

## TAXONOMIC PROBLEMS IN THE STUDY OF COCCOLITHS

by MAURICE BLACK

*The Eleventh Annual Address, delivered 6 March 1968*

ABSTRACT. From a review of Jurassic, Cretaceous, Tertiary, and Recent coccolithophorid and discoaster material, it is suggested that the abrupt appearance of some complex forms, hitherto difficult to classify, may be explained by mineralization of already existing unmineralized stocks; it also seems likely that some living un-mineralized forms may have fossil mineralized ancestors. Some recent work on uncalcified Haptophyceae reveals interesting parallels with the coccolithophorids. One new family, Stephanolithiaceae, is erected, and four specific names are recorded in new combination.

LIVING in the present oceans there are about 200 species of coccolith-bearing algae. About half of these fall quite naturally into two big families; the rest make up a peculiarly heterogeneous collection, with numerous monospecific genera which are very difficult to group into families or higher taxa. Attempts to devise a scheme of classification for these organisms have not been entirely successful. The simpler schemes tend to force very diverse genera into an inappropriately small number of families, as may be seen in many reports on quantitative plankton-surveys. Some of the more elaborate schemes try to solve the problem by building up a theoretical phylogenetic tree which is used as a basis of classification. For this purpose, the evidence has been drawn exclusively from the comparative morphology of living species, and up to the present palaeontological observations have been almost completely ignored. Twenty years ago, this may have been excusable, but it is not so today, for there is now enough information at hand for us to start establishing phylogenetic series on the evidence of the fossil record.

When we attempt to do this, one of the first results is the discovery that the two largest families, the Syracosphaeraceae and Zygosphaeraceae, each with more than 50 living species, have virtually no geological record at all. With the smaller taxa, the situation is quite different; many of the systematically isolated genera are found to have long ancestries, and some are survivors from once prosperous Mesozoic or Tertiary families. Clearly, these survivors are more closely related to their own fossil ancestors than they are to living genera of different parentage, and it is no longer reasonable to lump all the living coccolith-bearing algae into a single family, as has been done in some of the most recently published classifications (Kamptner 1958, pp. 68-71, Deflandre 1966, pp. 5-6).

Considerations such as these suggest that the time has now arrived when we must look carefully at the impact of palaeontological research upon the taxonomy of living forms. During the last two decades there has been a strong tendency to deny the possibility of recognizing fossil representatives of many living taxa above the rank of species. This is, of course, a strictly logical attitude, because the micropalaeontologist has to work largely with individual coccoliths, and some modern genera are defined in terms that take into account the way in which the coccoliths are assembled to form a complete skeleton. Nevertheless, I think it is an unnecessarily defeatist attitude, because it assumes that each fossil coccolith is to be considered as a completely isolated entity, with no

[*Palaeontology*, Vol. 11, Part 5, 1968, pp. 793-813, pls. 143-54.]

---

ancestors and no descendants. This, of course, is not true, and I hope to show that many living taxa can be traced back with reasonable confidence into the Tertiary, and a few can be followed still further into the Mesozoic. In this way, family relationships sort themselves out as phylogenetic lineages, and the theoretical difficulties of working with isolated coccoliths fall into the background.

#### PROBLEMS IN THE CLASSIFICATION OF LIVING COCCOLITHOPHORES

From the early days, it has been found satisfactory to identify and classify the living species on the basis of coccolith-structure. No two species are known which have exactly similar coccoliths, and, as a working hypothesis, it is not unreasonable to assume that this also holds good for extinct species. Coccolith-structure has likewise been relied upon extensively for the delimitation of genera, but other characters such as the shape of the cell and the presence or absence of a naked area at the flagellar pole have also been used to some extent in defining genera and higher taxa. Living taxa defined purely in terms of coccolith-morphology can be recognized with certainty when they are found as fossils, but characters involving the arrangement of coccoliths on the cell-surface are not as a rule observable in fossil material. With this difficulty in mind, some micropalaeontologists have argued that all fossil coccoliths should be assigned to provisional taxa until a complete coccosphere has been discovered. This practice has the serious disadvantage of requiring a dual nomenclature, with one set of names for living material and another for fossils, thus creating an artificial break between modern forms and their fossil ancestors.

In order to resolve this problem, we will first of all look more closely at some of the taxonomic difficulties presented by living coccolithophores, and then try to discover just how serious these difficulties really are when we try to work out some sort of phylogenetic story.

##### *Dimorphism of coccoliths*

Lohmann (1902) found that in some species the coccoliths covering a single individual were not all alike; for example, those round the flagellar pole might bear spines, whereas the ordinary body-coccolith did not. Usually the polar coccoliths are easily recognizable as straightforward modifications of the normal type, and Lohmann did not in general segregate species with this kind of dimorphism into separate genera. The only genus which he distinguished on these grounds was *Scyphosphaera*, which has an equatorial girdle of very large float-coccoliths. Taxonomic difficulties did not arise until 40 or 50 years later, when Kamptner (1941) and Deflandre (1952) took a much more serious view of coccolith-dimorphism, and removed all species with dimorphic coccoliths into separate genera. The consequent practical difficulty in naming fossil coccoliths was perhaps unnecessarily exaggerated, but the theoretical implications led Deflandre to abandon the use of a single classification for both living and fossil forms, and to create an independent taxonomic system for the fossils. The general adoption of this policy during the decade that followed did much to retard progress in the study of phylogenetic and taxonomic relationships among the fossil coccoliths.

Coccolith-dimorphism is likely to have been prevalent to much the same extent in

fossil as in living taxa, and although final proof is usually beyond our reach, it is not difficult to find fossil examples of morphological variants that have all the earmarks of dimorphic pairs. These are not uncommon in *Cretarhabdus* (Pl. 150, figs. 4, 5), *Deflandrius* (Pl. 151, figs. 4, 5), *Kamptnerius* (Pl. 152, figs. 5, 6), and *Rhabdolithina*; if fossil species with dimorphic coccoliths are not recognized as such, the worst that can happen is that two species with identical ranges appear in the fossil record instead of one.

#### *Pleomorphic life-histories*

Observations on the life-histories of species kept in culture have brought to light several examples in which a motile coccolith-bearing phase alternates with a sessile uncalcified phase which had previously been accepted as a member of a different genus (Parke 1961). This is particularly true of coastal species, whose non-motile phases tend to live attached to rocks. Distinct from these are the pelagic species, whose resting-stages take the form of calcified cysts, which in the absence of any solid support, remain suspended in sea-water. One of these species, *Crystallolithus hyalinus*, which bears organic scales, sometimes unmineralized (Pl. 154, figs. 1, 2), and sometimes covered with minute rhombohedra of calcite, has proved to be the motile phase of *Coccolithus pelagicus*, an encysted form with coccoliths of a totally different kind (Pl. 143, figs. 1, 2).

These unexpectedly complicated life-histories are interesting from a taxonomic point of view, because the individual phases are usually so different from each other that they were put into separate genera when first discovered. To judge from our knowledge of living species, we can hardly expect to find tangible evidence of pleomorphism in the fossil record. In the coastal species, all the known sessile phases are uncalcified, and hence unlikely to be preserved as fossils. In the pelagic species, on the other hand, it is only the heavily calcified cysts, or their component coccoliths, that stand much chance of being preserved; delicate motile forms like *Crystallolithus* soon disintegrate, and are never found in bottom deposits. Indeed, material from living cultures needs careful handling in the laboratory to prevent the organic scales from losing their cover of calcite crystals. The cysts, on the other hand, are often preserved entire, and good examples are quite common in rocks as old as the Kimeridge Clay (Pl. 143, fig. 6).

#### *Variation in response to external conditions*

Changes in external conditions can, in some circumstances, cause the organism to modify the appearance of its coccoliths, or even to cease calcification.

In most species that have been experimented upon, the principal effect of temperature-change is to alter the rate of cell-multiplication, without any significant effect upon coccolith-morphology. In *Coccolithus huxleyi*, however, the coccoliths grown in warm water are reported to be distinguishable from those grown at low temperatures (Pl. 145, figs. 1, 2); the two variants have been recorded in laboratory cultures (Watabe and Wilbur 1966) and in natural populations (McIntyre and Bé 1967).

*C. huxleyi* is kept in culture in several laboratories, and a number of separate strains are kept under constant observation. Some of these have been found quite suddenly to stop growing coccoliths, and to persist in a naked condition (Paasche 1964, p. 11). One cause of this change appears to be an enrichment in the supply of nutrients, particularly phosphate. An interesting point is that whereas some strains will resume growth

of coccoliths if the culture medium is adjusted to a composition more like natural seawater, others will not, and no known treatment will induce them to do so.

There are several very suggestive possibilities here in connection with the evolution and taxonomy of these algae; fixation of a single phase out of a pleomorphic life-history, independent development of ecological variants, and sudden changes from a naked to a calcified condition, could all lead to the introduction of apparently cryptogenetic forms into the geological record. Furthermore, some of these changes could take place very suddenly, owing to the extraordinarily fast rate of multiplication that is prevalent in these organisms (Parke and Manton 1962).

#### PHYLOGENETIC HISTORY OF SOME LIVING TAXA

Attempts to trace living coccolithophorids back into geological history lead to curiously divergent results. Some species such as *Coccolithus pelagicus*, *C. huxleyi*, and *Braarudosphaera bigelowi* lead back to flourishing and diverse complexes, which in the present oceans have been reduced to just one or two surviving representatives. The ancestral stocks show a good deal of evolutionary divergence, but a set of unifying family characters persists throughout. *Pontosphaera* provides an extreme example of divergence, for we not only get a hint of an evolutionary connection with the extinct Zygothaceae, but we also find here the first suggestion of a far-distant linkage with another living family, the Helicosphaeraceae. Other stocks seem to have been peculiarly stable throughout their geological history. *Calciosolenia* can be traced back to mid-Cretaceous times with very little change, and the coccoliths of *Braarudosphaera bigelowi* are specifically indistinguishable from fossils preserved in early Cretaceous rocks. In contrast with these are two flourishing modern families, the Syracosphaeraceae which are abundantly represented in contemporary Globigerina Ooze, but have not been found in deposits older than Quaternary, and the Zygosphaeraceae which are not represented in bottom deposits at all.

