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GEOLOGÍA

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CALCAREOUS NANNOFOSSILS IN MARINE SEDIMENTS

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1. Introduction

The term calcareous nannofossils is a relatively recent addition to the vocabulary of students of marine sediments. Although these minute objects have been known for well over a century they received little attention largely because of their small size. As sophisticated, easy to operate, high magnification microscopes became generally available, the usefulness of nannofossils in biostratigraphy became apparent and with the explosive expansion of ocean sediment studies brought, about largely by deep ocean drilling, the importance of calcareous nannofossils as a major component of pelagic sediment has become obvious. An inordinate amount of data on nannofossils has been generated as a result of the Deep Sea Drilling Project. The following treatment is not an attempt to summerize or even sample that pool of information. Rather, it is intended to introduce the interested student and non-specialist in a general way to this very important component of oceanic sediments, so that he will more readily understand and appreciate the numerous articles on the subject.

The term "calcareous nannofossils" or "nannoliths" generally includes a group of marine fossils most of which range in size from about one to ten microns, and which commonly constitute about half of the bulk of pelagic calcareous ooze. Best known among calcareous nannofossils are coccoliths, circular or elliptical bodies constructured of

two unequal discs connected by a tube. They are secreted by marine algae, and several coccoliths commonly form an interlocking "skeleton" or coccosphere around the parent cell. Nannofossil assemblages are nearly always dominated by coccoliths, but may also contain objects of distinctly different shapes such as the discoasters and sphenoliths through most of the Cenozoic, rhabdoliths, pentaliths and discoliths in the Mesozoic and Cenozoic, and the enigmatic nannoconnids in the Cretaceous.

In spite of their small size coccoliths as well as most other calcareous nannofossils exhibit a bewildering variety of shapes; however, virtually all have a regular symmetry - mostly radial or modified radial symmetry -- and a very orderly geometric arrangement of parts. An extensive list of terms with Latin or Greek roots is available to describe various nannofossils according to shape or appearance. In addition to these terms that are descriptive of gross morphology, and which are more or less applicable regardless of what mode of study is used, there are specialized terms that are useful only for a particular study technique such as cross-polarized light studies and electron optical imaging. Electron microscopy, both transmitted and scanning type, has the capability to resolve some of the smallest ultrastructural details, and consequently an inordinately large number of descriptive terms have been introduced and given special meaning in nannofossil studies. Most of these terms are not widely used, however, and many appear only once in the original description of a taxon. Following is a glossary of various terms and their definition, grouped according to the study technique in which they are used. Sources for these terms are chiefly the glossaries compiled previously by Hay, Mohler and Wade (1966); Reinhardt (1972); and Perch-Nielsen in Farinacci (1971). It should be

noted that this is not a comprehensive glossary. Many terms that have been introduced into the literature are superfluous and these have been left out. On the other hand, it is obvious that new terms are needed for describing some often recurring structures to substitute for cumbersome and lengthy descriptive phrases.

Descriptive morphologic terms useful for all modes of study (i.e. coccoliths divided by shape; see Text Figures

coccoliths - often used to refer to calcareous nannofossils in general; may refer only to placoliths

placoliths - two discs or shields connected at or near their center by a tube or collar; placoliths may be elliptical or circular
(example: Coccolithus pelagicus)

discoliths - elliptical discs, usually with a distinct, sometime thickened rim and a variable central area which may or may not be perforated. (Huxley's original description of discoliths as being imperforate seemingly was incorrect as most discoliths have perforations. Reinhardt (1972) includes caneoliths, dictyoliths, rhagoliths, ethmoliths and certain holococcoliths in this group, all of these being differentiated on the basis of ultrastructural detail largely resolvable only with electron microscopes.)
(example: Discolithina anisotrema)

lopadoliths - basket, cup or vase shaped nannofossils; discoliths with very high rim
(example: Scyphosphaera apsteinii)

cricoliths - elliptical rings constructed of multiple elements. (Many cricoliths are probably broken, corroded or partially developed coccoliths that normally are assigned to another category.)
(example: Pyrocyclus hermosus)

cycloliths - circular rings often constructed of multiple cycles of elements
(example: Cyclolithella nitescens)

zygoliths - elliptical ring, sometime of multiple cycles, with the center spanned by a bridge-like structure
(example: Zygodiscus sigmoides)

rhabdoliths - rod shaped objects, often attached to the center of a disc or zygolith
(example: Rhabdosphaera claviger)

caliptroliths - cap shaped coccoliths
(example: Caliptrosphaera)

pentaliths - nannoliths that have a five fold symmetry, sometimes pentagonal, often regularly polygonal, stellate or circular
(example: Braarudosphaera bigelowi)

asteroliths - star shaped nannoliths, also called "discoasters"
(example: Discoaster brouweri)

steloliths - column shaped or cylindrical nannofossils
(example: Fasciculithus tympaniformis)

sphenoliths - conical nannoliths constructed of radiating elements and often surmounted by a conical stem
(example: Sphenolithus heteromorphus)

ceratoliths - horseshoe shaped nannoliths
(example: Ceratolithus cristatus)

scapholiths - boat shaped nannoliths
(example: Scapholithus fossilis)

nannoconids - cylindrical or conical nannoliths with an axial canal
(example: Nannoconus colomi)

Structural terms applied to entire coccoliths (i.e. coccolith differentiated according to how they are constructed.)

ortholithid - nannoliths constructed so that the optic axes of all component cristallites are parallel, arranged either perpendicular to the surface of the nannolith or within the plane of the nannolith

heliolithid - nannoliths constructed of cristallites whose optic axes are arranged in a helicoidal pattern

heterolithid - nannoliths constructed of a heliolithid rim and with the center consisting of randomly arranged elements

Reinhardt (1972) characterizes these terms according to the behavior of the coccoliths in cross-polarized light, however, because nearly all coccoliths have a heliolithid or modified heliolithid type construction

Reinhardt's concepts are ambiguous.

holococcoliths - nannolith constructed entirely of one type and size of element, such as calcite rhombs or calcite prisms usually less than 0.1 micron in maximum dimension (rarely preserved)

heterococcoliths - nannolith constructed of elements of different size and shape (most coccoliths in sediments belong to this group)

2. Nannoliths as Particles

a. Morphology

Judging from modern coccolith secreting organisms, all nannofossils were at one time arranged on the surface of the parent organism. The side of the coccolith or other skeletal part facing toward the organism is usually concave and is termed the proximal side. The side facing away from the organism may be concave but more often is convex, and is termed the distal side. Nearly all calcareous nannofossils are constructed on a modified radial plan. In most cases this is obvious; in some it is not; in very few instances the plan of construction has no radial symmetry (e.g. ceratoliths), or derivation from a radial plan is difficult to trace (e.g. Triquetrorhabdulus rugosus). The radial symmetry is perhaps most obvious on a circular placolith (Figure 1) in which two discs (shields) are constructed of laths or plates (elements) arranged around a central axis. Frequently it can also be seen that the structure connecting the two shields (tube or collar) also is constructed of radially arranged elements. On some placoliths auxilary cycles of ele-

ments may also be developed and these, too, have radial symmetry. In most placoliths the plane of the individual structural members or elements is inclined to the surface of the shield and the arrangment can be more appropriately termed helicoidal; hence the term "heliolithid".

Starting from the circular placolith it is easy to visualize the same construction in elliptical placoliths, and only slightly more difficult to visualize the same type of construction in discoliths, lopadoliths, cricoliths, cycloliths, zygoliths and caliptroliths. Rhabdoliths often have a heliolithid base, and in some cases even isolated rods or stems that are never attached to a heliolithid base (e.g. Cretaceous microrhabdulids) plainly show a radial or axial symmetry. Pentaliths merely represent a radial arrangement of five segments. Among the asteroliths the number of rays may vary from three to more than thirty. (Instead of the terms "segments" or "elements" the radial members of asteroliths are referred to as "rays".) Steloliths (Fasciculithus) are morphologically very similar to certain asteroliths, and indeed, Prins (1971) considers the two groups to be closely related. In plan view these as well as the sphenoliths have radial symmetry. Ceratoliths have no symmetry, however, as Norris (1971) has shown the organism that secretes ceratoliths has its surface covered by a second type of coccolith, a cyclolith, which clearly has radial symmetry. This more normal type of coccolith is very delicate and is not preserved in the fossil record. Scapholiths have a peculiar 180 degree rotatory symmetry, which tended to develop as well among several nannofossil groups (i.e. Diadozygus, Diadorhambus, Isthmolithus), especially certain zygoliths. A modified radial symmetry is apparent among most of these, and it is not difficult to imagine that even the scapholith structure originated this way. Nannoconnids have axial symmetry, and most of the nannofossils that do

not readily fit into the above morphological categories also have a basic radial, axial, or spherical symmetry, including most of the holococcoliths.

b. Crystallography of Calcareous Nannofossils

A casual examination of coccoliths of the placolith type construction - by far the most frequently encountered morphology among nannofossils in sediment - may create the impression that placoliths, and indeed all coccoliths, are cristallographically extremely complicated. This is not entirely true. Kamptner (1954) determined the basic pattern of crystal arrangement for a number of different coccolith types, based on the images of the various coccoliths in cross-polarized light. He indicated that the "micellae" or crystallites of which coccoliths are constructed are arranged in a helicoidal pattern around an axis perpendicular to the plane of the coccolith. Black (1962) analyzed the crystallographic structure of coccoliths from electron micrographs and concluded that two crystal habits occur in coccoliths:

1. Hexagonal prisms in which the optic axis is parallel to the sides of the prism. The prisms are arranged parallel to one another and all have nearly the same dimensions. This type of crystallographic arrangement is known only among holococcoliths, which are rarely found in sediments.
2. Rhombohedral prisms in which all faces intersect the optic axis. The rhombohedra may be all of the same size and stacked or arranged in an orderly fashion as on certain holococcoliths (e.g. Crystallolithus hyalinus) or, more often, the rhombohedral shape is modified as in all heterococcoliths, so that frequently no natural crystal face is preserved. Heterococcoliths in the coccospheres of living

coccolithophores seldom have recognizable crystal faces. Coccoliths taken from sediment, however, may have distinctive crystal faces developed on their component elements and this condition becomes more prevalent with the age and degree of diagenetic alteration of the sediment.

In order to elucidate the crystallography of calcareous nannofossils it is best to start with the discoasters or asteroliths, a rather special group whose phyletic relationship to other coccoliths is somewhat ambiguous, but this point seems unimportant if not irrelevant from the standpoint of skeletal crystallography. Black (1972) illustrated by means of some very remarkable electron microscope photographs the nature and arrangement of calcite crystals in discoasters. Discoasters may be tabular, slightly to strongly biconvex or concave-convex in shape and are constructed of three or more radially arranged structural elements. When allowed to settle from suspension discoasters most often assume an orientation such that the axis of symmetry is perpendicular to the surface on which they rest, thus presenting a plan view. If viewed in cross-polarized light in this orientation discoasters are extinct, that is, they are not visible against the background, and they remain invisible, or at best, faintly visible, when rotated in a plane normal to the path of the light. This indicates that the optic axis of all rays of a discoaster are parallel to the light ray and normal to the plane of the asterolith. That this is indeed the case can be seen readily on Figure 2. These discoasters have undergone diagenetic alteration and in the process calcium carbonate was deposited in crystallographic continuity with each ray of the asterolith, resulting in formation of rhombohedral faces on the rays of the astroliths. Each ray of these discoasters has a median ridge

formed by one of the edges of the rhombohedron that intersects the optic axis. Thereby the six fold symmetry of these early Miocene discoasters is further accentuated by the trigonal symmetry of calcite. Black (1972) pointed out that opposite surfaces of the same asterolith would be slightly different: on one side the rhombohedra are arranged with an edge toward the center (edge to center or E-surface, Figure 2a) whereas on the opposite side rhombohedral faces would be turned toward the center (face to center or F-surface, Figure 2b). Adelseck et al. (1973) produced similar effects on discoasters by subjecting them to elevated temperature (300° C) and pressure (1 kilobar). In asteroliths that have more than six rays, as in the case with most Paleogene discoasters, the individual rays still retain the same crystal symmetry evident on six rayed specimens so that in preferred orientation the optic axis of each ray of the asterolith is parallel to the direction of illumination, and consequently the entire discoaster is at extinction in cross-polarized light.

