NANNOFOSSILS AND THEIR APPLICATIONS

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Preface

The present volume is the second that has been produced after a meeting of the INA, the International Nannoplankton Association. The meeting in London, which was attended by 50 participants from Europe, Africa, America and Asia was held from the 19–21st of August 1987. It was followed by a one day excursion to the Upper Cretaceous and Palaeogene sediments cropping out at the South coast of England. Having called the INA meeting in Vienna (1985) the third formal INA Meeting, the meeting in London can be called the fourth, if we consider the workshop held in 1986 in Woods Hole as an informal gathering.

The organising committee consisted of Shirley van Heck and Jason Crux, who also edited this volume, and Alan Lord, who was our host at University College. They were assisted by students and staff of the Micropalaeontology Unit who not only organised the viewing of the slides and the coffee, but also arranged three excellent buffet lunches. The conference party was held onboard a ship cruising up and down the Thames.

The scientific program started with an invited lecture by P. Westbroek on "Coccolithophorids and the integration between earth and life sciences" followed by presentations on living and Neogene coccoliths. The second day was dedicated to various aspects of Cretaceous, Jurassic and Triassic calcareous nannofossils. On the third day, talks included discussions on phylogenetic strategies and on geological processes and events and nannofossil distribution. The many posters on both coccolithophorids and silicoflagellates furnished ample food for discussions. The beginnings of a computer program on systematics of coccoliths (so far mainly Jurassic) were presented by H.J. and K.M. Dockerill, while J. Young demonstrated his program for computer-drawn coccoliths and discoasters. Most abstracts were published in a special edition of the INA Newsletter, 9/2 and a late one in 9/3.

The fieldtrip was organised by Jason Crux who was helped by Ray Milbourne, Nigel Robinson and David Ward.

Three localities were visited where Middle and Upper Albian was sampled at Copt Point near Folkestone, the classical locality treated in detail in the monographs of Black. The Turonian and Coniacian chalk was studied at the Langdon Stairs in the Cliffs of Dover and the basal part of the Thanetian stratotype at Pegwell Bay near Ramsgate. The fine day was concluded with a fine dinner in Canterbury.

INA thanks the organising committee and all those involved in a direct or indirect way in the organisation of the London Meeting, the Excursion and these Proceedings.

London,   Katharina Perch-Nielsen
September 1988   President I.N.A.

Introduction

This volume contains the proceedings of the International Nannoplankton Association London Meeting 1987. Of the 31 papers and posters presented at the meeting, 13 are included in this book. One additional paper is included which was scheduled for the meeting but which could not be presented because at the last moment the author was unable to attend.

The book has been divided into three parts, each focussing on a different aspect of nanno-plankton studies. Some papers focus on more than one aspect, and these have been grouped according to that aspect that seemed most prominent to the editors. Within each part the papers are ordered in stratigraphical sequence from young to old. Part I deals with pure morphology and systematics, containing papers on coccolith structure and growth (Young), phylogenetically based taxonomy (Aubry), taxonomy, structure and evolution of *Reticulo-fenestra* (Gallagher), crystallography and optical properties (Moshkovitz and Osmond), and conical nannofossils (Bown and Cooper). Part II focusses on ecological factors such as palaeobiogeography with papers on variation in assemblages during the last glacial cycle (Gard), temperature-controlled migration in the Aptian (Mutterlose), palaeogeography and bio-stratigraphy in the Lower Cretaceous (Crux), a comparison of North Atlantic assemblages in the Lower Cretaceous (Applegate, Bergen, Covington and Wise) and nannofossil provincialism in the Late Jurassic–Early Cretaceous (Cooper). Part III contains papers that show stratigraphical applications, such as Tortonian–Messinian stratigraphy (Flores and Sierro), Palaeocene stratigraphy (Varol), Palaeocene–Eocene stratigraphy of Turkey (Toker) and stratigraphical and palaeo-environmental importance of *Arkhangelskiella* (Girgis).

In general the editors have aimed to restrict the number of references with each paper, and the reader is referred to the contributions of Perch-Nielsen in Bolli, Saunders and Perch-Nielsen, 1985, *Plankton Stratigraphy*, Cambridge University Press, Cambridge, and to the references in the Loeblich and Tappan index and bibliography (1966–1972) and INA Newsletter (1979–1988).

It has been attempted to avoid nomen-claturally incorrect (invalid/illegitimate) names, but exceptions have been made for names that are in general use (such as *Discoaster*) or those for which no correct alternative was available.

To avoid lengthy and cumbersome citations in the text, the book contains a taxonomic index containing the full citation for the taxa. Names of taxa occurring only as part of a zonal name have not been included in this index, nor have informal names such as 'discoasters' or 'nanno-conids' been included. The page numbers (213) and plate numbers (13.1) have been included separately, and entries referring to introductions of new names, descriptions of taxa and pictures of holotypes are printed in bold.