#### *Coccolithus pelagicus* (Wallich) Schiller

Plate 143, figs. 1, 2

This is the most familiar of all coccoliths; it was discovered in samples of ooze raised from the floor of the North Atlantic Ocean during the first telegraph surveys, and was examined by Huxley and Wallich, and later by Murray and Blackman (1898). The living

---

#### EXPLANATION OF PLATE 143

- Figs. 1, 2. *Coccolithus pelagicus* (Wallich) Schiller, recent Globigerina Ooze, *Discovery II* Sta. 4269, Biscay Abyssal Plain. 1, No. 20175, oblique distal view,  $\times 4800$ . 2, No. 5000, details of central area, distal view,  $\times 5000$ .
- Fig. 3. *Coccolithus* sp. cf. *C. cavus* Hay and Mohler; No. 22279, Upper Oligocene, core DWBG 10, Pacific Ocean; distal view,  $\times 5300$ .
- Fig. 4. *Coccolithus* sp. cf. *C. marismontium* Black; No. 22284, Upper Oligocene, core DWBG 10, Pacific Ocean; proximal view,  $\times 6700$ .
- Figs. 5, 6. *Ellipsagelosphaera* sp. 5, No. 15230, Campanian Chalk, Belgorod, Russia; distal view,  $\times 8000$ . 6, No. 22874, Cambridge Greensand, Cherry Hinton Fields, near Cambridge; complete coccosphere (calcified cyst),  $\times 3700$ .
-

alga is confined to the North Atlantic, and is the only species that is known to have a preference for cold water; all attempts to find it in Antarctic waters of suitable temperature have failed. This was apparently not the case during the Pleistocene, for Allan Bé and his colleagues at the Lamont Observatory have found it in core-samples from the southern oceans at levels dated as belonging to the middle of the Wisconsin glacial episode (McIntyre and Bé 1967). In the Tertiary, there are very similar forms, but studies under the electron microscope show that they are specifically distinct (Pl. 143, fig. 3). The same generic form can be traced back to the Eocene, but once we pass into the Mesozoic, the species that superficially resemble *C. pelagicus* are obviously different in the finer details of their construction. When the coccoliths are examined under a petrological microscope, with the fossil lying flat on the slide, Tertiary and living species give an interference figure in which the distal shield plays no part, since the optic axes of the component calcite crystals are at right-angles to the plane of the shield. In the Mesozoic genus *Ellipsagelosphaera* this is not the case, and the crystals of the distal shield show strong birefringence, so that the optical figure takes a complicated form, due to the superposition of two black crosses, one produced by each shield. In addition, the Mesozoic species always have a corona of quadrate or keystone-shaped crystals lying on top of the distal shield, and marking off the central area (Pl. 143, fig. 5). Under an ordinary microscope the Tertiary and Mesozoic species look very much alike, but under a polarizing microscope or an electron microscope they are so obviously distinct that they are now placed in separate subfamilies.

In the Jurassic and Cretaceous there are also several other genera such as *Sollasites* (Pl. 144, figs. 1, 2), which resemble *Coccolithus* in a general way, but differ considerably in the finer details of their structure. They are clearly not on the main line of descent towards the *C. pelagicus* stock, but some of them may prove to be ancestral to certain other Tertiary and living forms.

*Cyclococcolithus leptoporus* (Murray and Blackman) Kamptner

Plate 144, figs. 3, 4; Plate 147, fig. 1

On theoretical grounds, Kamptner has argued that the circular outline is more primitive than the elliptical, and has insisted upon the taxonomic separation of these two shapes (compare Pl. 143, figs. 1–6, Pl. 144, figs. 3–7). He remarks:

'Above all else, one clear-cut taxonomic principle is decisive for subdivision . . . into tribes and subtribes: a sharper separation of the circular from the elliptical forms. A primitive character must be attributed to the circular outline, and a derivative character to the elliptical. . . . It is also *a priori* conceivable that the change-over from the circular to elliptical types has been achieved polyphyletically, and so to speak on a broad front' (Kamptner 1958, p. 64).

In accordance with this principle, he removed *Coccolithus leptoporus* to a new genus, *Cyclococcolithus*, and similarly split up other genera so that species with circular coccoliths could be put into different subtribes from those with elliptical coccoliths.

*Cyclococcolithus leptoporus* provides a convenient starting point from which to examine this taxonomic principle in relation to the geological record. This species is abundant in the living plankton, and is widely distributed. Very similar coccoliths are common in the Pliocene, and particularly so in core-samples from the ocean floor (Pl. 144, fig. 4).

In such deposits, the two discs of the placolith are apt to become separated, and many records of *Tiarolithus* and *Calcidiscus* from the Upper Tertiary are probably based upon dismembered specimens of *C. leptoporus* or closely related species. Other species are found in the Lower Tertiary, and the earliest record of the genus is from the Danian. These early forms occur associated with characteristically elliptical species of *Coccolithus*, and the two stocks were quite distinct from each other at the time of their first appearance in the early Tertiary. Thus the Tertiary record does not give much support to the idea that the circular shape is primitive; indeed, it tends to emphasize the complete independence of the elliptical forms rather than to provide any suggestion of their descent from circular ancestors.

This independent relationship is emphasized by a curiously similar state of affairs in the Upper Jurassic, for a different set of circular and elliptical types exist side by side in the Oxford and Kimeridge Clays. These include the genera *Cyclagelosphaera* and *Ellipsagelosphaera* (Noël 1965), which at first sight appear to be so much like *C. leptoporus* and *C. pelagicus* that they were originally recorded under these names. This resemblance, however, is illusory, for there are significant differences in micro-structure. It is remarkable that the two Jurassic genera each differ from their Tertiary analogues in exactly the same way: they both have strongly birefringent distal shields, surmounted by a well-developed corona (compare Pl. 143, fig. 3 and Pl. 144, fig. 3 with Pl. 143, fig. 5 and Pl. 144, fig. 5). Consequently, if we focus our attention on the minutiae of crystal-arrangement, we find that the Jurassic circular forms resemble their elliptical contemporaries more closely than they resemble modern circular forms. Are we then to unite the Jurassic genera, both circular and elliptical, into one family or subfamily, as Noël (1965) has done, or would it be more reasonable to keep the two shapes separate, regarding them as two parallel stocks that became independent at an early stage, and have remained so ever since?

An attempt to answer this question requires a closer look at the geological history of these two stocks. The elliptical forms are abundant throughout the Mesozoic and Cainozoic, and it may be that within this multitude of species there exists a continuous evolutionary thread leading from the Jurassic to the present day. The only serious break in this record is at the Cretaceous–Paleocene boundary, and there is not enough information available at present to reach a decision. The history of the circular placoliths is rather different. After the great abundance of *Cyclagelosphaera* (Pl. 144, fig. 5) in the Jurassic, there is a paucity of circular forms in the Cretaceous. The few examples that

## EXPLANATION OF PLATE 144

- Figs. 1, 2. *Sollasites horticus* (Stradner *et al.*) comb. nov. (= *Coccolithus horticus* Stradner *et al.*), Cambridge Greensand near Cambridge,  $\times 9600$ . 1, No. 4706, Barrington, distal view. 2, No. 21739, Cherry Hinton Fields, proximal view.
- Figs. 3, 4. *Cyclcoccolithus* spp., Lower Pliocene, core LSDH 78P, Pacific Ocean. 3, cf. *C. leptoporus* (Murray and Blackman) Kamptner, No. 22224, distal view,  $\times 4000$ . 4, No. 22210, group with some specimens in the 'Calcidiscus' condition,  $\times 2500$ .
- Fig. 5. *Cyclagelosphaera margereli* Noël; No. 17410, Oxford Clay (L. Oxfordian), Cambridge Experimental Borehole; distal view,  $\times 10\ 000$ .
- Fig. 6. *Markalius* sp. cf. *M. inversus* (Deflandre) Bramlette and Martini; No. 17199, Belemnite Marl (L. Turonian), Cherry Hinton, near Cambridge; proximal view,  $\times 6000$ .
- Fig. 7. *Ericsonia* sp.; No. 22295, Upper Oligocene, core DWBG 10, Pacific Ocean; proximal view,  $\times 6000$ .

are known, such as *Markalius* (Pl. 144, fig. 6), can hardly be regarded as linking *Cyclagelosphaera* with *Cyclococcolithus*, because they have a more complicated structure than either of these. They seem rather to be leading towards *Ericsonia* (Pl. 144, fig. 7) and other still more specialized forms that flourished in the Lower Tertiary. There is thus a gap extending throughout the Cretaceous period, during which they were apparently no representatives of the hypothetical *Cyclococcolithus* lineage. It seems, therefore, unlikely that the Tertiary species originated as an offshoot from *Cyclagelosphaera*, and it is more probable that they developed from an unknown ancestor early in the Tertiary.

The evidence from the geological record thus seems to alienate the Mesozoic circular forms from their modern analogues, and the evidence of morphology throws them into association with their elliptical contemporaries, in spite of the difference of shape.

*Coccolithus huxleyi* (Lohmann) Kamptner  
(= *Emiliana huxleyi* (Lohm.) Hay and Mohler 1967)

Plate 145, figs. 1, 2

The taxonomic position of this species is surrounded by interesting problems. It stands apart from *C. pelagicus* and all other living members of the genus in the peculiar construction of its shields, and its conspicuous central grid, which recalls the similar structures in many extinct forms. Mary Parke in Parke and Dixon (1964, p. 520) has pointed out that the motile phase lacks an obvious haptonema, and in this respect it resembles the Isochrysidales rather than the Coccolithophorales. Paasche (1964, p. 11) found in his cultures that coccolith-secreting individuals were without visible flagella, although these could be seen on some of the naked cells.

In the living plankton, it is undoubtedly the most vigorous and successful of the coccolith-bearing algae. It is distributed over the whole area of the oceans from the Antarctic convergence to the Arctic, and can invade brackish waters inaccessible to other pelagic species. Because of its great vigour and tolerance, it has provided material for more laboratory experiments than any other species.

*C. huxleyi* is apparently a very recent addition to the oceanic plankton. McIntyre and Bé (1967) have reported its first appearance in deep-sea cores as taking place within Brunhes Normal Zone (that is, less than 700 000 years ago, and more probably nearer to 100 000 years). They also report the presence of a coccolith intermediate between *C. huxleyi* and *Gephyrocapsa oceanica* in cores spanning the interval between 300 000 and 100 000 years. *G. oceanica* (Pl. 145, fig. 3) can be traced back into the Pliocene, and survives in the living plankton. Forms with the oblique bridge characteristic of *Gephyrocapsa* are unknown before the Pliocene, but the other characters of the genus, such as the large central opening with a bilateral grid, and the non-imbricate ray-elements, are strongly developed in a host of Lower Tertiary species of *Tremalithus* (Pl. 145, figs. 4–6). There is a great diversity of species with elaborate grids in the Middle and Upper Eocene, and the same type of coccolith can be traced back still further into the Mesozoic. The earliest representatives, with rather simpler grids, are found in the Lower Gault (Middle Albian) at Folkestone (Pl. 145, figs. 7, 8).