In contrast to discoasters, placoliths and virtually all other coccoliths do not go to extinction but instead yield some type of interference figure in cross-polarized light. On some placoliths (e.g. Cyclococcolithus leptoporus) only one shield contributes to the interference figure, while the other shield behaves optically precisely as discoasters do (Gartner, 1967; Bukry, 1971). On most placoliths, however, both shields as well as the collar contribute to the interference figure to a varying degree. Placoliths in coccospheres of living coccolithophores generally have no crystal faces on any structural elements as is true also of most pristine and well preserved placoliths recovered from clayey or marly sediment. Nanno-

fossils in chalk and chalk-ooze normally have undergone some diagenetic alteration with some secondary calcite deposition and overgrowth, although such specimens rarely have good crystal faces developed on any of the structural elements. Only rarely is preservation encountered that combines the pristine state of well preserved specimens with crystallographically continuous overgrowth so that crystal faces are clearly recognizable in electron micrographs (Figure 3a, 3b). The rhombohedra on the periphery of the shields of this placolith are clearly in crystallographic continuity with the elements of the shield. An oblique side view indicates that the optic axis (= crystallographic c-axis) is inclined to the plane of the placolith as well as to the radial direction. Both of these angles are difficult to measure precisely, although the projection of the optic axis of the individual elements into the plane of the placolith can be measured readily in cross-polarized light with the light microscope. The precise arrangement of the optic axes for individual elements usually is not the same in the two shields of a placolith, and the collar and any auxiliary cycles that may be present (e.g. Ericsonia) each contributes its own set of helicoidally arranged optic axes. The resulting interference figure may be exceedingly complex (e.g. Blackites - Figure 4).

It can be demonstrated that with few exceptions all nannofossils are constructed of variously shaped calcite crystallites arranged so that the optic axes of the elements form a helicoidal pattern, and that the true symmetry is rotational and not radial. Only among discoasters is there true radial symmetry of calcite crystals, although the morphological symmetry of most asteroliths is rotational since the individual rays of an unaltered discoaster are nearly always asymmetrical.

Ceratoliths do not have the symmetry of nannofossils in general. Although they are known to be constructed by algae closely related to other coccolithophores, the ceratoliths themselves are not homologous to the coccoliths. There exist in the fossil record also many rod-shaped objects that do not have the rotational symmetry of other nannofossils (e.g. Lithraphidites, Triquetrorhabdulus). In the case of Lithraphidites, similar species are known (i.e. Rhabdolekiskus aquitanicus) in which an elliptical disc of helicoidaly arranged elements is attached to one end of a rod. Very likely other rod shaped objects bear a similar relationship to the coccoliths of other coccolithophores, although it is possible that among some coccolithophores only rods without discs were constructed.

c. Chemical and mineralogical composition of calcareous nannofossils

The term "calcareous nannofossils" apparently is very appropriate indeed for coccoliths of various type in that they all seem to be made of nearly pure calcium carbonate, as several analyses indicate. Chemical analysis of bulk coccolith ooze samples by Vinogradov (1953) and by Goldberg and Arrhenius (1958) indicated the presence of Mg, Sr and Ba, and Thompson and Bowin (1969) measured Mg concentrations of 0.10 to 0.12% and Sr concentrations of 0.14 to 0.16%, along with traces of other elements. However, the source for these may have been sediment particles other than coccoliths. Shaffer (1971, and oral communication) analyzed isolated specimens of thirty species representing most major Cenozoic morphologic groups for Mg, Sr, Ba, and Fe by means of both dispersive and non-dispersive x-ray techniques in a combination scanning electron microscope - electron microprobe. He found that none of these elements was present in sufficient concentration to be

detected by the instrument (i.e. greater than 0.1%). Siesser (1977) analyzed nannofossils of Paleocene to Recent age from the southeastern South Atlantic for Al, Fe, K, Mg, Mn, Na, P and Si by means of a microprobe. None of these elements except phosphorus were present in sufficient concentration to be detected (i.e. 500 ppm). Phosphorus was present in concentrations of up to 0.3% and in one sample exceeded 2.5%. Hamano and Honjo (1969) have shown that organic material, presumably part of the matrix or template on which coccoliths are precipitated, may make up as much as 0.2% of fossil coccoliths. It is likely, therefore, that at least part of the phosphorus detected by Siesser is present in this residual organic matrix. From the available data it would seem that whatever impurities are present in the calcium carbonate that forms the mineralized parts of the calcareous nannofossils, are present in very low concentration under normal circumstances.

Calcium carbonate skeletons of marine organisms may take the crystal forms of aragonite or calcite, the latter being far more common in sediment. Calcite also seems to be the dominant mineral in coccoliths. Wilbur and Watabe (1963) found in cultures of Coccolithus huxleyi (= Emiliania huxleyi) that in a normal culture medium coccoliths are mineralized essentially as calcite with only traces of aragonite, whereas in a nitrogen deficient medium mineralization occurs in the three crystal phases of calcium: calcite, aragonite and vaterite. Nearly all analyses of naturally occurring coccoliths point to their being constructed of the mineral calcite. A specific reference to aragonitic composition is that of Tan Sin Hok (1927) who tested the mineralogy of discoasters with Mohr's salt (silver nitrate). Hart et al. (1965) determined an aragonite compo-

sition for a Cretaceous coccolith by means of electron diffraction. However, the specimen they used seems to be in a poor state of preservation and has been altered to the point where it cannot be readily identified with any known Cretaceous species. It is noteworthy that aragonite has not been identified in any of the nannofossil-foraminifer ooze recovered by the Deep Sea Drilling Project, even at the relatively shallow sites, except in instances where the aragonite is associated with non-pelagic constituents that were deposited from turbidity currents (see e.g. Zemmels, Cook and Matti, 1975 [leg 30] and other x-ray mineralogy sections in Deep Sea Drilling Project Initial Report).

3. Coccoliths as Skeletal Parts

a. The parent organism

Coccoliths are produced by a group of single celled algae, the coccolithophores (class Coccolithophyceae) which are included among the chrysophyta. Coccoliths are part of the external covering of the cell. Coccolithophores range in size from about 5 micrometers to more than 100 micrometers in maximum dimensions. Most coccolithophores are spherical to ovoid in shape, and these forms commonly attain diameters not greater than 25 micrometers. The larger species have fusiform cells, but this shape seems to be restricted to a relatively small number of modern forms (e.g. Calciosolenia). Though commonly regarded as flagellates, most coccolithophore cells lack flagella, at least in that stage of their life cycle in which they are most frequently encountered. When flagella are present they are paired, and may be equal or unequal in length. In some coccolithophores (i.e. Coccolithus pelagicus) both a flagella-bearing and a flagella-free

stage is known; the form with flagella is termed the motile stage, that without flagella the non-motile stage. The two stages produce coccoliths of entirely different morphology, one being a holococcolith (motile stage), the other a heterococcolith (non-motile stage) (for a detailed discussion see Parke and Adams, 1960).

In addition to flagella some coccolithophore cells may also bear a third appendage, the haptonema. However, coccolith formation is not associated with haptonema bearing cells, but seems to be confined to the non-motile stage or to the motile stage without haptonema (Parke, 1971, but see also Klaveness, 1973).

Detailed studies have been made of the life history of several coccolithophores and these studies are summarized by Paasche (1968). As Paasche points out the selection of species that have been cultured and studied probably is not representative because coccolithophores that are most easily cultured are those living in coastal waters. Several of these coastal species are known to have a benthic stage in their life cycle, a stage that may not exist in the life history of oceanic species.

b. Coccolith production

Two coccolithophores that have been maintained in culture successfully, Coccolithus pelagicus and Emiliania huxleyi (= Coccolithus huxleyi) are equally at home in coastal waters (hemipelagic realm) and in the oceanic realm. Neither of these two species has a known benthic phase. Coccolithogenesis has been observed in both species (Manton and Leedale, 1969; Wilbur and Watabe, 1963), as well as in a number of other species that are more restricted in their distri-

bution, and appears to proceed in a similar fashion in all species. Heterococcoliths are formed by calcification on a seemingly structureless organic matrix within large vesicles that originate in the Golgi region within the cell. When calcification is more or less complete the coccoliths are extruded to the surface of the coccolithophore where they are arranged to form a complete, sometimes interlocking, covering around the cell (Figure 5). In some species more than one layer of coccoliths is arranged around the cell.

Some coccolithophores produce two types of coccoliths (dimorphism) that are morphologically very different. On several species of Syracosphaera two different morphological types of coccoliths are arranged in two separate layers, one beneath the other. This type of dimorphism (dithecatism) results in two distinct coccospheres, one inside the other, and the two are termed the exotheca and endotheca (Okada and McIntyre, 1977). In dithecate coccolithophores only one of the two types of coccoliths, that of the endotheca, seems to be preservable, since none of the exothecal coccoliths have been recorded from sediment.

Another type of coccolith dimorphism (or polymorphism) is the modification of the basic coccolith morphology by the excessive development of one particular structure such as a central spine in certain species of Acanthoica and Syracosphaera, or unusually high development of the rim of a discolith as in Pontosphaera (see e.g. Schiller, 1930; Kamptner, 1937; Borsetti and Cati, 1976; Okada and McIntyre, 1977). Other types of dimorphism include pronounced spines developed at one or both poles in certain ovoid coccolithophores such as Ophiaster (Lohmann, 1913), and the presence of one relatively large horseshoe

shaped nannolith more or less hooked like a yoke around the coccolithophore cell (Norris, 1965). Many of the dimorphic coccoliths produced by modern coccolithophores are preserved in marine sediments, and their analogues are found also in Neogene sediments. It is reasonable to think, therefore, that dimorphism was common also among older Cenozoic and Mesozoic coccolithophores. An excellent case for this can be made for many Cretaceous coccolith species of the eiffellithalid type (e.g. Eiffellithus, Vekshinella) and podorhabdinalid type (e.g. Prediscosphaera, Cretarhabdus) of construction, among which many species are represented by specimens both with and without a prominent spine.

