Observations on heterococcolith rim structure and its relationship to developmental processes

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1.1 INTRODUCTION

Since the application of electron microscopy to nannoplankton research it has been possible to observe the fine structure of coccoliths. This has become a standard descriptive technique with invaluable results for the development of taxonomy. I have used some of the accumulated data in a slightly different way here, investigating certain geometrical aspects of coccolith morphology, and combining the results with information from studies of the development of living coccoliths. These approaches have been used to develop an enhanced understanding of the structure of coccoliths. A prime objective of this is to identify those aspects of the structure of coccoliths which are the result of architectural control, and so to separate other aspects which are of taxonomic significance, or which may be of adaptive significance.

A more direct impetus was provided by an attempt to write a computer program to generate, mathematically, illustrations of coccoliths. This is a useful end in itself, since accurate illustration is an essential means of communication in palaeontology, and diagrams provide a means of synthesising and interpreting data from electron microscope studies. Also, writing the program provided both a need for a model of coccolith geometry and a means of testing the predictions made by such a model. The program I have developed has enabled me to produce diagrams of a number of species. Similar illustrations have, of course, been produced by conventional techniques (e.g. Grün et al. 1974, Theodoridis 1984). However, computer-generated diagrams have the advantage that they can easily be redrawn, modified, and experimented with, although they are not necessarily faster to produce initially. Also there is potential for further development of the technique, to produce perspective illustrations, and to model birefringence patterns.

This paper deals with development of a model for heterococcolith development and geometry,
and its application to Neogene coccoliths, particularly reticulofenestrids. This model forms the theoretical basis for the computer program, details of which are given in Young (1987b, c).

1.2. SOME GEOMETRICAL ASPECTS OF COCCOLITH MORPHOLOGY

Circular coccoliths, and other nannofossils with radial symmetry, are geometrically simple, can easily be mathematically modelled, and do not readily yield much information on their mode of development. The same is not true for elliptical coccoliths, since the variable curvature of their rims needs to be accommodated by variation in the shape, size or spacing of the elements. Geometrical investigation of this effect is essential for modelling, and can provide clues to the controls on coccolith morphology.

The simplest way of mathematically deriving an elliptical form from a circular one is via a simple linear stretch. This type of transformation is illustrated in Figs. 1.1B and 1.1C. However, the resultant elliptical coccolith is not realistic, it differs from real coccoliths in a number of important ways, as discussed below.

The following terminology should be noted. (1) Placolith coccoliths are considered here as being divisible into two parts; the central area, which is enclosed by the tube (in many specimens the central area is an open aperture), and the rim, which consists of the tube, distal shield and outer part of the proximal shield (Fig. 1.2). (2) The term element is used in the conventional loose sense for the individual components of cycles. In particular cases these may be distinguished as rays, plates, etc. Where elements from different cycles appear to be united these larger units are referred to here as crystal units. (3) For convenience of reference, and computing, coccoliths are described as elliptical; in fact they probably have less regular oval shapes.

(a) Rim width and ellipticity variation

On the deformed coccolith the uniform stretching means that all circles become true ellipses of similar elongation (axial ratio = 1.3 in Fig. 1.C). As a consequence the rim width varies. It is greater at the ends of the coccolith (i.e. along the long axis) than at the sides, by a factor equivalent to the elongation.

Examination of electron micrographs of real coccoliths shows that a quite different relationship is the normal case. Characteristically the rim width is constant, and as a result the ellipticity varies, decreasing outwards. Thus the central area of most coccoliths is more strongly elliptical than their outer edge. As a result in many 'circular' coccoliths the central area is often distinctly elliptical (e.g. Calcidiscus leptopus, Cyclicargolithus floridanus).

This rim width constancy and ellipticity variation can be seen qualitatively by observing electron micrographs, and is apparent even with light microscopy. It can be demonstrated by measuring the length and width of the inner and outer margins of the rims of individual specimens. Fig. 1.3 gives data of this type, from my own and published micrographs. Rim width and axial ratio variation for sixty placolith coccoliths are plotted on two graphs. As these show, rim width is constant (Fig. 1.3A), and so the axial ratio of the coccolith perimeter is consistently lower than that of the central area (Fig. 1.3B). The correlation of rim widths is remarkably good, strongly suggesting that rim width constancy is a basic feature of coccolith geometry. It implies that rim elements are of similar length all round the coccolith.