Apart from the taxonomical index this volume contains a general subject index.

Part I

Morphology, Systematics and Evolution

The peculiar geometry of a rhombohedral crystal lends itself to the development of a great variety of elaborate patterns when groups of such crystals are forced to fit into a circular or elliptical framework, and the oblique direction of the optic axis leads to very distinctive interference effects in polarized light.

Black 1963

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1

Observations on heterococcolith rim structure and its relationship to developmental processes

Jeremy R. Young

Qualitative and quantitative observations are made on the structure and geometry of hetero-coccolith rims, using primarily published electron micrographs. This information is combined with a brief review of coccolith development during coccolithogenesis. A three-stage model for heterococcolith development is outlined: (1) formation of an organic base-plate; (2) uniform crystal nucleation around the edge of the base-plate, producing a proto-coccolith ring; (3) uniform element growth from this proto-coccolith ring. The application of this model to reticulofenestrid coccoliths and the effects of variable development at each stage are discussed. Its application to various other groups is outlined and its limitations noted.

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 bire-fringence 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 leptoporus, 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.
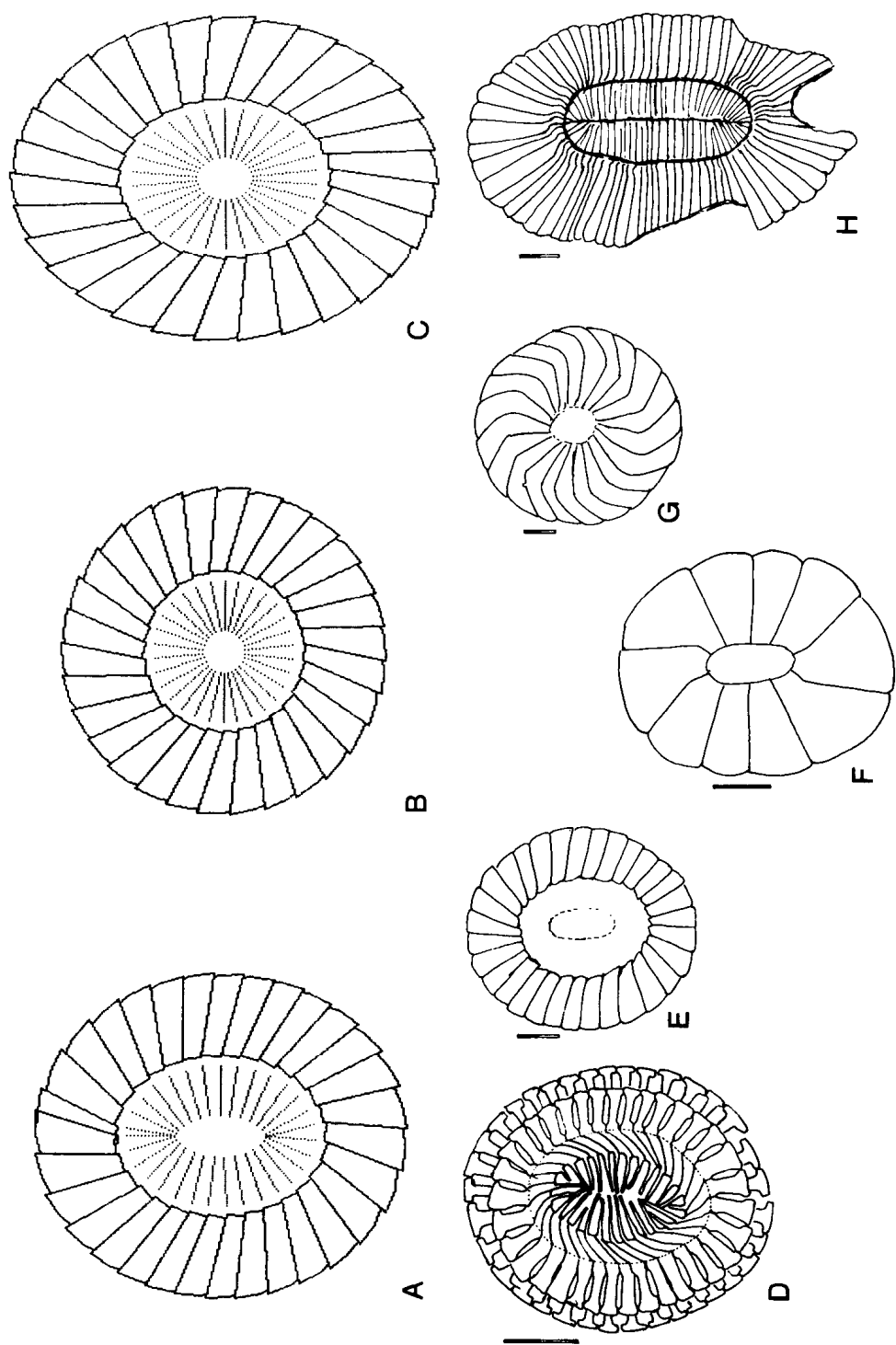
Fig. 1.1 — Coccolith rim geometry.