The taxonomic isolation of *C. huxleyi* from the rest of the genus *Coccolithus*, which is suspected from the peculiarities of the living alga, is thus confirmed by its long and independent geological history, and there can be little doubt that this species should be

removed to a separate genus, and possibly to a family independent of the Coccolithophoraceae.<sup>1</sup>

*Pontosphaera discopora* Schiller

Plate 146, figs. 1, 2

The genus *Pontosphaera* was created by Lohmann (1902) for species in which the coccoliths appear to be simple discs, with or without a shallow rim. The outline is elliptical, and the coccoliths are most commonly shaped like a shallow pie-dish. Specific diagnoses were originally based upon work under the biological microscope, and later studies in polarized light or under the electron microscope have led to the removal of several species to other genera. No electron micrographs of the type species, *P. syracusana*, have yet been published, but Mrs. Gaarder has generously allowed me to compare some of her excellent micrographs of this species with my Tertiary material. The coccoliths are large, with a floor perforated by about 750 very delicate pores, and the wall is constructed of about 200 very slender and steeply inclined calcite laths. *P. discopora* has similarly constructed but smaller coccoliths, with larger and less numerous pores. The Tertiary coccoliths discussed below have the same general type of structure, and can with reasonable confidence be referred to the same genus as *P. syracusana* and *P. discopora*.

Coccoliths of various species of *Pontosphaera* are not uncommon in modern Globigerina Ooze, particularly beneath the warmer parts of the oceans. In the Pliocene a form closely resembling *P. discopora* is occasionally found (Pl. 146, figs. 4, 5), but other species are rare or absent, and none of the modern perforated species has yet been identified with certainty in pre-Pliocene sediments. Nevertheless, coccoliths with all the characteristic features of *Pontosphaera* except the circular pores in the floor, are widely distributed throughout the Tertiary. There appear to be several lineages among these Tertiary species, each with a slightly different pattern in the structure of the floor. One of these is of special interest, since it appears to connect the living *P. discopora* with a complex of Eocene forms whose ancestry can probably be traced back to the Cretaceous. The proximal surface of the floor in this series has a bilateral arrangement of plates similar to that originally described by Kamptner in *P. scutellum*, and now known in a number of diverse Eocene forms (Pl. 146, fig. 6). The distal side has an entirely different

EXPLANATION OF PLATE 145

- Figs. 1, 2. *Coccolithus huxleyi* (Lohmann) Kamptner; recent oceanic deposits. 1, warm-water form, No. 3421, *Challenger* Sta. 338, S. Atlantic Ocean; distal view,  $\times 16\ 000$ . 2, cold-water form, No. 11612, *Discovery II* Sta. 3809, Galicia Bank; distal view,  $\times 20\ 000$ .  
 Fig. 3. *Gephyrocapsa oceanica* Kamptner; No. 18072, modern Globigerina Ooze, *Discovery II* Sta. 4288, Biscay Mts., proximal view,  $\times 8000$ .  
 Figs. 4-8. *Tremalithus* spp. 4, *T. danicus* (Black) comb. nov. (= *Dietyococites danicus* Black); No. 11819, Middle Oligocene, Grundf r, Denmark; proximal view,  $\times 6000$ . 5, *T. placomorphus* Kamptner; No. 22838, Lower Oligocene, Rodstenseje nr. Odder, Denmark; proximal view,  $\times 4000$ . 6, *T. dictyodus* (Deflandre and Fert) comb. nov. (= *Discolithus dictyodus* D. and F.); No. 22831, Lower Oligocene, Rodstenseje nr. Odder, Denmark (possibly reworked from M. Eocene); proximal view,  $\times 6100$ . 7, *T. burwellensis* Black; No. 14622, Cambridge Greensand (Cenomanian), Barrington near Cambridge; distal view with proximal shield showing through,  $\times 10\ 000$ . 8, *T.* sp., No. 13371, Lower Gault (M. Albion), Folkestone, Kent; proximal view,  $\times 8000$ .

<sup>1</sup> Since this lecture was delivered, a paper by W. W. Hay *et al* has been received, in which *C. huxleyi* has been formally transferred to a new genus, *Emiliana*.



appearance, with a pattern of concentrically arranged fibrous elements (Pl. 146, figs. 3, 7). This combination of patterns is also seen in several species of *Helicosphaera* (Pl. 147, figs. 1-3), and will be considered further in connection with the ancestry of that genus.

This constructional pattern can be picked up again in the late Cretaceous. Two species in the Santonian and Campanian have the same kind of wall-structure, and the same arrangement of plates on the proximal surface. One of these, *Pontolithina moorevillensis*, has two small perforations at the foci of the ellipse (Pl. 149, fig. 4). This species may well prove to be the ancestor of several Tertiary lineages. Obliteration of the two pores and an increase in the number of wall-elements would give a form very much like certain Eocene species, for example *P. versa* Bramlette and Sullivan (Pl. 146, fig. 6), *P. vadosa* Hay *et al.*, and possibly other forms like *Discolithus oamaruensis* Defl. Enlargement of the pores to make two circular windows would lead to such forms as *D. duocavus* Bram. and Sull. (L. Eocene) and *D. panarium* Defl. (M. Eocene).

There are also several Eocene species which differ in having numerous small circular pores, but which probably have a comparable floor-structure, since they give similar interference patterns in polarized light; their ultra-structure has not yet been examined under the electron microscope. *D. punctosus* Bram. and Sull. (L. Eocene) and *D. distinctus* Bram. and Sull. (M. Eocene) have this structure; they foreshadow the modern perforate species of *Pontosphaera*, but in the absence of any recognizable intermediates in the Upper Eocene and Miocene, we cannot say whether there is any direct phylogenetic connection. Possibly *D. vigintiforatus*, the type species of *Discolithus* from the Miocene of the Vienna basin, may yet prove to be on this line of descent.

There can be little doubt that *Pontosphaera* has a long geological history, and that many Tertiary species that have been referred to the rather unsatisfactory form-genus *Discolithus* actually fit quite naturally into one or other of the lineages of this complex. A derivation from some branch of the Mesozoic Zygolithaceae seems quite possible, and is indeed suggested by the presence in the Upper Cretaceous of forms that are intermediate between the two families (Pl. 149, fig. 4).

*Helicosphaera carteri* (Wallich) Kamptner  
(= *Helicopontosphaera kamptneri* Hay and Mohler 1967)

Plate 147, figs. 1, 2

In the present-day oceans, the genus *Helicosphaera* is represented by a single species whose coccoliths are peculiar in having a spiral brim which terminates in a characteristically flaring wing. Within this brim is an elliptical shield, shaped rather like the crown of a hat; it has bilaterally arranged plates on the proximal side, and concentric fibres on the distal, so that the structure is much the same as in many species of *Pontosphaera*.

This species has been customarily regarded as closely related to, and possibly derived from taxa such as *Coccolithus* with typical placoliths. Study of *H. carteri* under the electron microscope does not give much support to this idea; the coccoliths are clearly not mis-shapen placoliths, as is often assumed, and it is difficult to see how the spiral flange could have been derived from the two shields of a placolith. Compared with other living coccolithophorids, *H. carteri* stands very much by itself, and its geological history abundantly confirms its independence from the Coccolithophoraceae.

At the present day *H. carteri* is confined to the parts of the oceans lying roughly between latitudes 50° N. and S.; in bottom sediments its range is withdrawn a little towards the equator (McIntyre and Bé 1967, p. 585). In the Pliocene, forms that would be difficult to separate from this species are widely distributed, both in deep-sea cores and in samples collected on land. Similar forms, still very much like *H. carteri*, are abundant in the Upper Miocene, but here they are associated with several extinct species which are obviously quite different. In the underlying parts of the Miocene and in the Oligocene and Eocene there is a varied complex of extinct species, and the genus was evidently undergoing a burst of evolutionary diversification, possibly at its climax during the Oligocene.

In the early Eocene there are several species whose coccoliths lack the broad, flaring wing that is so characteristic of later species; they have a shape that does not depart much from an ovoid or even a regular ellipse. The earliest of these, *H. seminulum*, evolves from a Lower Eocene population in which this simple type (subspecies *seminulum*) is predominant (Pl. 147, fig. 4), to a Middle Eocene population in which the predominant subspecies *lophotus* is much more like a typical *Helicosphaera* (Bramlette and Sullivan 1961). The rim in subsp. *seminulum* shows little more than a suggestion of spiral structure, and in fact resembles the wall of an early Tertiary *Pontosphaera* crossed by an oblique wrinkle. The resemblance between these primitive species of *Helicosphaera* and some of the contemporary species of *Pontosphaera* is so close that they might reasonably be placed in the same genus, were it not that forms like *H. seminulum* are so plainly ancestral to other more typical species of *Helicosphaera*.

We have thus traced the ancestry of *H. carteri* back to an early stage when the genus was barely distinguishable from *Pontosphaera*, and we are now in a better position to assess its taxonomic status. It clearly has no close relationship with the Coccolithophoraceae, and must be placed in some other family. It has sprung from the same ancestors as the living *Pontosphaera*, and for this reason might be included in the Pontosphaeraceae. On the other hand, it can be argued that the divergence between the two stocks since the early Tertiary has been so profound that the living representatives can hardly be included in a single family, and I have proposed elsewhere that a new family, the *Helicosphaeraceae*, should be established for *H. carteri* and the numerous Tertiary species of which it is the sole survivor (Black 1968).

