

## 6. PLIOCENE-PLEISTOCENE COCCOLITH ASSEMBLAGES FROM THE SIERRA LEONE RISE—SITE 366, LEG 41

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### INTRODUCTION

The possibility that a continuous pelagic deep-sea section well above the CCD, representing the whole Cenozoic, was recovered from the Sierra Leone Rise at Site 366 (Hole 366A) makes this section an ideal profile for the Cenozoic zonation in tropic-subtropical latitudes.

The coccolith assemblages in these sediments reflect the development of the coccolith community in the Atlantic from Pliocene to Pleistocene without the adverse effects seen in higher latitudes during the glacial periods. For this reason Site 366 (Hole 366A) was chosen for an investigation of the late Tertiary and Pleistocene coccolith assemblages as an addition to the stratigraphical works of Cepek (this volume) and Bukry (this volume).

The samples come from the upper 50 meters of the section. Coccolith assemblages range from the *Discoaster surculus* Zone (NN 16) of the late Pliocene to the *Emiliana huxleyi* Zone (NN 21) of the late Quaternary.

### METHOD

Grain-size fractions (<2, 2-6, 6-20  $\mu\text{m}$ ), separated by a modified Atterberg method (Fütterer, this volume) were investigated with a scanning electron microscope. Between 500 and 1000 specimens per sample were counted on SEM micrographs. Additionally, up to about 5000 specimens were examined on the screen in order to check the first or last occurrence of stratigraphically important species.

An exact count of coccoliths and the representation of the percentage-abundance of the dominant species (Figure 1) is only possible for the fractions >2  $\mu\text{m}$ , because the coccoliths in the fraction <2  $\mu\text{m}$  are often obscured by fine debris. Frequently species cannot be counted, so their frequencies are estimated. This applies especially to the closely related and morphologically similar *Gephyrocapsa* species (*G. ericsonii*, *G. aperta*, *G. protohuxleyi*) and *Emiliana huxleyi* which form a considerable, occasionally even predominant, portion of the coccolith assemblages. If these species were added to Figure 1, it would reduce the percentages considerably. However, the development of the coccolith community can be sufficiently evaluated through the counted species, inasmuch as those common species not shown in the diagram either have unknown ecological relationships (*Gephyrocapsa ericsonii* and *G. aperta*) or are extremely eurythermal (*Emiliana huxleyi*).

Table 1 gives a summarized representation of the coccolith assemblages. The estimated abundances of the species in the fraction <2  $\mu\text{m}$  are included. The capital letters in Table 1 mean: A (abundant) = more than 30%, C (common) = 10% to 30%, F (few) = 0.5% to 10%, R (rare) = less than 0.5%. Species seen only sporadically on the screen, but not found on the micrographs, are marked in Table 1 with "r."

The counts of the dominant coccolith species have also been subjected to a factor analysis with varimax rotation of the factors (Program FACTO, Scientific Subroutine Package, Programmers Manual, IBM).

The samples have been divided into two groups using the results of factor analysis: Sections 1-1 to 2, CC (with *Gephyrocapsa oceanica*) and Sections 3-1 to 6-3 (with *Pseudoemiliana lacunosa*). Because the number of samples was far too small for this method, the resultant factors have been used only for a hypothetical grouping of the species according to their joint biogeographically effective ecological affinities (Figure 2).

### PRESERVATION

The preservation of coccoliths is normally good. A few of the specimens occasionally show the effects of dissolution where delicate structures like grilles (e.g., in *Gephyrocapsa* and *Pseudoemiliana*) are mostly destroyed. Several times some specimens of a certain species (e.g., *Helicosphaera carteri*) in the same sample show rather deep grooves of dissolution while others are overgrown with secondary calcite (Plate 2, Figures 4 and 6).

Bottom assemblages deposited even in less than 3000 meters of water in equatorial regions are incomplete (McIntyre and Bé, 1967) and the proportions of species are changed by selective dissolution of the coccoliths sinking down through the water column or lying at the sea floor. The coccolith assemblages are not only affected by selective dissolution but also by breakage. This process begins during the sedimentation of the coccoliths and continues during the preparation of the samples. Certain species often show a more or less strong fragmentation evidently produced during the preparation of the strewn slide (Plate 2, Figures 2 and 8). An investigation of complete fossil coccolith assemblages without technical alteration of their composition seems to be impossible.

Drilling disturbances cannot be ruled out, but seem to play a minor role in sections of Core 366A. These samples show the normal coccolith succession of the late Cenozoic. Down-hole contamination is seen by

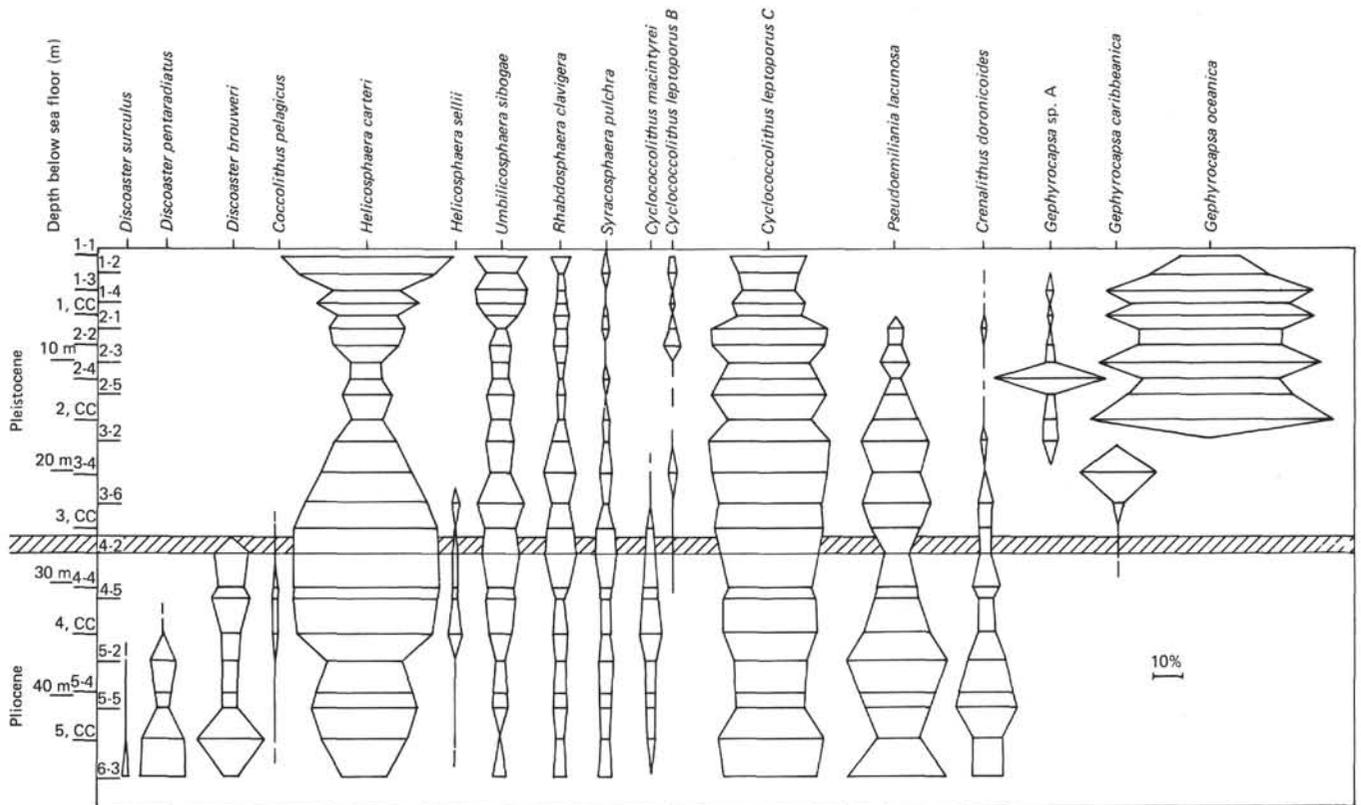


Figure 1. Portions of common coccolith species in the late Pliocene and Pleistocene of Hole 366A.

isolated occurrences of young species in core-catcher samples (*Gephyrocapsa caribbeanica* in Sample 4, CC, *Gephyrocapsa protohuxleyi* in Sample 2, CC).

## RESULTS

The greatest numbers of coccoliths are found in the fraction 2 to 6  $\mu\text{m}$  in which they form from 30% to more than 50% of the sediment. The portion of the coccoliths is smaller in the fractions  $<2 \mu\text{m}$  and 6 to 20  $\mu\text{m}$ . This is particularly evident in the fraction 6 to 20  $\mu\text{m}$  of Pleistocene sediments where the coccoliths (without considering *Thoracosphaera*) form usually less than 10% and occasionally even less than 3% of the sediment.

An investigation of coccolith assemblages has to take into consideration both the evolution and the ecology of coccolithophorids because of the mutual dependence between them. A major part of the evolutionary processes is either caused or influenced by changes of the biotope. It is well known that the first or last occurrence of certain species in different locations may have happened at different time levels because of ecological reasons. As an example, Wise (1973) described the different relations of the first occurrence of *Gephyrocapsa caribbeanica* to the last occurrence of *Discoaster brouweri* at the Pliocene/Pleistocene boundary for several regions. Often one distinguishes between the "first" and "first common" and the "last" and "last common" occurrence of a certain species, whereby some stratigraphers take the first or the last "common occurrence" for the stratigraphically more important event. This demonstrates to what extent ecologically caused factors, such as the frequency of

species in a community, are used for mere biostratigraphical purposes.