Although all available evidence indicates that the calcification of all heterococcoliths is accomplished in approximately the same manner within the coccolithophore cell, holococcolith formation has not been observed inside the cell, and Manton and Leedale (1969) speculate that the motile phase of Coccolithus pelagicus (i.e. Crystallolithus hyalinus) may construct its holococcoliths by calcifying outside the cell. Holococcoliths are very rare in Recent and sub-Recent sediments. Most holococcolith species are known only from plankton samples where they are always found attached to a cell. The rare occurrences of fossil holococcoliths are nearly always associated with clayey sediments of hemipelagic deposits. Curiously there is one interval of the Cenozoic, the Middle Eocene to Early Oligocene, where holococcoliths are encountered more often than anywhere else, though why this is so is by no means clear. [For a discussion of fossil holococcoliths see Gartner and Bukry, 1969; Wind and Wise, 1978.]

With the exception of the Coccolithus pelagicus/Crystallolithus hyalinus relationship it is not known whether any other holococcolith

species also has a heterococcolith producing stage in its life cycle.

In addition to coccoliths, coccolithophores also form uncalcified organic scales which, however, are not preservable. Of two types of organic scales found on coccolithophore cells, one type usually is considerably smaller than the other and appears to bear no relation to coccolith formation. The larger type of scale, however, frequently is associated with calcification, and may be attached to the base (proximal side) of the coccolith. Organic scales, too, are formed within vesicles that originate in the Golgi area. [For detailed discussions of coccolithogenesis see for example Wilbur and Watabe, 1963; Manton and Leedale, 1969; Gayral and Fresnal, 1976.]

Rate of coccolith production has been observed for two species in laboratory cultures. Following decalicification by lowering the pH of the culturing medium, Coccolithus huxleyi (= Emiliania huxleyi) acquired a complete new coccosphere of about 15 coccoliths within 15 hours, whereas a species of Cricosphaera required 40 hours to rebuild its coccosphere (Paasche, 1968). Under natural condition rates of coccolith production probably vary within wide limits, depending largely on the amount of nutrients and light that are available. Extremely high rates of coccolith production (tens of millions to more than 100 million cells/l seawater) by Coccolithus huxleyi (= Emiliania huxleyi) have been observed during spring and summer blooms in fjords and along the adjacent west coast of Norway (Braarud, 1945; Berge, 1962), which may be partially attributable to pollution of the fjords by sewage but may also result from unusual upwelling or overturning of nutrient rich waters because of abnormal hydrographic conditions. Honjo (1976) calculates that turnover time of coccolithophore populations in tem-

perate and tropical regions of the Pacific is 4 to 10 days, with each coccolithophore producing an average of 20 coccoliths.

c. Distribution of Coccolithophores

The distribution of living coccolithophores over large areas of the world's oceans has recently been studied by McIntyre and Bé (1967), McIntyre, Bé and Roche (1970), Okada and Honjo (1973) and Honjo and Okada (1974). In the Atlantic coccolithophores have been found in surface waters from about 70°N to about 60°S. Two species, Cyclococcolithus leptoporus and Emiliania huxleyi, have notably wide temperature tolerences, and they seem to be equally at home in tropical and in boreal or austral latitudes. One species only, Coccolithus pelagicus, is restricted to high northern latitudes, and has not been recorded living in the southern hemisphere, although its coccoliths are present in surface sediments in high austral latitudes. McIntyre and Bé (1967) recognized four coccolithophorid floral provinces in the Atlantic, these provinces being arranged roughly symmetrically about the equatorial Atlantic with their boundaries corresponding to isotherms (Figure 6). Greatest diversity of species was found in the tropical and subtropical provinces, with ten species of coccolithophores recorded in each. The Arctic and Antarctic floral provinces yielded only three and two species, respectively, of placolith bearing coccolithophores. It should be noted that McIntyre and Bé studied only part of the coccolithophorid flora, and while their results are necessarily incomplete, they do seem to reflect general trends. In a more comprehensive study Okada and McIntyre (1974) noted that a fairly large number of species may occur in cold water in the North Atlantic,

but they did not elaborate on the composition of the flora they examined.

In the Pacific, too, McIntyre, Bé and Roche (1970) found that the ranges of ten of the common coccolithophores and some of their morphotypic variants are bounded approximately by surface water isotherms. Okada and Honjo (1973) identified some 90 species of coccolithophores living in the Pacific along a north-south transect from 50°N and 15°S although they list only fifteen of these. The largest number of coccolithophore cell per liter of water occurred in the subarctic province (north of about 43°N) with a second high in the equatorial region (from about 10°N to 15°S). The smallest number of cells per liter was found in the central North Pacific between about 10°N and 33°N. They found the highest diversity of coccolithophores between about 25°N and 35°N and in the equatorial region from about 8°N to perhaps 15°S (see Honjo and Okada, 1974, Figure 11, 12). Notably low diversity was found north of 35°N latitude and to a lesser extent, within parts of the central North Pacific from about 8°N to about 23°N. The authors recognized not only a horizontal (latitudinal) structure in the coccolithophore community but also a vertical structure within the photic zone with a distinct discontinuity at about 130 meters separating the lower photic layer dominated by heavily calcified genera such as Florisphaera and Thorosphaera from the middle photic layer in which delicate species dominate.

4. Coccoliths as Sediment

a. Sedimentation

Coccolith production is generally associated with photosynthesis,

although under laboratory conditions coccolith production has been observed to occur even in the absence of light. However, there is no field evidence to suggest that significant amount of calcification of coccoliths takes place below the photic zone. It must be assumed, therefore, that for practical purposes all coccoliths are produced within the upper 200 m of the oceans. All of the coccoliths accumulating on the ocean floor must, therefore, settle through the overlying water column.

Given the small size of coccoliths and taking into account the generally none too compact shape, the settling velocity would be expected to be quite low. Honjo (1976) measured settling velocities for coccoliths of Emiliania huxleyi at 4^{o}, 10^{o} and 18^{o}C, and found that settling speed ranged from less than 1 μm/sec to about 1.6 μm/sec. Taking into account thermal convection, subsurface advection, and eddy diffusion he estimates that in a 5000 m deep ocean a large and a small modern coccolith would settle to the bottom in about 50 to 150 years, respectively. With such long settling times ocean currents should distribute coccoliths far beyond the area where they were produced; that is, the coccoliths of tropical coccolithophores should be found in all extratropical areas. This is not the case, however (Honjo's Paradox 1). The distribution of coccoliths in bottom sediment corresponds fairly closely (within about 200 km) to the distribution of the parent organsim (Okada and Honjo, 1973). Honjo (1976) also points out that a coccolith settling slowly by itself through the water column could not possibly reach the sea floor because it would be dissolved in transit (Honjo's Paradox 2). Nevertheless, coccoliths do occur in great abundance at depths to which they could not have settled singly.

The answer, of course, is that coccoliths do not settle singly, but rather that they are packaged relatively undamaged into compact fecal pellets after passing through the gut of various grazing zooplankton, and that these pellets settle to the bottom much faster than would individual coccoliths (Honjo, 1975; Roth, Mullin and Berger, 1975; Honjo, 1976; 1977). Honjo (1976) measured sinking rates of naturally occurring fecal pellets, and his data suggest that in a 5000 m deep ocean coccoliths enclosed in fecal pellets would reach the bottom in 22 to 100 days. In addition to greatly increasing the rate of descent, fecal pellets further protect coccoliths from dissolution in that the pellets are held together and coated by a mucose organic substance. Although this organic coating is quickly degraded by bacteria in the warm surface waters, bacterial degradation is greatly reduced at the temperatures prevailing below the thermocline. Thus fecal pellets that descend blow the thermocline, and particularly those produced below the thermocline by grazers that migrate vertically, would constitute an efficient mechanism for transporting coccoliths to the floor of the deep oceans, the more so if recycled and repackaged by filter feeders along the way.

The rate at which coccoliths are delivered to the sediment on the ocean floor is largely unknown. Honjo (1976) estimates that in the equatorial Central Pacific (10^{o}N, 155^{o}W) the calcium carbonate precipitated annually by coccoliths is about 9.6 g per m^2. He calculated that about 8% of the coccoliths produced in the photic zone are dissolved during descent to the ocean floor, and that the remainder are assumed to reach the bottom. If a density of 1.5 g/cm^3 is assumed for pelagic ooze then Honjo's figures yield a sedimentation

rate of about 0.6 cm per 1000 years of coccoliths. If it is further assumed that about 50% of the calcareous component in pelagic ooze consists of coccoliths and about 50% of planktonic foraminiferal tests, then the sedimentation rate obtained for this area is just over 1 cm per 1000 years. At DSDP site 167 (07^{o} 04.1'N, 176^{o} 49.5'W), which probably has comparable productivity to Honjo's locality, and which is located in 3176 m of water, well above the regional CCD, the interval above the Discoaster brouweri extinction (ca. 1.65 m.y) is represented by 18 m of sediment, yielding a sediment accumulation rate of a little more than 1 cm per 1000 years, or approximately the same as was obtained from Honjo's data. These calculations, though crude, suggest that transfer of coccolith carbonate from the photic zone to the ocean floor is relatively efficient, and that dissolution of coccoliths occurs principally on the sea floor. Adelseck and Berger (1975) found this to be the case also for larger foraminifers and for pteropods.

b. Accumulation

The production of coccoliths is for obvious reasons dependent on the fertility of the surface waters. The accumulation rate on the other hand, is controlled largely by dissolution of carbonate on the ocean floor. Consequently the distribution of coccoliths on the ocean floor is closely related to the depth of the calcite compensation depth (CCD) and to sea floor topography. (The calcite compensation depth is itself related in a complex way to surface productivity and the deep circulation in the oceans. Recently the calcite compensation depth has been related to the degree of undersaturation of the deep ocean with respect to calcium carbonate. For a review see Berger, this volume.) Wherever sea floor topography rises above the calcite

compensation depth, calcareous sediments, including coccoliths, are found on the ocean floor. The actual distribution of coccoliths in modern sediments follows closely the distribution of calcium carbonate and can, therefore, be inferred from calcium carbonate distribution maps such as that of Lisitzin (1972, Figure 58).