*Braarudosphaera bigelowi* (Gran and Braarud) Deflandre

Plate 147, fig. 5

In 1935 a new species, thought to be a *Pontosphaera*, was recorded in plankton hauls from the Bay of Fundy (Gran and Braarud 1935); this was re-examined by Deflandre,

EXPLANATION OF PLATE 146

Figs. 1-7. *Pontosphaera* spp. 1-3, *P. sp. cf. P. discopora* Schiller, recent Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean. 1, No. 11393, proximal view,  $\times 7200$ . 2, No. 11318, distal view,  $\times 8000$ . 3, No. 11319, details of distal surface,  $\times 24\ 000$ . 4, 5, *P. sp. cf. P. discopora* Schiller, Pliocene, Cisano nr. Albenga, Italy. 4, No. 16852, proximal view,  $\times 4800$ . 5, No. 16854, oblique proximal view,  $\times 4000$ . 6, 7, *P. versa* (Bramlette and Sullivan) comb. nov. (= *Discolithus versus* B. and S.), Eocene, Tuilerie de Donzacq, Landes, France. 6, No. 15855, proximal view,  $\times 6000$ . 7, No. 15834, distal view,  $\times 6000$ .

who showed that its coccoliths were entirely different from any previously known form. They consist of five peculiarly shaped calcite plates arranged to form a regular pentagon, and twelve of these pentoliths fit together to make a dodecahedral skeleton enclosing an encysted cell. The species was re-named *Braarudosphaera bigelowi*, and a new family was based upon it (Deflandre 1947). At that time little was known about its geological history, which we now know to be quite remarkable. Coccoliths with exactly the same structure have been found at various levels in the Tertiary, and are abundant in the Upper Bracklesham Beds of the Sussex coast. They have also been found, though less abundantly, throughout the Cretaceous system, and except for an increase in size in the older specimens, are specifically indistinguishable from recent material. No other species of coccolithophorid has a stratigraphical range at all comparable with this, and at first sight it might be thought that we have here an extreme example of specific stability. This is no doubt true of the main lineage of *B. bigelowi* itself, but in the Tertiary we are confronted not only with a multiplicity of other species of *Braarudosphaera* itself, but in addition an exuberant development of two closely related genera, *Micrantholithus* and *Pemma* (Pl. 147, fig. 6), all with coccoliths constructed on the same pentolith system. Detailed phylogenies have still to be worked out, but some of the simpler forms are so close to *B. bigelowi* that there can be little doubt about their origin.

*B. bigelowi* is an unquestionable example of a single living species that is the sole survivor of an important and diversified Tertiary family whose ancestry can be traced back well into the Mesozoic. This point is stressed because there are several other species in the living plankton with very much the same kind of history, resulting in a taxonomic isolation which is equally real, but by no means always so obvious.

#### CALCIOSOLENIACEAE Kamptner

Plate 148, figs. 1, 2

Most coccolithophorids have a spherical, egg-shaped, or pear-shaped body. The Calciosoleniaceae differ in being cylindrical or fusiform, and their coccoliths instead of being circular or elliptical, take the form of a narrow parallelogram (Pl. 148, fig. 1). There are probably four or five living species, and although the family characters are unmistakable, their systematics at generic and specific levels are not easy. Fossil representatives are never common, but have been found at intervals in the geological column down to the Cretaceous, the earliest British occurrence being at the base of the Cenomanian (Pl. 148, fig. 2); Stradner (in Stradner *et al* 1968) has recently announced the discovery of similar specimens in the Albian of Holland. The interesting feature of this record is that the earliest specimens differ so little from living material: the family characters with all their eccentricities are fully developed at the first appearance, there is no clue at all about relationships to other coccolith taxa, and no suggestion of any evolutionary change during the long interval from the middle Cretaceous to the present day.

#### LIVING FAMILIES WITH NO KNOWN GEOLOGICAL RECORD

We have now considered a number of isolated species in the living plankton, many of which have turned out to be survivors of once flourishing families that are otherwise

extinct. In contrast with these are the two largest living families, the Syracosphaeraceae and Zygosphaeraceae, which have no fossil record behind them. Both families have more than 50 species, and together they account for more than half the living coccolithophorids. The Zygosphaeraceae are all holococcoliths: that is, they are constructed of minute rhombohedra or prisms of calcite, each enclosed in an organic membrane. Such structures are very delicate, and would probably break down into their component crystals soon after falling to the sea floor; this may well be the reason why they are not found in the Globigerina Ooze or other oceanic deposits. This, however, can hardly be true of the Syracosphaeraceae, which are much more robustly constructed. Many species of *Syracosphaera* are, indeed, found abundantly in the modern Globigerina Ooze, and their absence from the Pliocene and older deposits therefore calls for some different explanation. (W. W. Hay and his colleagues have recently referred two Tertiary species to this genus (*S. bisecta* Hay *et al.* 1966, p. 393, and *S. clathrata*, 1967, p. 449). *S. bisecta* has been re-examined by Bramlette and Wilcoxon (1967, p. 102), who regard it as a species of *Coccolithus*, and until more is known about the wall-structure of *S. clathrata*, its reference to *Syracosphaera* cannot be regarded as fully established.) The obvious conclusion that the Syracosphaeraceae are, in fact, post-Tertiary additions to the oceanic plankton is probably correct, and will be considered later in relation to the abrupt appearance of other cryptogenic families in earlier times.

## EXPLANATION OF PLATE 147

- Figs. 1-4. *Helicosphaera* spp. 1, 2, *H. carteri* (Wallich) Kamptner, recent Globigerina Ooze. 1, No. 18030, *Discovery II* Sta. 4288, Biscay Mts., proximal view,  $\times 7200$ . Also *Cyclococcolithus leptoporus* (M. and B.) Kamptner, distal view. 2, No. 13137 from *Challenger* Sta. 338, S. Atlantic Ocean; distal view,  $\times 7200$ . 3, *H.* sp., No. 22839, Lower Oligocene, Rodstenseje nr. Odder, Denmark; proximal view,  $\times 3200$ . 4, *H. seminulum* Bramlette and Sullivan; No. 14293, Middle Eocene, core DWBG 23B, Pacific Ocean; proximal view,  $\times 6700$ .
- Figs. 5, 7. *Braarudosphaera* spp. 5, *B. bigelowi* (Gran and Braarud) Deflandre; No. 15730, Yazoo Formation (Upper Eocene), Clarke County, Mississippi; complete coccolith of five plates,  $\times 4000$ . 7, *B. africana* Stradner; No. 16057, Sutterby Marl (Aptian), borehole Alford, Lincs., 101-7 ft.; complete coccolith,  $\times 4000$ .
- Fig. 6. *Pemma papillatum* Martini; No. 15871, Yazoo Formation (Upper Eocene), Clarke County, Mississippi; single plate,  $\times 5000$ .

## EXPLANATION OF PLATE 148

- Fig. 1. *Calciosolenia* sp., No. 13131, recent Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean; proximal view,  $\times 10\ 000$ .
- Fig. 2. *Scapholithus* sp., No. 20678, Chalk Marl, (Cenomanian), Folkestone, Kent; proximal view,  $\times 13\ 000$ .
- Figs. 3, 4. *Syracosphaera* spp. 3, *S. hystrica* Kamptner; No. 2573, recent Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean; distal view,  $\times 16\ 000$ . 4, *S. pulchra* Lohmann; No. 18062, recent Globigerina Ooze, *Discovery II* Sta. 4288, Biscay Mts.; proximal view,  $\times 6000$ .
- Fig. 5. *Loxolithus armilla* (Black) Noël, holotype, No. 2807, Burwell Rock (Cenomanian), Great Shelford nr. Cambridge; distal view,  $\times 8000$ .
- Figs. 6, 9. *Rhabdolithina* spp. 6, *R.* sp., No. 18616, Sutterby Marl (Aptian), borehole, Alford, Lincs., 101-7 ft.; oblique proximal view,  $\times 6000$ . 9, *R.* sp., No. 13501, Lower Gault (Albian), Folkestone, Kent; oblique proximal view,  $\times 8000$ .
- Fig. 7. *Staurolithites* sp., No. 21747, Cambridge Greensand (Cenomanian), Cherry Hinton Fields nr. Cambridge; distal view,  $\times 8000$ .
- Fig. 8. *Zygodolites diplogrammus* Deflandre; No. 22337, Mooreville Chalk (Santonian), nr. Eutaw, Alabama; distal view,  $\times 5300$ .

## EXTINCT FAMILIES

In examining the fossil representatives of living families, we have not found it necessary to employ a dual classification with the extinct species segregated into parataxa. We can approach the extinct families in much the same way, and follow the well-tried palaeobotanical practice of treating them as being made up of closely related organ-genera. Much depends upon the choice of characters that are relied upon for the definition of genera or families, and there must always be an element of personal opinion in making this selection. Quite clearly, we cannot follow any hard and fast rules, for some kinds of criteria that are of great value in certain families are worthless in others. For example, in the Zygolithaceae and Podorhabdaceae, the number of crystals in the marginal shields or rings is variable, even within a single species; in the Deflandriaceae, however, the number is always 16 (Pl. 151, fig. 2), and in the Braarudosphaeraceae it is 5 throughout the whole family (Pl. 147, fig. 5). In a large number of families the structure of the outer margin of the coccolith follows a characteristic pattern, and can be used as a primary basis of classification. Thus, the Zygolithaceae all have an architecture based upon the loxolith-ring (see below and Pl. 148, fig. 5); the Coccolithophoraceae have two marginal shields of radial elements (Pl. 143, fig. 4; Pl. 144, fig. 2; Pl. 145, fig. 3), and the Podorhabdaceae have yet another type of rim (Pl. 150, figs. 1, 6). The presence or absence of a central spine is also of unequal significance in different families. Such structures are characteristically present in the Rhabdosphaeraceae, but never in the Coccolithophoraceae. In the Podorhabdaceae, on the other hand, the coccoliths of some genera, such as *Polypodorhabdus* (Pl. 150, fig. 1) always have spines, but in others, such as *Cretarhabdus*, some coccoliths in a single species may have spines and others not (Pl. 150, figs. 4, 5). This state of affairs is also known in some living genera, such as *Syracosphaera*.

## ZYGOLITHACEAE Noël

Plate 148, figs. 5-9; Plate 149, figs. 1-5

A large number of Mesozoic coccoliths have an outer wall that consists of narrow, steeply inclined laths of calcite, giving a structure rather like the wall of a barrel that has been given a sharp twist, so that the staves run obliquely instead of straight up and down (Pl. 148, figs. 6, 9). The resulting loxolith-ring resembles the wall of *Pontosphaera* in its general plan of construction, but differs in normally having no floor, and in having a much smaller number of staves, which are also coarser and more robust. The numerous genera which make up the family are defined by the various structures that bridge or partly close the opening within the ring.

The name *Loxolithus* was proposed by Denise Noël (1965) for species consisting of an unmodified ring (Pl. 148, fig. 5); many fossils preserved in this condition are in fact damaged specimens of other genera, having lost the bridge or central cross that was originally present. In *Zygoolithus* there is a bridge along the shorter axis of the ellipse on the proximal side (Pl. 148, fig. 8). *Pontolithus* has a grid on the proximal side and a distal bridge (Pl. 149, figs. 2, 3), and *Staurolithites* has a central cross (Pl. 148, fig. 7). In several genera the proximal side of the loxolith-ring is closed by a floor, sometimes solid, but frequently pierced by pores (Pl. 149, fig. 1). In *Rhagodiscus* the floor consists

of a mosaic of little granules, and the addition of a prominent spine gives a rhabdolith-like appearance to *Rhabdolithina* (Pl. 148, figs. 6, 9).