The ecological affinities of the individual coccolithophorid species are more or less changed by processes of evolution. No doubt, this has its effect upon the composition of the coccolith community and simulates a modification of the ecological conditions.

The stratigraphic and paleoecologic results of this investigation are represented successively below.

## BIOSTRATIGRAPHY (TABLE 1)

The late Pliocene is divided by the successive extinction of the last *Discoaster* species: the last occurrence of *Discoaster surculus* in Sample 5-2, 73-75 cm, and the last occurrence of *Discoaster pentaradiatus* in Sample 4, CC. The distance between the last occurrences of these two species is relatively small. Thus, the *Discoaster pentaradiatus* Zone (NN 17), which lies between these events, comprises a rather short interval of time. In addition, *Discoaster surculus* appears only in very small portions of the assemblages in the upper part of Zone NN 16 (*Discoaster surculus* Zone). This is the reason why the bottom boundary of the *Discoaster pentaradiatus* Zone is not determined exactly.

*Discoaster tamalis* (= four-rayed *Discoaster brouweri*, Plate 5, figure 2) occurs only in a few specimens in Zone NN 16. Its disappearance cannot be used as a significant boundary against the *Discoaster pentaradiatus* Zone (compare Bukry, 1971a, 1973).

The last occurrence of *Discoaster brouweri* is observed in Sample 4-2, 60-62 cm. The Pliocene/Pleistocene boundary is placed between this sample and



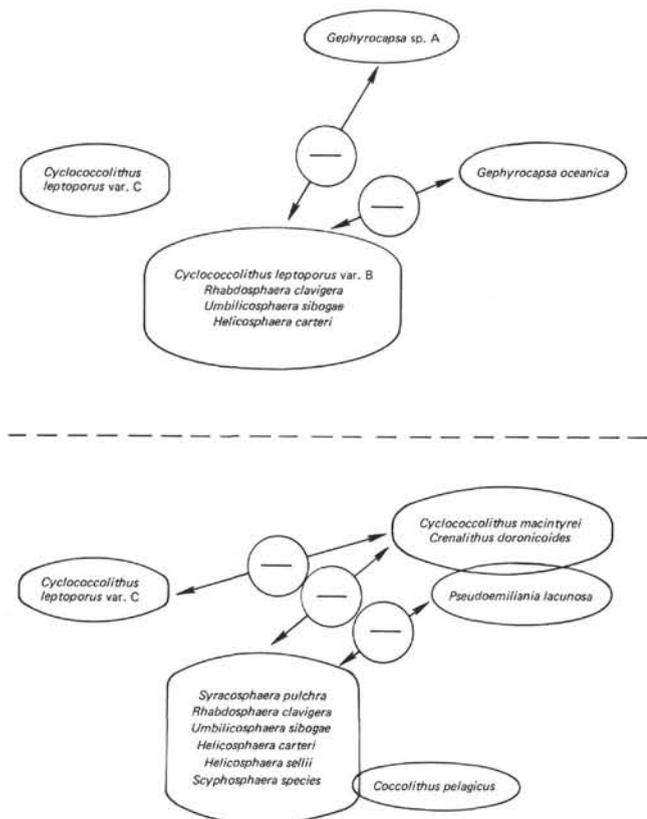


Figure 2. Community relations of common coccolith species as inferred from their frequencies in late Pliocene and Pleistocene assemblages of Hole 366A. Above: Samples 41-366A-1-1 to 2, CC; below: Samples 41-366A-3-1 to 6-3.

Sample 4-1, 62-64 cm. This boundary is marked by the following additional events: (1) *Gephyrocapsa caribbeanica* appears shortly before the Pliocene/Pleistocene boundary and shows a slight overlapping in Sample 4-2 with *Discoaster brouweri*. A few extremely rare specimens in Sample 4, CC are probably due to down-core contamination. (2) *Ceratolithus rugosus* (Plate 5, Figures 8, 9) has its last occurrence in Section 4-2. (3) *Coccolithus pelagicus*, which is not very frequent in the Pliocene, is not found above Sample 3, CC, except for a few specimens in the top sample (1A-1, 71-73 cm).

The final occurrence of the following species occurs a few meters above the Pliocene/Pleistocene boundary in the *Pseudoemiliana lacunosa* Zone (NN 19): *Helicosphaera sellii* in Sample 3-6, 33-35 cm and *Cyclcoccolithus macintyreii* which occurs relatively frequently in the late Pliocene in Sample 3-4, 68-70 cm.

*Gephyrocapsa caribbeanica* splits into *Gephyrocapsa oceanica* and *Gephyrocapsa sp.A.* in the middle of the *Pseudoemiliana lacunosa* Zone. From here on (Sample 2, CC), *Gephyrocapsa oceanica* forms a considerable portion of the community. *Gephyrocapsa sp. A.* is a form usually identified as *Gephyrocapsa caribbeanica* Boudreaux and Hay (1967), but which can be separated from this species on biometric grounds. Therefore, I use it as a distinct species.

The upper boundary of the *Pseudoemiliana lacunosa* Zone (Gartner, 1969) is marked by the last occurrence of *Pseudoemiliana lacunosa* in Sample 2-1, 68-70 cm. Accumulation rates in Hole 366A between 2 cm/10<sup>3</sup> yr in the late Pleistocene and 1.2 cm/10<sup>3</sup> yr in the early Pleistocene are found by comparing the absolute age and depth of the first appearance of *Emiliana huxleyi* (0.2 m.y.) and *Gephyrocapsa oceanica* (0.9 m.y.) and the last occurrence of *Discoaster brouweri* (1.8 m.y.), respectively. The extinction of *Pseudoemiliana lacunosa* at Site 366 can be estimated as occurring 300,000 years ago using the above-defined accumulation rates. This is in good agreement with the age of extinction of this species in the Caribbean (275,000 yr B.P.) calculated by Gartner (1972).

The *Pseudoemiliana lacunosa* Zone represents a stratigraphic interval of about 1.5 m.y. duration and is considerably longer than the following *Gephyrocapsa oceanica* Zone (NN 20). This is unsatisfactory, and several authors have tried to subdivide this interval differently. The initial division by Boudreaux and Hay (1967) defined the *Gephyrocapsa caribbeanica* Zone in the lower part and the *Gephyrocapsa oceanica* Zone on top of it. This latter zone does not begin with the last occurrence of *Pseudoemiliana lacunosa*, but with the first occurrence of *Gephyrocapsa oceanica*, which is considerably earlier (Table 2). This division could be used for Hole 366A because below the first and very abundant occurrence of *Gephyrocapsa oceanica* there is a definitely marked horizon (Sections 3-2 and 3-1) in which *Gephyrocapsa oceanica* as well as *Gephyrocapsa caribbeanica* are missing, and only *Gephyrocapsa sp. A.* forms a minor portion of the assemblage.

However, in principle one has to take into account that *Gephyrocapsa oceanica* has evolved from *Gephyrocapsa caribbeanica*. A definite determination in a transitional period, at least of individual specimens is almost impossible because of overlapping morphological variations. This probably leads different investigators to different results.

Bukry (1971a), in his attempt to establish concurrent multiple range zones which are based on key species and the nature of the associated coccolith assemblage, named *Crenalithus daronicoides* as a zone-fossil for the range between the last common occurrence of *Discoaster brouweri* and the first common occurrence of *Gephyrocapsa oceanica*. This range is characterized by an assemblage in which, besides *Cyclcoccolithus leptoporus* and *Cyclolithella annula*, *Crenalithus daronicoides* is prominent. *Crenalithus daronicoides* occurs at Hole 366A in the early Pleistocene in slowly decreasing portions and less frequently than in the late Pliocene. The continuous occurrence of this species ends with the appearance of *Gephyrocapsa oceanica* (Figure 1). Yet since that time to the present, *Crenalithus daronicoides* is found discontinuously and rarely. Therefore, in the section at Site 366 the stratigraphic interval of the *Crenalithus daronicoides* Zone is not characterized by *Crenalithus daronicoides*.

Bukry (1971a, 1973), Geitzenauer (1972), Roth (1974), and other subdivide the *Crenalithus daronicoides* Zone. Apart from a different naming of the lower

TABLE 2  
Quaternary Nannofossil Zonations

Boudreaux and Hay (1967)	Gartner (1969) Martini and Worsley (1970) Roth (1973)	Bukry (1971, 1973)	Geitzenauer (1972)	Roth (1974)
<i>Emiliana huxleyi</i> Zone	<i>Emiliana huxleyi</i> Zone (NN 21)	<i>Emiliana huxleyi</i> Zone	<i>Emiliana huxleyi</i> Zone	<i>Emiliana huxleyi</i> Zone
<i>Gephyrocapsa oceanica</i> Zone	<i>Gephyrocapsa (oceanica)</i> Zone (NN 20)	<i>Gephyrocapsa oceanica</i> Zone	<i>Gephyrocapsa</i> Zone	<i>Gephyrocapsa oceanica</i> Zone
<i>Gephyrocapsa caribbeanica</i> Zone	<i>Pseudoemiliana (lacunosa)</i> Zone (NN 19)		<i>Pseudoemiliana lacunosa</i> Zone	
		<i>Crenalithus daronicoides</i> Zone	<i>Emiliana annula</i> Subzone	<i>Pseudoemiliana lacunosa</i> Zone
<i>Discoaster brouweri</i> Zone	<i>Discoaster brouweri</i> Zone	<i>Discoaster brouweri</i> Zone	<i>Discoaster brouweri</i> Zone	<i>Cyclococcolithus macintyreii</i> Zone

division (Bukry: *Emiliana annula* Subzone, Geitzenauer: *Coccolithus daronicoides* Zone, Roth: *Pseudoemiliana lacunosa* Zone) which leads to a certain confusion, the interval of this division is defined uniformly by the authors as the time period between the extinction of *Discoaster brouweri* and the first occurrence of *Gephyrocapsa caribbeanica* (Table 2). This subdivision has significance only where *Gephyrocapsa caribbeanica* clearly appears after the extinction of *Discoaster brouweri*. This seems to be the case especially in higher latitudes; in tropical and subtropical regions, as at Site 366, the occurrences of both species overlap. Therefore, a subdivision of the early Pleistocene cannot be made here.