(b) Element orientation

If the distorted coccolith is compared with the circular coccolith from which it was derived (Figs. 1.1B and 1.1C), it can be seen that the angular separation of the elements is increased along the sides of the distorted coccolith and decreased at the ends. Thus the elements fan strongly at the sides and only slightly at the ends. This again is the reverse of the normally observed relationship on real coccoliths. As shown by the tracings, Figs. 1.1D–1.1H, maximum fanning occurs around the ends, where the curvature is greatest, whilst the elements along the sides are often sub-parallel.
Fig. 1.1 — Coccolith geometry.

A)–C) Computer-generated diagrams: (A) elliptical coccolith, as modelled by my program, based on E; (B) circular coccolith derived from A; (C) elliptical 'coccolith' formed by stretching B.

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(c) Element spacing

In the distorted coccolith the element spacing is directly related to the angular divergence, and so is maximum along the edges and minimum at the ends. This again is the reverse of the generally observed relationship, since usually elements are broader at the ends of elliptical coccoliths than along their sides (Figs. 1.1D–1.1H). Closer examination shows that this is predominantly an effect of the outer margin. By contrast, around the inner margin of coccolith rims element spacing usually appears to be more or less uniform. The variation in the width of the ends of the elements is thus primarily a product of the variation in angular divergence, or ray fanning.

![Diagram of biometric parameters](image)

**Fig. 1.2 — Biometric parameters.**

Key to the features plotted in Figs. 3, 7 and 9. Abbreviations; CAL, central area length; CL, coccolith length; RW, ray width (averaged from 3 to 6 rays).

The fanning effect is shown particularly clearly by elongated coccoliths such as *Ellipsolithus macellus* (Fig. 1.1H). A related effect is shown by central area elements; in real coccoliths (e.g. *Emiliania huxleyi*, Fig. 1.1D) these tend to be bunched at the ends, instead of converging uniformly on the centre. Both these effects suggest that the orientation of elements is more closely related to the orientation of the rim (i.e. the local tangent), than to radial directions from the centre of the coccolith.

This aspect of the geometry of coccoliths is hard to measure reliably, without high quality enlarged micrographs. It can, however, be qualitatively observed in virtually any micrographs of Mesozoic or Tertiary coccoliths.

![Biometric data plots](image)

**Fig. 1.3 — Biometric data illustrating rim width constancy.**

(A) Scatter plot of rim width variation in 60 coccoliths. (B) Plot of axial ratios (length:width), illustrating that the axial ratio of the central area is consistently higher than that of the coccolith perimeter. Dotted lines indicate equal abscissa and ordinate values.
1.3 COCCOLITH DEVELOPMENT DURING COCCOLITHOGENESIS

An alternative approach to looking at the final form of coccoliths is to examine how they actually develop. Coccolithogenesis in heterococcolith producing phases is an intracellular process closely associated with organic scale formation. The process has been followed in detail in three species, *Coccolithus pelagicus* (Parke and Adams 1960, Manton and Leedale 1969), *Emiliania huxleyi* (Wilbur and Watabe 1962, Klaveness 1976, Westbroek et al. 1984), and *Pleurochrysis carterae* (Manton and Leedale 1969, Outka and Williams 1971, van der Wal et al. 1983).

Although there are important differences in coccolith structure and cell organisation in these three species the sequence of coccolith development is similar in all three. So a general pattern can be suggested, as shown in Fig. 1.4.

In each case an organic base-plate scale has been observed to form before calcification starts (Fig. 1.4A). In the case of *E. huxleyi* this was not identified until the study of Westbroek et al. (1984), although it was illustrated by Wilbur and Watabe (1962). In the other species base-plate formation prior to calcification is well documented.

Initial calcification occurs around the rim of this base-plate, producing a ring of simple elements (Fig. 1.4B). This ring of elements forms the basis of subsequent coccolith development and can conveniently be referred to as the proto-coccolith ring. Good examples are illustrated in Klaveness (1976) and Leadbeater and Morton (1973); in them the elements appear to be uniformly spaced around the ring. Several workers have suggested that the base-plate is important at least in providing a frame of reference for the nucleation sites (Manton and Leedale 1969, Outka and Williams 1971, Westbroek et al. 1984).