Not all coccoliths are equally resistant to solution, however, so that nannofossil assemblages immediately above the CCD may contain two or three species whereas the overlying water column may support a flora of 30 to 50 species. Several detailed studies have been made of the relative solubilities of coccolith species (McIntyre and McIntyre, 1971; Schneidermann, 1972; Roth and Berger, 1975). The data from these three studies are substantially in agreement although derived from different ocean basins or from different parts of the same ocean basin. In all cases Cycloccolithus leptoporus was found to be most resistant to solution, whereas Discosphaera tubifera is in each case considered one of the species least resistant to solution. There is some difficulty in comparing data from the three studies because the samples came from areas of the ocean basins that have vastly different bottom water mass characteristics and different vertical structure of the water column. It is not possible to compare the dissolution depth of a particular species in the Atlantic and the Pacific because the calcite compensation depth is at different levels beneath the surface. To correct for this a regional CCD was hypothesized for the entire sample set in each study. On Figure 7 the data from all three studies have been replotted in such a way as to show the height above the regional CCD at which the species first appears. The regional CCD for this purpose is arbitrarily taken to be the level below which no iden-

tifiable coccoliths were recovered, which is essentially equivalent to the deepest occurrence of Cyclococcolithus leptoporus. In general McIntyre and McIntyre (1971) indicate greater resistance to solution for most species than do Schneidermann (1972) and Roth and Berger (1975). This may be entirely attributable, however, to the distribution of sampling stations. The first named authors used samples from the North and South Atlantic and from the Indian Ocean, including the adjacent Antarctic area. Schneidermann's samples on the other hand are taken entirely from the equatorial Atlantic while Roth and Berger used samples mainly from the equatorial and southern Pacific Ocean. Two species for whose depth range relative to the CCD there is very poor agreement are Cyclococcolithus fragilis and Cyclolithella annula. Not surprisingly both of these species may be difficult to identify, and the concept of these species vary from author to author. Cyclococcolithus fragilis is a common but delicate modern species which is rarely found in sediments. A similar but apparently much more resistant form, Oolithotus antillarum, has been identified by McIntyre and Bé (1967) to be a variant of Cyclococcolithus fragilis in which the collar and pore is not centrally placed in the distal shield but is in an eccentric position. It is not clear whether all authors used the same concept of this species, but it may be useful to keep them separated in the future since they do seem to have different solubilities. As to Cyclolithella annula, it, too, is either represented by several distinct variants (see e.g. Neosphaera coccolithomorpha in Okada and McIntyre, 1977), or more than one biological species produces rather similar coccoliths.

c. Post depositional changes

The preservational state of coccoliths and other calcareous nannofossils varies greatly in deep sea sediments. Perfect preservation is probably non-existent in calcareous ooze, and pristine coccoliths can be found only in plankton tows, or in marly sediments which have not been buried deeply and in which there is sufficient clay to inhibit any circulation of interstitial waters. Post depositional changes of nannofossils involve both dissolution and precipitation of calcite. Even at relatively shallow depths such as oceanic ridges and rises some species are dissolved before burial, while others are etched and yet others remain virtually undamaged. With increasing water depth or proximity of the CCD, etching and corrosion become more pronounced. McIntyre and McIntyre (1971) illustrate the effects of progressive dissolution of two species, Emiliani huxleyi and Gephyrocapsa oceanica. Both of these species are rather distinctive when well preserved, but both become unrecognizable when severely corroded.

Some dissolution no doubt continues to occur after burial, but unless the dissolved calcium carbonate is flushed out of the sediment or is able to diffuse out, further dissolution would be quickly inhibited unless an equal amount of calcite is precipitated. This indeed seems to be the case in all calcareous ooze and chalk, specimens being characterized by corrosion and dissolution of some constitutents and by overgrowth and calcification of others. Roth and Thierstein (1972) and Bukry (1973) have devised scales for qualitative determination of etching or corrosion on the one hand, and overgrowth and calcification on the other hand. Adelseck et al. (1973) were able to simulate diagenetic etching and overgrowth over a period of only a month by subjecting

the samples to a pressure of up to 3 kb at a temperature of up to 300°C.

Several descriptive studies have been made of the diagenesis and lithification of calcareous ooze, including the role of, and affect on, calcareous nannofossils (e.g. Wise and Hsu, 1971; Wise and Kelts, 1972; Schlanger et al., 1973; Schlanger and Douglas, 1974; Roth and Berger, 1975; Matter et al., 1975; van der Lingen and Packham, 1975; Wise, 1977). It is generally observed that while some species are selectively dissolved other species acquire an overgrowth of calcite. In Cenozoic sediment discoasters are the most active site of calcite precipitation. Often the calcifying species acquire euhedral crystal faces, and their size may be increased several fold. Wise (1977) has pointed out that many of the mid Cenozoic discoaster "species" are probably overgrowth stages of a single species, Discoaster deflandrei. Sphenoliths are also highly succeptible to overgrowth. In a pristine state Sphenolithus abies is constructed of radially arranged crystallites connected by delicate, membrane-like structures (Figure 8a). With progressive lithification all trace of such membranes is lost and the species assumes the appearance of a cluster of massive calcite crystals with euhedral faces (Figure 8b). Among coccoliths the pattern of overgrowth appears to be more complex in that some species of coccoliths, and sometimes one particular shield of a coccolith species, tends to be overgrown while the other shield is etched or dissolved. Cyclococcolithus leptoporus and Coccolithus pelagicus are two species in which the proximal shield may be destroyed while the distal shield reamins. In both of these species the distal shields are so constructed that the crystallographic c-axes (optic axes) of all elements are parallel

to one another, and normal to the plane of the shield (in discoasters the crystallographic arrangement of component parts is similar). The optic axes of the elements of the proximal shield on the other hand are helicoidally arranged. Several authors have made reference to these different crystallographic orientations of component structural elements as a possible reason for preferential overgrowth or dissolution. The argument is weak, however, because several species that are succeptible to overgrowth have the optic axes of the component elements arranged helicoidally (e.g. Cyclicargolithus floridanus and the very durable Cretaceous species Watznaueria barnesae) while some species that are not found with calcite overgrowths are constructed much like Coccolithus pelagicus (e.g. Cyclococcolithus formosus), or like Cyclococcolithus leptoporus (e.g. Umbilicosphaera sibogae). Clearly there must be something in the construction and ultrastructure of coccoliths other than crystallographic orientation of component elements that determines their succeptibility to overgrowth or dissolution.

As coccoliths are etched they tend to break apart and produce a fine matrix of crystallites whose affinity is no longer clear. In ooze that is being dissolved as on the sea floor near the CCD these crystallites have irregular shapes and no euhedral faces. In ooze that is undergoing lithification the crystallites, though of no specific shape, usually have several euhedral faces and are generally much more robust. It appears, therefore, that the process of overgrowth and lithification involves a constant transfer of calcite from the more soluble to the less soluble particles.

Schlanger and Douglas (1974) consider depth of burial to be the principal driving force in diagenesis and lithification of pelagic

carbonates, recognizing, however, that the sediments themselves may vary in their diagenetic potential, which in turn may be a function of water depth, sedimentation rate, surface temperature, surface productivity the ratio of foraminifera plus coccoliths to discoasters, the ratio of maximum size to minimum size, and the predation rate. There are probably other important factors as well, notably the presence and nature of non-carbonate impurities, which may influence diagenesis greatly both to promote and inhibit it.

Although coccoliths are a major constituent of calcareous ooze in ocean basins, over most of the continental shelf area of the world they are generally not significant contributors to the sediment. But, coccolithophores are by no means lacking in the water column in these areas. Indeed the largest concentrations of coccolithophores have been recorded from relatively shallow coastal waters (Braarud, 1945; Berge, 1962). Very probably cocoliths contribute larger amounts of carbonate sediments per unit to the continental shelves than to the deep ocean basins owing largely to the greater productivity of the former. Nevertheless, coccoliths may go unnoticed in shelf sediments because of the dilution by detrital sediments or by other biogenic carbonates. An example of the former would be the continental shelf of the northern Gulf of Mexico where coccoliths may be relatively rare in the predominantly detrital sediment, even though they are produced in abundance in the water column. An example of the second type would be Belize lagoon where significant numbers of coccoliths may be present in carbonate muds (Scholle and Kling, 1972), which, however, is composed primarily from the comminuted skeletal parts of shallow water plants and invertebrates.

It has been noted that the nannofossil assemblages from different areas such as an oceanic area and continental shelf or slope area, may differ in species composition even though the samples are essentially of the same age (Bukry, 1970; Bukry et al., 1971). Endemism has been invoked as one possible reason, and in some instances it appears to be an adequate explanation. For example, the late Eocene-early Oligocene species Bramletteius seraculoides often is very abundant in pelagic ooze, but is rare in hemipelagic sediments. In most instances endemism is more characteristic of the hemipelagic environment, however. Numerous species of pentaliths (Braarudosphaera, Micrantolithus, Pemma) are known from hemipelagic deposits, yet virtually none of these species occurs in oceanic sediments (Bramlette and Sullivan, 1961; Sullivan, 1964; 1965). Curiously the same "endemic" pentalith species are found on most continents, which might indicate that their absence from oceanic sediments is a preservation artifact (for a discussion, see e.g. Bybell and Gartner, 1972). For modern coccolithophores there is no quantitative evidence to indicate that the floras over a shelf area are significantly different from the flora of the open ocean, except by inference from the record of coccoliths in Recent sediments. Certain modern species that are common in hemipelagic muds are only rarely found in deep sea calcareous ooze (e.g. Pontosphaera, Scyphosphaera, all holococcoliths). Many of these species, however, have been reported in plankton samples taken far from land, and their absence from sediment is most probably attributable to the fact that all these species like the holococcoliths disintegrate readily into their component crystallites, thereby either being quickly dissolved or becoming unrecognizable.

Thus it is not all clear to what extent endemism is characteristic of modern coccolithophores in regard to oceanic to hemipelagic variability, and modern distribution patterns cannot serve completely as a model to explain the distinctly different fossil assemblages that are often found in strata of the same age but deposited in different sedimentary settings.

5. Geological History of Coccoliths

a. Origin and evolution

Coccolith-like objects have been described and illustrated from several Paleozoic and Mesozoic sediments, and although some of these objects resemble coccoliths, this resemblance is superficial or may be an artifact of fossilization or of sample preparation. In any case the pre-Jurassic record of coccoliths is primarily one of more or less random, curious objects of uncertain origin and affinity. The earliest unequivocal "coccolith" Crucirhabdus primulus, is found in the earliest Jurassic (lower Liassic) beds.

No obvious predecesor to this species is known but judging from the complexity of this earliest coccolith it is reasonable to assume that the organisms that started to secrete calcareous coccoliths in earliest Jurassic time had undergone considerable development and evolution prior to that time, though probably forming its scales or skeletal parts of a substance that was not preserved in the fossil record.

Following their first appearance, coccoliths evolved and radiated rapidly during the early Jurassic. A detailed evolutionary scheme has

been constructed by Prins (1969) for the lower and middle Lias (early Jurassic) during which time three major nannofossil lineages developed and, although that scheme seems unrealistically detailed, the criteria set down by Prins have provided the basis on which the comprehensive classification of Hay (1977) is constructed. The three major groups that had differentiated by the end of middle Lias are the Eiffellithales, the Podorhabdinales and the Coccolithales. The ancestral species, Crucirhabdus primulus, is clearly constructed on the eiffellithalid plan in that its base consists of a single cycle of small and tightly imbricating elements, the central area being spanned by some type of cross-bar structure which may or may not bear a stem on the convex side (Figure 9). Among Eiffellithales the nature (geometry) of the central structure seems to be the most useful criterion for differentiating various genera. Lower Liassic nannofossil assemblages are dominated by various species of Eiffellithales of the same basic construction, but during the middle Lias the Podorhabdinales and Coccolithales make their appearance at approximately the same time. The former have the base constructed of two distinct cycles of elements, the elements being generally much larger than in Eiffellithales and only slightly imbricated (Figure 10). Podorhabdinales, too, have various types of cross-bars which may or may not bear a stem or rod on the convex side (it is interesting that nearly every type of cross-bar structure found among Eiffellithales is also found among Podorhabdinales).

Coccolithales also are constructed of two distinct cyles of elements, the two cycles being connected near the center by a tube or collar (Figure 11). Coccolithales may or may not have a central

structure, and never bear a stem. These three structural types dominate nannofossil assemblages throughout the Mesozoic, and although several other groups evolve, most of them are more or less clearly traceable to one of these three. Hay (1977) lists 32 genera for Jurassic sediments, approximately 85 genera for the Cretaceous, and 75 to 80 genera for the Cenozoic exclusive of living genera known only from plankton tows. The largest diversity of genera and species occurs in Late Cretaceous sediments, where it is not unusual to encounter forty or more species in an assemblage. Modern sediments typically yield assemblages of 20 to 30 species. Haq (1973) documented nannoplankton species diversity from the Jurassic to Recent and his data indicate the highest diversity occurs during periods of widespread epicontinental seas as in Companian and Maastrichtian time and during early Eocene time (Figure 12). Haq interprets this to mean that diversity is highest during periods of equable climates, and lowest when seasonal temperature fluctuations are greatest.