The earliest Zygolithaceae are found in the Lias, but there is no great variety of structure until the Lower Cretaceous, when specialized forms begin to appear, leading up to the spectacular diversity of genera and species in the Albian and Cenomanian. High in the Upper Cretaceous there are species with a new type of floor-structure, in which the plates are arranged very much as in early species of *Pontosphaera* and *Helicosphaera* (compare Pl. 149, fig. 4 with Pl. 146, fig. 6 and Pl. 147, fig. 3). These have been mentioned already in connection with the ancestry of these two genera.

#### PODORHABDACEAE Noël

Plate 150, figs. 1-6

This is an exclusively Mesozoic family which made its first appearance in the Oxfordian, when five well-differentiated genera appeared simultaneously without any known ancestors. Most of these continue throughout the upper part of the Jurassic and the Lower Cretaceous. An additional genus, *Cretarhabdus*, appears in the Berriasian and continues with undiminished vigour to the top of the Maestrichtian, when this genus, and with it the whole family quite suddenly became extinct (Bramlette and Martini 1964). The characters of the family may be seen in Plate 150, figs. 1-6; there is an elliptical shield with a narrow rim consisting of two layers of keystone-shaped crystals surrounding a very large central area, from which arises a tall spine. The several genera which make up the family are distinguished from each other by the structures occupying the central area (compare Pl. 150, figs. 1, 2, 3, 5); in most of them the central spine is supported by four buttresses constructed of fibrous crystals. This is an architectural feature which is not confined to the Podorhabdaceae (Pl. 149, fig. 6; Pl. 151, fig. 3; Pl. 152, fig. 1), and its taxonomic significance will be discussed on a later page.

#### EXPLANATION OF PLATE 149

- Fig. 1. *Zygolithus* sp. with perforated floor; No. 22407, Cambridge Greensand (Cenomanian), Hauxton Mill near Cambridge; proximal view,  $\times 8000$ .  
 Figs. 2, 3. *Pontolithus flabellus* (Stradner), comb. nov. (= *Coccolithus flabellus* Stradner, Cambridge Greensand (Cenomanian). 2, No. 22881, Cherry Hinton Fields, proximal view,  $\times 6000$ . 3, No. 11510, Barrington, distal view,  $\times 8000$ .  
 Figs. 4, 5. *Pontolithina* spp. 4, *P. moorevillensis* Black, No. 22362, Mooreville Chalk (Santonian), nr. Eutaw, Alabama; proximal view,  $\times 4800$ . 5, *P.* sp., No. 22899, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; distal view,  $\times 4800$ .  
 Fig. 6. *Eiffelithus turriseiffeli* (Deflandre) Reinhardt, No. 22114, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; distal view with characteristically oblique spine,  $\times 4000$ .

#### EXPLANATION OF PLATE 150

- Fig. 1. *Podorhabdus cylindratus* Noël, No. 22798, Upper Oxford Clay (L. Oxfordian), Cambridge Experimental Borehole, 220 ft. 3 in.-221 ft. 3 in.; distal view,  $\times 4800$ .  
 Fig. 2. *Polypodorhabdus madingleyensis* Black, No. 17413, Oxford Clay, locality as 1; distal view,  $\times 9600$ .  
 Fig. 3. *Ethmorhabdus gallicus* Noël, No. 22799, Oxford Clay, locality as 1; distal view,  $\times 7200$ .  
 Figs. 4-6. *Cretarhabdus* spp., Cambridge Greensand (Cenomanian) nr. Cambridge. 4, No. 21766 with spine, Hauxton Mill; distal view,  $\times 4800$ . 5, No. 21763 without spine, Cherry Hinton Fields; distal view,  $\times 9600$ . 6, No. 22867, Cherry Hinton Fields, side view,  $\times 4800$ .

## DEFLANDRIACEAE Black 1967

Plate 151, figs. 1-5

More than a century ago Sorby described a remarkable coccolith from the Chalk; it has a ring of sixteen granules from which arise four flying buttresses supporting a peculiarly constructed stalk. Bramlette and Martini (1964) have shown that Sorby's coccolith belongs to one of several closely similar species that existed in the Upper Cretaceous, and which they united into the genus *Deflandrius*. The earliest species is found in the Gault (Pl. 151, fig. 1); it has all the family characters fully developed, and has no known ancestors. Three distinct, but very similar species are very abundant in the Upper Cretaceous right up to the top of the Maestrichtian, when the whole family became extinct.

The main differences between this family and the Podorhabdaceae are to be found in details of ultra-structure. Otherwise the two families share the same basic architectural plan: a spine supported by four buttresses arising from a granular ring. Quite recently, this structural plan has been found to be developed in a remarkably similar way among the uncalcified Haptophyceae, notably in several species of *Chrysochromulina*. This discovery raises the possibility that the ancestors of both the *Deflandriaceae* and *Podorhabdaceae* may have belonged to such uncalcified stocks in which the family characters were already developed, and only needed the ability to calcify in order to make their appearance on the geological record.

## GONIOLITHACEAE Deflandre

Plate 151, fig. 6

This is perhaps the most remarkable of the extinct families. It was founded by Deflandre (1957) upon a single species, *G. fluckigeri*, which he discovered in the Eocene of north-west Germany and the Oligocene of Basses Alpes. The coccolith is pentagonal in outline, with a granular centre and radially constructed border. More recently, Martini (1964) has discovered a complete cyst in the Clayton Formation (Danian) of Alabama; in this unique specimen, twelve of the pentagonal coccoliths are fitted together to form a regular dodecahedron, giving a configuration exactly like the cysts of *Braarudosphaera*, but with an entirely different coccolith-structure. Martini has shown that *G. fluckigeri* ranges from the Lower Maestrichtian to the Rupelian, in the later occurrences apparently re-worked. The only observable difference between earliest and latest autochthonous specimens is a slight increase in size. Although *Goniolithus* is always a rare fossil, it has a wide geographical distribution: Denmark, France, Germany, English Channel (submarine core-samples), Tunisia, Alabama, and Texas. At the time of writing, the family still includes only the single species.

## STEPHANOLITHIACEAE fam. nov.

Plate 152, figs. 1-3

The genus *Stephanolithion* was created by Deflandre (1939) for a peculiar species of coccolith from the Oxford Clay of Calvados, which he named *S. bigoti*. It differs from other coccoliths in having a set of radial spines extending beyond the marginal ring;

moreover, each spine consists of a single scalenohedron, a crystal habit that is most unusual among the coccolithophorids. Two more species have subsequently been discovered: *S. speciosum*, also from the Oxford Clay, and *S. laffitei* from the Portlandian of Algeria. *S. bigoti* is known from the Callovian, but is only common in the Oxfordian; in England it appears to be confined to the Upper Oxford Clay. *C. laffitei* is now known to occur throughout the Cretaceous System, becoming extinct at the top of the Maestrichtian.

*Stephanolithion* stands so far apart from other coccoliths that it cannot be fitted into any existing family, and I propose a new family name, Stephanolithiaceae, with the characters of the single included genus.

#### DISCOASTERACEAE Tan Sin Hok

Plate 153, figs. 1-9

The discoasters are usually considered to be taxonomically distinct from the coccoliths, but it would be unrealistic to ignore the likelihood that they are the products of similar planktonic algae, possibly in an encysted condition. They are mentioned here because they illustrate particularly clearly the taxonomic importance of crystal-orientation, which these organisms were able to control with great precision. In most species of *Discoaster* no crystal outlines are visible; nevertheless, the orientation of the crystals can be determined optically, and they are invariably found to be arranged so that the c-axis lies parallel with the axis of symmetry of the discoaster. In a smear-slide prepared so that the fossils lie flat against the cover-slip, they consequently remain dark in all positions between crossed nicols, and show the maximum refractive index for calcite. This property is constant for all discoasters, and at once distinguishes them from typical coccoliths.

The general appearance of the discoasters can be seen in Plate 153, figs. 1-8. They

#### EXPLANATION OF PLATE 151

Figs. 1-5. *Deflandrius* spp. 1, *D. cantabrigensis* Black, No. 22863, Cambridge Greensand (Cenomanian), Cherry Hinton Fields nr. Cambridge; side view,  $\times 6000$ . 2, 3, *D. spinosus* Bramlette and Martini. 2, No. 22187, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; oblique distal view,  $\times 4000$ . 3, No. 20144, Upper Chalk (Campanian), borehole at Holton nr. Halesworth, Suffolk; distal view,  $\times 8000$ . 4, 5, *D. cretaceus* (Arkhangelski) Bramlette and Martini. 4, No. 18481, Upper Chalk (Santonian), nr. Salisbury, Wilts.; oblique proximal view of short-stalked form,  $\times 6000$ . 5, No. 22321, Mooreville Chalk (Santonian), nr. Eutaw, Alabama; oblique proximal view,  $\times 6000$ .  
Fig. 6. *Goniolithus fluckigeri* Deflandre, No. 22888, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; damaged coccolith,  $\times 10\ 000$ .

#### EXPLANATION OF PLATE 152

Figs. 1-3. *Stephanolithion* spp. 1, *S. bigoti* Deflandre, No. 22783, Upper Oxford Clay (L. Oxfordian), Cambridge Experimental Borehole; distal view,  $\times 4000$ . 2, 3, *S. laffitei* Noël, Lower Gault (M. Albian), Folkestone, Kent. 2, No. 13503, proximal view,  $\times 10\ 000$ . 3, No. 13537, oblique distal view,  $\times 8000$ .  
Fig. 4. *Neococcolithes* sp., No. 22923, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; proximal view,  $\times 10\ 000$ .  
Figs. 5-7. *Kamptnerius magnificus* Deflandre, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama,  $\times 4000$ . 5, No. 22902, form with narrow wing, distal view. 6, No. 22928, form with expanded wing, distal view. 7, No. 22925, form with narrow wing, proximal view.



consist of calcite crystals grouped round a central axis, giving a snow-flake pattern. In *Marthasterites* (Pl. 153, fig. 9) the whole structure appears to consist of a single calcite crystal. In *Discoaster* each ray is crystallographically distinct, as may be seen from the etch-patterns which are all too common on corroded specimens, or from the crystal faces that are sometimes seen in exceptionally well-preserved specimens (Pl. 153, fig. 1).