The *Gephyrocapsa oceanica* Zone (NN 20), defined as the interval between the last occurrence of *Pseudoemiliana lacunosa* and the first appearance of *Emiliana huxleyi*, is only represented by Sample 1, CC. *Emiliana huxleyi* frequently occurs in Sample 1-4, 43-45 cm. *Gephyrocapsa protohuxleyi* appears as a rare, but relatively conspicuous member of the coccolith assemblage in Samples 1-4 and 1, CC.

The stratigraphic results outlined above agree with the findings of Cepek (this volume).

### PALEOECOLOGY

The ecological limits of species used to interpret ecological conditions must be identical within the time interval of interest. The evolution of new and the extinction of old species implies changing ecological relations within the community.

The development of the coccolith community in the Pliocene and Pleistocene, characterized by a rapid

evolution and the expansion of several species, cannot be interpreted meaningfully without acknowledging changes not only in the living conditions, but also in the ecological relations of a number of species. Under these changing conditions, a rigid scheme of relationships between climate and the development of the coccolithophorid community cannot be established. Primarily, the individual species have to be investigated with respect to evolution and changes of ecological preferences, in order to be able to interpret the development of the community.

The number and sampling density of the samples investigated from Hole 366A are not sufficient to give detailed information on the evolutionary process of the coccolith community or any linkage to the paleo-oceanography at the Sierra Leone Rise before and during the Pleistocene. The results so far indicate only major trends.

The genus *Discoaster* is not considered here because from the few samples in which the genus occurs, no information can be gained about favorable living conditions for this group under extinction.

### *Cyclococcolithus leptoporus* var. C

*Cyclococcolithus leptoporus* var. C shows a nonvarying abundance (Figure 1) in the section from Hole 366A. Most of the other common coccolith species show significant oscillations of frequency. These fluctuations are not always easy to interpret, but are related to the ecological changes during the late Pliocene and the Pleistocene. Evidently, *Cyclococcolithus leptoporus* var. C was not influenced by these changes. A slight increase of the relative frequency of this species at the Pliocene/Pleistocene boundary, two

maxima of frequency in the Pleistocene, and a slight decrease in the late Quaternary are calculation effects caused by a strong change in the portions of other species rather than a reaction of this species to a changed environment. The ecological insensitivity of *Cyclococcolithus leptoporus* var. C is clearly indicated by the fact that it is not correlated, with the exception of a negative correlation with *Crenolithus dornicoides* with the frequencies of other species.

### Tropical-Subtropical Species Group

This group of species is characteristic of warm water in tropical to subtropical regions (McIntyre and Bé, 1967). The assemblage includes *Helicosphaera carteri*, *Umbilicosphaera sibogae*, *Rhabdosphaera clavigera*, *R. stylifera*, *Cyclococcolithus leptoporus* var. B (only in the upper part of the section observed), *Helicosphaera sellii* (only in the lower part of the section), and, with low statistical reliability due to the small portions of this species in the coccolith assemblages *Syracosphaera pulchra*. These species have positive correlations with each other and are clearly distinguished from other species of the assemblage. Therefore, almost identical ecological affinities may be assumed for them. Several species of the genus *Scyphosphaera* are associated with this group (Plate 4, Figures 1-11).

The changes of the relative frequencies of *Helicosphaera carteri*, one of the most abundant species, are the most apparent and strongest. This species comprises up to 35% of the flora from the upper part of the *Discoaster surculus* Zone to the lower part of the *Pseudoemiliana lacunosa* Zone. Its portion decreases significantly and reaches minima of only 7% of the flora in the upper part of the early Pleistocene *Pseudoemiliana lacunosa* Zone (Samples 2, CC to 2-3, 73-75 cm). This is apparently related to decreasing surface-water temperatures. Afterwards, there is a gradual increase to almost 40% abundance.

Because the relative frequency of this species is also influenced by the portions of the coccolith species, the ratio of *Helicosphaera carteri* to *Cyclococcolithus leptoporus* var. C (expressed as the percentage of *H. carteri* in the pair *H. carteri* + *C. leptoporus* var. C) was calculated as a control because the frequencies of these two species show no positive or negative correlation (Figure 3). *Helicosphaera carteri* rises to over 60% of the flora in Zone NN 16 and stays that high to the end of the Pliocene. The values start to decrease at the beginning of the Pleistocene and reach minima of 25% to 30% in the center of the *Pseudoemiliana lacunosa* Zone (NN 19). From then on, there is a relatively steady increase to almost 70% in the top of Sample 1-1, 71-73 cm. The changes of this ratio reflect developments caused by a general cooling during the Pleistocene. The changes of this ratio cannot be directly related to the climatic events or even to the changes of water temperature. This is shown by the lack of effects of climatic oscillations on the uncorrected graph of the frequency percentages (Figure 1). However, the changes of this ratio do show how *Helicosphaera carteri*, the dominant species among the tropical-subtropical flora, is quantitatively repressed during the

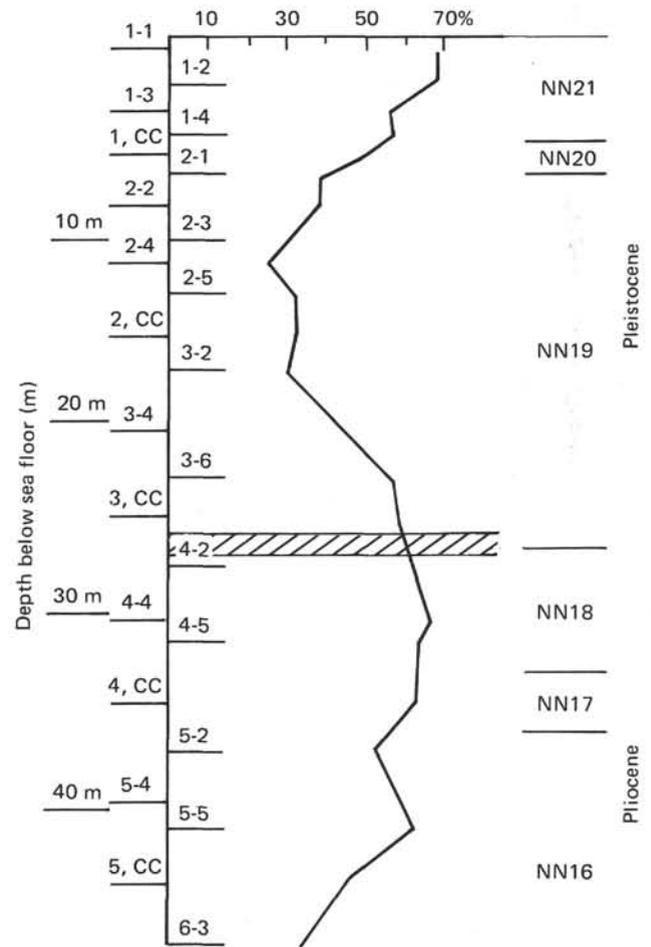


Figure 3. Ratio  $\frac{\text{Helicosphaera carteri}}{\text{H. carteri} + \text{C. leptoporus var. C}}$  in the late Pliocene and Pleistocene of Hole 366A.

climatic deterioration of the Pleistocene, and how it later gradually stabilized and even expanded without the restoration of the original, favorable environment. Selection and adaptation to changed environments played an important role in this process.

A direct positive correlation exists between *Helicosphaera carteri* and the closely related form *Helicosphaera sellii*. This species occurs in low percentages in the late Pliocene and is only slightly more frequent in the *Discoaster pentaradiatus* (NN 17) and the *Discoaster brouweri* Zone (NN 18) in which *Helicosphaera carteri* forms a high proportion of the flora. *Helicosphaera sellii* decreases rapidly in abundance in the beginning of the Pleistocene and it becomes extinct in the lower *Pseudoemiliana lacunosa* Zone.

The portions of *Umbilicosphaera sibogae* also show a clear correlation to *Helicosphaera carteri*, although this species does not reach the abundance of *Helicosphaera carteri*. The positive correlation between *Helicosphaera carteri* and *Rhabdosphaera clavigera*, *Cyclococcolithus leptoporus* var. B, and *Syracosphaera pulchra* is not as good. These species form only a small part of the assemblage and therefore do not show clear changes of their frequencies. But the data indicate that these

species preferred almost the same living conditions as *Helicosphaera carteri*.

*Cyclococcolithus leptoporus* var. B belongs to the tropical-subtropical assemblage, and *Cyclococcolithus macintyreii* (late Pliocene) has a significant negative correlation with this group. Although these two forms cannot be directly correlated with each other because of a small overlapping of their occurrences, this suggests that their ecological affinities were different.