A very radical reduction in diversity of coccolithophores occurred at the end of the Maastrichtian when virtually all Cretaceous species became extinct. Several interesting hypotheses have been suggested to explain this event, and among these the nutrient depletion hypothesis proposed by Bramlette (1965) has in various forms enjoyed much popularity, although many paleontologists favored some sort of cosmic event as a most likely explanation. Recently an entirely different explanation has been proposed, one that invokes a layer of brackish water on the surface of all oceans to cause the extinction of the stenohaline Upper Cretaceous coccolithophore species (Gartner and Keany, 1978).

Detailed evolutionary studies have been done only in limited ways

for calcareous nannofossils. In addition to the study of Prins (1969) of the Liassic coccoliths, Rood and Barnard (1972) have examined the stratigraphic relationship among various species of Stephanolithion and Diadozygus in the middle and upper Jurassic; Lauer (1974) has studied the evolution of the various genera of Arkhangelskiellacea in the upper Cretaceous. In the Cenozoic Gartner (1969) has studied the evolution of the genus Chiasmolithus; Prins (1972) has studied the discoasters; Roth, Franz and Wise (1972) have studied the genus Sphenolithus; Haq (1973) has summarized information on Helicosphaera; and Gartner and Bukry (1975) have examined the ceratoliths in some detail.

b. Calcareous nannofossil biostratigraphy

The biostratigraphic utilization of calcareous nannofossils began with the studies of Bramlette and his co-workers (Bramlette and Riedel, 1954; Bramlette and Sullivan, 1961; Bramlette and Martini, 1964; Martini and Bramlette, 1963), and Stradner's study of Mesozoic nannofossils (Stradner, 1963). The most notable advances in nannofossil biostratigraphy were made, however, during the first five years of the Deep Sea Drilling Project (1968-1973). This project provided much of the impetus as well as a great deal of the material for students of nannofossils, and the result has been publication of astonishingly detailed and accurate zonations based on coccoliths, discoasters and other associated nannofossils. Comprehensive zonations for the Cenozoic have been prepared by Bukry (1971 and subsequent updated versions) and by Martini (1971). Several partial and more or less comprehensive zonations also have been prepared for the Jurassic and Cretaceous. Sissingh (1977) and Thierstein (1977) have

presented two useful zonations for the Cretaceous; the fact that the two schemes are not totally in agreement reflects perhaps the imperfect understanding of the Cretaceous nannofossil succession. For the Jurassic, zonations have been prepared by Barnard and Hay (1974) and by Th'erstein (1977) and the discrepencies between these two zonations reflect in large measure the lack of useful sections of marine sediments for much of the Jurassic. Nannofossil biostratigraphy has recently been reviewed elsewhere (Gartner, 1977), and the reader is referred to this paper and references therein for a more detailed treatment of the subject. For a general overview of the succession of calcareous nannofossil species, range charts for select marker species of the Jurassic, Cretaceous and Cenozoic are given in Figures 13, 14, and 15. Although no specific zonation is given for the Cretaceous or for the Cenozoic, the range charts include most of the markers used in various zonations and are compatible with the zonations in so far as the zonations reflect accurately the ranges of marker species.

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Text - Figure 1a, 1b, 1c. Placolith; 1a - distal view; 1b - side view; 1c - proximal view.

Text - Figure 2a, 2b. Discolith; 2a - side view; 2b - distal view.

Text - Figure 3a, 3b. Lopadolith; 3a - side view; 3b - distal view.

Text - Figure 4a, 4b. Cricolith; 4a - side view; 4b - plan view.

Text - Figure 5a, 5b. Cyclolith; 5a - plan view; 5b - side view.

Text - Figure 6a, 6b, 6c. Zygoliths; 6a, 6b - distal views; 6c - side view.

Text - Figure 7a, 7b, 7c. Rhabdoliths; 7a, 7c - side views; 7b - distal views of basal disc.

Text - Figure 8a, 8b. Caliptrolith; 8a - proximal view; 8b - side view.

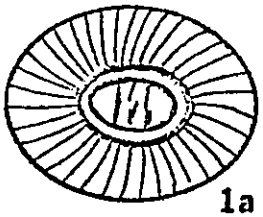
Text - Figure 9a, 9b. Pentalith; 9a - plan view; 9b - side view.

Text - Figure 10a, 10b, 10c. Asteroliths; plan view.

Text - Figure 11a, 11b. Stelolith; 11a - plan view; 11b - side view.

Text - Figure 12a, 12b, 12c. Sphenoliths; 12a, 12b - side view; 12c - plan view.

Text - Figure 13. Ceratolith.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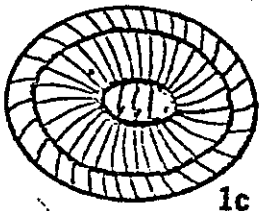
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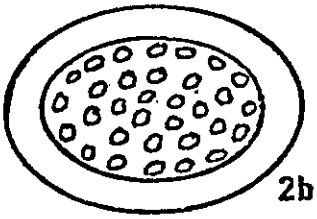
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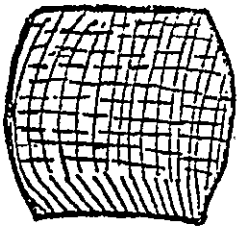
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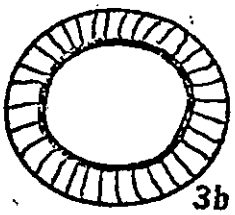
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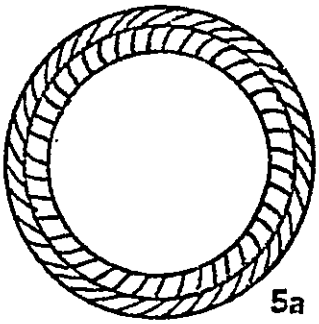
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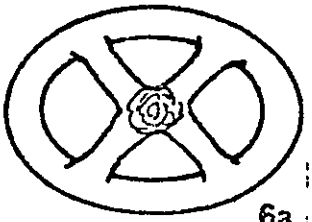
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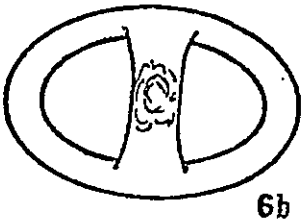
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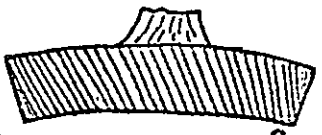
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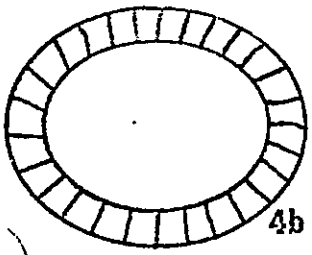
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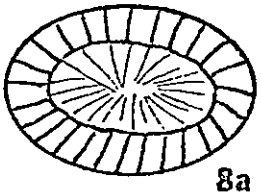
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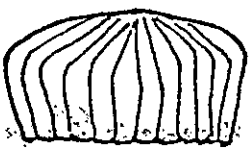
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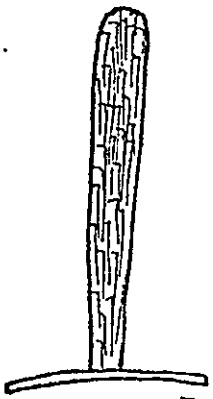
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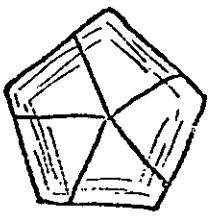
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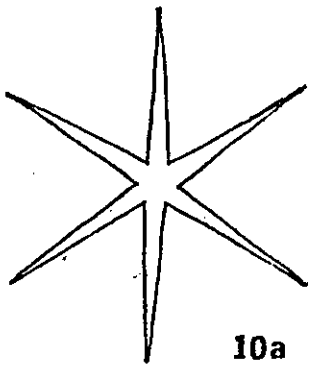

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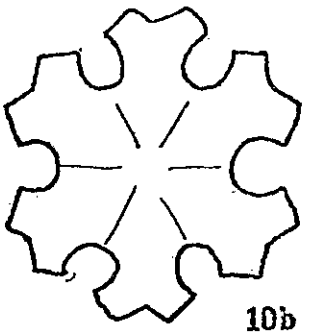

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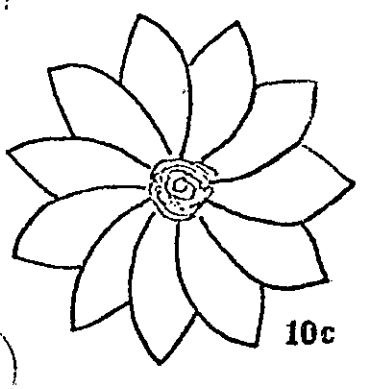

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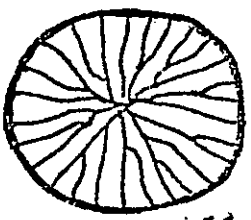

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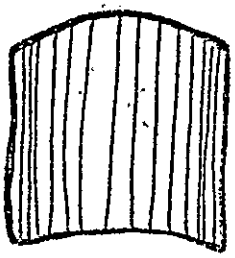

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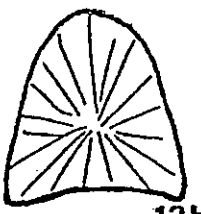

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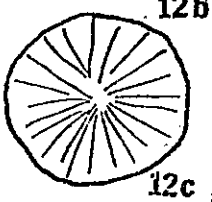

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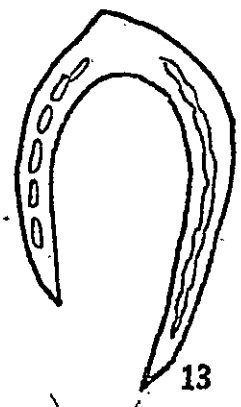

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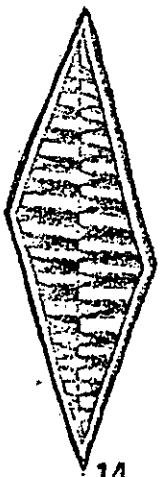

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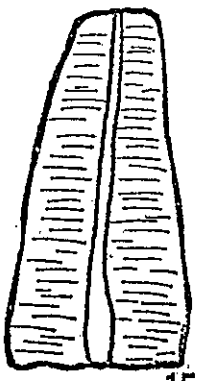

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Figure 1. Cyclococcolithus leptoporus (Murray and Blackman), a typical coccolith in three different views. a. Proximal view (x 6000); b. side view (x 10000); c. distal view (x 6000). Scanning electron microscope photographs by M. P. Chen.

Figure 2. Late Oligocene discoasters probably of the same species but showing different aspects of preservation. Specimens a and b have experienced calcite overgrowth and show primarily crystal faces of calcite rhombohedra. The optic axis of the calcite crystallites is normal to the plane of the discoaster. Specimen a shows the E-surface of the discoaster; specimen b shows the F-surface; specimen c is a well preserved example of Discoaster deflandrei from the same stratigraphic level. Very probably specimens a and b were originally similar to specimen c. Transmission electron microscope photographs of self shadowed carbon replicas. a. x 10000; b. x 5000; c. x 10000.