*Marthasterites* is found in the Upper Cretaceous and in the Lower Eocene; *Discoaster* is confined to the Tertiary, appearing in the Paleocene and becoming extinct at the top of the Pliocene or just within the Pleistocene, according to the horizon adopted for the base of the Quaternary. Reported discoveries of living Discoasteraceae are at present unconfirmed.

Constancy of crystal-arrangement is equally prevalent among the coccoliths; its optical effects, however, are much more complicated when the crystal-axes are not all parallel, but they are none the less of great taxonomic significance, and are relied upon extensively in systematic work. In the *Braarudosphaeraceae* the crystals are arranged round a central axis, much as in the Discoasteraceae, but the orientation is quite different, with the rhombohedron faces lying approximately in the plane of the coccolith (Pl. 147, fig. 5). In *Stephanolithion* the radial spines are scalenohedra with the optic axes at right angles to the central axis of the coccolith (Pl. 152, fig. 1). In the majority of coccoliths, the arrangement is much more complicated, with the optic axes arranged in a pattern that almost invariably involves some kind of screw symmetry.

#### RELATIONS WITH UNCALCIFIED STOCKS

The geological histories of the various coccolithophorid stocks discussed above clearly do not all follow the same pattern. On the one hand there are long-ranging stocks such as the Coccolithophoraceae, Pontosphaeraceae, and Zygothaceae, with a great number of species spread out through a considerable span of geological time. These pass through phases when generic and specific distinctions are blurred, and evolutionary divergence was evidently taking place. The Coccolithophoraceae, for example, passed through such phases in Albian-Cenomanian times, again in the Eocene, and apparently once more in the Pleistocene. The taxonomic problems involved in this state of affairs are those familiar in any actively evolving group of organisms, and call for no special comment here.

In contrast with such normally evolving stocks, there are others which behave quite differently; these arrive on the scene abruptly, with all their characters ready-made. Some of them, for example *Gonolithus*, *Deflandrius*, and *Stephanolithion*, persist perhaps for the length of a geological period with little or no change, and then just as abruptly become extinct; others, such as the *Podorhabdaceae*, appear equally abruptly, but undergo noticeable evolutionary changes before they become extinct. In each of these cryptogenic stocks, there is a well-defined architectural plan which we have taken as characteristic of the family, and which is fully perfected in the earliest known species. It looks very much as though the architectural plan had already been elaborated before the fossil record started, and I think we have to consider seriously the possibility that the beginning of the fossil record for such a family simply marks the change-over to calcification in a stock whose scales were previously unmineralized.

Of course, we can hardly hope to find any tangible evidence of a palaeontological

nature to support this speculation, but fortunately there are other lines of investigation open to us. The most promising of these is an inquiry into the existing unmineralized stocks themselves, with a view to finding out what linkages may exist between these and the coccolith-bearing algae.

Recent work on the uncalcified Haptophyceae has indeed brought to light some very interesting parallels with the coccolithophorids. The various species of *Chrysochromulina* have been found to bear delicate organic scales, which in their architectural construction are very similar to some coccoliths. It is a little surprising to find that the most elaborately constructed scales, although quite unlike the majority of living forms, can be readily matched among extinct taxa.

In spite of their extreme tenuity, these scales apparently consist of two layers which are differently sculptured, and if calcified would produce entirely different crystal patterns. The simplest scales are elliptical discs, with sharply etched radiating lines on the proximal surface, and a less clearly defined series of concentric rings or a vague spider's web pattern on the distal side (Pl. 154, figs. 1, 2). Scales of this kind are also well-known in *Crystallolithus hyalinus*, where they provide the support upon which calcite crystals are secreted (Parke and Adams 1960). In addition to these simple scales, most species of *Chrysochromulina* also carry larger and more elaborate scales, in which the distal layer is modified in various ways, often producing a central spine. The large scales of *C. chiton* (Parke *et al.* 1958, figs. 16, 17, 28, 29) are shaped like pie-dishes, with sloping walls on the distal surface, much like those of *Pontosphaera* (Pl. 146, fig. 5). *C. ericina* (Parke *et al.* 1956, figs. 17-19) has scales shaped like rhabdoliths with very long spines, reminiscent of some Tertiary species of *Rhabdosphaera*. In several other species the spines are differently constructed, and do not resemble those of *Rhabdosphaera*, but are

## EXPLANATION OF PLATE 153

Figs. 1-8. *Discoaster* spp. 1, *D.* sp. showing crystal faces; each of the six rays is a separate rhombohedron, with triad axis at right-angles to page; No. 22291, Upper Oligocene, core DWBG 10, Pacific Ocean;  $\times 6100$ . 2, *D. elegans* Bramlette and Sullivan, No. 11890, Middle Oligocene (reworked from Eocene?), Grundf or, Denmark;  $\times 3000$ . 3, *D. barbadiensis* Tan Sin Hok, No. 11949, Middle Oligocene (reworked from Eocene?), Grundf or, Denmark;  $\times 4500$ . 4, *D. lodoensis* Bramlette and Riedel, No. 15771, Eocene, Tuilerie de Donzacq, Landes, France;  $\times 1900$ . 5, *D. strictus* Stradner, No. 11899, Middle Oligocene (reworked from Eocene?), Grundf or, Denmark;  $\times 3000$ . 6, *D. deflandrei* Bramlette and Riedel, No. 15830, Eocene, Tuilerie de Donzacq, Landes, France;  $\times 4000$ . 7, *D. hamatus* Martini and Bramlette, No. 16969, damaged specimen, Pliocene, core DWBP 119, Pacific Ocean;  $\times 4000$ . 8, *D. brouweri* Tan Sin Hok, No. 22197, Pliocene, core LSDH 78P, Pacific Ocean;  $\times 3000$ .

Fig. 9. *Marthasterites tribrachiatus* (Bramlette and Riedel) Deflandre, No. 10485, Lower Eocene, R snaes, Denmark;  $\times 2500$ .

## EXPLANATION OF PLATE 154

Figs. 1-3. *Crystallolithus hyalinus* Gaarder and Markali (= motile phase of *Coccolithus pelagicus*), strain No. LB 913/12 (Plymouth 182), Culture Collection of Algae and Protozoa, Botany School, Cambridge;  $\times 16\ 000$ . 1, No. 22909, two scales in proximal view. 2, No. 22911, two scales in distal view. 3, No. 22915, scale and calcite rhombohedra detached during preparation.

Fig. 4. *Scyphosphaera* sp., No. 18028, ordinary coccolith, proximal view; recent Globigerina Ooze, *Discovery II* Sta. 4269, Biscay Mts.;  $\times 6000$ .

Figs. 5-7. *Scyphosphaera* sp., ordinary coccoliths; modern Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean. 5, No. 11316, distal view,  $\times 6000$ . 6, No. 11317, detail, distal surface,  $\times 20\ 000$ . 7, No. 11308, detail, proximal surface,  $\times 80\ 000$ .

remarkably like those of certain Mesozoic genera. In these species the spine is supported by four buttresses which arise from the distal surface of the scale. *C. alifera* (Parke *et al.* 1956, fig. 76) has buttresses which do not reach the marginal rim, much as in the Cretaceous *Eiffellithus* (Pl. 149, fig. 6). In *C. ephippium* (Parke *et al.* 1956, figs. 38, 39) the buttresses are arranged exactly as in the Jurassic *Polypodorhabdus* (Pl. 150, fig. 2); they extend from the marginal rim to the centre, dividing the scale into four quadrants, each of which is ornamented by radial striae on the proximal surface. In the large spined scales of *C. pringsheimii* (Parke *et al.* 1962, figs. 21, 22, 29) the supports of the tall spine are no longer in contact with the surface of the scale except at the outer margin, but behave like flying buttresses; the whole arrangement is an astonishing duplication of the Upper Cretaceous *Deflandrius* (Pl. 151, fig. 3). *C. pringsheimii* is unusual in having so many as four different kinds of scale, each of which could serve as a template for the orderly disposition of calcite-crystals to give a familiar coccolith pattern.

Enough has been said to show that there is a very significant parallel between the calcified and uncalcified Haptophyceae. Several of the living species of *Chrysochromulina* could indeed be regarded as uncalcified survivors of familiar Mesozoic families. It would be asking too much of coincidence to believe that the few living species of *Chrysochromulina* have contrived to reconstruct in their uncalcified scales just those features that were required to start off the Podorhabdaceae in the Oxfordian, the Deflandriaceae in the Albian, and the Pontosphaeraceae and Helicosphaeraceae sometime near the beginning of the Tertiary. I think it is at least as reasonable to suppose that this remarkable genus is indeed a survival from a protean stock that existed in early Mesozoic times, and by selective calcification of its organic scales has given birth to these ancient families.

## REFERENCES

- BLACK, M. 1968. The systematics of coccoliths in relation to the geological record. In *The micropalaeontology of oceans*, edited by B. M. Funnell and W. R. Riedel, Cambridge University Press.
- BRAMLETTE, M. N. and MARTINI, E. 1964. The great change in calcareous nannoplankton fossils between the Maestrichtian and the Danian. *Micropalaeontology*, **10**, 291–322.
- and SULLIVAN, F. R. 1961. Coccolithophorids and related nannoplankton of the early Tertiary in California. *Ibid.* **7**, 129–88.
- and WILCOXON, J. A. 1967. Middle Tertiary calcareous nannoplankton of the Cipero section, Trinidad, W.I. *Tulane Stud. Geol.* **5**, 93–131.
- DEFLANDRE, G. 1939. Les stéphanolithes, représentants d'un type nouveau de coccolithes du Jurassique supérieur. *C. r. hebd. Séanc. Acad. Sci. Paris*, **208**, 1331–3.
- 1947. *Braarudosphaera* nov. gen., type d'une famille nouvelle de coccolithophoridés actuels à éléments composites. *Ibid.* **225**, 439–441.
- 1952. Coccolithophoridae. In *Traité de Zoologie*, ed. P. P. Grassé, Paris: Masson.
- 1959. Sur les nannofossiles calcaires et leur systématique. *Rev. Micropaléont.* **2**, 127–52.
- 1966. Commentaire sur la systématique et la nomenclature des nannofossiles calcaires. *Cahiers Micropaléont.*, ser. 1, no. 3, C.R.N.S., Paris. 9 pp.
- and FERT, C. 1954. Observations sur les coccolithophoridés actuels et fossiles en microscopie ordinaire et électronique. *Annls. Paléont.* **40**, 115–76.
- GAARDER, K. R. 1967. Observations on the genus *Ophiaster* Gran (Coccolithineae). *Sarsia*, **29**, 183–92.
- GRAN, H. H. and BRAARUD, T. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine. *J. biol. Bd. Can.* **1**, 297–467.
- HALLDAL, P. and MARKALI, J. 1955. Electron microscope studies on coccolithophorids from the

