even subtropical conditions.

In our opinion, the base of the *E. brouweri* Zone (NN18 ; 2.40 Ma), which is marked by a drastic decrease in the number of specimens of *Eu-discoaster*, corresponds with a major paleoenvironmental turnover in the Pliocene Mediterranean from an alternating subtropical-temperate to an alternating temperate-cool climatic regimen. This event is related to the onset of the first glaciation on the northern hemisphere. The subsequent Late Pliocene/Early Pleistocene episode shows calcareous nannofloras of predominantly cool-transitional and subpolar nature. We recorded two short-term influxes (2.06 and 1.91 Ma) and

one longer term influx (1.72-1.67 Ma) of very cool waters in latest Pliocene times, and one prolonged cold period in the Early Pleistocene (1.50 until beyond 1.30 Ma).

We would like to conclude this paper by stating that, in addition to yielding very good biostratigraphic markers, changes in the calcareous nannofossil taphocoenoses are valuable indicators for paleoenvironmental changes. Detecting and interpreting such events requires detailed quantitative floral analyses, a sound and preferably biometrical species concept, and, especially, a furthering of the insight into the environmental parameters, determining the geographical and temporal distribution of the modern calcareous nannoplankton species. Because of their numerical importance in the geological record, the Noëlaerhabdaceae seem to offer a great potential for the biostratigraphy, paleoclimatology and paleoceanography of the Cenozoic.

Assuming that our main paleoenvironmental changes fit in a system of contemporaneous changes on a global scale, it would be logical to use major events for biostratigraphic boundaries of higher rank (e.g. zonal boundaries) and to use the subordinate events for lower-rank boundaries (e.g. subzonal boundaries). Many of the Pliocene zonal boundaries of the Standard Zonation (Martini and Worsley, 1970) seem to correspond with minor paleoenvironmental events. However, we prefer using the 'lingua franca' of the Standard Zonation until the exploration and evaluation of the microfossil record have reached the stage of the integration of biostratigraphic and ecostratigraphic units.

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Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>	<i>E. tamalis</i>	<i>E. browneri</i>	<i>E. surculus</i>	<i>E. variabilis</i>	Indet. 5-rayed	Indet. 6-rayed
CP2350	63	0	0	0	8	1	0	28
2353	49	0	0	3	6	0	0	42
2356	61	0	0	1	9	3	0	26
2359	57	0	0	0	10	5	0	28
2362	72	0	0	0	4	8	0	16
2366	10	0	0	0	0	13	0	77
2205	21	0	0	0	18	7	0	54
2208	88	0	0	0	5	2	0	5
2209	52	0	0	2	24	8	1	13
2210	48	0	0	1	5	15	0	31
2211	47	0	0	2	15	8	0	28
2212	35	0	0	0	1	21	0	43
2214	16	0	0	0	42	0	0	42
2215	81	0	0	2	11	0	0	6
2216	12	0	0	0	48	1	0	39
2217	42	0	0	0	24	0	0	34
2219	14	0	0	0	43	1	0	42
2221	84	0	0	0	4	1	0	11
2222	64	2	0	6	9	3	0	16
2223	22	2	0	2	36	1	0	37
2224	19	16	0	10	21	0	4	30
2225	42	6	0	13	7	1	1	30
2226	19	1	0	7	20	0	0	53
2227	23	4	0	3	32	0	1	37
2228	42	4	0	3	36	0	1	14
2229	70	6	0	8	4	0	3	9
2230	79	11	0	6	1	0	1	2
2231	35	22	0	24	5	0	1	13
2232	70	10	0	12	5	1	0	2
2233	27	2	0	1	48	1	0	21
2234	44	4	0	7	26	1	0	18
2235	45	17	1	9	16	0	1	11
2236	50	1	0	2	28	0	0	19

Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>	<i>E. tamalis</i>	<i>E. browneri</i>	<i>E. surculus</i>	<i>E. variabilis</i>	Indet. 5-rayed	Indet. 6-rayed
CP2237	35	8	1	8	32	0	0	16
2238	59	2	1	1	23	0	0	14
2239	41	7	2	1	22	1	0	26
2240	3	14	2	3	52	0	0	26
2241	4	55	6	25	4	0	0	6
2242	26	24	6	13	23	1	0	7
2243	6	26	2	53	2	1	0	10
2244	1	12	0	14	49	0	0	24
2245	2	18	5	22	14	0	0	39
2246	2	4	2	10	52	0	0	31
2247	1	18	4	4	49	1	0	23
2248	5	15	6	10	36	0	0	28
2249	2	12	7	5	41	1	0	32
2250	0	1	0	2	55	0	0	42
2252	0	40	12	35	2	0	0	11
2255	1	6	5	6	50	1	0	31
2257	1	0	0	56	5	0	0	38
2259	0	9	5	7	53	0	0	26
2261	0	21	0	69	5	0	0	15
2262	0	4	0	15	43	0	0	37
2263	1	10	7	10	37	1	0	34
2265	0	9	8	10	42	1	0	30
2267	0	9	7	7	63	2	0	12
2270	0	14	9	14	39	1	0	23
2272	0	5	2	3	67	0	0	23
2273	2	15	13	13	22	0	0	35
2274	0	7	5	2	62	1	0	23
2275	0	25	10	25	23	0	0	17
2276	0	19	32	16	4	1	0	28
2277	0	35	18	13	7	1	0	26
2278	0	17	19	23	5	0	0	36
2279	0	20	8	31	13	1	0	27
2280	0	27	16	35	5	0	0	17

Table XXIV: Distribution chart of the species of *Eu-discoaster* in section Aghios Vlassios (N=100).

Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>			<i>E. tamalis</i>	<i>E. browneri</i>	<i>E. surculus</i>	<i>E. variabilis</i>	Indet. 5-rayed	Indet. 6-rayed
CP2001	0	21	19	8	28	0	1	23		
2004	1	6	4	2	26	1	0	60		
2007	0	9	5	2	53	0	2	29		
2010	2	3	1	5	36	0	0	53		
2012	0	11	4	13	30	0	0	42		
2016	0	14	4	16	7	0	0	59		
2121	1	9	2	6	53	0	0	29		
2023	0	21	21	18	18	1	0	21		
2025	0	1	5	9	59	0	0	26		
2027	0	33	39	15	5	0	0	8		
2032	2	22	19	27	5	2	0	23		
2035	1	15	21	18	5	0	0	40		
2037	0	27	19	23	7	0	0	24		
2041	0	27	30	27	2	0	0	14		
2044	1	30	15	22	10	0	0	22		
2047	0	16	16	14	30	0	0	24		
2049	2	11	19	13	14	1	0	40		
2052	1	34	21	20	1	0	0	23		
2053	1	25	11	22	6	1	0	34		
2054	1	29	21	12	3	0	0	34		
2055	6	18	12	18	11	0	0	35		
2056	15	15	13	11	17	1	0	28		
2057	3	24	21	14	7	0	0	31		
2058	5	15	24	10	16	0	0	30		
2059	43	6	7	8	13	1	0	22		
2060	13	25	12	10	13	0	0	27		
2061	9	27	16	15	2	0	0	31		
2062	8	30	24	12	12	0	0	14		
2063	0	5	6	42	3	0	0	44		
2064	24	12	9	14	10	0	0	31		
2065	50	8	6	9	3	0	0	24		
2067	16	24	19	10	0	0	0	31		
2070	14	16	15	27	7	1	0	20		
2072	58	11	5	2	9	1	2	12		
2074	36	20	16	10	2	2	1	13		
2076	44	20	10	5	14	0	0	7		
2079	17	27	20	5	4	5	0	22		
2083	1	30	16	7	18	0	0	28		

Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>			<i>E. tamalis</i>	<i>E. browneri</i>	<i>E. surculus</i>	<i>E. variabilis</i>	Indet. 5-rayed	Indet. 6-rayed
CP2087	16	26	12	4	7	0	1	34		
2089	20	14	10	3	19	0	0	34		
2092	0	32	52	2	1	0	0	13		
2095	10	28	15	2	17	0	0	28		
2100	25	19	19	9	10	3	0	15		
2103	1	40	17	5	10	2	0	25		
2107	1	29	15	8	22	2	0	23		
2109	3	16	22	3	18	1	0	37		
2113	0	25	27	4	14	0	0	30		
2116	2	21	19	2	6	1	0	49		
2120	3	21	13	2	23	0	0	38		
2122	12	14	12	3	21	0	0	38		
2124	17	14	6	6	19	0	0	38		
2128	9	24	12	4	9	2	0	40		
2129	14	13	11	1	37	0	0	24		
2130	15	8	9	1	40	0	0	27		
2131	10	21	17	2	27	0	0	23		
2132	6	33	29	3	13	1	0	15		
2134	14	25	30	4	7	1	0	19		
2135	12	14	11	3	36	0	0	24		
2136	10	11	9	3	32	0	0	35		
2137	20	7	10	6	39	0	0	18		
2138	13	22	25	6	22	1	0	11		
2139	28	15	31	2	8	0	0	16		
2140	7	29	36	6	1	1	0	20		
2141	41	15	8	1	15	0	0	20		
2143	14	12	15	4	33	0	0	22		
2146	31	5	32	3	19	1	0	9		
2150	13	7	15	0	32	0	0	33		
2152	3	24	23	4	19	0	2	25		
2154	24	12	1	2	27	0	1	33		
2158	34	24	2	2	28	0	2	8		
2162	0	8	10	5	32	0	1	44		
2166	32	5	5	1	29	0	0	28		
2169	4	11	7	4	35	1	4	34		
2171	27	9	5	3	35	1	0	20		
2173	8	10	7	1	55	0	0	19		

Table XXV: Distribution chart of the species of *Eu-discoaster* in the Finikia section (N=100).

Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>	<i>E. tamalis</i>	<i>E. browneri</i>	<i>E. sarculus</i>	<i>E. variabilis</i>	Indet. 6-rayed
JT11.516	84	0	0	5	2	0	9
11.517	55	0	0	5	8	6	26
11.518	49	12	0	31	1	0	7
11.519	21	10	0	35	5	0	29
11.520	64	10	0	9	3	0	14
11.521	78	5	0	6	1	0	10
11.522	66	15	0	11	3	0	5
11.523	88	1	0	7	0	0	4
11.524	28	14	0	48	0	0	10

Table XXVI: Distribution chart of the species of *Eu-discoaster* in section Singa IA (N=100).

Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>	<i>E. tamalis</i>	<i>E. brouweri</i>	<i>E. surculus</i>	<i>E. variabilis</i>	Indet. 5-rayed	Indet. 6-rayed
CP4051	31	0	0	30	0	1	0	38
4055	2	0	0	14	5	0	0	79
4058	82	0	0	10	1	0	0	7
4060	31	0	0	11	8	1	0	49
4061	11	0	0	2	10	0	0	77
4062	15	0	0	1	6	2	1	75
4063	4	0	0	0	9	0	1	86
4068	37	0	0	0	10	0	0	53
4071	70	0	0	1	0	5	0	24
4075	0	0	0	1	12	6	1	80
4078	88	0	0	1	2	3	0	6
4080	61	1	0	5	5	4	1	23
4084	81	2	1	0	2	2	0	12
4089	5	0	0	6	3	16	0	70
4093A	37	0	0	2	10	2	0	49
4097	23	0	0	1	26	2	0	48
4099A	51	0	0	0	13	0	0	36
4099B	40	1	0	10	1	1	1	46
4100	35	0	0	0	18	2	0	45
4100A	90	2	0	0	0	0	0	8
4100B	26	11	0	26	8	0	0	29
4100C	13	26	0	37	2	1	2	19
4101	1	32	0	32	3	0	0	32
4102	11	43	2	23	4	0	0	17
4102A	17	17	1	25	6	0	3	31
4102B	14	31	6	23	5	1	0	20
4103	4	38	7	38	0	0	0	12
4103A	3	59	5	11	1	0	0	20
4104	0	59	14	12	3	0	0	12
4104A	4	33	5	39	0	0	0	19
4105	0	24	9	21	12	0	0	34
4106	0	31	10	22	9	1	0	27
4107	1	21	10	22	8	1	0	37
4108A	0	35	12	32	0	0	0	21
4110	1	23	8	16	18	0	0	34
4111	0	22	7	12	19	0	0	40
4112	0	26	11	18	14	0	0	31
4113	0	36	5	18	3	0	0	38
4114	0	6	7	3	46	0	0	38
4115	0	15	5	17	16	2	0	45
4117	2	41	12	27	1	0	0	17
4118	1	37	13	25	3	0	0	21
4119	0	41	20	16	9	0	0	14
4120	0	17	10	18	7	0	0	48
CP4121	0	29	19	25	3	0	0	24
4122	0	23	14	12	8	0	0	43
4124	0	21	15	10	15	0	0	39
4126	2	19	15	14	20	0	0	30
4127	0	34	23	20	2	1	0	20
4128	3	21	20	9	20	0	0	27
4129	0	20	18	6	9	0	0	47
4130	34	16	32	5	3	0	0	10
4131	16	25	25	7	7	0	0	20
4132	42	33	11	9	3	0	0	2
4133	76	11	5	3	4	0	0	1
4134	12	37	19	5	1	0	0	26
4135	0	41	31	9	4	1	0	14
4136	8	25	33	5	10	0	0	19
4137	2	26	22	6	17	0	0	27
4138	1	28	14	5	22	0	0	30
4139	2	24	31	9	7	0	0	27
4140	22	30	11	9	3	0	0	25
4142	2	26	42	3	8	0	0	19
4143	0	24	34	3	4	0	0	35
4145	0	39	14	16	5	0	0	26
4147	5	22	18	2	16	0	0	37
4148	8	32	35	10	5	0	0	10
4150	10	33	19	2	10	0	0	26
4153	0	34	32	4	17	0	0	13
4155	0	10	13	4	14	0	0	59
4157	19	11	6	3	20	0	0	41
4160	6	29	24	2	22	0	0	17
4162	2	20	11	6	17	0	0	44
4165	3	22	27	13	16	0	0	19
4168	5	10	22	15	16	0	0	32
4170	22	1	1	26	4	0	0	46
4171	3	6	7	4	9	0	0	71
4172	20	0	0	3	15	0	0	62
4174	8	11	12	6	11	0	0	52
4175	29	1	1	4	3	0	0	62
4176	2	16	18	16	10	0	0	38
4177	6	0	5	6	4	1	0	78
4178	8	0	1	3	15	0	2	71
4179	1	1	0	2	31	1	0	64
4180	11	0	1	0	8	0	0	80
4181	1	0	0	4	21	0	0	74
4182	0	1	0	2	27	0	0	70

Table XXVII: Distribution chart of the species of *Eu-discoaster* in the Punta di Maiata section (N=100).

Samples	<i>E. quintatus</i>	<i>E. asymmetricus</i>	<i>E. tamalis</i>	<i>E. browneri</i>	<i>E. sureulus</i>	<i>E. variabilis</i>	Indet. 6-rayed
JT5701	0	19	16	9	4	0	52
5702	8	41	24	9	2	0	16
5703	5	32	18	6	9	0	30
5704	1	4	9	7	24	0	55
5705	3	6	6	5	12	0	68
5706	2	16	9	14	14	0	45
5707	7	12	12	23	17	0	29
5708	0	0	2	4	19	0	75
5709	0	4	6	9	29	0	52
5710	12	0	0	0	23	0	65
5711	3	11	14	2	21	0	49
5712	20	1	1	0	8	0	70
5713	9	11	8	10	18	0	44
5714	26	1	1	1	14	0	57
5715	3	12	11	19	11	0	44
5716	7	3	0	5	5	0	80
5717	14	1	0	2	22	0	61
5718	2	0	0	3	26	0	69
5719	16	0	0	1	39	0	44
5720	8	3	0	3	20	0	66
5721	0	0	1	4	40	1	54
5722	0	0	0	6	22	0	72
5723	16	2	0	0	42	0	40
5724	26	0	0	0	13	0	61
5725	20	12	17	15	5	0	31
5726	0	3	11	1	17	0	68
5727	10	0	2	25	26	0	37
5728	4	0	0	8	31	0	57
5729	2	2	0	24	13	0	59
5730	1	5	0	0	28	0	66
5731	54	0	0	1	17	0	28
5732	7	2	0	7	28	2	54
5733	1	0	0	3	28	0	68
5734	3	0	0	8	19	0	70
5735	61	0	0	0	8	1	30
5736	9	1	0	8	31	0	51
5737	19	0	0	2	29	0	50
5738	31	0	1	5	23	0	40
5739	1	0	1	4	26	1	67
5740	27	1	0	1	13	0	58
5741	2	1	0	5	29	0	63
5742	69	0	0	2	2	0	27

Table XXVIII: Distribution chart of the species of *Eu-discoaster* in section Punta Piccola (N=100).

Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>	<i>E. tamalis</i>	<i>E. triradiatus</i>	<i>E. browneri</i>	<i>E. surevulus</i>	<i>E. variabilis</i>	Indet. 6-rayed
CP3751	38	0	0	0	8	3	0	51
3752	73	2	0	0	5	2	2	16
3753	7	27	2	0	41	3	0	20
3754	0	31	16	0	3	0	0	50
3755	0	16	7	0	17	7	1	52
3756	0	14	6	0	15	22	0	43
3757	1	23	18	0	17	9	0	32
3758	0	41	33	0	11	1	0	14
3759	0	15	8	0	2	2	0	73
3760	3	23	29	0	5	11	0	29
3761	55	18	11	0	3	0	0	13
3762	5	21	13	0	0	4	0	57
3763	9	26	9	0	1	12	0	43
3764	3	23	37	0	2	4	0	31
3765	0	13	67	0	1	2	1	16
3766	9	25	18	0	3	4	0	41
3767	12	9	13	0	10	14	0	42
3768	21	0	1	0	1	24	0	53
3769	3	1	0	0	0	46	0	50
3770	70	2	2	0	0	5	0	21
3771	1	15	19	0	11	24	0	30
3772	6	1	2	0	5	36	1	49
3773	21	1	1	0	22	7	0	48
3774	28	0	0	0	15	6	1	50
3775	69	2	2	0	3	0	1	23
3775C	83	2	1	0	0	0	0	14
3776	71	2	0	0	0	5	0	22
3777	60	1	1	0	6	3	1	28
3778	13	3	3	0	31	6	2	42
3783	1	0	0	0	54	0	1	44
3784	5	5	1	0	49	6	3	31
3785	1	1	1	0	73	2	0	22
3787	1	1	1	63	21	0	0	14

Table XXIX: Distribution chart of the species of *Eu-discoaster* in the Monte San Nicola section (N=100).

Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>	<i>E. tomajis</i>	<i>E. triradiatus</i>	<i>E. browneri</i>	<i>E. surculus</i>	<i>E. variabilis</i>	Indet. 6-rayed	Total number of discoasters per 10,000 nannofossils	Traversal length in mm. (10,000 nannofossils)
GR1170	3	2	0	0	8	5	0	44	62	32.25
1172	18	3	0	0	0	1	0	13	35	18.75
1173	2	1	5	0	4	2	0	17	31	15.75
1174	6	0	0	0	0	0	0	25	31	19.50
1176	26	0	0	0	1	5	0	7	39	20.50
1179	9	0	0	0	0	8	0	39	56	34.00
1182	0	0	0	0	1	5	0	14	20	13.25
1184	6	0	1	0	4	9	1	61	82	14.25
1185	4	0	0	0	3	1	0	11	19	74.50
1186	2	1	0	0	0	4	0	30	37	12.75
1187	0	0	0	0	13	0	0	22	35	37.50
1189	20	0	0	0	9	7	0	27	63	13.75
1191	0	0	0	0	16	0	0	17	33	38.00
1192	8	0	0	0	2	2	0	17	29	14.75
1196	23	0	0	0	26	2	1	40	92	36.75
1199	39	0	0	0	39	4	1	61	144	45.00
1201	27	0	0	0	2	28	0	37	94	30.25
1203	3	0	0	0	0	0	0	28	31	24.75
1207	14	0	0	0	2	0	0	7	23	18.25
1209	18	0	0	0	10	4	0	6	38	30.75
1211	39	0	0	0	3	0	0	15	57	24.00
1214	37	1	1	0	5	0	0	6	50	47.75
1215	17	0	0	1	3	0	1	6	28	31.75
1216	40	4	0	1	23	0	1	17	86	72.00
1217	1	0	0	0	0	0	0	0	1	22.00
1218	1	0	0	0	0	0	0	0	1	36.25
1219	1	0	0	0	0	0	0	0	1	27.50
1220	1	0	0	0	0	0	0	2	3	49.00
1222	3	0	0	0	0	0	0	3	6	27.75
1225	0	0	0	0	0	0	0	0	0	38.25

Table XXX: Frequency of the species of *Eu-discoaster* in 10,000-counts in section Francocastello.

Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>	<i>E. tamatis</i>	<i>E. triradiatus</i>	<i>E. browneri</i>	<i>E. sureulus</i>	<i>E. variabilis</i>	Indet. 6-rayed	Total nr. of discoasters per 10,000 nannofossils	Traverse length in mm. (10,000 nannofossils)
CP3751	20	0	0	0	10	2	0	19	51	19.50
3752	10	1	0	0	3	2	0	2	18	7.50
3753	0	3	0	0	12	0	0	1	16	16.00
3755	1	6	2	0	7	9	0	26	51	5.25
3757	0	6	4	0	4	1	0	8	23	12.75
3759	0	1	0	0	1	0	0	7	9	5.50
3761	15	4	3	0	1	1	0	3	27	8.75
3763	1	1	2	0	1	2	0	4	11	4.75
3765	0	4	21	1	2	0	0	8	36	8.25
3767	7	4	7	0	4	4	0	16	42	17.50
3769	2	0	0	0	6	24	0	17	49	20.25
3770	115	3	2	0	8	12	0	29	169	21.75
3771	1	7	17	0	4	7	0	15	51	18.00
3773	5	0	1	0	7	7	0	10	30	17.50
3774	4	0	0	0	6	2	0	6	18	17.25
3775	27	0	1	0	3	0	0	3	34	37.50
3775C	64	0	1	0	1	1	0	5	72	40.00
3776	3	1	0	0	0	2	0	2	8	20.25
3777	20	0	0	0	6	1	0	2	29	13.50
3778	4	1	0	0	2	0	1	2	10	29.25
3779	3	0	1	0	0	0	1	4	9	15.50
3780	1	1	1	0	2	1	1	11	18	34.50
3781	0	1	0	0	1	0	0	0	2	10.75
3782	1	0	0	0	1	0	2	2	6	18.75
3783	0	0	0	0	11	0	0	2	13	9.75
3784	0	1	0	0	2	0	0	2	5	31.25
3785	0	1	0	0	11	0	0	1	13	22.25
3786	3	0	0	0	3	0	0	2	8	29.00
3787	0	0	0	16	12	0	0	5	33	21.00
3788	0	0	0	0	2	0	0	0	2	23.50
3789	2	0	0	0	2	0	1	0	5	12.25
3790	0	0	0	0	1	0	0	3	4	23.00
3792	0	0	0	0	1	0	0	1	2	12.75
3793	2	0	0	0	0	0	0	8	10	23.75
3795	1	0	0	0	2	1	0	2	6	23.00
3797	1	0	1	0	1	0	0	6	9	18.50
3799	0	1	0	0	0	0	0	3	4	20.00
3801	1	0	1	0	0	0	0	4	6	28.25
3803	3	0	0	0	1	0	0	8	12	60.00

Table XXXI: Frequency of the species of *Eu-discoaster* in 10,000-counts in section Monte San Nicola.

Sample	<i>E. quintatus</i>	<i>E. asymmetricus</i>	<i>E. tamalis</i>	<i>E. triradiatus</i>	<i>E. browneri</i>	<i>E. surculus</i>	<i>E. variabilis</i>	Indet. 6-rayed	Total number of discoasters per 10,000 nannofossils	Traverse length in mm. (10,000 nannofossils)
JT9235	0	4	3	0	21	15	0	12	55	18.00
9236	7	6	3	0	7	11	0	19	53	9.25
9239	10	0	0	0	6	3	1	7	27	25.00
9241	2	1	0	0	4	2	0	9	18	11.50
9245	1	1	1	0	6	0	1	16	26	22.00
9246	0	0	1	0	2	1	0	3	7	14.50
9249	0	2	4	0	8	5	0	9	28	18.10
9252	12	0	0	0	1	3	0	2	18	32.00
9255	13	1	0	0	1	4	0	4	23	11.50
9256	3	0	0	0	7	3	1	20	34	10.75
9260	0	0	0	0	1	2	0	2	5	12.50
9261	2	0	0	0	12	1	0	10	25	33.00
9265	1	0	0	0	5	1	0	8	15	19.50
9266	19	0	0	0	5	0	1	6	31	170.00
9269	0	0	0	0	6	4	0	11	21	17.00
9270	0	0	0	0	1	1	0	5	7	10.50
9273	2	0	0	0	8	3	0	5	18	14.75
9275	33	0	0	0	10	0	0	1	44	11.25
9276	23	0	0	0	3	2	0	4	32	17.50
9277	3	0	0	0	4	3	0	9	19	22.00
9281	50	0	0	0	2	0	0	1	53	27.50
9283	44	0	0	0	1	0	1	1	47	33.75
9286	22	0	0	0	0	2	0	4	28	31.00
9315	23	0	0	0	0	0	0	3	26	21.25
9319	9	0	0	0	0	1	1	3	14	30.25
9323	28	0	0	0	5	0	0	1	34	13.00
9327	16	0	0	0	3	0	0	1	20	18.50
9329	20	0	0	0	3	0	0	1	24	26.25
9330	1	0	0	0	1	0	0	0	2	43.50
9335	2	0	0	0	0	0	0	3	5	25.50
9339	0	0	0	0	0	0	0	1	1	24.50
9343	0	0	0	0	1	0	0	3	4	81.00
9347	1	0	0	0	0	0	0	1	2	31.00
9351	0	0	0	0	0	0	1	0	1	39.00
9355	1	0	0	0	0	0	0	0	1	35.00
9358	0	0	0	0	0	0	0	0	0	15.75
9360	0	0	0	0	1	0	0	3	4	14.00
9366	0	0	0	0	1	0	0	0	1	16.75
9370	1	0	0	1	4	0	0	1	7	14.75
9374	0	0	0	0	0	0	0	1	1	14.75

Table XXXII: Frequency of the species of *Eu-discoaster* in 10,000-counts in section Singa II/III.

Plate 1

(all magnifications X 6000)

- Fig.1 Coccosphere of *Reticulofenestra minutula* (Gartner) Haq & Berggren, emend.
Finikia, CP2171, NN16-17D.
- Fig.2 Coccosphere of *Emiliana ovata* Bukry
Aghios Vlassios, CP2261, NN16-17A.
- Fig.3 *Reticulofenestra minutula*
Kalithea I, GR2714, NN12-13B.
- Figs.4,5 *Reticulofenestra minutula*
Aghios Vlassios, CP2261, NN16-17A.
- Fig.6 *Reticulofenestra pseudumbilicus* (Gartner) Gartner
Kalithea I, GR2717, NN12-13B.
- Figs.7,8 *Reticulofenestra minutula*
Fig.7 : Lido Rossello, CP4220, NN18A.
Fig.8 : Vrica, JT6269, NN19A.
- Fig.9 *Gephyrocapsa caribbeanica* Boudreaux & Hay
Levkos, GR3139, NN19B.
- Fig.10 *Reticulofenestra minutula*
Monte San Nicola, CP3770, NN16-17D.

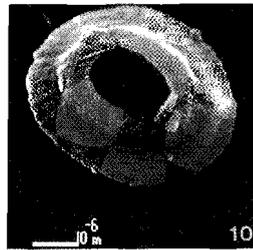
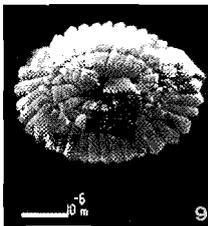
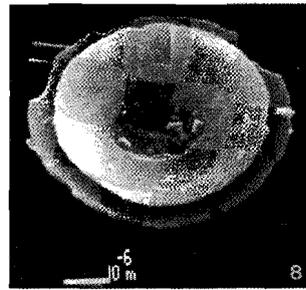
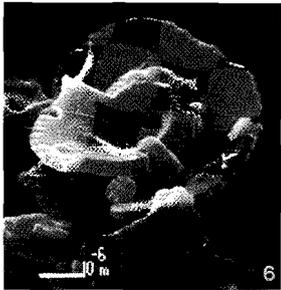
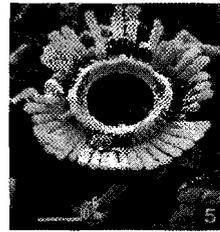
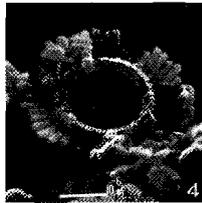
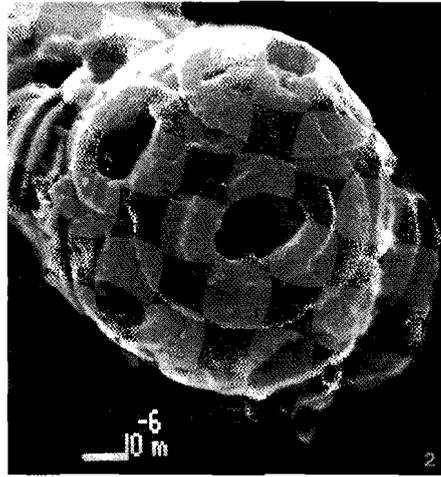
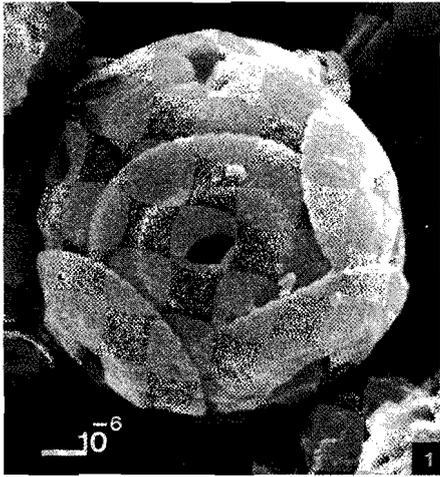