During subsequent coccolith growth (Figs. 1.4C and 1.4D) the elements remain attached to the base-plate, so it is unlikely that they move relative to each other. Hence the element spacings and orientations determined by the initial nucleation should be retained during coccolith growth.

In *E. huxleyi*, growth occurs in upward, outward and inward directions so that the proto-coccolith ring approximates to the inner margin of the proximal shield (Wilbur and Watabe 1962, Westbroek et al. 1984). In *Umbilicosphaera sibogae* var. *foliosa*, for which this stage of coccolithogenesis has been described by Inouye and Pienaar (1984), growth occurs in a very similar manner. *Pleurochrysis carterae* is also similar, although there is little or no outward growth—the coccolith remains a ring-shaped cricolith rather than developing into a placolith (Outka and Williams 1971, van der Wal et al. 1983).

In *Coccolithus pelagicus* the coccolith development stages were not so readily discernible. It appears likely, however, from the illustrations of Manton and Leedale (1969) that in this species too growth occurs outward and upward from the proto-coccolith ring (their Figs. 22–28), so that it corresponds to the base of the tube, and that in the mature coccolith the base-plate is attached to the inside edge of the proximal shield (their Figs. 16, 17 and 31).
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1.4 A BASIC MODEL FOR HETERO-COCCOLITH DEVELOPMENT

The mode of development from one, or a very few, proto-coccolith rings, and the clear succession of stages which occurs during coccolithogenesis, provide a useful sequential framework for the interpretation of final coccolith morphology, as summarised below.

1) Formation of the base-plate scale: this is a critical precursor to coccolith development since the base-plate acts as a template for crystallite nucleation. Its shape and size is thus one of the main influences on the ultimate form of the coccolith—it is responsible for the ellipticity of elliptical coccoliths.

2) Crystal nucleation, around the base-plate: it is at this stage that the number, spacing, and orientation of the elements is fixed. The limited observations from coccolith geometry, and the few available illustrations of actual protococcolith rings, suggest that, at least to a first approximation, the elements are uniformly
1.5 RETICULOFENESTRID STRUCTURE

To test the developmental model it needs to be applied to real coccoliths. This involves digression into taxonomy, so only one group is discussed in detail here: the reticulofenestrids, which form a coherent, abundant, and well-known group, with an interesting range of structures. In addition, coccolithogenesis has been extensively studied in the principal living species, *Emiliania huxleyi*.

The term reticulofenestrid is used here for coccoliths with similar rim structure to *Reticulofenestra*. This includes all the Late Eocene to Recent Noelaerhabdaceae, but excludes the earlier genera *Toweius* and *Prinsius*, which have a significantly different rim structure (see e.g. Perch-Nielsen 1985). Representative reticulofenestrid species are illustrated in Fig. 1.5.

Basic reticulofenestrid structure is discussed first, to show how it can be related to growth from a proto-coccolith ring. Then each of the three stages of coccolith development suggested above is looked at in turn to see how it affects aspects of morphology and variation in the group.

(a) Basic structure

Most reticulofenestrids consist on the proximal side of a shield constructed of a single cycle of rays and a grill flooring the central opening (examples in Figs. 1.5D and 1.5G). On the distal side two cycles of elements are visible, an outer cycle forming the distal shield and a discrete inner cycle of smaller ‘cover plates’ overlying the distal shield. A central tube connects the proximal and distal shields, and this consists of two cycles: an outer tube cycle with clockwise imbrication of the elements, and an inner tube cycle—termed the wall—with anticlockwise imbrication (i.e. the tops of the elements are offset in an anticlockwise sense from the bottoms of the elements). Thus a total of six cycles can be identified (proximal and distal shield, outer tube, wall, cover plate, and grill cycles). However, closer examination shows that the elements of the various cycles are connected.

The cover plates arise from the elements of the wall, which in turn are connected to the rays of the proximal shield, and so to the grill. These relationships are readily apparent in suitable micrographs and have been noted by many authors (e.g. Hay et al. 1966, Perch-Nielsen 1971, Edwards 1973, Romein 1979).