(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.

(D)–(H) Tracings of coccoliths (scale bars, 1μm; sources Roth 1970, Bukry 1971, 1974, Perch-Nielsen 1971, 1977): (D) *Emiliania huxleyi*, proximal; (E) *Coccolithus pelagicus*; (F) *C. crater*; (G) *Calcidiscus leptoporus*; (H) *Ellipsolithus macellus*, proximal.
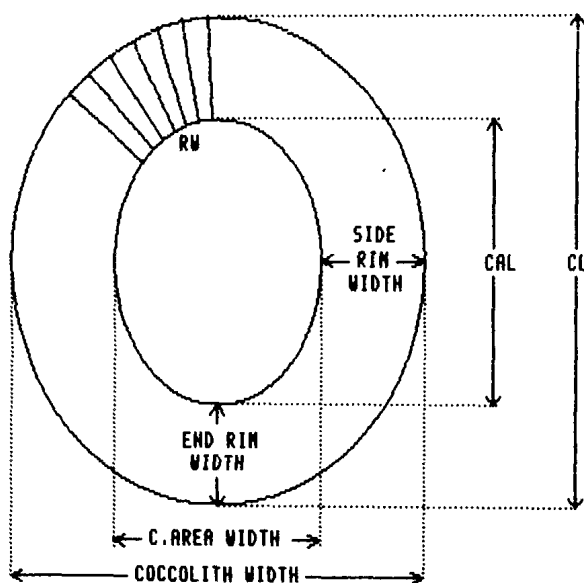
Fig. 1.2 — Biometric parameters.
Key to the features plotted in Figs. 3, 7 and 9. Abbreviations; CAL, central area length; CL, coccolith length; RW, ray width (averaged from 3 to 6 rays).

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.

(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.

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.

A — Rim width at sides vs rim width at ends (μm)
- P.LACUHOSA
- OTHER RETICULOFENESTRIDS
- COCCOLITHACEAE

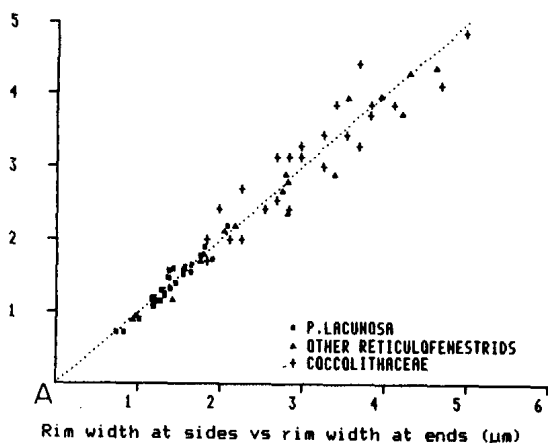B — Coccolith axial ratio vs central area axial ratio

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.
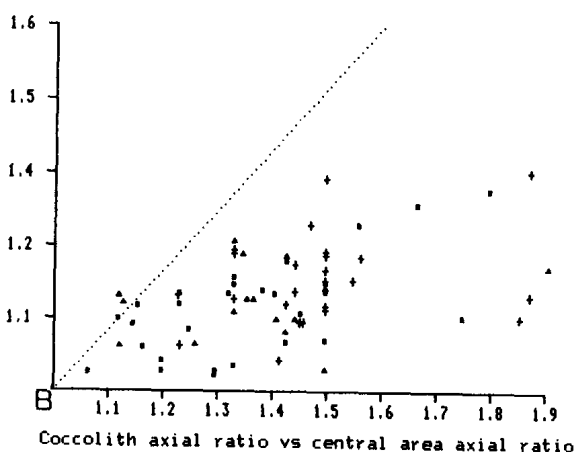
(d) Discussion

This succession of mismatches between the coccolith morphology derived by stretching a circular coccolith and that of real coccoliths makes it plain that coccolith morphology is not controlled in this manner. The rim width data suggest that the distortion implicit in the derivation of an elliptical coccolith from a circular one is primarily confined to the central area, whilst the rim is only indirectly affected. Support for this concept is provided by the, tentative, evidence that the orientation and spacing of elements is constant around the inner margin of the rim. Thus it is attractive to consider coccoliths as being formed from elements of constant basic form with coccolith structure determined by the form of the elements, their orientation and positions. Analogous structures can be created with a pack of playing cards.