Plate 2

(all magnifications X 6000)

- Fig.1 ? *Gephyrocapsa caribbeanica*
Levkos, GR3139, NN19B.
- Figs.2,3 ? *Emiliana huxleyi* (Lohmann) Hay & Mohler
Adriatic Sea, Core IN68-38, Adria 404-4, NN21.
- Fig.4 Intercentral specimen *Reticulofenestra minuta* / *Reticulofenestra minutula*
Kalihea I, GR2714, NN12-13B.
- Fig.5 *Reticulofenestra pseudumbilicus*, small specimen
Lido Rossello, CP4220, NN18A.
- Fig.6 *Emiliana ovata*
Finikia, CP2007, NN16-17A.
- Figs.7,8 *Reticulofenestra pseudumbilicus*, small specimens
Kalihea I, GR2711, NN12-13B.
- Fig.9 *Emiliana huxleyi*
Laboratory culture A-92, Department of Biochemistry, State University of Leiden.
- Fig.10 *Emiliana ovata*
Aghios Vlassios, CP2261, NN16-17A
- Figs.11-13 Intercentral specimens *Reticulofenestra minuta* / *Reticulofenestra minutula*
Fig.11 : Aghios Vlassios, CP2357, NN12-13B.
Fig.12 : Kalihea I, GR2714, NN12-13B.
Fig.13 : Kalihea I, GR2714, NN12-13B.
- Figs.14,18 *Gephyrocapsa caribbeanica*
Bianco-sample, NN19B.
- Figs.15-17 *Gephyrocapsa* sp.
Figs.15,17 : Aghios Vlassios, CP2261, NN16-17A.
Fig.16 : Finikia, CP2027, NN16-17A.

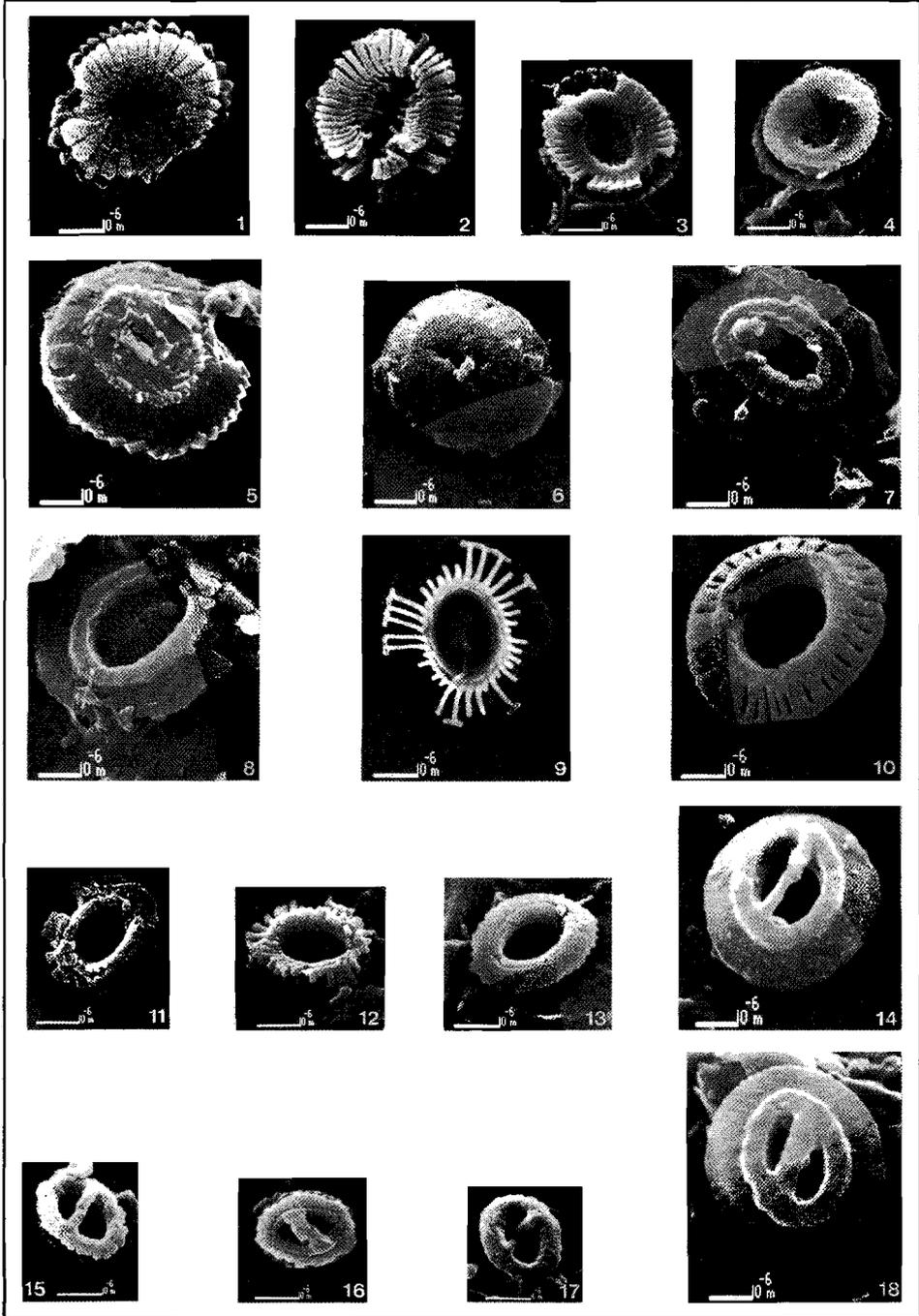


Plate 3

(all magnifications X 6000)

- Fig.1 *Emiliana huxleyi*
Laboratory culture A-92, Department of Geochemistry, State University of Leiden.
- Figs.2,3 *Reticulofenestra pseudoumbilicus*
Kalihea I, GR2711, NN12-13B.
- Fig.4 *Reticulofenestra minutula*
Kalihea I, GR2711, NN12-13B.
- Figs.5-7 *Reticulofenestra pseudoumbilicus*
Kalihea I, GR2711, NN12-13B.
- Fig.8 *Reticulofenestra minuta* Roth
Kalihea I, GR2711, NN12-13B.
- Fig.9 Fragment of *Reticulofenestra pseudoumbilicus*
Kalihea I, GR2711, NN12-13B.
- Fig.10 Fragment of ? *Reticulofenestra minutula*
Kalihea I, GR2711, NN12-13B.
- Figs.11-13 *Gephyrocapsa* sp.
Levkos, GR3139, NN19B.
- Fig.14 *Gephyrocapsa caribbeanica*
Levkos, GR3139, NN19B.
- Fig.15 ? *Gephyrocapsa caribbeanica*
Levkos. GR3139, NN19B.

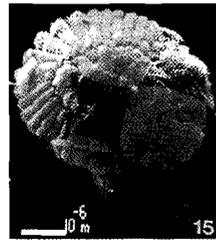
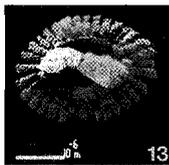
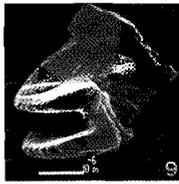
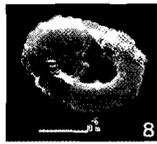
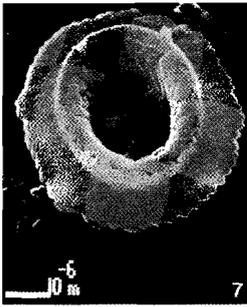
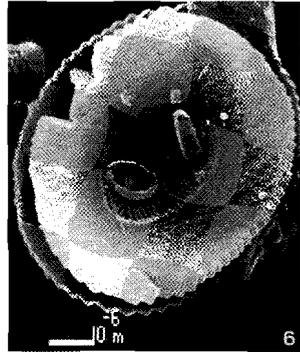
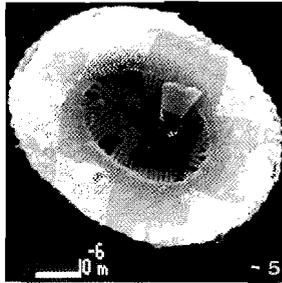
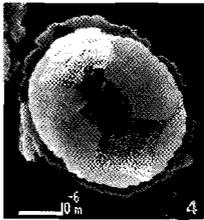
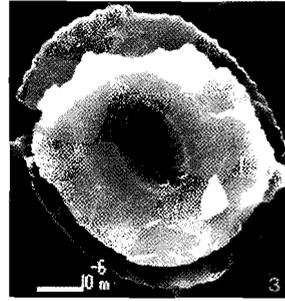
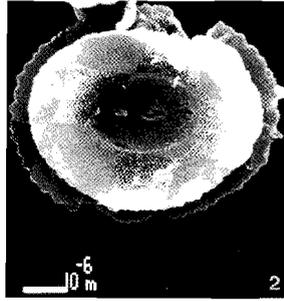
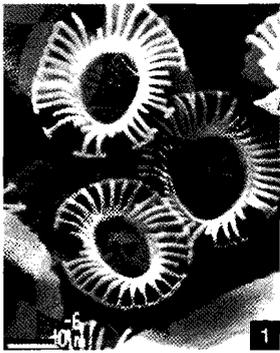


Plate 4

(all magnifications X 3000)

- Fig.1 *Reticulofenestra pseudumbilicus*, distal views
Kalithea I, GR2711, NN12-13B.
Fig.1a : SEM.
1b : same specimen, LM.
- Figs.2,3 *Reticulofenestra minutula*, distal views
Punta di Maiata, CP4116, NN16-17A.
Fig.2a : SEM.
2b : same specimen, LM.
Fig.3a : SEM.
3b : same specimen, LM.
- Fig.4 *Gephyrocapsa caribbeanica*, distal views
Levkos, GR3140, NN19B.
Fig.4a : SEM.
4b : same specimen, LM.
- Figs.5,6 *Reticulofenestra pseudumbilicus*, proximal views
Kalithea I, GR2711, NN12-13B.
Fig.5a : SEM.
5b : same specimen, LM.
Fig.6a : SEM.
6b : same specimen, LM.
- Figs.7,8 *Reticulofenestra minutula*, proximal views
Punta di Maiata, CP4116, NN16-17A.
Fig.7a : SEM.
7b : same specimen, LM.
Fig.8a : SEM.
8b : same specimen, LM.
- Figs.9,11,12 *Reticulofenestra antarctica* (Haq) nov. comb.
Fig.9 : Kalithea I, GR2661, NN12-13A.
Fig.11 : Kalithea I, GR2681, NN12-13A.
Fig.12 : Singa Varda, JT11.481, NN12-13A.
- Figs.10,13 *Reticulofenestra antarctica* (a) and *Reticulofenestra minuta* (b)
Fig.10 : Kalithea I, GR2681, NN12-13A.
Fig.13 : Singa Varda, JT11.481, NN12-13A.