Similarly, the distal shield rays continue into the outer tube cycle, and this again merges with the proximal shield. These connections are only visible in fortuitously oriented specimens, and so are not well established. They are, however, clearly shown in the micrographs of Perch-Nielsen (1971, Plate 24.3, and noted p. 31), Bramlette and Wilcoxon (1967, Plate 1.3), and Steinmetz and Stradner (1984, Plate 26.4).

Thus all the various apparently distinct elements are interconnected at the base of the tube (Fig. 1.6). As such the conventionally recognised ‘elements’ can be seen to be rather arbitrary parts of larger units. These units have a remarkably elaborate four-part structure, but presumably are single calcite crystals, and so are referred to here as crystal units. An interesting aspect of the structure, shown in Fig. 1.6, is that the opposite imbrication directions of the wall and outer tube result in the cover plates and
Fig. 1.5 — Reticulofenestrid coccoliths.
Computer-generated diagrams of eight species. Note the following. (1) Each diagram set consists of distal view (left), proximal view (right) and cross-section (bottom). (2) Diagrams are not drawn to a common scale, and the cross-sections are at larger
Fig 1.5 (cont)
scales than the plan views. (3) Central area details and cross-sections are schematic. (4) All diagrams are based on information from many sources rather than single specimens.
distal shield rays of single crystal units being offset. As a result, although the distal shield and wall are formed from the same cycles of crystal units, they do not fuse during diagenesis.

In the particular case of *Emiliania huxleyi* this structure, with the various elements being parts of larger crystal units, was suggested by the observations on coccolithogenesis of Wilbur and Watabe (1962) and subsequently demonstrated by X-ray diffraction examination of individual crystal units by Watabe (1968).

Light microscopy also suggests this interconnection of elements—all the components of the coccoliths show similar optical behaviour in both plan and side view. The central grill is rarely visible in cross-polarised light but this is almost certainly a result of its extreme thinness rather than different optical orientation.

This structural interpretation, with all the elements traceable to a common origin at the base of the tube (Fig. 1.6), provides strong support for the concept of their growing from a proto-coccolith ring corresponding to the base of the tube, which is a critical prediction of the model outlined above. Conversely the model provides an explanation for the structure of the crystal units.

**Fig. 1.6 — Reticulofenestrid crystal unit structure.**

Simplified drawing of a single reticulofenestrid crystal unit, showing its complex multi-element construction. For clarity all elements are shown as of similar thickness; in fact the column elements are rather thicker. Also, kinks in the rays, grill complexities, etc. are omitted.

(b) **Effect of proto-coccolith size and ellipticity**

An obvious consequence of the growth model is that one of the primary controls on coccolith morphology is the size and shape of the proto-coccolith ring, which in turn is related to the base-plate size and shape. Usually shape, or ellipticity, seems to show a low degree of variation within species, and size rather more. An interesting example of the effects of combined variation in these factors is provided by the *Pseudoemiliania lacunosa—Reticulofenestra doronicoides* group (the name *Pseudoemiliania lacunosa* is adopted here since it has nearly universal currency; it may, however, not be strictly valid—van Heck pers. commun. 1988).

This group is usually regarded as consisting of two or more species, with *R. doronicoides* being a typical small elliptical reticulofenestrid, and *P. lacunosa* a slightly larger circular to sub-circular form with a broad central area, numerous elements and slitting between the rays of the distal shield (Fig. 1.5E). There is, however, a continuous range of morphotypes between these end-members, and it is probably more valid to regard the entire group as a single species. This interpretation was based initially on my own, mainly qualitative, light microscope observations, but
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the range and style of variation is also clear from published illustrations and descriptions (e.g. McIntyre et al. 1967, Samtleben 1979, Nishida 1979, Pujos 1985). Similar interpretations of the taxonomy of the group have been made by McIntyre et al. (1967) and Samtleben (1979).

The large number of morphological variables make the group ideal for biometric investigation. I have conducted a crude study of this type, using about forty electron micrographs of P. lacunosa, mainly from the literature. Graphs from this data set are given in Fig. 1.7, and a synthetic series of diagrams based on it is given in Fig. 1.8. Unfortunately it is not possible to identify precisely the proto-coccolith ring location, particularly since distal views have had to be used to get a reasonably sized data set. However, since element growth is predominantly outward, the edge of the central area provides a practical approximation. Variation in central area size and shape in P. lacunosa can thus be used to investigate the effect of variation in proto-coccolith size and shape.