#### **Coccolithus pelagicus**

*Coccolithus pelagicus* occurs in low proportions only in the Pliocene, with a small maximum of frequency in Zones NN 17 and 18. This species disappears from the community at the beginning of the Pleistocene. Similar observations are reported by Smith and Beard (1973) from the Gulf of Mexico; and Müller (1974) from the Western Indian Ocean. The occurrence of the low numbers of *Coccolithus pelagicus* with the highest frequencies of the tropical-subtropical species group and then the disappearance of this form at a time when the surface-water temperatures probably decreased are incompatible with the present occurrence of *Coccolithus pelagicus* in regions with relatively low water temperatures (6° to 14°C).

A comparison of late Tertiary and Quaternary coccolith assemblages from different regions in the Pacific (Bukry, 1971b) reveals that *Coccolithus pelagicus* in the late Pliocene occurs in cool as well as tropical climates, but disappeared from the tropical region in the Pleistocene. One explanation of the discrepancy between the present occurrence of this species and its pre-Pleistocene occurrence is the assumption that its ecological affinities, at least as far as the preferred water temperatures are concerned, have changed since the end of the Pliocene. This could have been a result of a process of evolution or selection of a population which prefers lower water temperatures than the original eurythermal species but without changes in morphological features. Only this population survived the climatic deterioration of the Pleistocene. Such a selective process could explain the significant stenothermy of the Recent *Coccolithus pelagicus* as well as the fact that this species, which in the Pliocene had a worldwide distribution, today only occurs in the northern hemisphere.

The uncertainty of paleoecological conclusions raised based on the occurrence of species with apparently known ecological limits is demonstrated by this example.

#### **Pseudoemiliana-Gephyrocapsa Group**

An interpretation of the different proportions of *Gephyrocapsa*, *Crenalithus daronicoides*, and *Pseudoemiliana lacunosa* contribute to the coccolith assemblages during the Pliocene and the Pleistocene is difficult. This is partly because these species are systematically related and, in a rapid evolution during the Pleistocene, partially emerge from each other. Thus the probability exists that they substitute for each other ecologically in the community. The taxonomic separation is difficult for some of these forms because

of morphological similarities and overlapping variations which are caused by the close relationship. Therefore, several different criteria have been used. Gartner (1969) assumes that the name *Pseudoemiliana lacunosa* comprises at least two different species of round and oval placoliths which have in common "radial slits in the distal shield." It has been impossible to separate definitely these two different species because of numerous transitional forms. The arrangement and number of slits on the distal shield vary widely; specimens are found with more than 30 slits as well as those with only one (Plate 3). Placoliths of the same size and the same oval shape which show no slit are not grouped with *Pseudoemiliana lacunosa*, but are specified as *Crenalithus daronicoides*. However, is the difference between one and no slit, with respect to real systematic boundaries, in fact more important than the difference between one and 30? Also, the differentiation is not always certain between *Crenalithus daronicoides*, which is seen as the ancestor of *Gephyrocapsa*, and the various species of this genus. Cocospheres have been found in sediments off west Africa which showed coccoliths with a bridge, certainly *Gephyrocapsa*, and others with no bridge which, if isolated, would have been called *Crenalithus daronicoides*.

It is understandable that in this uncertain "triangular relationship" which exists between *Crenalithus*, *Gephyrocapsa*, and *Pseudoemiliana* the counts of species which were published by various authors are not always directly comparable. For example, the high percentages of *Crenalithus daronicoides* which McIntyre et al. (1967) present for the coccolith assemblages directly below and above the Pliocene/Pleistocene boundary in the Atlantic, can be explained because the authors apparently did not differentiate between *Pseudoemiliana lacunosa* and *Crenalithus daronicoides*.

*Crenalithus daronicoides* occurs in decreasing portions in the coccolith assemblages of the late Pliocene and the lower part of the Pleistocene from Hole 366A. The oscillations of abundances of this species show a slight positive correlation with *Cyclococcolithus macintyreii* and *Pseudoemiliana lacunosa*. During the time of their cooccurrence, *Crenalithus daronicoides* and *Pseudoemiliana lacunosa* show a strong negative correlation with the tropical-subtropical species group. Therefore, it may be assumed that both species substitute for each other under similar, although not completely identical, living conditions. However, these conditions are clearly distinct from those preferred by the tropical-subtropical species group. In addition, a good negative correlation occurs between *Crenalithus daronicoides* and *Cyclococcolithus leptoporus* var. C, but its significance is unknown.

Gartner (1972) observed *Pseudoemiliana lacunosa* of early Pleistocene age from the Caribbean and the eastern equatorial Pacific which shows higher abundances during minima of temperature than during maxima. The trend changes shortly before its extinction and *Pseudoemiliana lacunosa* occurs with higher percentages during periods with higher surface-water temperatures. Although the number of samples from

Hole 366A is not sufficient to observe this rapid change, it is apparent that in the upper part of Zone NN 19 (Sample 2, CC to Section 2-1) the portions of *Pseudoemiliana lacunosa* are positively correlated with the tropical-subtropical species group. The change in trend occurs at a time of the evolution and the abundant occurrence of *Gephyrocapsa oceanica*. *P. lacunosa* was eventually influenced by the latter because *G. oceanica* displaced *Pseudoemiliana lacunosa* from its biotope.

*Gephyrocapsa oceanica* is the most frequent species in the upper part of the Pleistocene, probably because it was best adapted to the living conditions which prevailed in this region. Its contribution to the flora fluctuates from 30% to more than 60%, and it has a strongly negative correlation with all common species of the coccolith assemblage. The strongest negative correlation exists with the tropical-subtropical species group, such as *Helicosphaera carteri*. A correlation with *Pseudoemiliana lacunosa* can be seen which leads to the assumption that both species successively preferred the same living conditions and probably held a similar position in the community. Today *Gephyrocapsa oceanica* occurs in water of the same temperatures as the group characterized by *Helicosphaera carteri*. Therefore, the gross differences of the proportions of these species at Hole 366A do not imply any particular water temperature above the Sierra Leone Rise or sea-surface temperature oscillation during the Pleistocene. The observation that *Gephyrocapsa oceanica* has undergone an infraspecific evolution during the late Pleistocene is also contradictory to a paleoecological interpretation. The earlier populations of this species (Sample 2, CC to Section 2-4) are readily distinguishable by a larger angle of the bridge from the later ones (Sections 2-3 to 1-1). Although a direct connection between the morphological evolution of the species and a change of its ecological affinities cannot be readily assumed, it nevertheless cannot be excluded. A new species which clearly shows an evolution is still not a reliable indicator for ecological conditions.

*Gephyrocapsa* sp. A (*G. caribbeanica* of many authors) is a eurythermal form which tolerates considerably lower water temperatures than does *Gephyrocapsa oceanica*. Investigations in the late Pleistocene and Holocene north of the Cape Verde Islands reveal that during the glacial periods this species formed a higher percentage of the coccolith assemblage than *Gephyrocapsa oceanica*. The samples from Hole 366A with one exception (Sample 2-4, 68-70 cm), have *Gephyrocapsa* sp. A in low proportions. Along with the composition of the entire coccolith flora, this indicates the living conditions on the Sierra Leone Rise during the Pleistocene in general were similar to those which existed 15° farther north during the warm interglacial periods.

Sometimes the frequent occurrence of *Gephyrocapsa caribbeanica* is also taken as an indicator for lower water temperatures. This is the result of this form being identified with *Gephyrocapsa* sp. A. However, *Gephyrocapsa caribbeanica* is the ancestor, not only of *Gephyrocapsa* sp. A, but also of *Gephyrocapsa oceanica* with

which it also shows morphological overlappings. Therefore, it cannot be equalized in its ecological affinities with either of its successors, and is beyond an evaluation.

## CONCLUSIONS

A comprehensive study of the relative percentages of the common coccolith species in assemblages from Hole 366A reveals the following results (Figure 2). In the late Pliocene, the coccolithophorid flora is characterized by two groups of species. One group comprises the tropical-subtropical species of which *Helicosphaera carteri* shows the highest percentages. The other group is characterized by *Pseudoemiliana lacunosa* and *Crenalithus dornicoides*. Both groups apparently preferred different living conditions. The proportions of the species within the groups are positively correlated but between the groups the correlations are negative.

The development of the coccolith community is not caused only by changes of the ecological conditions, but also by the evolution of coccolith species and the changes of their ecological affinities. The proportions of the tropical-subtropical species group were considerably suppressed in the early Pleistocene. However, the number of species was only slightly lower, with the exception of a strong decrease of the warm-water *Scyphosphaera*. The impoverishment which occurred during the Pleistocene in higher latitudes did not occur in the low latitudes. *Gephyrocapsa caribbeanica* evolves at the Pliocene/Pleistocene boundary from which *Gephyrocapsa oceanica* emerges in the middle Pleistocene. From here on, this species characterizes the coccolith community and probably holds the same position which formerly was held by *Pseudoemiliana lacunosa* and *Crenalithus dornicoides*. *Gephyrocapsa* sp. A, a eurythermal species which prefers cool-water temperatures, forms only small portions of the flora. In the upper part of the core another increase of the tropical-subtropical species group can be found, but from this a change of climate should not be inferred.

*Cyclcoccolithus leptoporus* var. C occurs with the same relative proportions, thus showing only a minor influence by the fluctuating Pleistocene changes of environment in this region.

## ACKNOWLEDGMENT

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## REFERENCES

- Boudreaux, J.E. and Hay, W.W., 1969. Calcareous nannoplankton and biostratigraphy of the Late Pliocene-Pleistocene-Recent sediments in the Submarex cores: Rev. Esp. Micropaleont., v. 1, p. 249-292.