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 hetero-coccolith 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).
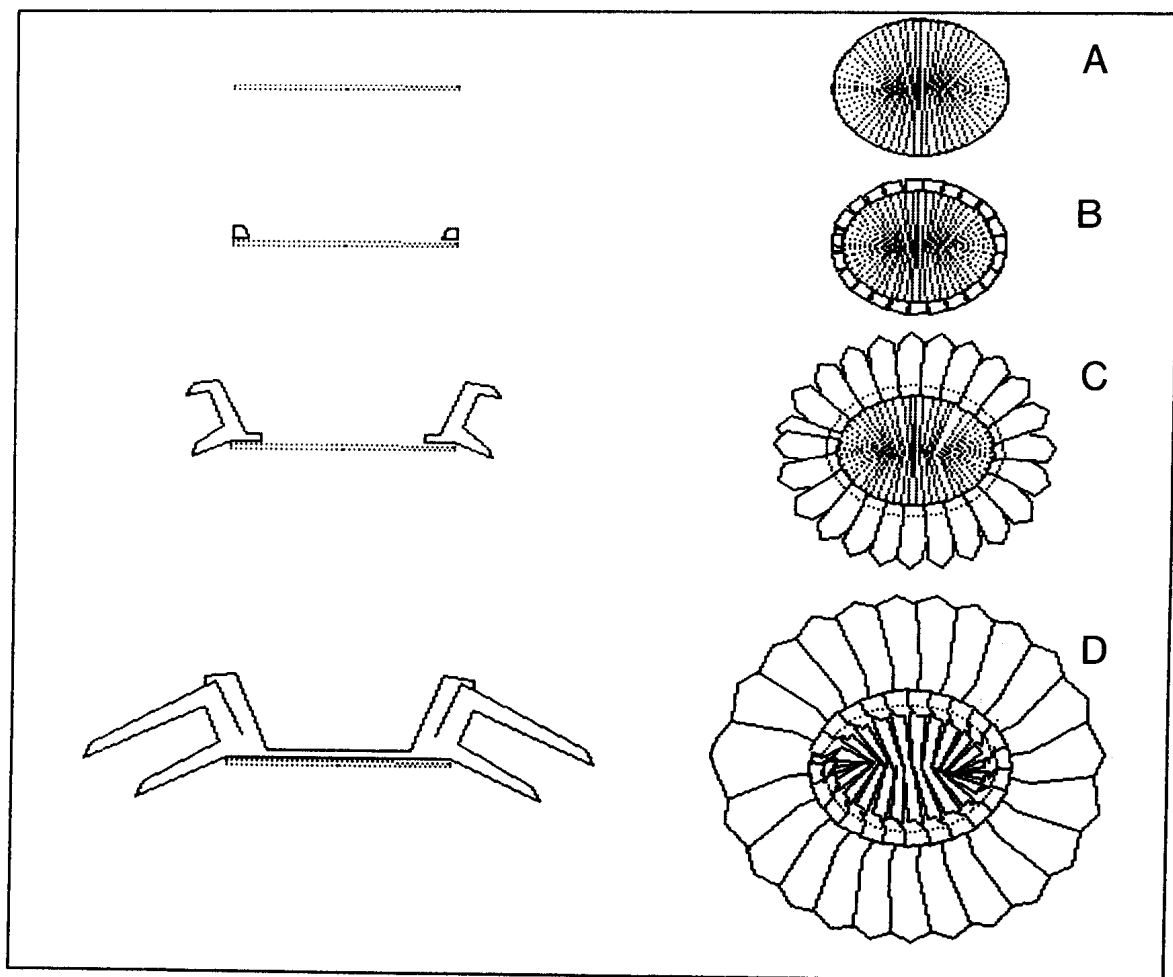
Fig. 1.4 — Coccolith development.
Series of diagrams showing intracellular coccolith development. Organic base-plate scale shown by dotted lines. Left — sections, right — plan views (distal side): (A) base-plate only; (B) base-plate and proto-coccolith ring; (C) partially formed coccolith; (D) final form.

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 proto-coccolith rings, suggest that, at least to a first approximation, the elements are uniformly

spaced at this stage, with a constant orientation relative to the base-plate margin.

(3) Element growth: this occurs in various directions but leaves the proto-coccolith ring on the proximal surface of the coccolith. Rim cycles are formed by outward growth of elements, and so have different structures from central area features which are formed by inward growth of elements. The constant width of coccolith rims suggests that elements develop to uniform lengths during this process. All the elements of a cycle also tend to have similar shapes, apart from width variation due to differences in curvature of the ring. The asymmetry introduced by elliptical base-plates appears to be compensated for by variable lateral expansion of elements or by their overlapping to varying degrees. The basic form, initial spacing, and orientation of the crystal units do not seem to be affected by the variable curvature.

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