As shown in Fig. 1.7A central area length and width are strongly correlated but not directly proportional; central area ellipticity decreases with increasing size (see also Figs. 1.7B and 1.8). As a result central area width, which is related to both increasing central area size and decreasing ellipticity, shows greater variation (0.5–3.0 μm) than either coccolith length (3–7 μm) or central area length (1–3 μm). It proved the most discriminating parameter to plot other data against.

The parameters which are most nearly independent of central area width are rim width (Fig. 1.7C) and element spacing around the central area edge (Fig. 1.9B). The variation in these parameters is low and apparently random, or related to other controls. This is of interest since it suggests that variation can occur in one phase of the coccolith development process with little effect on the other phases.

An inevitable consequence of the low rim width variation is that central area size increases relative to coccolith size as the central area width increases (Fig. 1.7D). Similarly, since initial element spacing is approximately constant, the number of rays increases with central area width (Fig. 1.7E).

The number of slits between rays increases very markedly (from 0 to 50), with central area width. This is partially an effect of the increasing number of rays, but in addition the percentage of rays with slits increases (Fig. 1.7F). The cause of this is not clear, but slitting and the change to broader more open coccolith shapes might both be mechanisms for reducing calcite usage, and so could be parallel responses to a single external factor. The distribution of slits around the coccoliths appears to be random, as modelled in Fig. 1.8.

Summary: a number of superficially independent changes in coccolith morphology can be seen to be related to the single control of increase in base-plate size, with faster increase in width than length. This is demonstrated in the diagrams of Fig. 1.8; the only parameters changed in the program were central area width, ellipticity, and degree of slitting.

Interestingly there are analogous cases of correlation in these features, except for slitting, in other groups, notably *Reticulofenestra pseudoumbilicus–rotaria*, and *Calidiscus leptoporus–macintyrei*; variation in the *Coccolithus pelagicus* group also shows some such features. More generally variation in base-plate size and shape appears to be an important process in producing interspecific and intraspecific variation.

(c) Nucleation related features

The second phase of coccolith development is crystal nucleation, when the spacing and orientation of crystal units are determined.

It is readily apparent from electron micrographs that there is little variation in the orientation of the elements between the various reticulofenestrid species. Also, between crossed-nicols all reticulofenestrids show birefringence in plan view, and have similar interference figures. This suggests that the crystallographic orientation of the crystal units is constant.

More surprisingly crystal unit spacing also appears to be remarkably constant within the
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Fig. 1.7 — *Pseudoemiliania lacunosa* biometric data. Data from measurements of photographs of *P. lacunosa* (s.l.) specimens, illustrating variation in various parameters with aperture width. Open symbols represent the computer-generated specimens of Fig. 1.8. Dotted lines in A show axial ratio Coccolith openness (D) 100 × central area length/coccolith length.
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group as a whole. This can be demonstrated by direct measurement of the width of the rays at the inner margin of the proximal shield (assuming again that this approximates to the protococcolith ring). Measurements of ray width in a range of species, mainly from published micrographs, are given in Fig. 1.9A. The ray widths only show a two-fold variation (0.1–0.2 μm), in comparison with a ten-fold variation in coccolith length. A similar pattern is shown by the results from within the single species *P. lacunosa* (Fig. 1.9B). The accuracy of the measurements is not high—with errors likely from inaccurate quotation of magnifications, specimen tilting, and choice of location to measure elements. These problems should, however, increase rather than decrease the variability.

Qualitatively the low variability in crystal unit spacing is reflected in the common observation that reticulofenestrids have very narrow rays, rarely resolvable by light microscopy. The only exceptions, such as *Cyclicargolithus floridanus*, have broad rims and narrow central areas (Fig. 1.5C).

**Summary:** The low variation in both crystallographic orientation and crystal unit spacing suggests that the nucleation processes were relatively constant during evolution of the reticulofenestrids. As such they are of importance as distinctive higher level taxonomic features of the group.