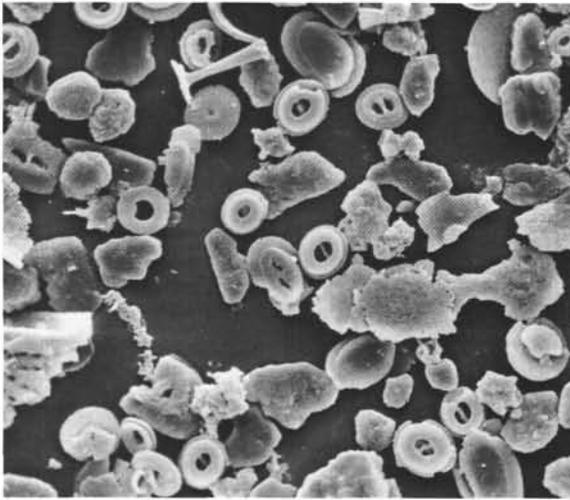
- Bukry, D., 1971a. Cenozoic calcareous nannofossils from the Pacific Ocean: San Diego Soc. Nat. Hist. Trans., v. 16, p. 303-327.
- , 1971b. Coccolith stratigraphy, Leg 6, Deep Sea Drilling Project. In Fischer, A.G., Heezen, B.C., et al., Initial Reports of the Deep Sea Drilling Project, Volume 6: Washington (U.S. Government Printing Office), p. 965-1004.
- , 1973. Coccolith stratigraphy, eastern equatorial Pacific, Leg 16, Deep Sea Drilling Project. In van Andel, T.H., Heath, G.H., et al., Initial Reports of the Deep Sea Drilling Project, Volume 16: Washington (U.S. Government Printing Office), p. 653-711.
- Gartner, S., Jr., 1969. Correlation of Neogene planktonic foraminifer and calcareous nannofossil zones: Gulf Coast Assoc. Geol. Soc. Trans., v. 19, p. 585-599.
- , 1972. Late Pleistocene calcareous nannofossils in the Caribbean and their interoceanic correlation: Paleogeography, Paleoclimatology, and Paleoecology, v. 12, p. 169-191.
- Geitzenauer, K.R., 1972. The Pleistocene calcareous nannoplankton in the subantarctic Pacific Ocean: Deep-Sea Res., v. 19, p. 45-60.
- Hay, W.W., Mohler, H., Roth, P.H., Schmidt, R.R., and Boudreaux, J.E., 1967. Calcareous nannoplankton zonation of the Cenozoic of the Gulf Coast and Caribbean-Antillean area, and transoceanic correlation: Gulf Coast Assoc. Geol. Soc. Trans., v. 17, p. 428-480.
- Martini, E. and Worsley, T., 1970. Standard Neogene calcareous nannoplankton zonation: Nature, v. 225, p. 289-290.
- McIntyre, A. and Bè, A.W.H., 1967. Modern Coccolithophoridae of the Atlantic Ocean—I. Placoliths and cyrtoliths: Deep-Sea Res., v. 14, p. 561-597.
- McIntyre, A., Bè, A.W.H., Preikstas, R., 1967. Coccoliths and the Pliocene-Pleistocene boundary: Progr. Oceanography, v. 4, p. 3-25.
- Müller, C., 1974. Calcareous nannoplankton, Leg 25 (Western Indian Ocean). In Simpson, E.S.W., Schlich, R., et al., Initial Reports of the Deep Sea Drilling Project, Volume 25: Washington (U.S. Government Printing Office), p. 579-633.
- Roth, P.H., 1973. Calcareous nannofossils—Leg 17, Deep Sea Drilling Project. In Winterer, E.L., Ewing, J.I., et al., Initial Reports of the Deep Sea Drilling Project, Volume 17: Washington (U.S. Government Printing Office), p. 695-795.
- , 1974. Calcareous nannofossils from the northwestern Indian Ocean, Leg 24, Deep Sea Drilling Project. In Fisher, R.L., Bunce, E.T., et al., Initial Reports of the Deep Sea Drilling Project, Volume 24: Washington (U.S. Government Printing Office), p. 969-994.
- Smith, L.A. and Beard, J.H., 1973. The Late Neogene of the Gulf of Mexico. In Worzel, J.L., Bryant, W., et al., Initial Reports of the Deep Sea Drilling Project, Volume 10: Washington (U.S. Government Printing Office), p. 643-677.
- Wise, S.W., Jr., 1973. Calcareous nannofossils datum levels associated with the Pliocene-Pleistocene boundary: SEPM—Calcareous Nannofossil Symp., Houston, Proc., p. 126.

## PLATE 1

Scanning electron micrographs of Pliocene  
and Pleistocene coccolith assemblages.

- Figure 1 Assemblage with *Gephyrocapsa oceanica*, *Helicosphaera carteri*, *Cyclococcolithus leptoporus*, *Rhabdosphaera clavigera* (*Gephyrocapsa oceanica* Zone, NN 20). Sample 366A-1, CC. 1600 $\times$ . 10 kv.
- Figure 2 Assemblage with *Gephyrocapsa caribbeanica*, *Helicosphaera carteri*, *Cyclococcolithus leptoporus*, *Rhabdosphaera clavigera*, *Umbilicosphaera sibogae*, *Syracosphaera pulchra*, *Pseudoemiliana lacunosa*, *Ceratolithus cristatus*, and a "Polcoccolith" (*Pseudoemiliana lacunosa* Zone, NN 19). Sample 366A-3-4, 68-70 cm. 1600 $\times$ . 10 kv.
- Figure 3 Assemblage with *Helicosphaera carteri*, *H. sellii*, *Pseudoemiliana lacunosa*, *Cyclococcolithus leptoporus*, *Ceratolithus cristatus*, *Rhabdosphaera clavigera* (*Pseudoemiliana lacunosa* Zone, NN 19). Sample 366A-3, CC. 1600 $\times$ . 10 kv.
- Figure 4 Assemblage with *Helicosphaera carteri*, *Cyclococcolithus leptoporus*, *Discoaster brouweri*, *Syracosphaera pulchra*, *Pontosphaera syracusana*, *Pontosphaera* sp., *Scyphosphaera pulcherrima*, *Coccolithus pelagicus*, *Umbilicosphaera sibogae* (*Discoaster brouweri* Zone, NN 18). Sample 366A-4-2, 60-62 cm. 1600 $\times$ . 10 kv.
- Figure 5 Assemblage with *Discoaster brouweri*, *Helicosphaera carteri*, *Cyclococcolithus leptoporus*, *Umbilicosphaera sibogae*, *Pseudoemiliana lacunosa*, *Rhabdosphaera clavigera*, *Syracosphaera pulchra* (*Discoaster brouweri* Zone, NN 18). Sample 366A-4-4, 64-66 cm. 1600 $\times$ . 10 kv.
- Figure 6 Assemblage with *Discoaster pentaradiatus*, *D. brouweri*, *Helicosphaera carteri*, *Cyclococcolithus leptoporus*, *C. macintyreii*, *Rhabdosphaera stylifera*, *Syracosphaera pulchra* (*Discoaster surculus* Zone, NN 16). Sample 366A-5, CC. 1600 $\times$ . 20 kv.

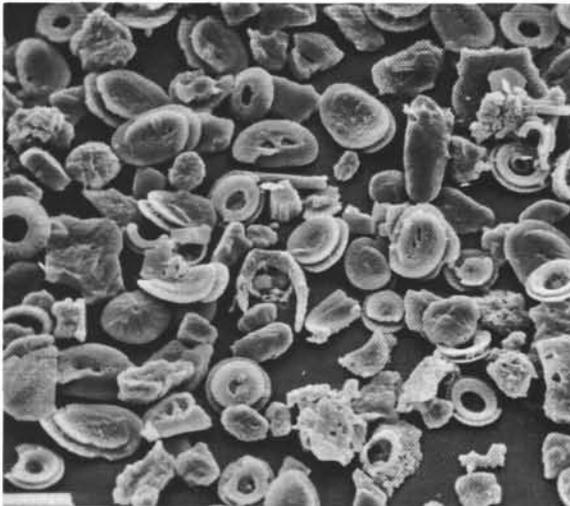
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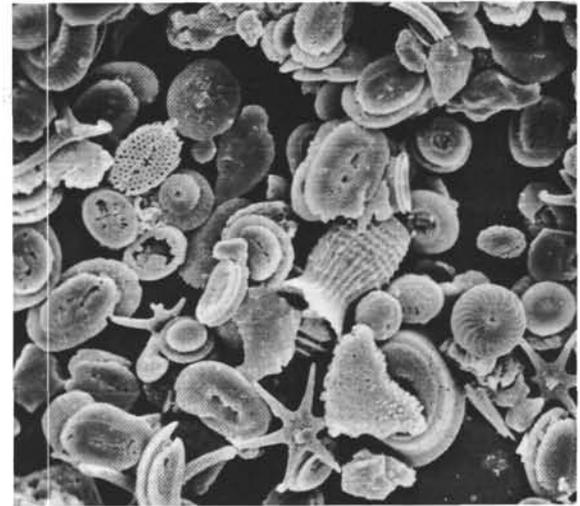
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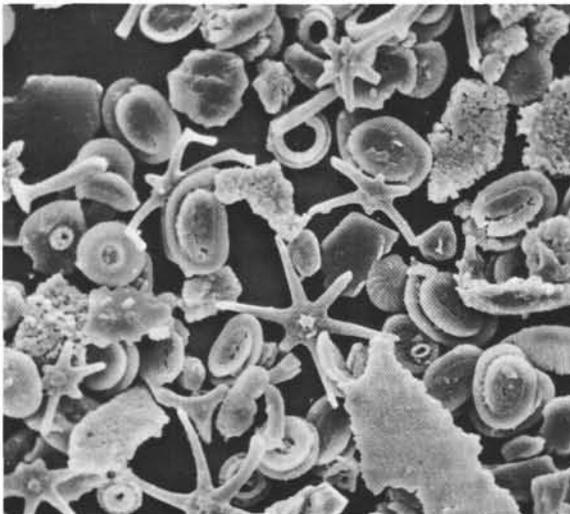
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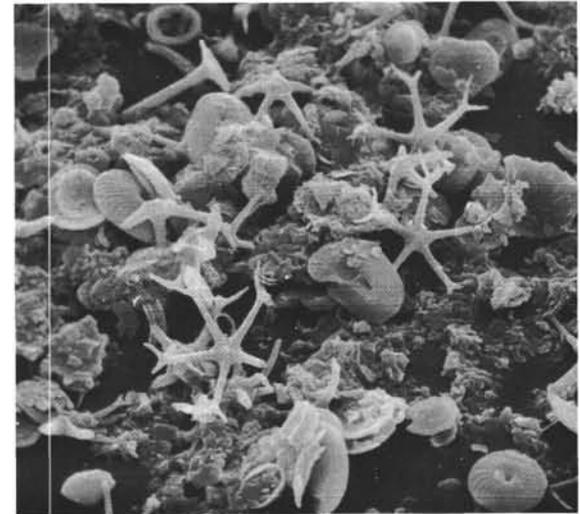
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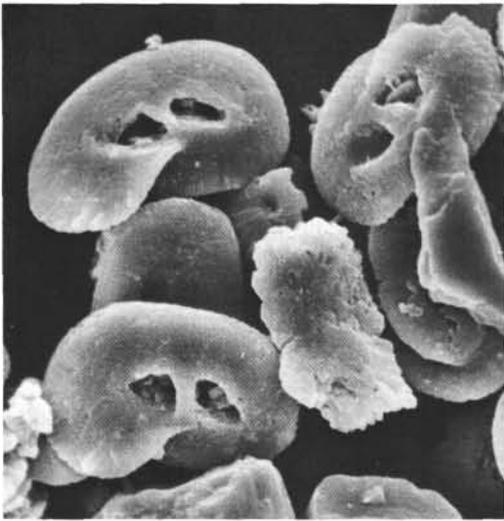