Figure 3. Specimens of the Oligocene coccolith Cyclicargolithus foridanus on which calcite overgrowth has occurred on periphery of the shield in crystallographic continuity with the tip of each element of the shield. a. Proximal view; b. side view. Note on b (arrow) that the optic axis of the calcite rhombohedron is approximately normal to the surface of the photograph. Transmission electron microscope photographs of self shadowed carbon replicas; x 1000.

Figure 4. Blackites sp., the base of a late Middle Eocene rhabdolith which is constructed of four or five distinct cycles of elements or calcite crystallites, the crystallographic orientation of the elements in each cycle being different as is indicated by the cross-polarized light image (c). a. Transmission electron microscope photograph of a self shadowed carbon replica, x 10000; b. phase contrast, x 2500; c. cross-polarized light, x 2500.

Figure 5. Coccosphere of the late Neogene to Recent species Umbilicosphaera sibogae showing the arrangement of individual coccoliths on the surface of a coccosphere. Scanning electron microscope photograph of a specimen filtered from a near surface water sample in the South Atlantic; x 10000.

Figure 6. Coccolithophorid floral zones of the Atlantic Ocean. I-tropical; II-subtropical; III-transitional; IV-subarctic and subantarctic. (Redrawn in part from McIntyre and Be, 1967).

Figure 7. Solubility of several coccolith species relative to the regional CCD. Because the data are from various ocean basins, they were replotted relative to a hypothetical CCD which corresponds to the lowest occurrence of Cyclococcolithus leptoporus, the most solution resistant species. Dissolution levels for other species are plotted in meters above this hypothetical CCD.

Figure 8. Sphenolithus abies from late Miocene sediments. a. A well preserved specimen from a clayey ooze showing the honeycomb morphology of the species; b. an overgrown and recrystallized specimen from a clay free calcareous ooze in which the radial arrangement of the structural elements is accentuated by overgrowth. Scanning electron microscope photographs by M. P. Chen, x 10000.

Figure 9. Eiffelithaled plan of rim construction with two examples from the Early Cretaceous. a. Side view; b. plan of view of Chiastozyus, a Cretaceous genus; c. oblique view of Parhabdolithus asper; d. distal view of Vekshinella; c,d. scanning electron microscope photographs, x 10000.

Figure 10. Podornabdinalid plan of rim construction with two examples from the Cretaceous. a. Side view; b. plan view, both of a Cretarhabdus like form; c. oblique side view of Cretarhabdus surirellus; d. distal view of Cretarhabdus conicus; c,d. Scanning electron microscope photographs, x 10000.

Figure 11. Coccolithalid plan of construction with two examples from the Cretaceous. a. Cross-section of a placolith; b. distal view; c. proximal view of Watznaueria barnesae, x 10000; d. coccosphere of Watznaueria barnesae, x 5000.

Figure 12a. Species diversity of calcareous nannoplankton through the Jurassic and Cretaceous. Shaded areas represent new species. The inset is the oxygen-isotope paleotemperature curve of Dorman (1968) for Europe, and triangles at the top mark periods of widespread sea level maxima (from Haq, 1973).

Figure 12b. Species diversity of calcareous nannoplankton through the Cenozoic. Shaded area represents new species. Paleotemperature curve (inset) is that of Devereux (1967) for New Zealand. Triangle at top marks the period of widespread seas (from Haq, 1973).

Figure 13. Ranges of various nannofossil species used as biostratigraphic markers in the Jurassic according to Barnard and Hay (1976) (from Gartner, 1977).

Figure 14. Ranges of various nannofossil species used as biostratigraphic markers in the Cretaceous (from Gartner, 1977).

Figure 15. Ranges of various nannofossil species used as biostratigraphic markers in the Cenozoic (from Gartner, 1977).