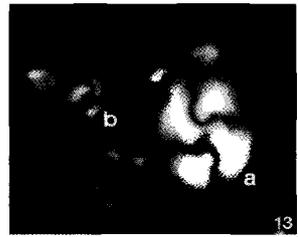
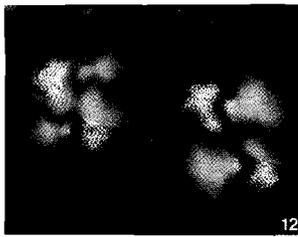
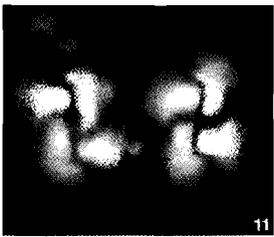
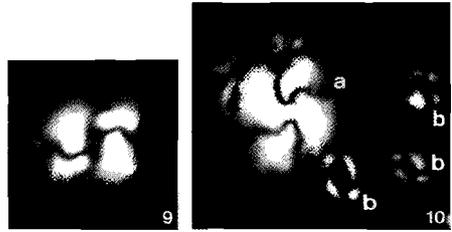
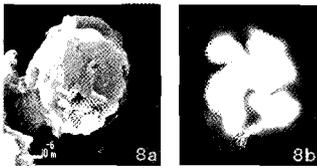
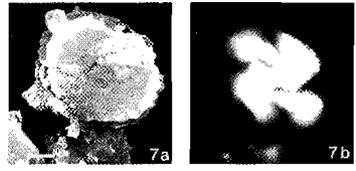
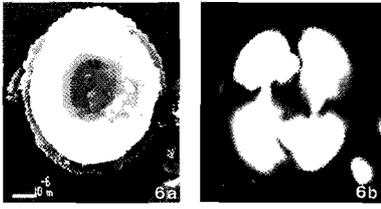
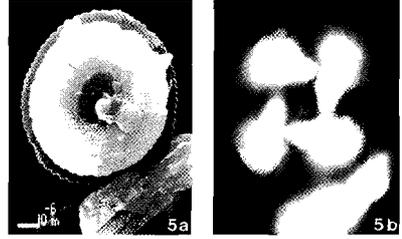
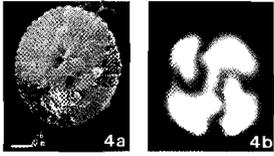
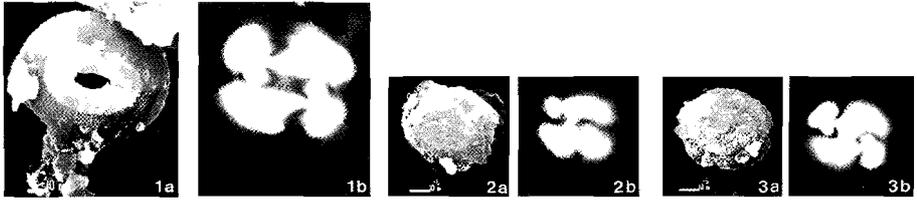


Plate 5

(all magnifications X 3000)

- Fig.1 *Reticulofenestra minuta*
Kalihea I, GR2681, NN12-13A.
- Figs.2-6 *Reticulofenestra minutula*
Fig.2 : Singa I, JT9119, NN12-13A.
Fig.3 : Punta di Maiata, CP4108A, NN14-15B.
Fig.4 : Punta Piccola, JT5736, NN16-17E.
Fig.5 : Singa III, JT9330, NN18A.
Fig.6 : Singa III, JT9339, NN18A.
- Fig.7 *Reticulofenestra pseudoumbilicus* (a), *Reticulofenestra minutula* (b), *Reticulofenestra minuta* (c), and intercentral specimens *R. minuta* / *R. minutula* (d)
Kalihea I, GR2706, NN12-13B.

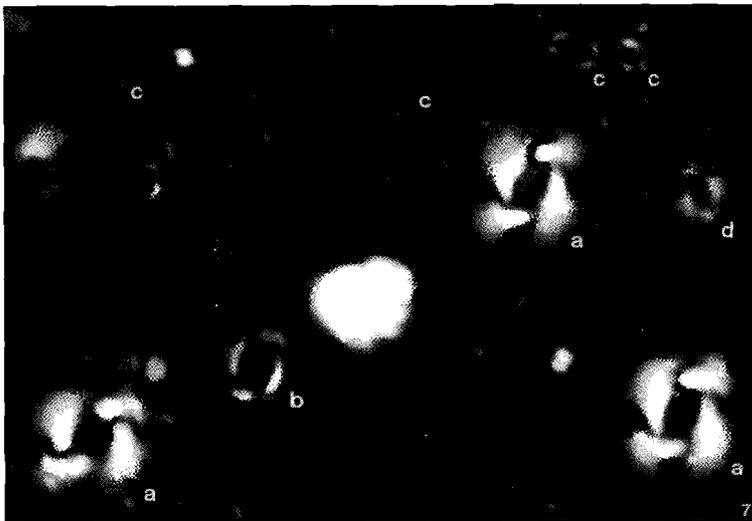
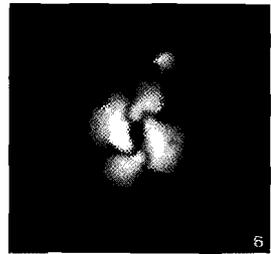
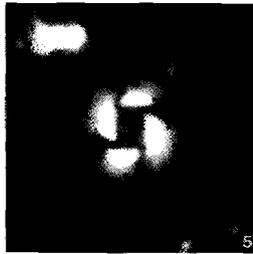
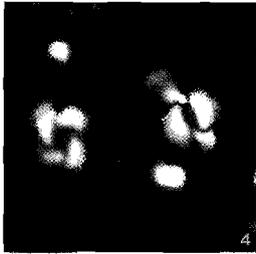
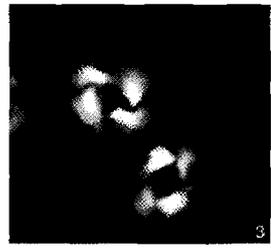


Plate 6

(all magnifications X 3000)

- Fig.1 *Reticulofenestra pseudoumbilicus* (a), *Reticulofenestra minutula* (b), and *Reticulofenestra minuta* (c)
Singa I, JT9001, NN12-13B.
- Figs.2,4,5 *Reticulofenestra pseudoumbilicus*
Fig.2 : Singa I, JT8985, NN12-13B.
Fig.4 : Singa I, JT9119, NN12-13C.
Fig.5 : Singa I, JT9126, NN12-13C.
- Fig.3 *Reticulofenestra pseudoumbilicus* (a) and an *R. minuta* / *R. minutula* intercentral specimen (b)
Singa I, JT9119, NN12-13C.
- Figs.6-11 *Emiliana ovata*
Fig.6 : Aghios Vlassios, CP2244, NN14-15B.
Fig.7 : Aghios Vlassios, CP2249, NN16-17A.
Fig.8 : Aghios Vlassios, CP2255, NN16-17A.
Figs.9,10 : Aghios Vlassios, CP2275, NN16-17A.
Fig.11 : Aghios Vlassios, CP2276, NN16-17A.

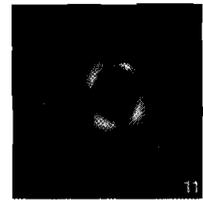
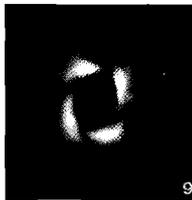
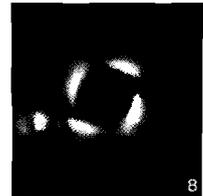
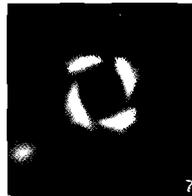
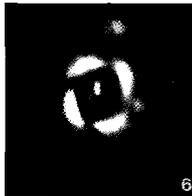
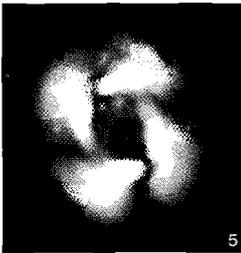
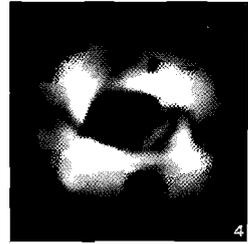
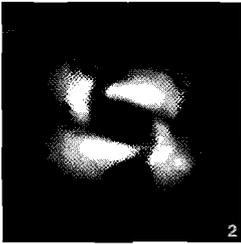
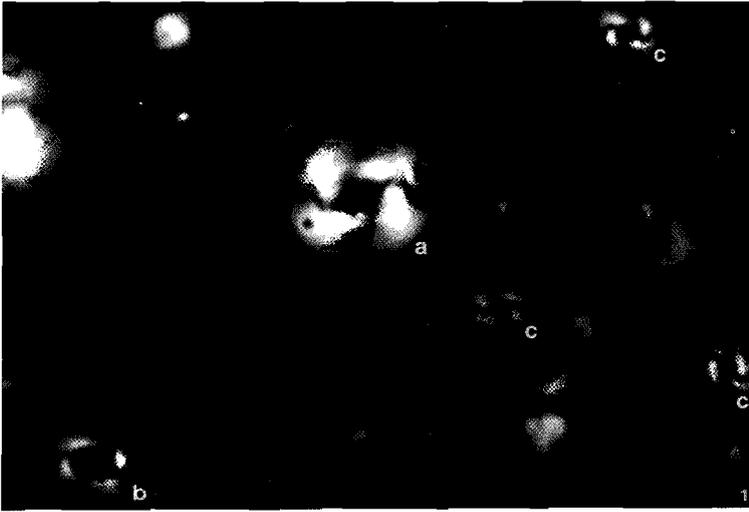


Plate 7

(all magnifications X 3000)

Figs.1-8

Emiliana ovata

Fig.1 : Finikia, CP2023, NN16-17A.