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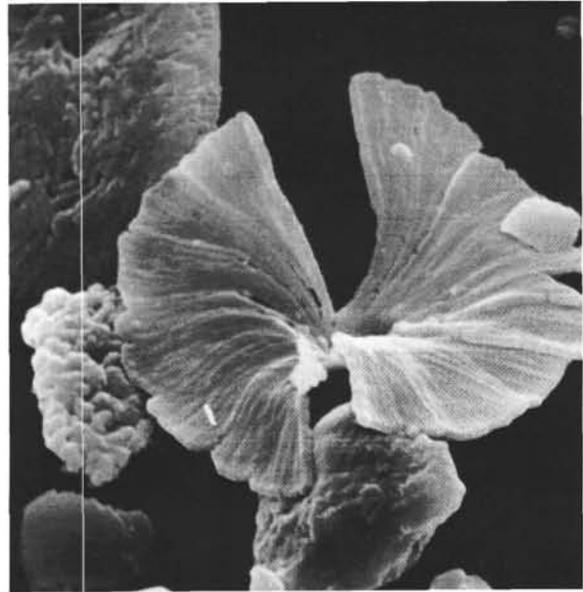
PLATE 2

- Figure 1 *Helicosphaera sellii* (Bukry and Bramlette).  
Sample 366A-4-4, 64-66 cm. 4000 $\times$ . 10 kv.
- Figure 2 *Umbellosphaera irregularis* Paasche.  
Sample 366A-1, CC. 8000 $\times$ . 10 kv.
- Figure 3 *Helicosphaera carteri* (Wallich) Kamptner.  
Specimen with heavy overgrowth.  
Sample 366A-3-4, 68-70 cm. 8000 $\times$ . 10 kv.
- Figure 4 *Helicosphaera carteri* (Wallich) Kamptner.  
Slightly corroded specimen.  
Sample 366A-1, CC. 5000 $\times$ . 10 kv.
- Figure 5 *Craspedolithus declivus* Kamptner.  
Sample 366A-2, CC. 8000 $\times$ . 10 kv.
- Figure 6 *Helicosphaera carteri* (Wallich) Kamptner.  
Partly recrystallized specimen.  
Sample 366A-1, CC. 8000 $\times$ . 10 kv.
- Figure 7 *Umbellosphaera irregularis* Paasche.  
Sample 366A-1, CC. 8000 $\times$ . 10 kv.
- Figure 8 *Discoaster perplexus* Bramlette and Riedel.  
Partly broken specimen.  
Sample 366A-3-4, 68-70 cm. 8000 $\times$ . 10 kv.

PLATE 2



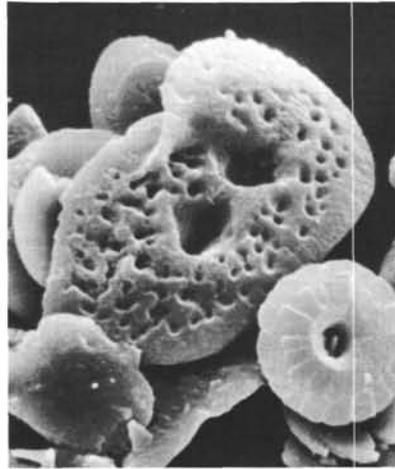
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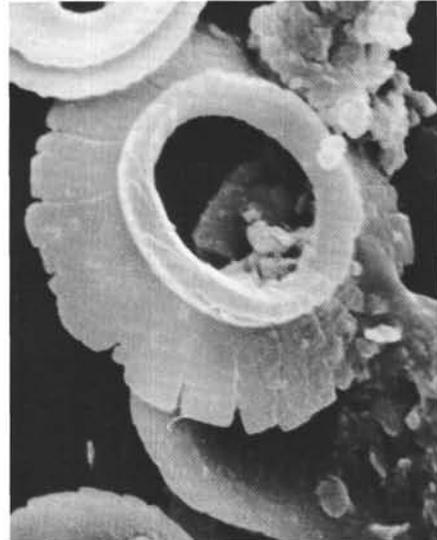
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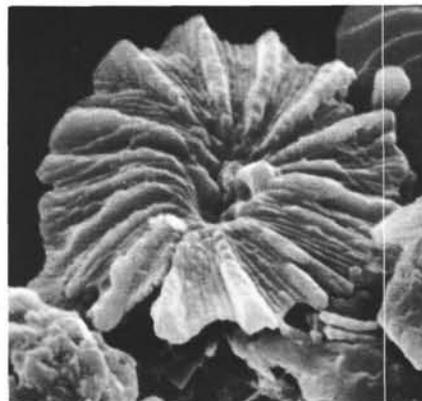
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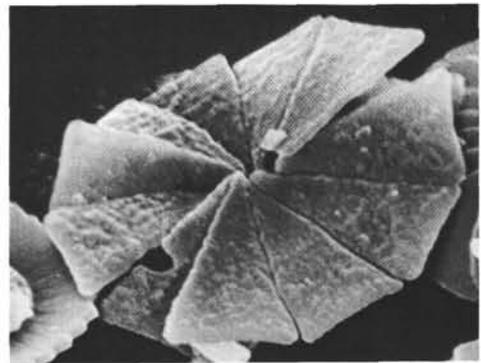
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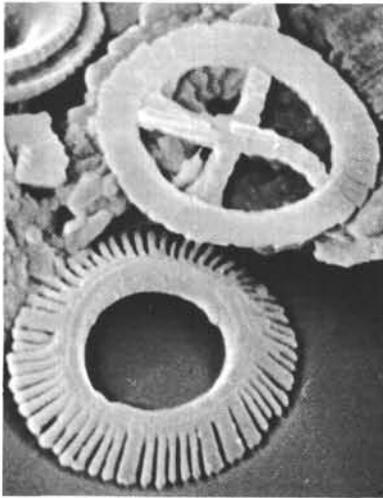


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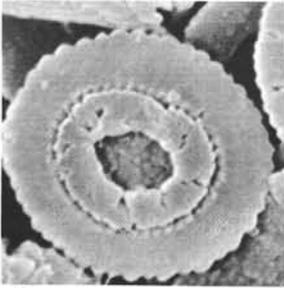
## PLATE 3

- Figure 1 *Cruciplacolithus neohelis* (McIntyre and Bè) and *Pseudoemiliana lacunosa* (Kamptner) Gartner.  
Sample 366A-4, CC. 8000×. 10 kv.
- Figure 2 Two specimens of *Pseudoemiliana lacunosa* (Kamptner) Gartner.  
Sample 366A-3-6, 33-35 cm. 8000×. 20 kv.
- Figure 3 *Pseudoemiliana lacunosa* (Kamptner) Gartner.  
Sample 366A-4, CC. 8000×. 10 kv.
- Figure 4 *Crenalithus daronicoides* (Black and Barnes).  
Sample 366A-4, CC. 8000×. 10 kv.
- Figure 5 Two specimens of *Pseudoemiliana lacunosa* (Kamptner) Gartner.  
Sample 366A-6-3, 83-85 cm. 8000×. 10 kv.
- Figure 6 *Pseudoemiliana lacunosa* (Kamptner) Gartner.  
Sample 366A-3-6, 33-35 cm. 8000×. 20 kv.
- Figure 7 *Gephyrocapsa protohuxleyi* McIntyre.  
Sample 366A-1-4, 43-45 cm. 10,000×. 20 kv.
- Figure 8 *Gephyrocapsa aperta* Kamptner.  
Sample 366A-4-2, 60-62 cm. 10,000×. 10 kv.
- Figure 9 *Crenalithus daronicoides* (Black and Barnes).  
Sample 366A-6-3, 83-85 cm. 8000×. 10 kv.
- Figure 10 *Crenalithus daronicoides* (Black and Barnes).  
Sample 366A-6-3, 83-85 cm. 10,000×. 20 kv.
- Figure 11 *Gephyrocapsa ericsonii* McIntyre and Bè.  
Sample 366A-4-2, 60-62 cm. 10,000×. 10 kv.
- Figure 12 *Gephyrocapsa ericsonii* McIntyre and Bè.  
Sample 366A-1-4, 43-45 cm. 8000×. 20 kv.
- Figure 13 *Pseudoemiliana lacunosa* (Kamptner) Gartner.  
Sample 366A-2, CC. 8000×. 10 kv.
- Figure 14 *Gephyrocapsa caribbeanica* Boudreaux and Hay.  
Sample 366A-3-6, 33-35 cm. 8000×. 20 kv.
- Figure 15 *Gephyrocapsa caribbeanica* Boudreaux and Hay.  
Sample 366A-3-6, 33-35 cm. 8000×. 20 kv.