FIG. 1

a

b

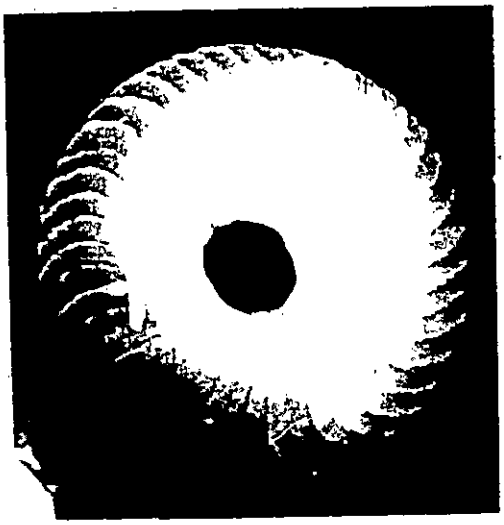

FIG 2

FIG. 3

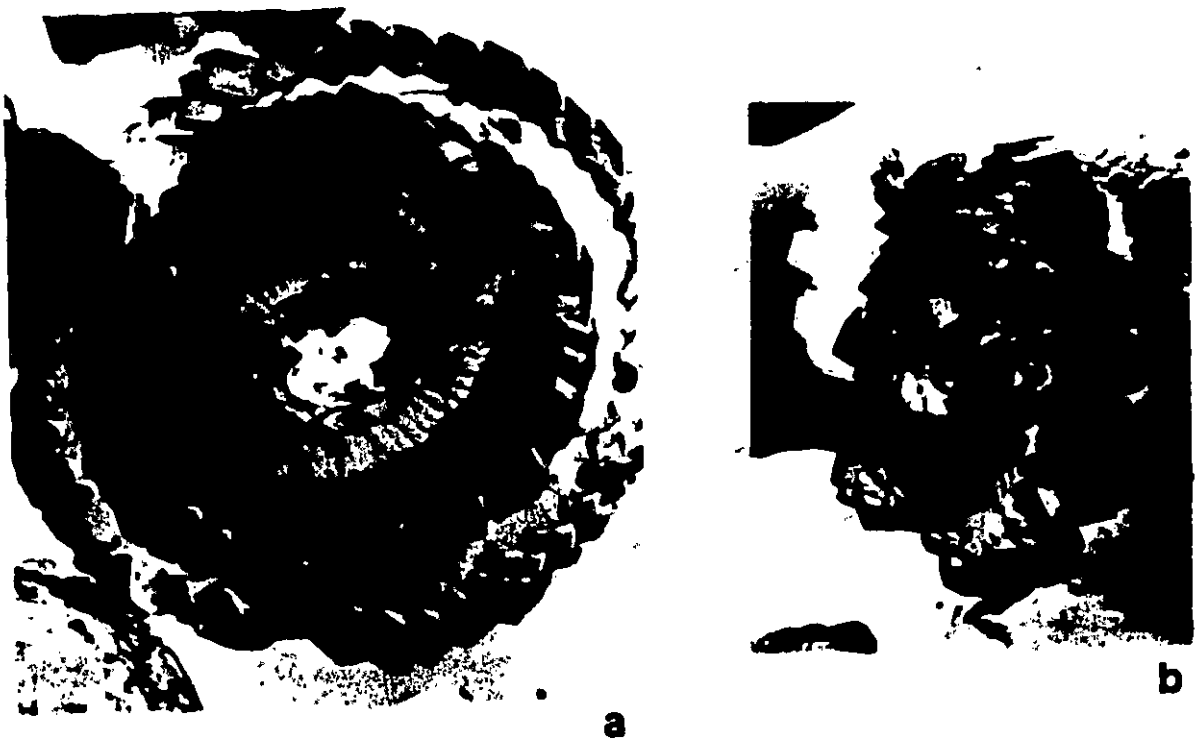

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FIG. 4

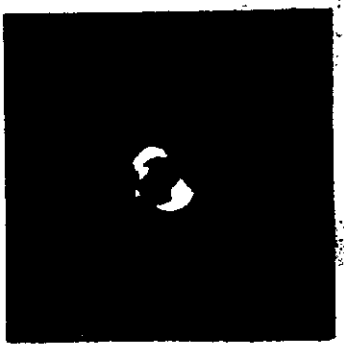

FIG. 5

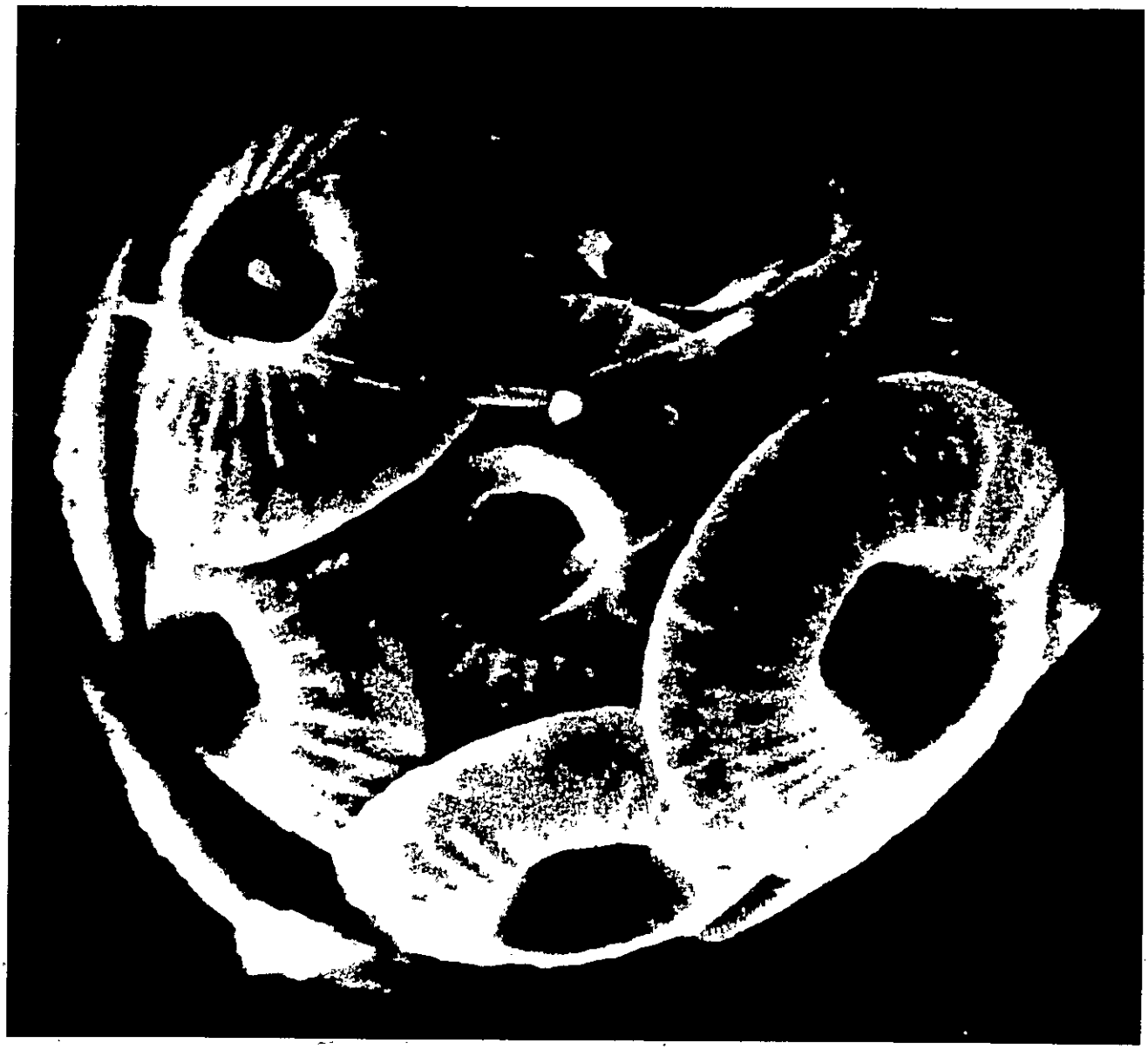

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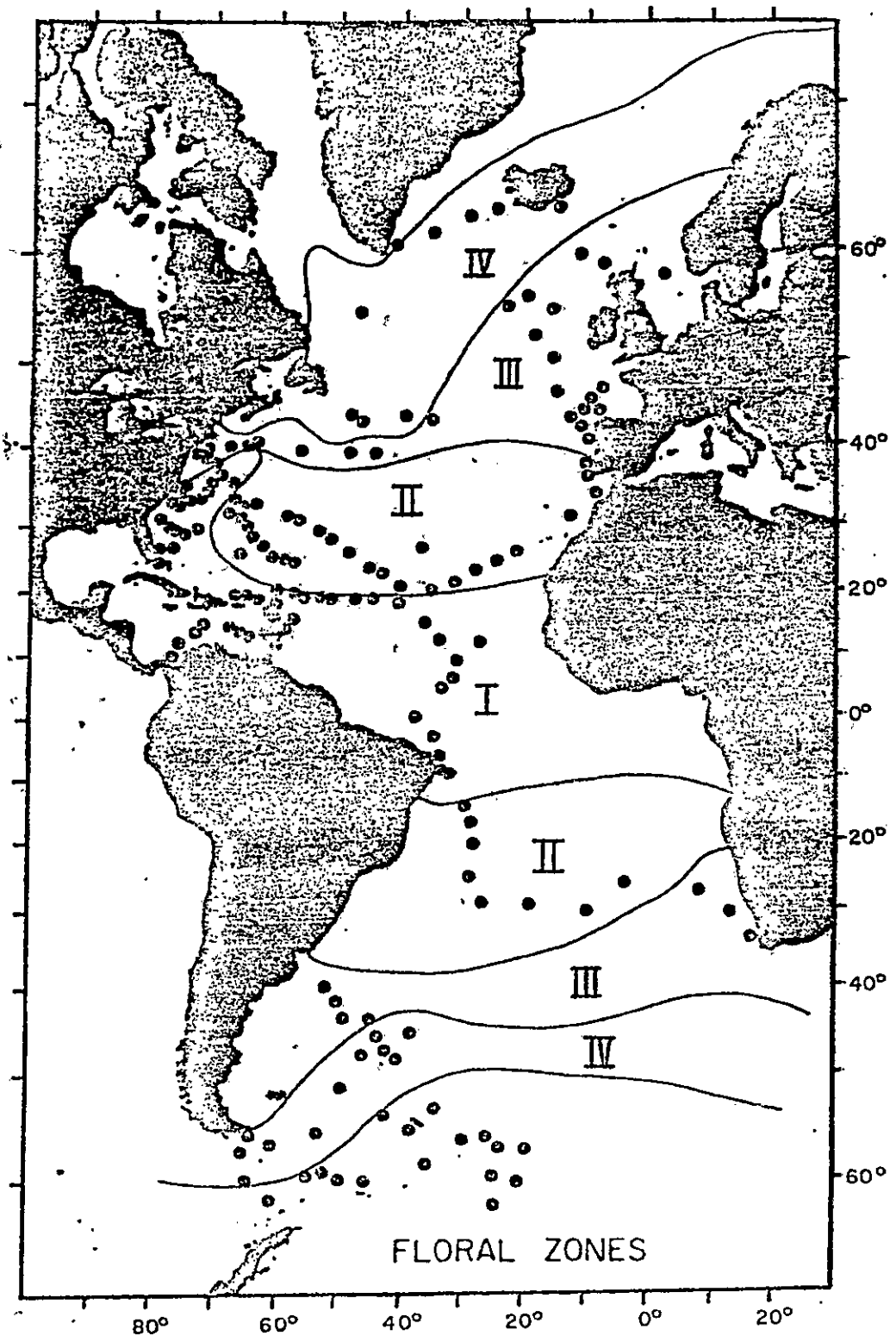
FIG. 6


IV
III
II
I
II
III
IV
60°
40°
20°
0°
20°
40°
60°
80°
60°
40°
20°
0°
20°
FLORAL ZONES

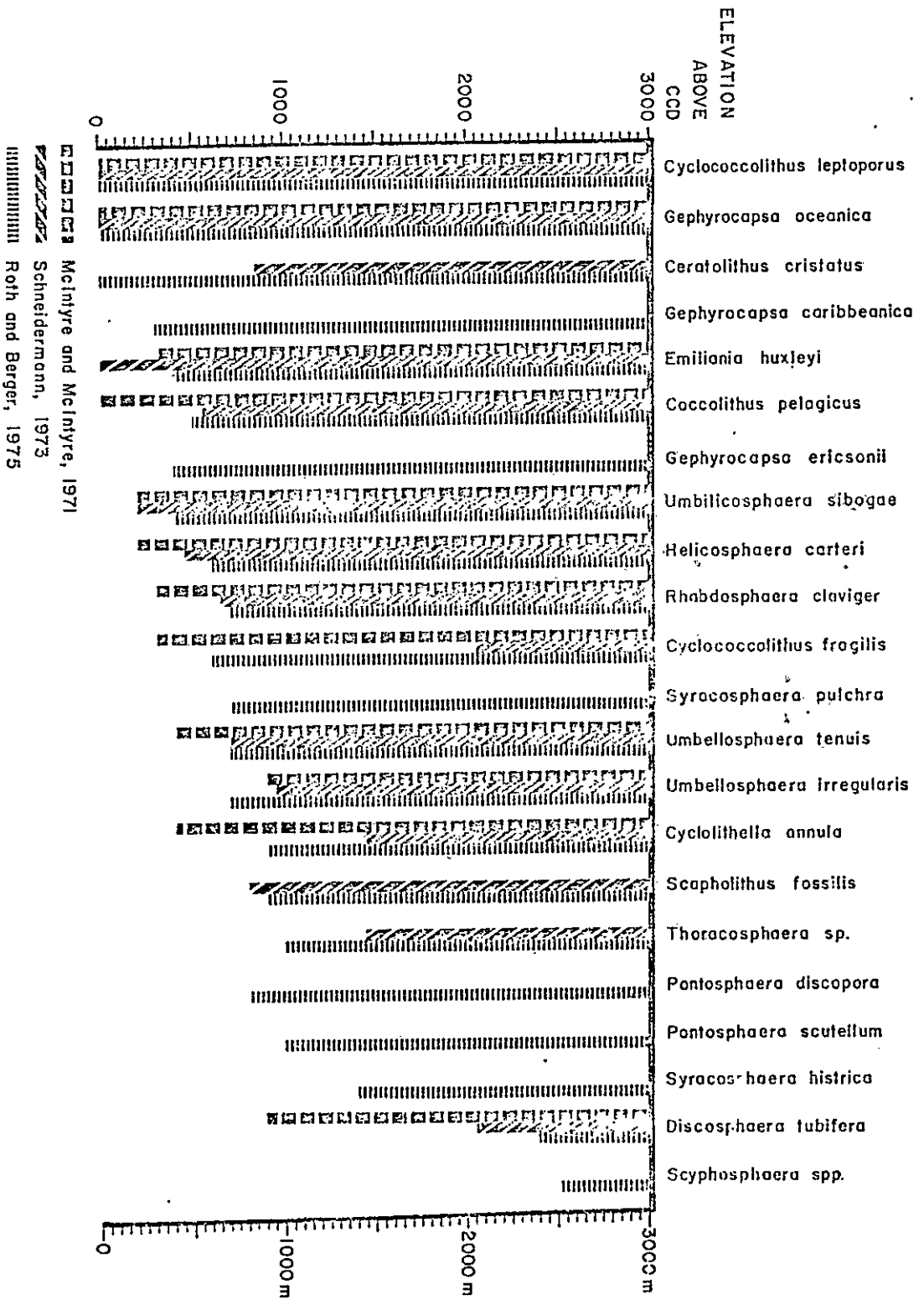

ELEVATION ABOVE CCD
0
1000
2000
3000
Cyclococcolithus leptoporus
Gephyrocapsa oceanica
Ceratolithus cristatus
Gephyrocapsa caribbeanica
Emiliania huxleyi
Coccolithus pelagicus
Gephyrocapsa ericsonii
Umbilicosphaera sibogae
Helicosphaera carteri
Rhabdosphaera claviger
Cyclococcolithus fragilis
Syracosphaera pulchra
Umbellosphaera tenuis
Umbellosphaera irregularis
Cyclolithella annula
Scapholithus fossilis
Thoracosphaera sp.
Pontosphaera discopora
Pontosphaera scutellum
Syracosphaera histrica
Discosphaera tubifera
Scyphosphaera spp.
0
1000 m
2000 m
3000 m
McIntyre and McIntyre, 1971
Schneidermann, 1973
Roth and Berger, 1975