**Element growth variation**
Apart from the slitting mentioned above, reticulofenestrid crystal units are remarkably similar in all species. Constant features include the four-part structure (Fig. 1.6), the imbrication directions, and kinks in both the proximal and the distal shield rays (Fig. 1.5). Most reticulofenestrid coccoliths also have pointed ray tips, but this is probably related to the crystallography of the elements, and may in part be of diagenetic origin. The grill and wall cycles show most variation in mode and degree of development, and so are important in subdivision of the group.

In *Cyclicargolithus floridanus* and other Early Miocene and Oligocene reticulofenestrids the
wall elements, or a limited number of them, overlap onto the distal shield as cover plates (Fig. 1.5C). In most later reticulofenestrids there are no discrete cover plates; instead, a raised collar occurs around the central area (Fig. 1.5E). This is formed jointly by the wall cycle elements and the distal shield elements, which butt against them. A third type of development is for the wall to terminate flush with, or slightly below, the edge of the distal shield, without development of a collar or cover plates (Fig. 1.5G). This morphology is most characteristic of *Emiliania huxleyi*, but is also seen in some *Gephyrocapsa* specimens.

In all three cases the wall cycle can be thickened inwards to close the central area. Forms with this development are often placed in a separate genus, *Dictyococccites*. However, specimens of *Emiliania huxleyi* with closed central areas have been illustrated by several authors (e.g. Black 1968, Heimdal and Gaarder 1981), and this type of variation seems more likely to be of ecological than taxonomical significance. Probable exceptions are *Dictyococccites bisectus* (Fig. 1.5B) in which the central area is closed by a plug of inward-growing cover plates, and *Dictyococccites daviesii* in which a limited number of wall elements contribute to an expanded grill.

The general variability of wall cycle development is continued by two more radical structures. In *Gephyrocapsa* wall elements on opposite sides of the distal shield become elongated and arch over to form a bridge (Fig. 1.5H). The bridges always show the same diagonal orientation (NE-SW in distal view), and frequently the elements fail to meet precisely, with an anticlockwise offset. Etched specimens show that each half of the bridge is formed from two to five wall elements. *Noelaerhabdus* (a Late Miocene Paratethyan genus, Jerković 1970) has a single asymmetrically placed spine, similarly formed from a few wall elements (Fig. 1.5F).

The development of different structures from the wall is thus a consistent theme in reticulofenestrid variation. These new structures are thus produced by modification of the crystal units rather than by production of new crystal units. Moreover, the basic crystal unit structure is not changed; instead the final phase of its development is modified. In this respect the different structures fit well with the model proposed above. In contrast, the spine of *Noelaerhabdus* and the bridge of *Gephyrocapsa* show that crystal units in one part of the cycle can develop quite different forms to those in other parts of the cycle. This is an important modification of the general pattern of similar development of all crystal units. Here final coccolith form appears to be regulating element development, rather than vice versa. Some degree of interplay is nonetheless evident, in the offset of the bridge...
halves in *Gephyrocapsa*, and in the eccentricity of the spine of *Noelaerhabdus*. Also malformed *Gephyrocapsa* specimens with three or more half bridges grown from different parts of the wall sometimes occur (e.g. Okada and McIntyre 1977, Plate 3). In all these respects the final structure is distorted from symmetrical perfection by the developmental process.

Summary: It appears that basic crystal unit structure is constant in reticulofenestrates. Major modifications are mainly confined to addition of extra features and are usually taken as generic level features. Intraspecific variation can produce changes in the degree of development, causing variations in rim width, in degree of slitting, and in central area closure.

### 1.6 EXTENSION OF THE MODEL TO OTHER GROUPS

The following notes briefly outline the extent to which the three-phase–proto-coccolith ring model can be applied in other coccolith families. Only Neogene groups are discussed since I know these best.

(a) **Coccolithaceae**

The Coccolithaceae, like the reticulofenestrates, are placoliths. Coccolithogenesis has been studied in two species, *Coccolithus pelagicus* and *Umbilicosphaera sibogae*, and, as discussed above, coccolith development in them is very similar to that in *E. huxleyi*. The family is more heterogeneous than the reticulofenestrates. It contains at least three discrete groups: *Coccolithus* (plus *Chiasmolithus, Cruciplacolithus, and Clausicoccus*), *Umbilicosphaera*, and *Calcidiscus*. Within each of these groups there is a constant rim structure analogous to that of the reticulofenestrates, and similar variation patterns in such features as ellipticity, ray number and central area width can be recognised.