- Norwegian Sea, the Gulf Stream and the Mediterranean. *Avh. norske VidenskAkad. Oslo*, 1955 (1), 30 pp.
- HAY, W. W., MOHLER, H. P., ROTH, P. H., SCHMIDT, R. R., and BOUDREAUX, J. F. 1967. Calcareous nannoplankton zonation of the Cenozoic of the Gulf Coast and Caribbean-Antillean area and transoceanic correlation. *Trans. Gulf-Cst Ass. geol. Socs.* **17**, 428-80.
- and WADE, MARY E. 1966. Calcareous nannofossils from Nal'chik (Northwest Caucasus). *Ecl. Geol. Helv.* **59**, 379-400.
- KAMPTNER, E. 1958. Betrachtungen zur Systematik der Kalkflagellaten, nebst Versuch einer neuen Gruppierung der Chryomonadales. *Arch. Protistenk.* **103**, 54-116.
- LOHMANN, H. 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten. *Ibid.* **1**, 89-165.
- MCINTYRE, A. and BÉ, A. W. H. 1967. Modern Coccolithophoridae of the Atlantic Ocean—I. Placoliths and Cyrtoliths. *Deep Sea Res.* **14**, 561-97.
- MARTINI, E. 1964. Ein vollständiges Gehäuse von *Goniolithus fluckigeri* Deflandre. *Neues Jb. Geol. Paläont. Abh.* **119**, 19-21.
- MURRAY, G. and BLACKMAN, V. H. 1898. On the nature of the coccospheres and rhabdospheres. *Phil. Trans. R. Soc., B*, **190**, 427-41.
- NOËL, DENISE. 1965. *Sur les coccolithes Jurassiques Européens et d'Afrique du Nord*. C.N.R.S., Paris. 209 pp.
- PAASCHE, E. 1964. A tracer study of the inorganic carbon uptake during coccolith formation and photosynthesis in the coccolithophorid *Coccolithus huxleyi*. *Physiologia Pl.*, suppl. 3, 82 pp.
- PARKE, MARY. 1961. Some remarks concerning the class Chrysophyceae. *Br. phycol. Bull.* **2**, 47-55.
- and ADAMS, IRENE. 1960. The motile (*Crystallolithus hyalinus* Gaarder and Markali) and non-motile phases in the life history of *Coccolithus pelagicus* (Wallich) Schiller. *J. mar. biol. Ass. U.K.* **39**, 263-74.
- and DIXON, P. S. 1964. A revised check-list of British marine algae. *Ibid.* **44**, 499-542.
- MANTON, IRENE, and CLARKE, B. 1956-62. Studies on marine flagellates. *Ibid.* **35**, 387-414; **37**, 209-28; **42**, 391-404.
- SCHILLER, J. 1930. Coccolithineae. In Rabenhorst's *Kryptogamen-Flora*, **10** (2), 89-266.
- STRADNER, H., ADAMIKER, D., and MARESCH, O. 1968. Electron microscope studies on Albian calcareous nannoplankton. *Verh. K. ned. Akad. Wet.* **24** (4), 107 pp.
- WATABE, N. and WILBUR, K. M. 1966. Effects of temperature on growth, calcification and coccolith form in *Coccolithus huxleyi* (Coccolithineae). *Limnol. Oceanogr.* **11**, 567-75.
- WILBUR, K. M. and WATABE, N. 1963. Experimental studies on calcification in molluscs and the alga *Coccolithus huxleyi*. *Ann. N.Y. Acad. Sci.* **109** (1), 82-112.

## APPENDIX

*Localities of deep-sea samples mentioned in the explanation of plates*H.M.S. *Challenger*

Station 338: dredge, 21° 15' S., 14° 02' W., about 900 miles S. of Ascension Is., South Atlantic Ocean.

R.R.S. *Discovery II*

Station 3809: dredge, northern slope of Galicia Bank, 42° 56' N., 11° 47' W., about 120 miles W. of Cape Finisterre.

Station 4269: trigger-weight core, Biscay Mts., W. of Bay of Biscay.

Station 4288: dredge, Biscay Abyssal Plain, Bay of Biscay.

## Scripps Institution of Oceanography

DWBG 10: core sample, specimens from 11 to 27 cm. 6° 54' N., 131° 00' W., central Pacific Ocean.

DWBG 23B: core sample, specimens from 10 to 12 cm. 16° 42' S., 145° 48' W., between Tuamotu Archipelago and Tahiti.

DWBP 119: core sample, specimens from 398 to 400 cm.  $27^{\circ} 54' S.$ ,  $106^{\circ} 53' W.$ , about 200 miles ESE. of Easter Is.

LSDH 78PG core sample, specimens from 250 to 270 cm.  $4^{\circ} 30' S.$ ,  $168^{\circ} 03' E.$ , between Gilbert Is. and Solomon Is.

MAURICE BLACK  
Department of Geology  
Sedgwick Museum  
Cambridge

Typescript received 21 May 1968



1



2



3



4

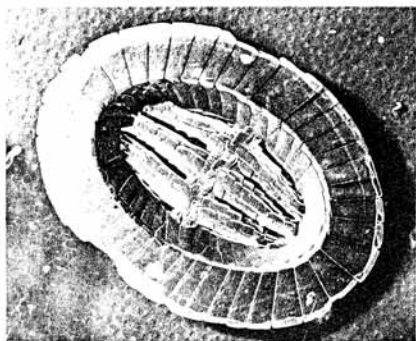


5

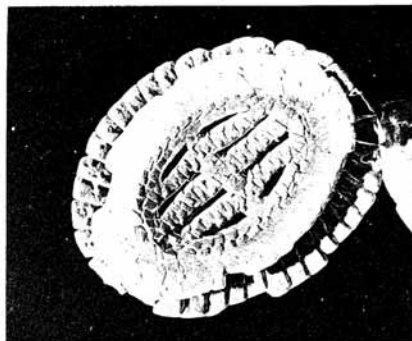


6

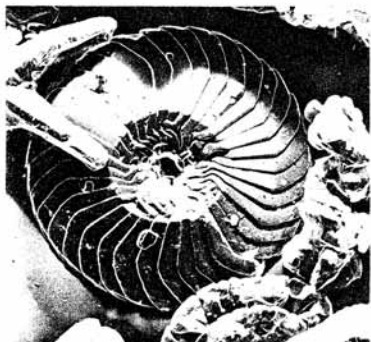
BLACK, Living, Tertiary and Cretaceous coccoliths



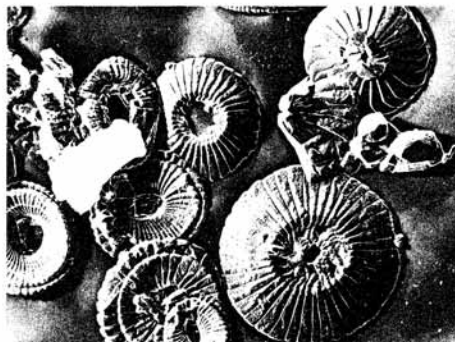
1



2



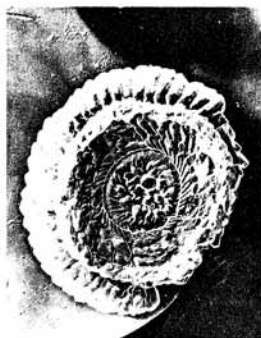
3



4



5

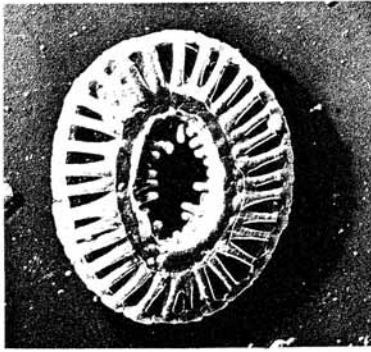


6



7

BLACK, Cretaceous, Tertiary and Jurassic coccoliths



1



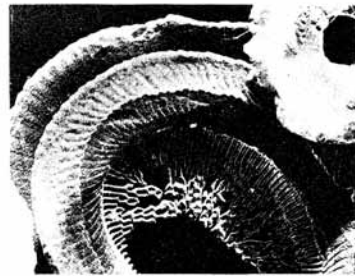
2



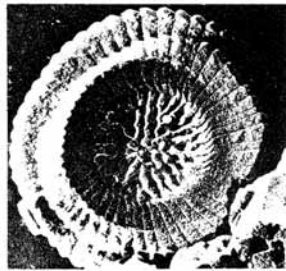
3



4



5



6

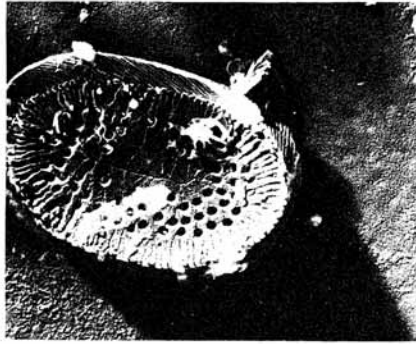


7

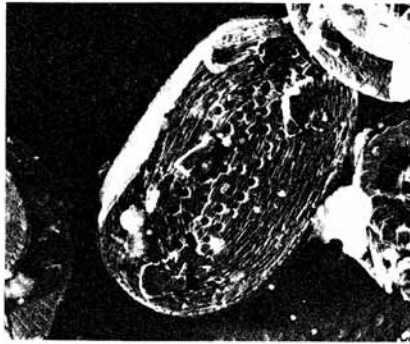


8

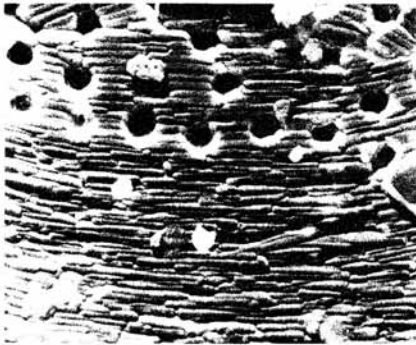




1



2



3



4



5



6



7

BLACK, Living and Tertiary coccoliths



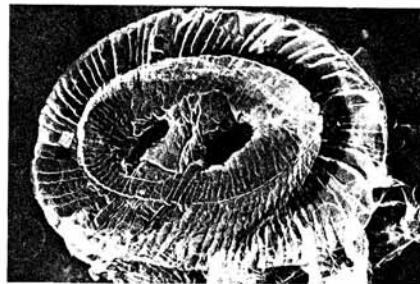
1



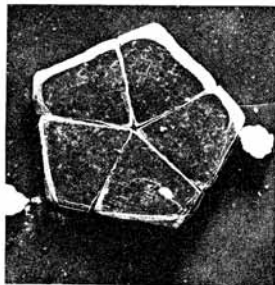
2



3



4



5



6



7

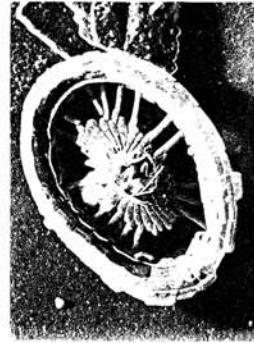
BLACK, Living, Tertiary and Cretaceous coccoliths