Fig. 7

FIG. 8

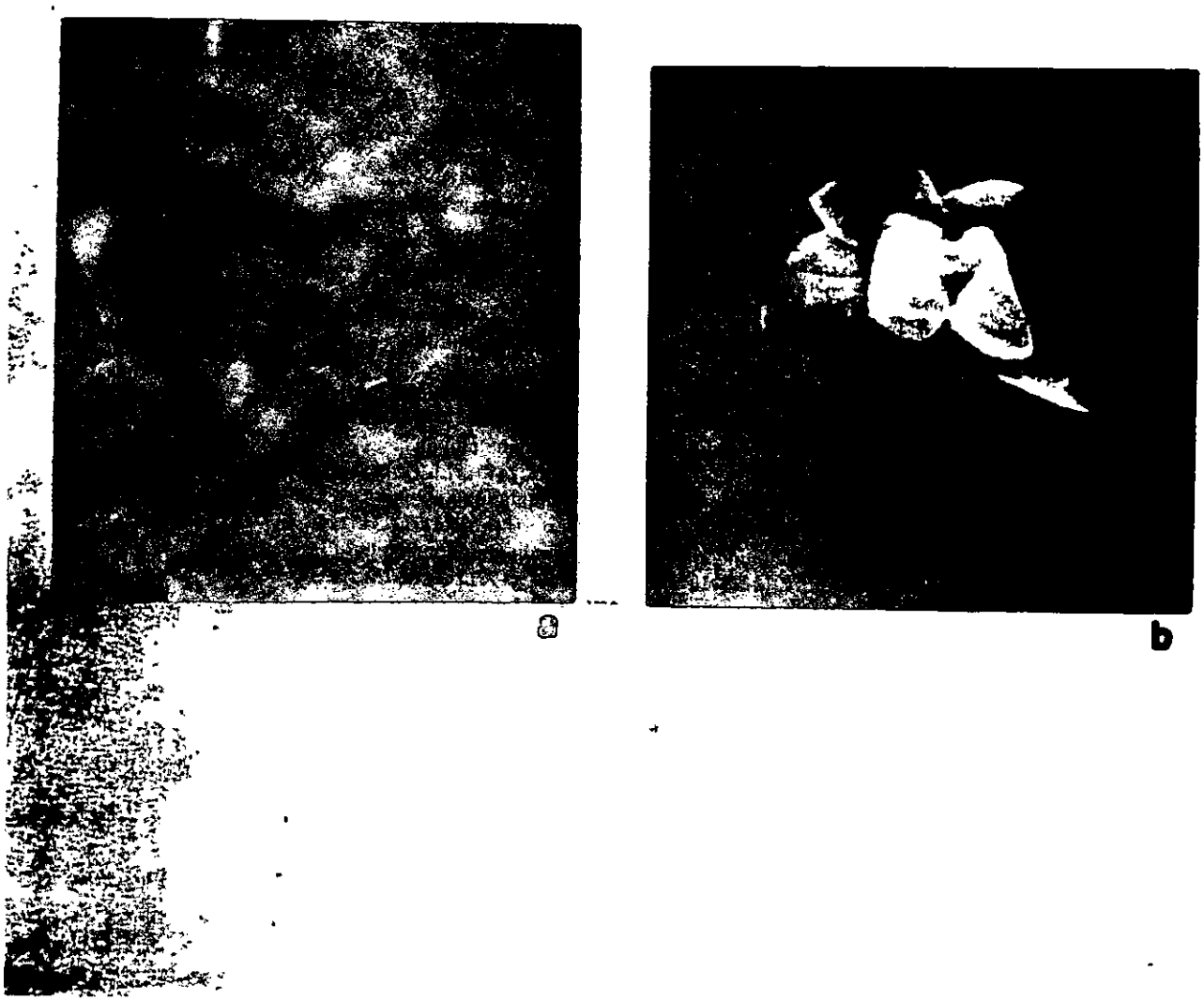
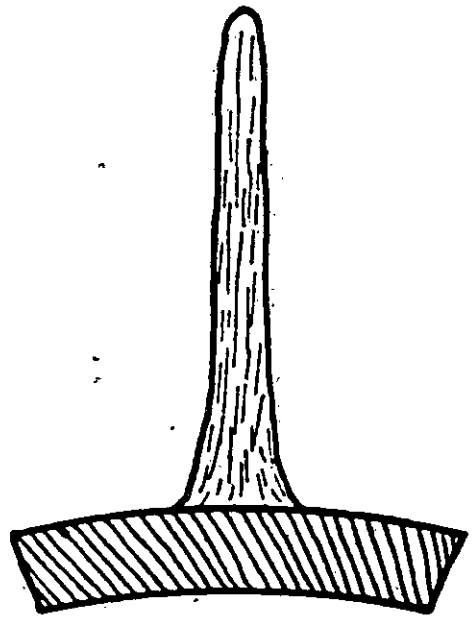
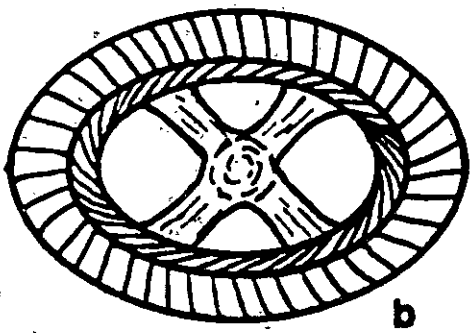


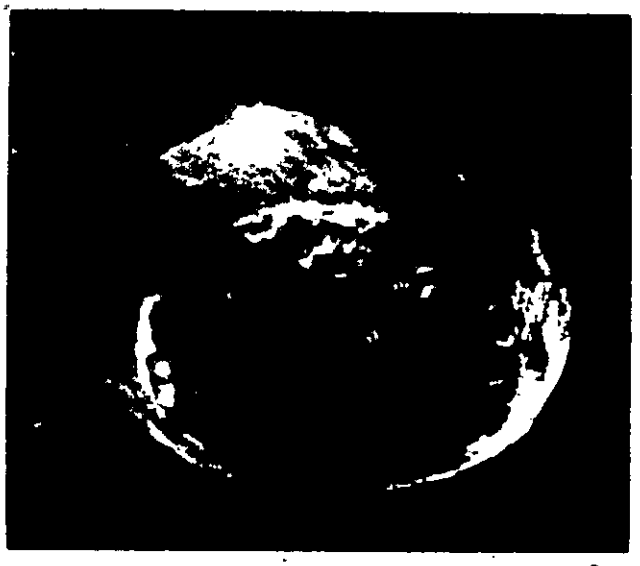
FIG. 9



a



b



c

d

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FIG. 10

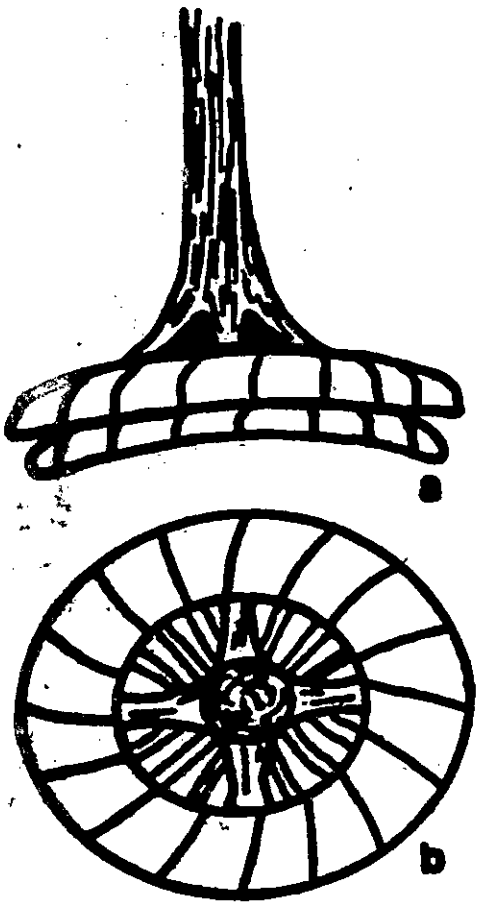
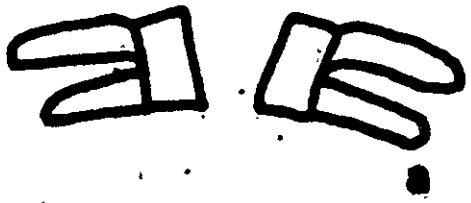
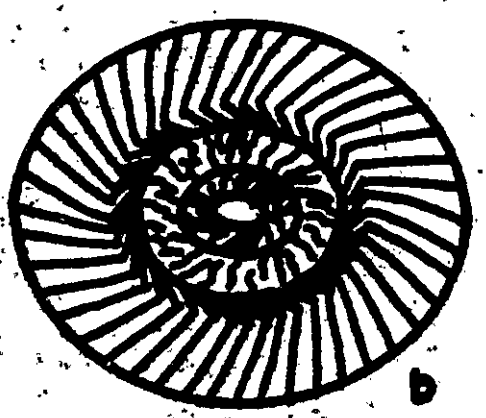


FIG. 11



a



b

c

d

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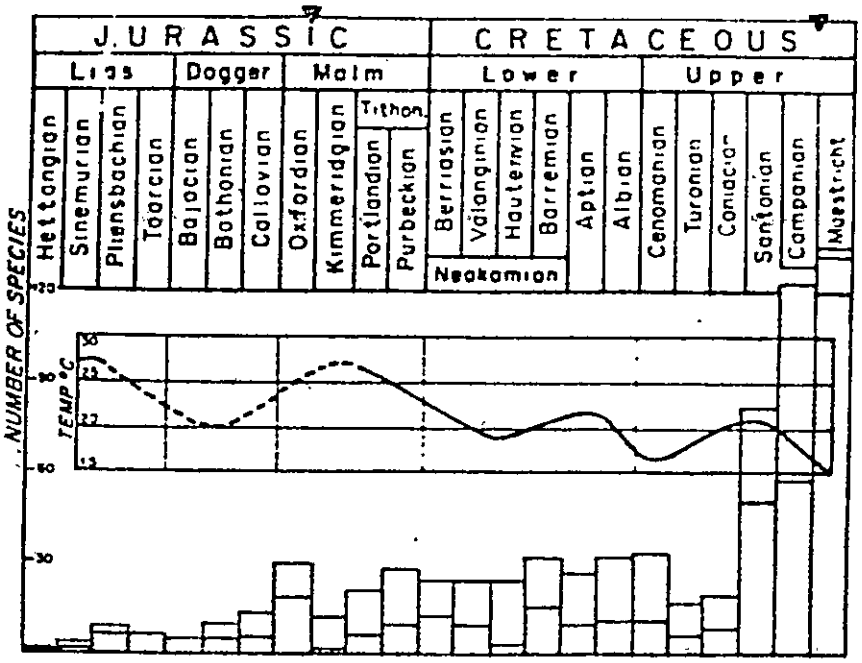
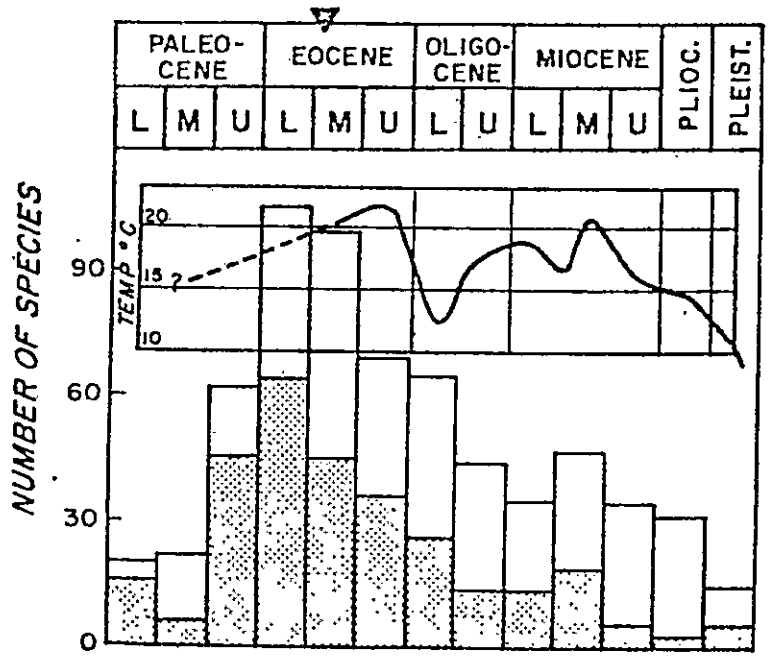

JURASSIC
CRETACEOUS
Lias
Dogger
Malm
Lower
Upper
Hettangian
Sinemurian
Pliensbachian
Toarcian
Bajocian
Bathonian
Callovian
Oxfordian
Kimmeridgian
Tithon.
Portlandian
Purbeckian
Berriasian
Valanginian
Hauterivian
Barremian
Aptian
Albian
Neokomian
Cenomanian
Turonian
Coniacian
Santonian
Campanian
Maastricht
NUMBER OF SPECIES
TEMP °C

12a


PALEO-CENE
EOCENE
OLIGO-CENE
MIOCENE
PLIOC.
PLEIST.
L
M
U
NUMBER OF SPECIES
TEMP °C
90
60
30
0
20
15
10

12b