Fig.2 : Finikia, CP2139, NN16-17D.

Fig.3 : Punta Piccola, JT5723, NN16-17E.

Fig.4 : Singa III, JT9330, NN18A.

Fig.5 : Singa III, JT9411, NN18B.

Fig.6 : Singa III, JT9438, NN18B.

Fig.7 : Singa III, JT9485, NN18B.

Fig.8 : Singa IV, JT9637, NN19A.

Figs.9-29

Gephyrocapsa spp.

Photograph-pairs a,b : in b the microscope's stage has been rotated in clockwise direction over 45 degrees, relative to the position in a.

Figs.9-10 : Singa IA, JT11.497, NN12-13C.

Figs.11,12 : Singa IA, JT11.497, NN12-13C.

a : *R. minuta*

Figs.13,14 : Singa IA, JT11.497, NN12-13C.

Figs.15,16 : Singa IA, JT11.499, NN12-13C.

Fig.17 : Singa IA, JT11.500, NN12-13C.

Fig.18 : Aghios Vlassios, CP2214, NN12-13C.

Figs.19-22 : Singa IA, JT11.519, NN14-15A.

Figs.23,24 : Aghios Vlassios, CP2244, NN14-15B.

Figs.25-27 : Aghios Vlassios, CP2268, NN16-17A.

Fig.28 : Aghios Vlassios, CP2268, NN16-17A.

a : intercentral specimen *R. minuta* / *R. minutula*

Fig.29 : Punta di Maiata, CP4114, NN16-17A.

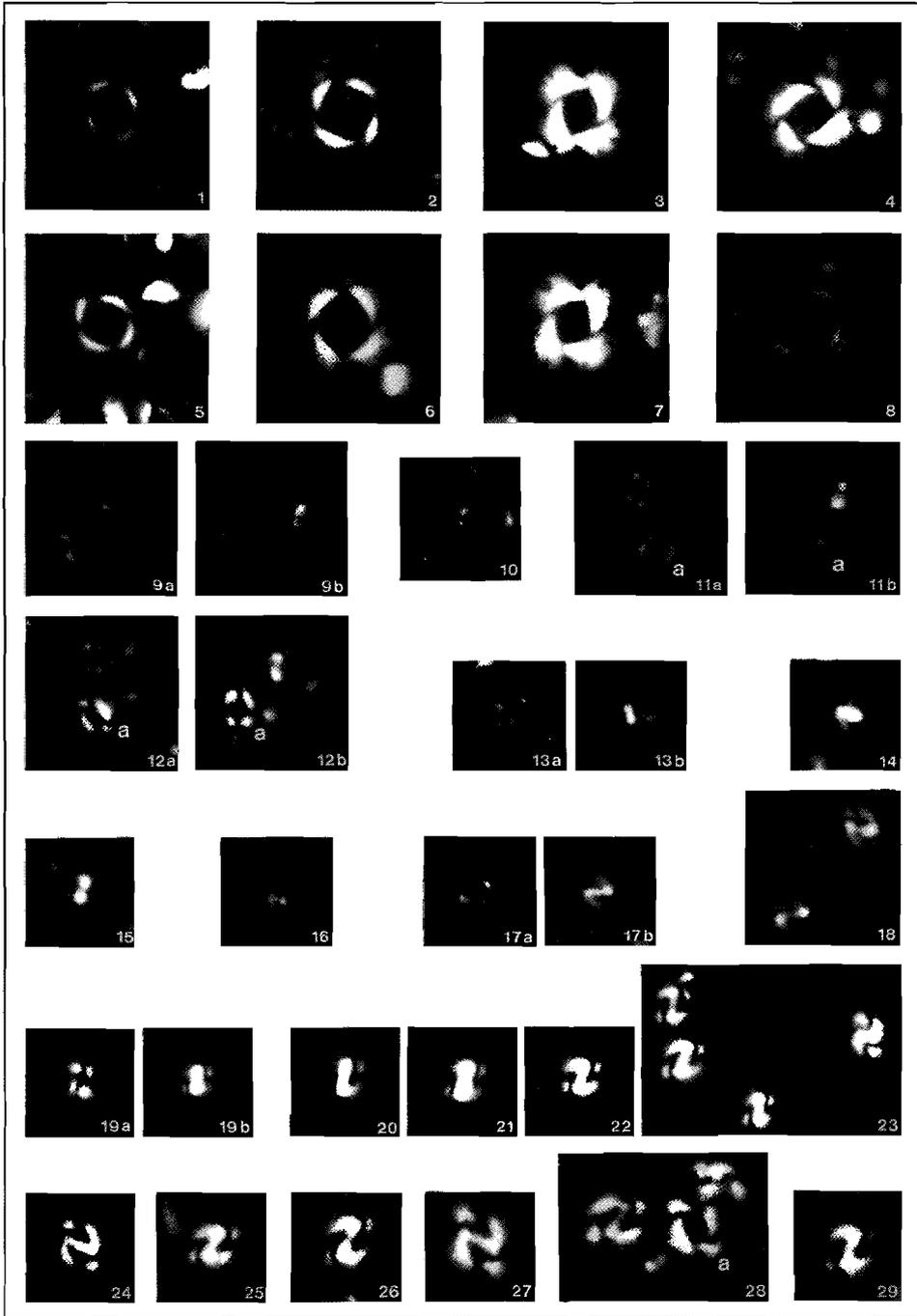


Plate 8

(all magnifications X 3000)

- Figs.1-19 *Gephyrocapsa* spp.
Figs.1,2 : Punta di Maiata, CP4124, NN16-17B.
Fig.3 : Singa III, JT9411, NN18B.
Fig.4 : Singa III, JT9411, NN18B.
 a : *R. minuta*
Figs.5,6 : Singa III, JT9438, NN18B.
Figs.7-10 : Singa III, JT9485, NN18B.
Figs.11-17 : Singa IV, JT9629, NN19A.
Figs.18,19 : Singa IV, JT9676, NN19B.
- Figs.20-25 *Gephyrocapsa caribbeanica*
Figs.20,24 : Singa IV, JT9670, NN19B.
Figs.21,23 : Singa IV, JT9676, NN19B.
Figs.22,25 : Singa IV, JT9676, NN19B.
 a : *Gephyrocapsa* sp.

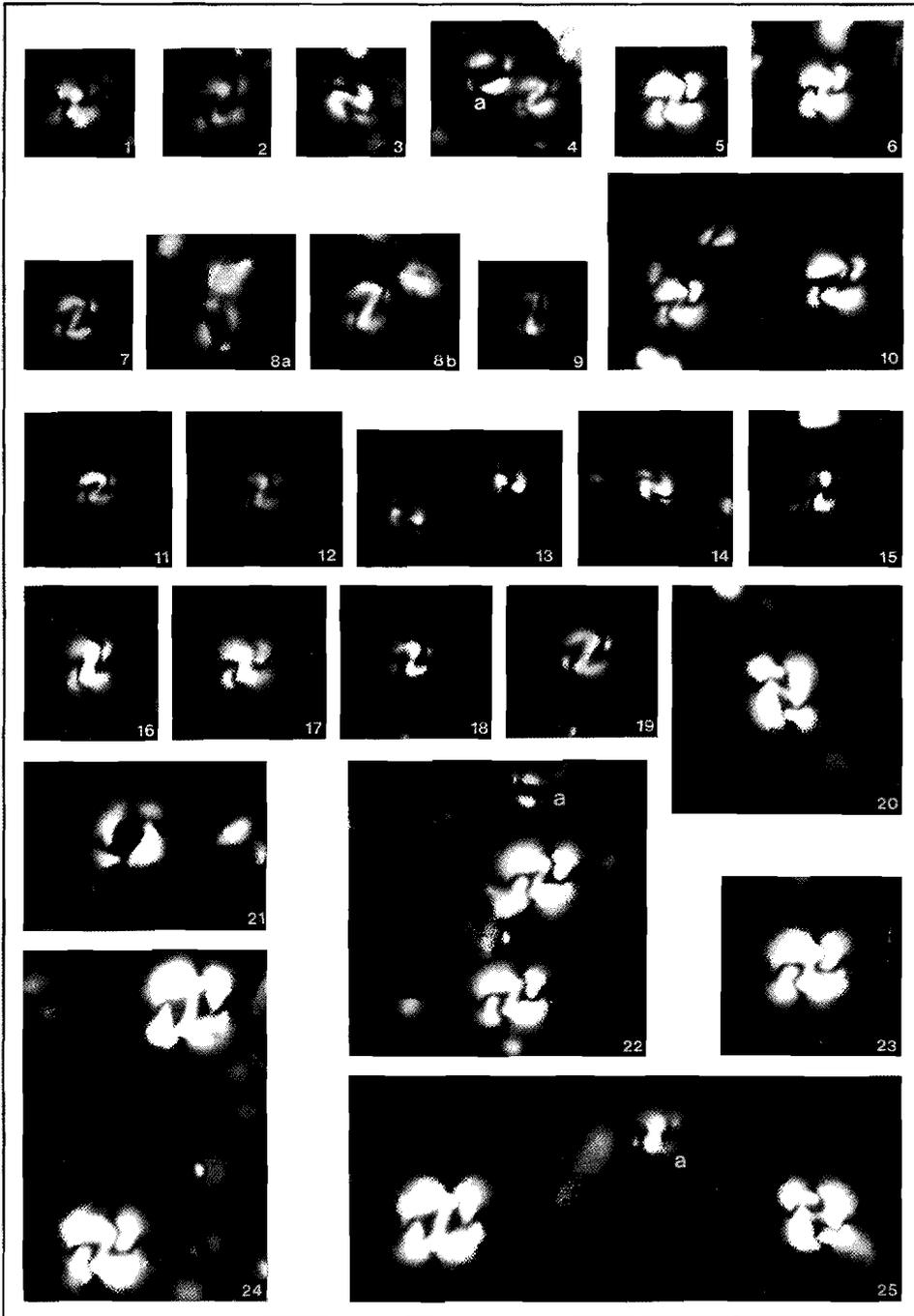


Plate 9

(all magnifications X 3000)

- Fig.1 *Reticulofenestra* sp.
Punta di Maiata, CP4108A, NN14-15B.
- Fig.2 a : *Reticulofenestra* sp.
b : *R. minutula*
c : *Gephyrocapsa* sp.
Punta di Maiata, CP4108A, NN14-15B.
- Fig.3 a : *Reticulofenestra* sp.
b : *R. minutula*
c : *R. minuta*
Punta Piccola, JT5715, NN16-17D.
- Figs.4,5 *Calcidiscus macintyre* (Bukry & Bramlette) Loeblich & Tappan
Fig.4a : Singa II, JT9235, NN16-17D, normal light.
4b : same specimen, crossed nicols.
Fig.5a : Singa IV, JT9629, NN19A, normal light.
5b : same specimen, crossed nicols.
- Figs.6-10 *Sphenolithus* spp.
Fig.6 : Finikia, CP2023, NN16-17A.
Figs.7,8 : Aghios Vlassios, CP2273, NN16-17A.
Figs.9,10 : Punta di Maiata, CP4115, NN16-17A.