However, all the Coccolithaceae have at least two discrete cycles of crystal units, since the proximal and distal shields show contrasting optical behaviour, and the proximal shield is usually bicyclic. My interpretation of the structure is that there are two discrete rim cycles (Fig. 1.10A). An upper rim cycle (non-birefringent) forms the distal shield, outer tube, and upper part of the proximal shield. The lower rim cycle (birefringent) forms the lower part of the proximal shield. This obviously requires two separate sets of crystal nuclei. The plates of Manton and Leedale (1969, Figs. 28 and 31) provide striking evidence for this. They show the edge of the base-plate curving up during protococcolith formation, and separate crystals developing on either side of it, thus forming a double proto-coccolith ring.

In the *Coccolithus* group, further complexity is provided by the presence of a wall (i.e. inner tube elements, Fig. 1.10A). This is birefringent like the proximal shield, but is composed of many cycles of small elements. It is difficult to envisage these as all being connected to the proximal shield; instead it seems likely that they too require separate nucleation, which considerably increases the amount of crystal nucleation. Central area structures, such as the cross in *Cruciplacolithus*, are formed from similar elements and so unlike the central area structures in reticulofenestrates do not show any relation to the rim geometry.

(b) **Helicosphaeraceae**

The coccoliths, or helicoliths, of *Helicosphaera* consist of three main parts; proximal plate, flange and blanket (cf. Theodoridis 1984; see Fig. 1.15Q). *Helicosphaera* has not been grown in culture, so there is no information on coccolithogenesis in the genus. Norris (1971) has, however, illustrated a base-plate scale on *H. carteri*, entirely covering the proximal plate, and Gaarder (1970) recorded similar observations. Hence this is a likely position for the protococcolith ring. Strong support for this is provided by the form of the elements of the proximal plate, which show ray bunching and wedging inward, suggesting inward growth. The proximal plate can thus be interpreted as a normal cycle, but grown inwards, like the grills in the reticulofenestrates. The flange is composed of
the same number of elements as the proximal plate, and they have similar optical orientations (Young 1987b), so the elements of these two units are probably two components of a single cycle of crystal units. The flange, however, is a strongly modified cycle, with apparently considerable variation in crystal unit structure and length, producing the spiral effect. This is quite different from the uniform rim development of placolith coccoliths, and indicates a significant modification of the coccolith development process. It has a direct functional significance; the specialised rim form allows unusually regular and close interlocking of the coccoliths on the coccosphere (Young 1987a).

The proximal plate (and so proto-coccolith ring) shape is also irregular. It is often somewhat tapered or rhomboidal rather than truly

\textit{Coccolithus}

A

\textit{Pontosphaera}

B

\textit{Helicosphaera}

C

Fig. 1.10 — Schematic cross-sections through typical Coccolithaceae, Pontosphaeraceae and Helicosphaeraceae. Densely stippled parts are formed of numerous irregular cycles of concentrically arranged elements, which are birefringent in plan view. The other parts are cycles of larger elements, suggested to have developed from proto-coccolith rings located at the edges of the base-plate scales; arrow-heads indicate postulated directions of crystal growth. Except for the lower rim cycle of \textit{Coccolithus} (light stipple) these cycles are not birefringent in plan view.

\textit{ALL DRAWINGS ERRORS}
elliptical. Nucleation processes, as in the other groups, appear more constant, with a characteristic orientation and spacing of the elements. A separate problem is provided by the blanket. The elements of this unit have different optical orientations from those of the flange and proximal plate. However, they are floored by the proximal plate, and so must have nucleated on this rather than the organic base-plate.

(c) Pontosphaeraceae
The Pontosphaeraceae have a structure analogous to that of the Helicosphaeraceae, with proximal plate, flange and an inner–upper blanket of smaller elements (Fig. 1.10C). Guarder (1970) has illustrated a base-plate scale entirely covering the proximal plate on an ordinary coccolith of Scyphosphaera apsteinii. The flanges in both the Helicosphaeraceae and the Pontosphaeraceae display anticlockwise element imbrication, but otherwise have very different structures and forms. The relationship between the two families is by no means certain, but in terms of the coccolith development they appear to be similar.