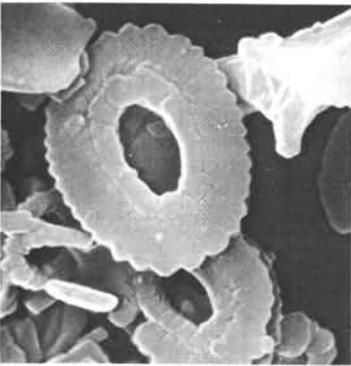
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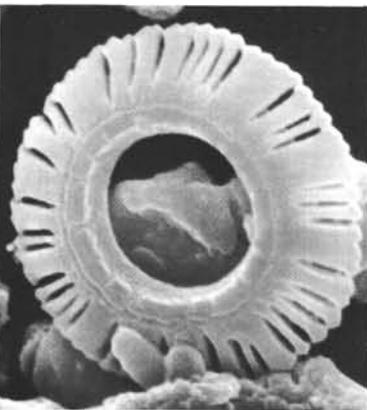
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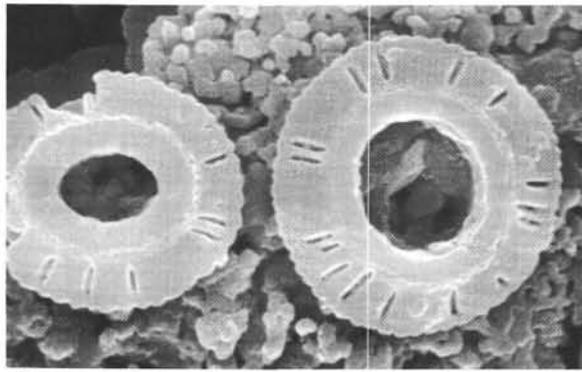
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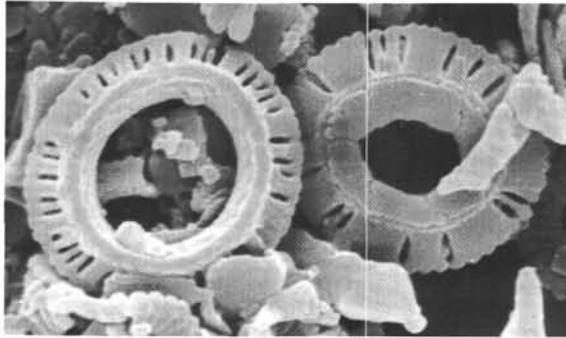
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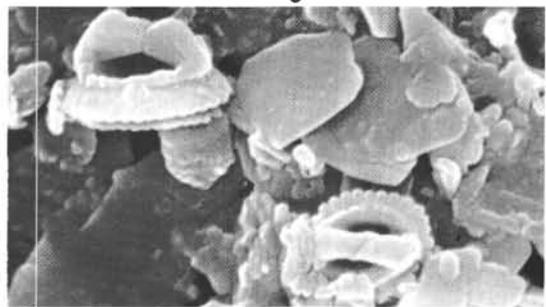
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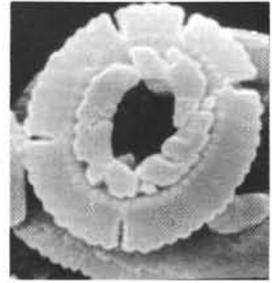
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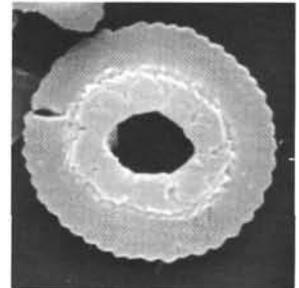
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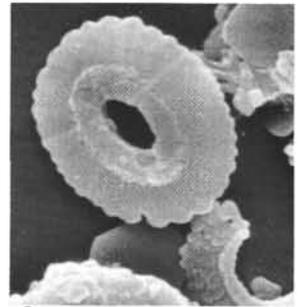
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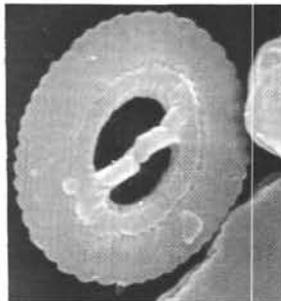
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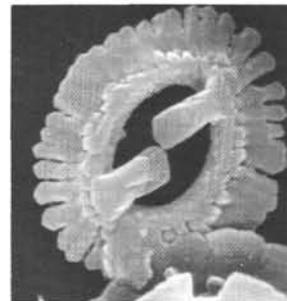
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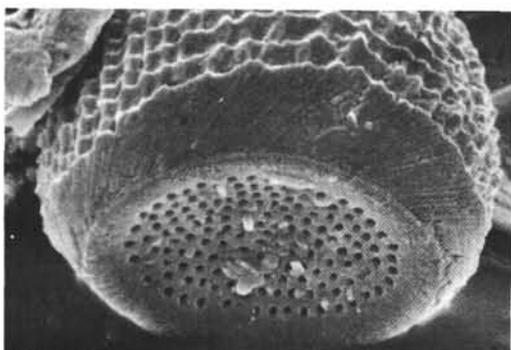
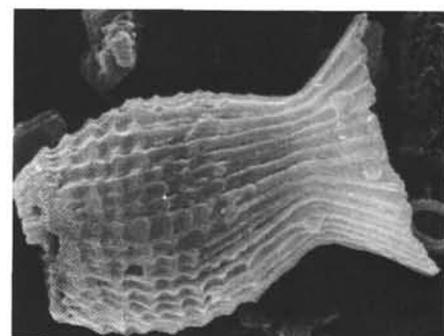
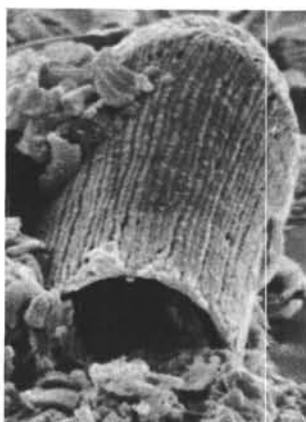
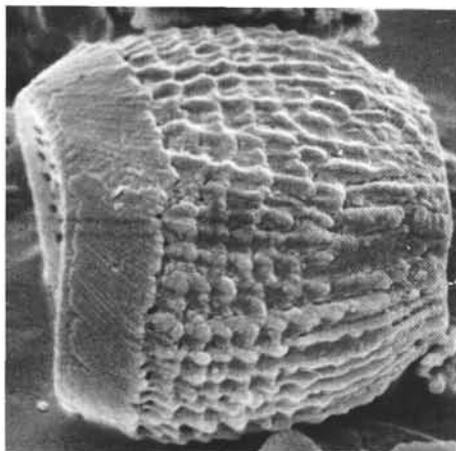
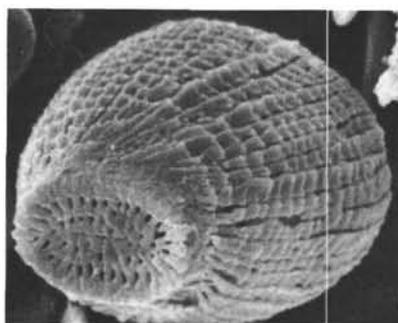
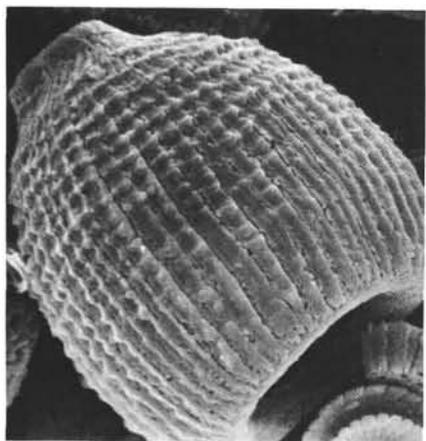
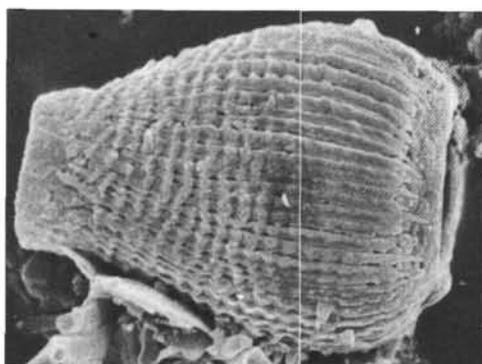
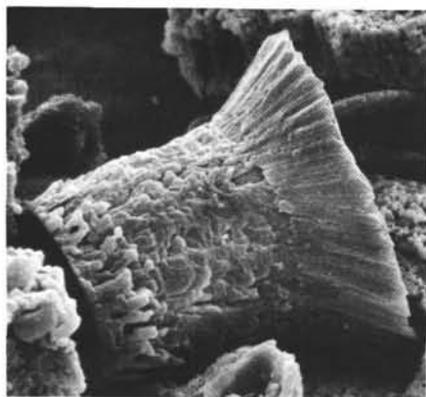