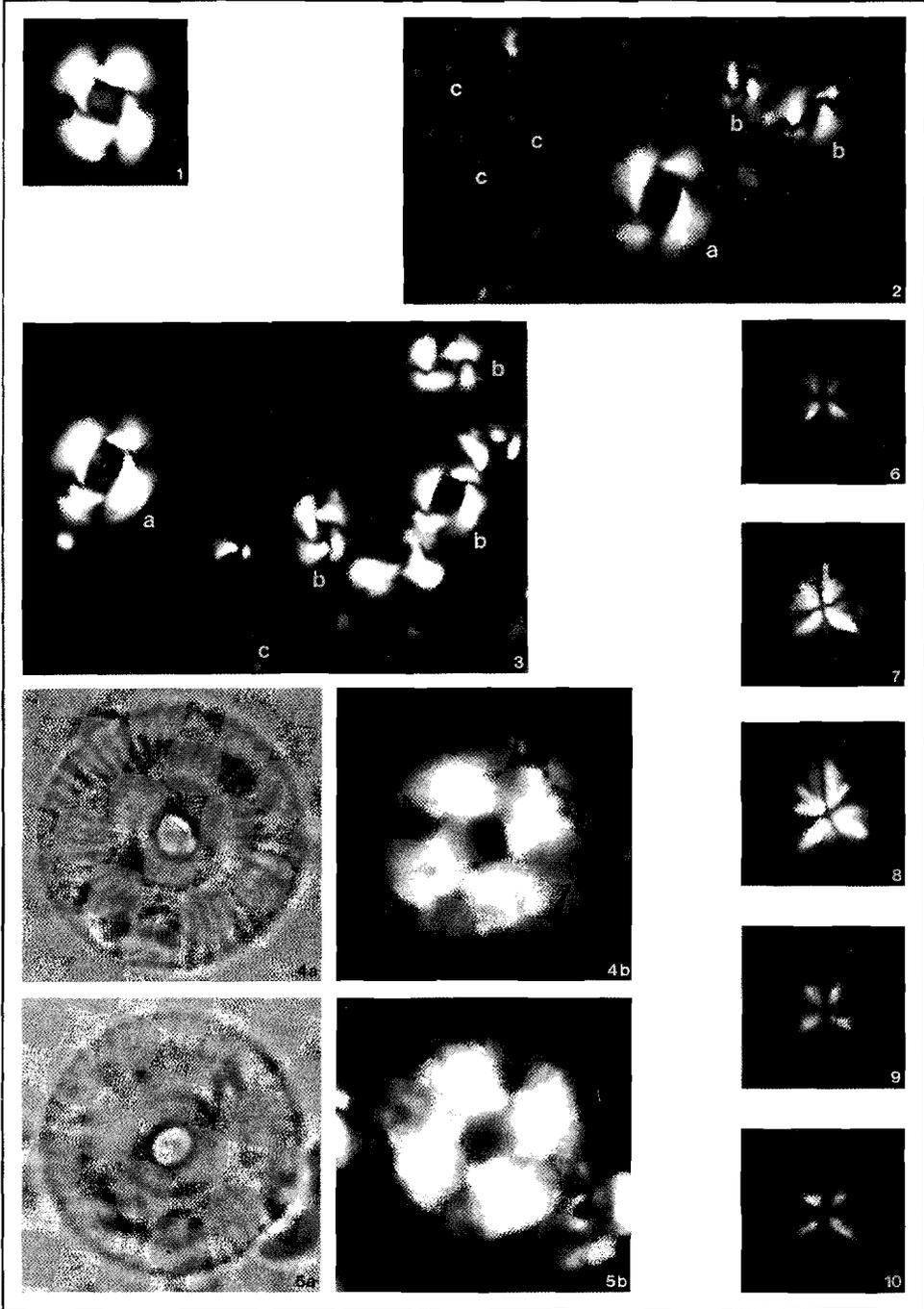


Plate 10

(all magnifications X 3000)

Figs.1-6

Eu-discoaster quintatus (Bukry & Bramlette) nov. comb.

Fig.1a : Aghios Vlassios, CP2238, NN14-15A, normal light.

1b : same specimen, crossed nicols.

Fig.2a : Singa II, JT9275, NN16-17F, normal light.

2b : same specimen, crossed nicols.

Fig.3a : Singa II, JT9275, NN16-17F, normal light.

3b : same specimen, crossed nicols.

Fig.4a : Singa II, JT9281, NN16-17F, normal light.

4b : same specimen, crossed nicols.

Fig.5a : Singa II, JT9281, NN16-17F, normal light.

5b : same specimen, crossed nicols.

Fig.6a : Monte San Nicola, CP3775C, NN16-17F, normal light.

6b : same specimen, crossed nicols.

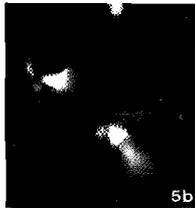
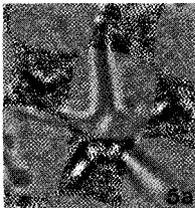
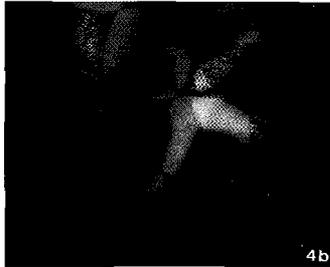
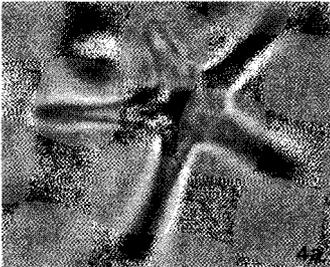
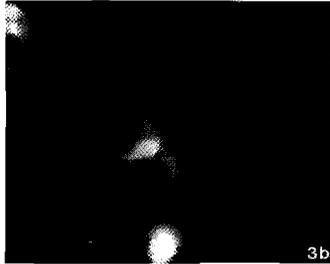
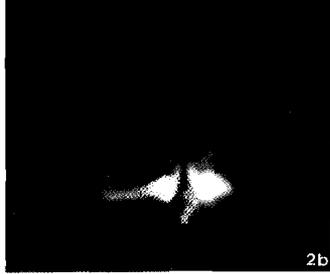
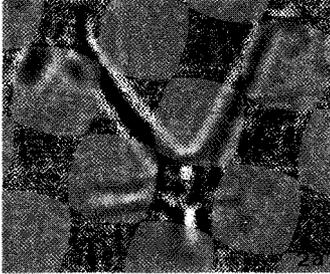
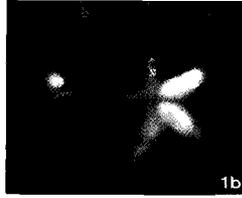
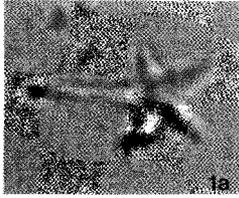


Plate 11

(all magnifications X 3000)

- Figs.1-4 *Eu-discoaster variabilis* (Martini & Bramlette) Theodoridis
Figs.1,2 : Aghios Vlassios, CP2362, NN12-13B.
Figs.3,4 : Aghios Vlassios, CP2366, NN12-13C.
- Figs.5-9 *Eu-discoaster surculus* (Martini & Bramlette) Theodoridis
Figs.5,6 : Aghios Vlassios, CP2233, NN14-15A.
Figs.7,8 : Singa II, JT9235, NN16-17D.
Fig.9 : Monte San Nicola, CP3772, NN16-17E.
- Figs.10,11 Indeterminable six-rayed *Eu-discoaster* spp.
Francocastello, GR1184, NN16-17E.