There are also distinct similarities between the blanket elements in these two groups and the wall elements of the Coccolithaceae. In all cases they are small, sub-vertically oriented, lath-like, elements arranged in numerous irregular concentric cycles. They show strong birefringence in plan view, with an oblique extinction cross.

These elements thus differ from the rim cycles discussed above in that they are not arranged in regular cycles, did not nucleate on the edge of the base-plate, and have very simple structure. It would appear that they are the product of a different type, or fourth phase, of development, characterised by formation of numerous small crystal units, with less precise distribution in cycles, and less precise regulation of growth. Structures formed from these elements tend to be rather variable, and they are widely used for species level taxonomy.

(d) Holococcoliths
The diagnostic feature of holococcoliths is that they are formed of numerous minute identical elements. These holococcolith elements do not interconnect to form larger crystal units and are not arranged in uniform cycles; instead, elements show similar orientations over large zones, forming irregular pseudo-crystals. Also, few elements are in contact with the base-plate. Plainly the concept of development from a proto-coccolith ring is not applicable to holococcoliths. A quite different developmental model is needed to interpret their morphology. This is also suggested by evidence that they form by extracellular calcification (Manton and Leedale 1963, Rowson et al. 1986), and they show entirely different styles of morphological variation to heterococcoliths.

(e) Other groups
The model of development from a proto-coccolith ring is probably applicable to Syracosphaeraceae, Calcirosoleniaceae, Zygodiscaceae and most Mesozoic heterococcoliths, but I have not examined them in detail. Discoasters and sphencococcoliths can readily be envisaged as developing in an analogous manner, but with little or no base-plate development.

Groups with structures which appear to reflect different development processes include Rhabdosphaeraceae—spirally arranged cycles of small elements (but rim is analogous), Braarudosphaeraceae—layered ultrastructure, and Ceratolithaceae and Triquetrorhabdulaceae—completely different shape and structure.

1.7 SUMMARY
(1) Examination of coccolith morphology suggests that the three-phase pattern of heterococcolith cycle development observed in studies of coccolithogenesis is of general application. The phases are base-plate formation, crystal nucleation, and element growth. The first two stages produce a proto-coccolith ring, the third develops it into a coccolith.
(2) Both nucleation and growth processes are usually uniform around cycles, except where
elements interfere with each other. Departures from this pattern, such as flange development in *Helicosphaera* and bridge formation in *Gephyrocapsa*, probably require functional explanations.

(3) Structural complexity in heterococcoliths is primarily a result of elaborate crystal unit structure, rather than production of numerous separate cycles of crystal units. This can be a valuable perspective for elucidating coccolith structure and looking for homologous structures within families.

(4) Intraspecific variation can occur, and evolution operate, during any of the developmental phases, with varying effects on final form. Some aspects, however, are more stable than others. Most stable are nucleation-related features—element spacing, orientation and number of cycles. Crystal unit structure is only slightly less stable, but element length and degree of calcification are both, and independently, liable to intraspecific variation. Base-plate—and so proto-coccolith ring—diameter is similarly variable, and in some species is accompanied by shape variation.

![Diagram of coccolith growth]

Fig. 1.11 — Allometric coccolith growth.
Three large coccoliths (B)–(D) derived from a smaller one (A) without variation in initial ray spacing, and consequently showing variation in form: (A), (B) increase in proto-coccolith ring width only (e.g. *P. lacunosa*); (A)–(C) balanced increase in rim and ring width (e.g. *R. pseudoumbilicus*); (A)–(D) increase in rim width only (e.g. some *E. huxleyi* specimens).
An important result of the stability of crystal unit spacing is that larger coccoliths inevitably differ from smaller ones of the same species—whether the size variation is caused by variation in proto-coccolith ring diameter, rim width, or a combination of the two (Fig. 1.11).

This model is applicable to the development of typical rim, flange, and proximal plate cycles in Neogene heterococcoliths. It does not appear to be directly applicable to some central area structures, to blanket elements, or to holococcoliths.

The model is directly applicable to the problem of mathematically describing coccoliths, and forms the theoretical basis of a computer program used to produce illustrations of coccoliths.

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1.9 REFERENCES

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Observations on heterococcolith rim structure