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## PLATE 4

- Figure 1 *Scyphosphaera* cf. *S. campanula* Deflandre.  
Sample 366A-5-5, 63-65 cm. 3000 $\times$ . 10 kv.
- Figure 2 *Scyphosphaera apsteini* Lohmann.  
Sample 366A-6-3, 83-85 cm. 4000 $\times$ . 10 kv.
- Figure 3 *Scyphosphaera pulcherrima* Deflandre.  
Note the round finely perforate basal plate.  
Sample 366A-3, CC. 4000 $\times$ . 10 kv.
- Figure 4 *Scyphosphaera recurvata* Deflandre.  
Sample 366A-3, CC. 3000 $\times$ . 10 kv.
- Figure 5 *Scyphosphaera apsteini* Lohmann.  
Note the elliptical basal plate.  
Sample 366A-3, CC. 4000 $\times$ . 10 kv.
- Figure 6 *Scyphosphaera pulcherrima* Deflandre.  
Sample 366A-3, CC. 4000 $\times$ . 10 kv.
- Figure 7 *Scyphosphaera* sp. 3.  
Sample 366A-4-4, 64-66 cm. 4000 $\times$ . 10 kv.
- Figure 8 *Scyphosphaera* sp.  
Sample 366A-6-3, 83-85 cm. 4200 $\times$ . 10 kv.
- Figure 9 *Scyphosphaera pulcherrima* Deflandre.  
Sample 366A-3-6, 33-35 cm. 4000 $\times$ . 20 kv.
- Figure 10 *Scyphosphaera* sp. 3 (same specimen as Figure 7).  
Oblique view at the round basal plate.  
Sample 366A-4-4, 64-66 cm. 4000 $\times$ . 10 kv.
- Figure 11 *Scyphosphaera* sp. 2.  
Sample 366A-3, CC. 4000 $\times$ . 10 kv.

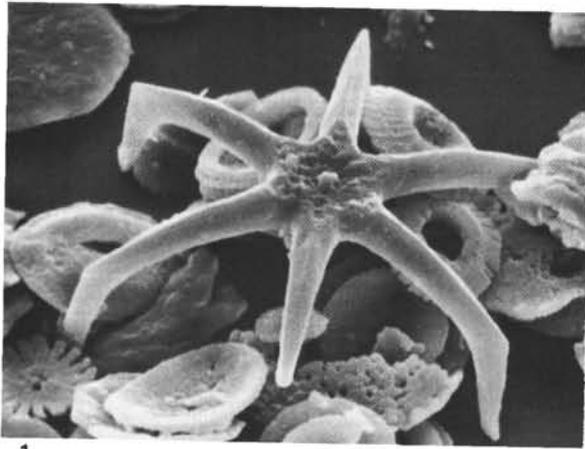
PLATE 4



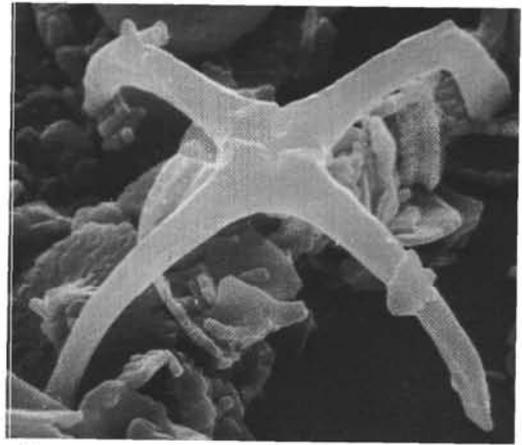
## PLATE 5

- Figure 1 *Discoaster brouweri* Tan.  
Sample 366A-4-4, 64-66 cm. 4000×. 10 kv.
- Figure 2 *Discoaster brouweri* Tan (= *D. tamalis* Kamptner).  
Sample 366A-6-3, 83-85 cm. 8000×. 20 kv.
- Figure 3 *Discoaster pentaradiatus* Tan.  
Three-rayed specimen.  
Sample 366A-6-3, 83-85 cm. 4000×. 20 kv.
- Figure 4 *Discoaster brouweri* Tan.  
Three-rayed specimen.  
Sample 366A-4, CC. 4000×. 10 kv.
- Figure 5 *Discoaster pentaradiatus* Tan.  
Sample 366A-6-3, 83-85 cm. 4000×. 20 kv.
- Figure 6 Three specimens of *Discoaster pentaradiatus* Tan.  
Sample 366A-5, CC. 4000×. 20 kv.
- Figure 7 *Ceratolithus cristatus* Kamptner.  
Sample 366A-1-1, 71-73 cm. 4000×. 10 kv.
- Figure 8 *Ceratolithus rugosus* Bukry and Bramlette.  
Sample 366A-4-4, 64-66 cm. 4000×. 10 kv.
- Figure 9 *Ceratolithus rugosus* Bukry and Bramlette.  
Sample 366A-4, CC. 4000×. 10 kv.
- Figure 10 *Ceratolithus cristatus* Kamptner.  
Sample 366A-3, CC. 4000×. 10 kv.

PLATE 5



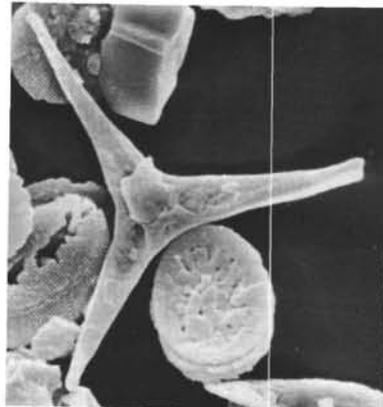
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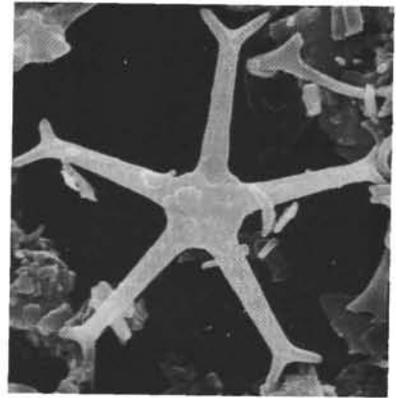
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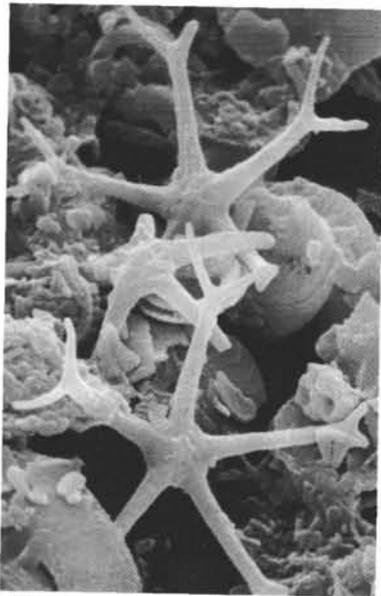
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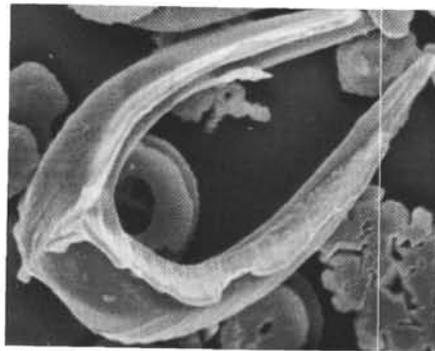
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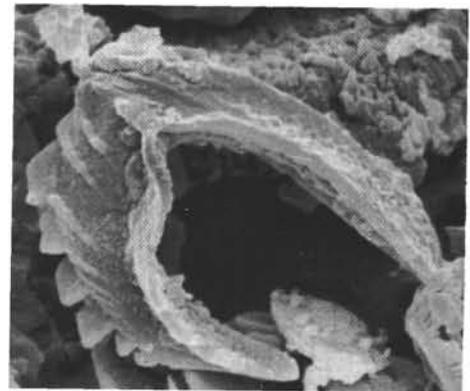
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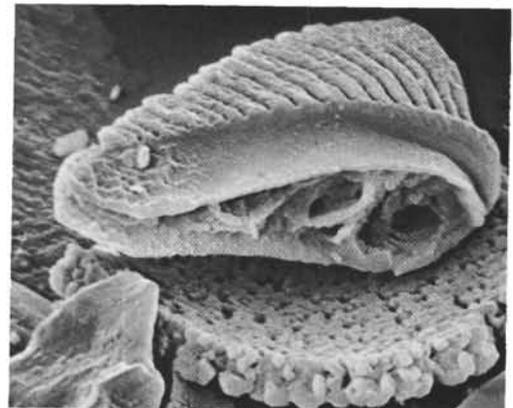
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