1



2



3



4



5



6



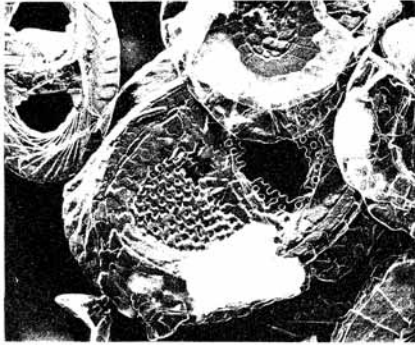
7



8



9



1



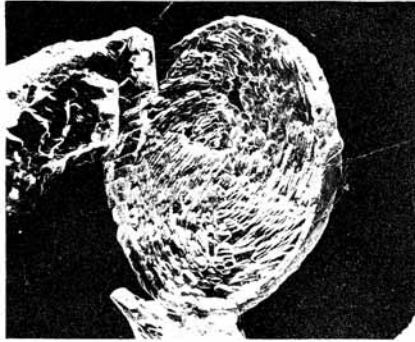
2



3



4

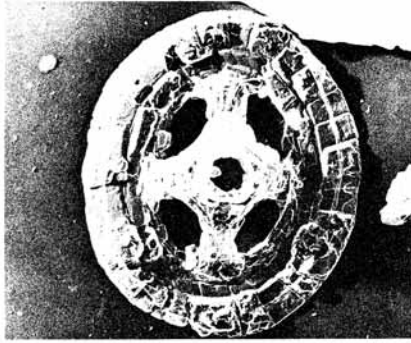


5



6

BLACK, Cretaceous coccoliths



1



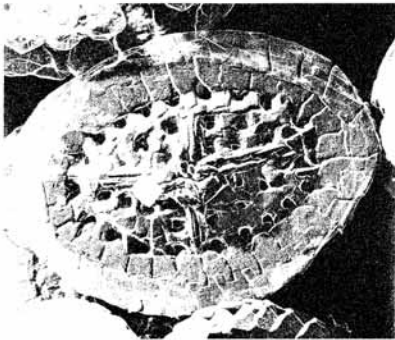
2



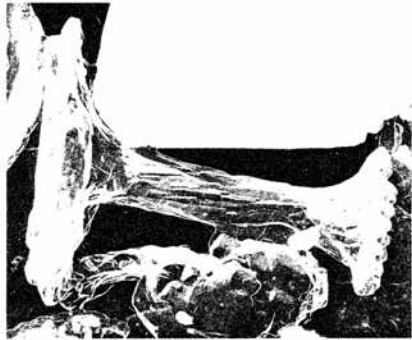
3



4



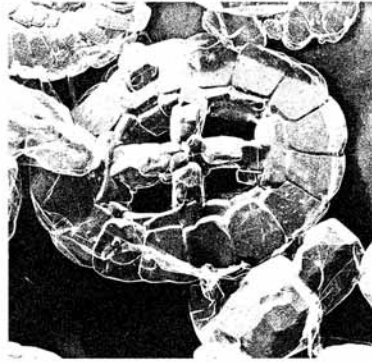
5



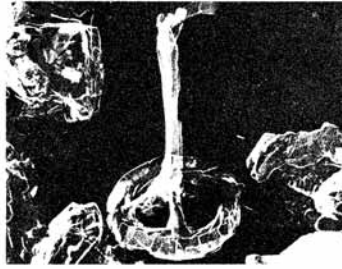
6



1



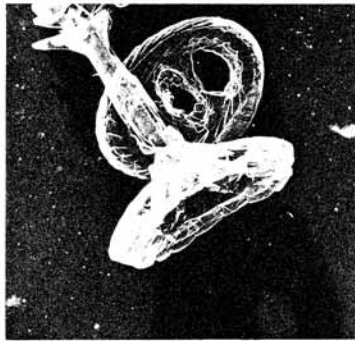
2



3



4

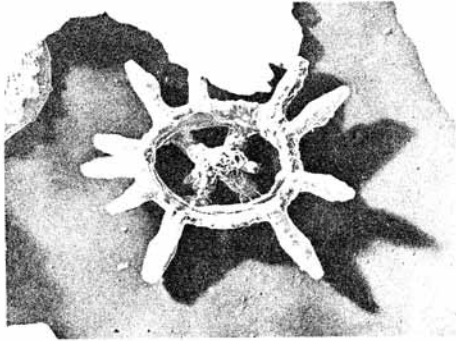


5

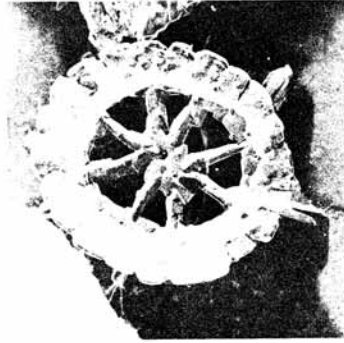


6

BLACK, Cretaceous coccoliths



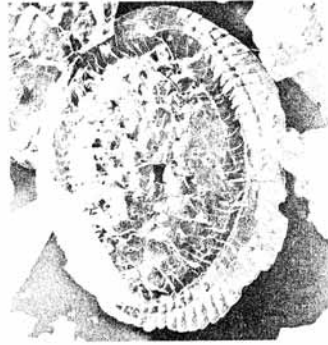
1



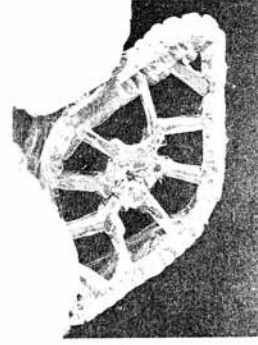
2



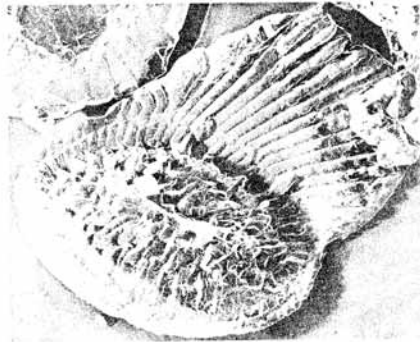
3



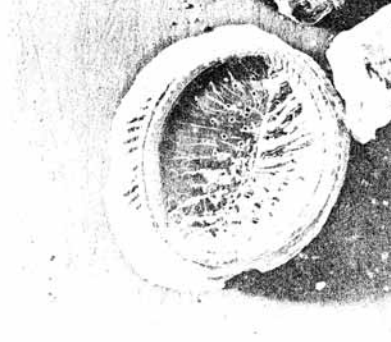
4



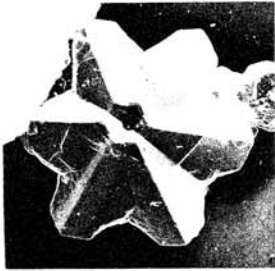
5



6



7



1



2



3



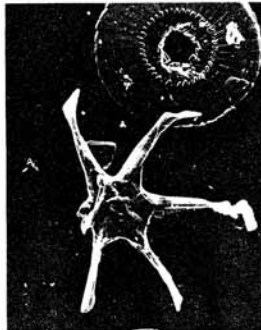
4



5



6



7



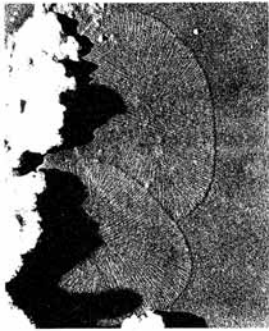
8



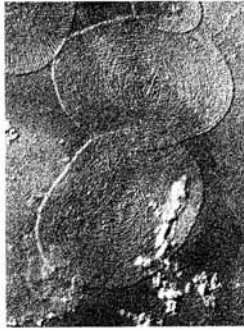
9

BLACK, Tertiary discoasters





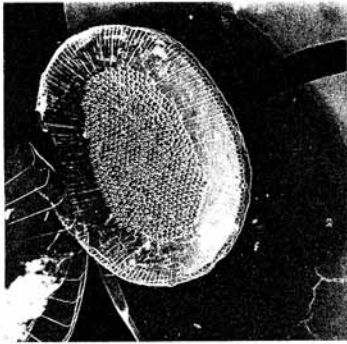
1



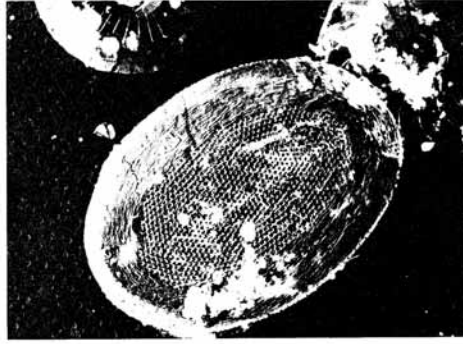
2



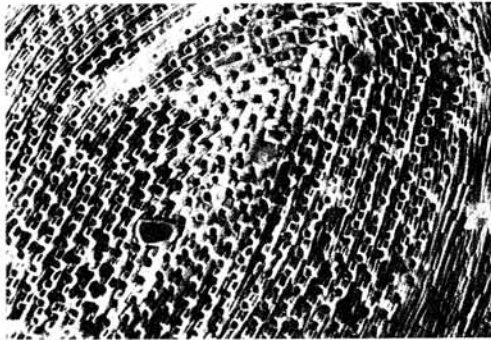
3



4



5



6



7

BLACK, Living uncalcified Haptophyceae and coccoliths

---