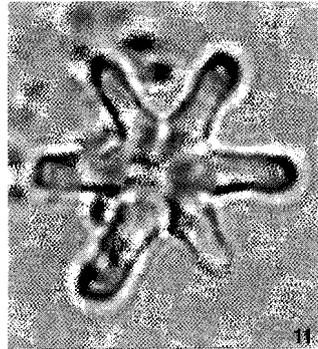
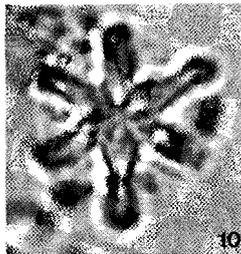
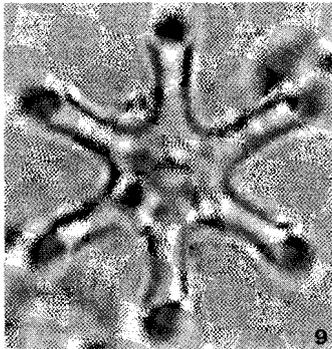
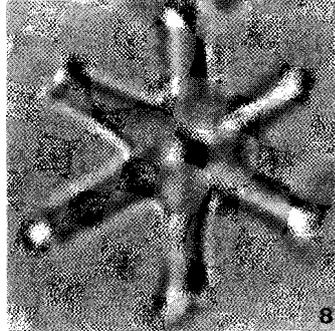
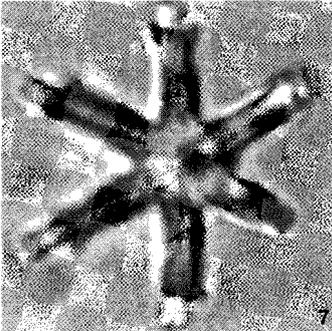
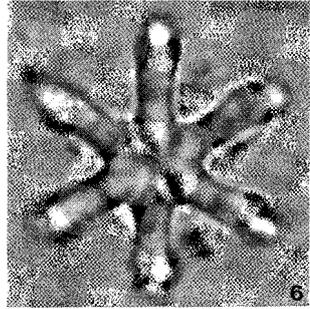
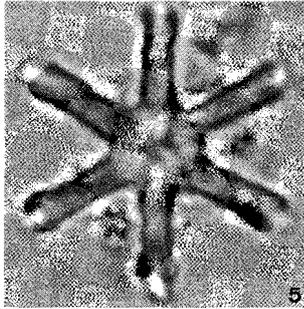
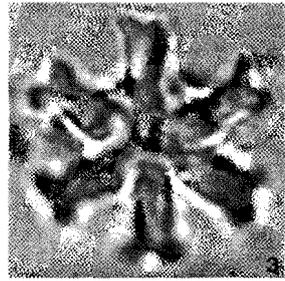
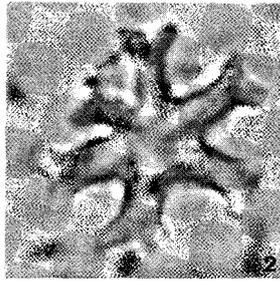
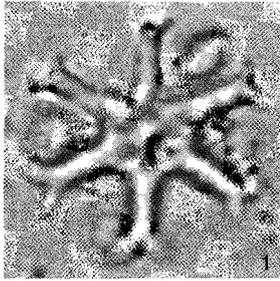


Plate 12

(all magnifications X 3000)

- Figs.1-5 *Eu-discoaster brouweri* (Tan Sin Hok) Theodoridis
Fig.1 : Singa IA, JT11.524, NN14-14A
Fig.2 : Punta Piccola, JT5737, NN16-17E.
Figs.3,4 : Monte San Nicola, CP3785, NN18A.
Fig.5 : Monte San Nicola, CP3787, NN18B.
- Figs.6-10 *Eu-discoaster asymmetricus* (Gartner) Theodoridis
Fig.6 : Singa IA, JT11.522, NN14-15A.
Fig.7 : Punta di Maiata, CP4103, NN14-15B.
Fig.8 : Aghios Vlassios, CP2276, NN16-17A.
Fig.9 : Singa II, JT9235, NN16-17D.
Fig.10 : Monte San Nicola, CP3775, NN16-17F.
- Fig.11 *Eu-discoaster tamalis* (Kamptner) Theodoridis
Punta di Maiata, CP4103, NN14-15B.

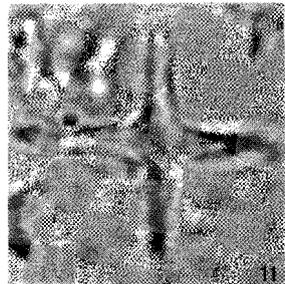
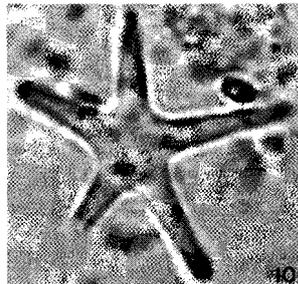
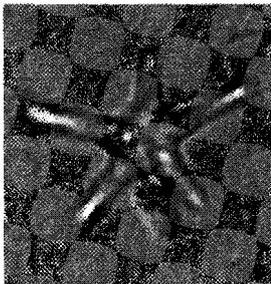
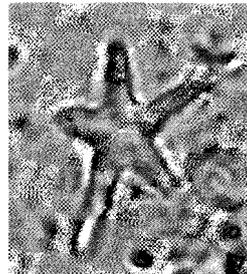
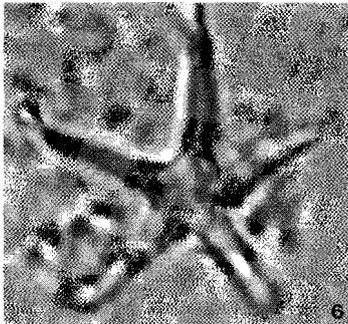
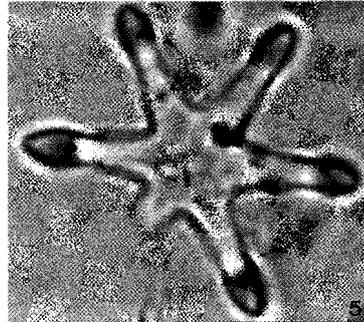
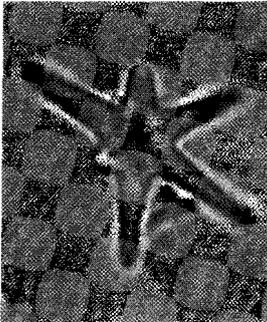
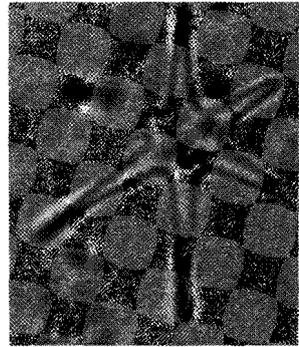
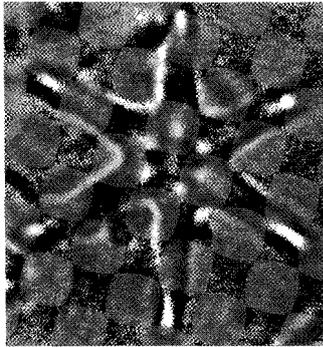
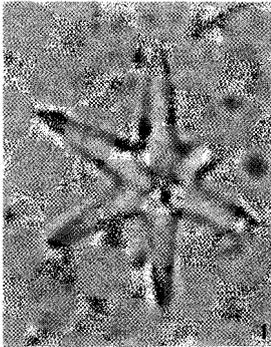
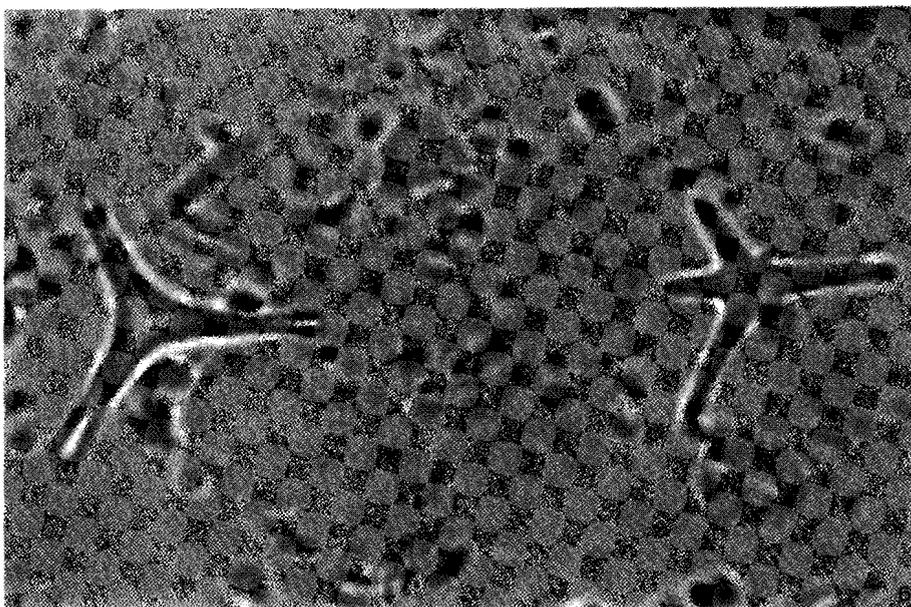
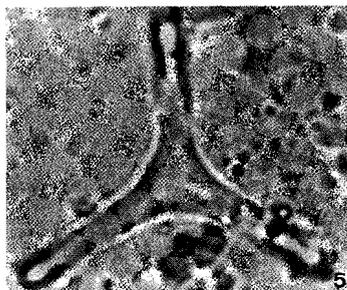
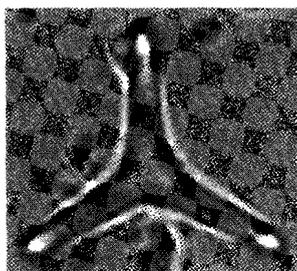
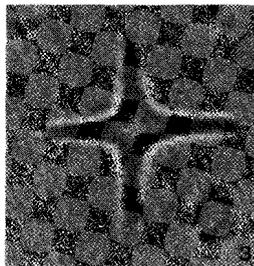
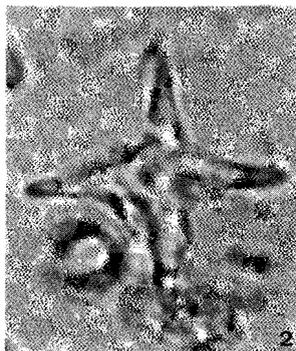
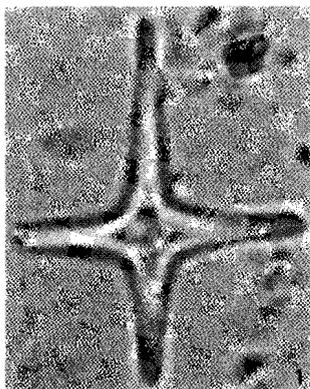


Plate 13

(all magnifications X 3000)

- Figs.1-3 *Eu-discoaster tamalis* (Kamptner) Theodoridis
Fig.1 : Aghios Vlassios, CP2276, NN16-17A.
Fig.2 : Punta di Maiata, CP4153, NN16-17D.
Fig.3 : Singa II, JT9235, NN16-17D.
- Figs.4,5 *Eu-discoaster triradiatus* (Tan Sin Hok) nov. comb.
Monte San Nicola, CP3787, NN18B.
- Fig.6 *Eu-discoaster triradiatus* and *Eu-discoaster brouweri*
Monte San Nicola, CP3787, NN18B.



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