

# PROPOSALS FOR A REVISED CLASSIFICATION SYSTEM FOR CALCAREOUS NANNOPLANKTON

We have recently been working on a new version of *A Stratigraphical Index of Calcareous Nannofossils* (Bown, in press). During this work we needed to address the question of the classification of nannofossils, and attempted a comprehensive generic-level review. We had originally intended to publish this in the book but space constraints prevented this. In addition, since one of the problems of classification is a lack of consensus, it seemed sensible to proceed on a broader basis. So, following consultation with various INA committee members, we decided to publish a working draft classification here in good time for subsequent discussion at the Puerto Rico INA Conference, at which we will host a workshop during which the following papers will be thoroughly discussed. Eventually, it is our intention to publish a final version of these papers, incorporating the results of these workshop discussions, as a handbook which will be distributed to all members of the INA. We have set out the classification in three separate papers. First, a discussion of the higher-level approach adopted and its relationship to previous classifications, followed by separate sections on Mesozoic and Cenozoic nannofossils. The Mesozoic/Cenozoic divide follows the precedent of Perch-Nielsen (1985a, b), and for much the same reasons: most major groups are predominantly confined to one era or other, so that grouping Mesozoic and Cenozoic nannofossils together in taxonomic sequence results in awkward alternations between the two eras.

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# HIGHER CLASSIFICATION OF CALCAREOUS NANNOFOSSILS

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## **Classification development**

The starting point for this overview was the comprehensive review and classification of nannofossils of Perch-Nielsen (1985a, b), complimented by, in particular, the Jurassic nannofossil classification of Bown (1987, 1996) and the classification of extant haptophytes by Jordan and co-workers (Kleijne, 1993; Green & Jordan, 1994; Jordan & Kleijne, 1994; Jordan & Green, 1994; Jordan *et al.*, 1995). Important earlier sources for these classifications include Parke & Dixon (1976), Hay (1977), Okada & McIntyre (1977) and Tappan (1980). In order to provide a comprehensive synthesis, we paid special attention to taxonomic papers published since 1985, as catalogued in the INA Bibliography and Index of Taxa. For the Tertiary, the reviews of Aubry (1984 *et seq.*) were invaluable sources, although they are based on a slightly different taxonomic philosophy.

## **Top-down subdivisions vs bottom-up groupings**

Two main approaches can be identified in the classification of calcareous nannofossils. The *top-down subdivision* approach has attempted to classify the range of nannofossils into well-defined subdivisions using clear-cut criteria based on major aspects of shape or structure. For instance, Deflandre (1950) divided all nannofossils into ortholiths and helioliths based on whether they showed radial calcite orientations (helioliths) or were formed of single calcite crystals (ortholiths, including the constituent segments of pentoliths). The *bottom-up grouping* approach, by contrast, has been based on organisation of species into genera and of genera into families based on multiple similarities of morphology, existence of intergradational morphologies and stratigraphic distribution. The latter, bottom-up, approach is, we believe, more productive and leads to a more natural classification, and it is the predominant method applied in Perch-Nielsen (1985a, b). This forms the basis for our formal classification into genera, families and orders. The top-down subdivision approach is, however, valuable for organising taxa of uncertain inter-relationship and so we apply a system of this type to arrange the higher taxa we recognise in a logical sequence, and in some cases to provide arbitrary subdivisions of particular taxa.

## ***Incertae sedis* and informal categories**

A key objective of classification is to systematise our existing knowledge. Conversely, an obvious pitfall of classification is to provide, via spurious pigeon-holing, the impression of knowledge where none exists. To avoid this we have attempted to discipline ourselves and only to include genera within families (or families within orders) where there is good positive evidence for doing so. As a consequence, the classification is not comprehensive - many genera are left as of uncertain family/order, and many families are not assigned to an order. We do not apologise for this, since it is a simple reflection of the limits of current knowledge.

## **Use of orders as well as families**

The only higher taxonomic category which has been universally applied is family and we continue to use families as the main level of classification. However, in revising the classification, we considered that exclusive use of families was unduly

restrictive and that, with around 50 families, important relationships would be obscured.

We decided to use orders (Figure 1), rather than to subdivide families, in order to retain as many taxa as possible at their current level, the alternative being to reclassify many well-established families as subfamilies. Also, orders have previously often been used in nannofossil classifications, notably by Hay (1977), Tappan (1980) and Bown (1987). The principle potential problem here is discordance with use of orders in the classification of modern haptophytes. Classifications of modern haptophytes have, following Parke & Green (*in* Parke & Dixon, 1976), usually recognised four orders: Coccosphaerales (coccolith-bearing), Prymniales (typical non-coccolith-bearing haptophytes, haptonema well developed), Isochrysidales (haptonema diminutive, including some coccolith-bearing genera), and Pavloales (with the flagella of unequal lengths, the longer flagellum with hairs and scales, haptonema diminutive). Recent work on molecular genetics, cytology and biochemistry, have unequivocally established the distinctive nature of the Pavloales and they are now separated as a discrete class or subclass (Green & Jordan, 1994). The subdivision of the remaining haptophytes into the other three orders has not, however, been supported by subsequent studies, with the result that Green & Jordan (1994) recommended subsuming all these orders into the single subclass Prymnesiophycidae, order Prymniales. Given this abandonment of the traditional ordinal-level classification of extant haptophytes there is no obvious problem in introducing a new ordinal-level classification based in the first place on coccolith morphology, although obviously future research on aspects of haptophyte biology is liable to result at least in modifications of this classification. Nonetheless, this is not an area where we are especially dogmatic, and debate on use of particular levels of classification would be welcome.

#### **Paraphyletic and polyphyletic taxa**

We have not attempted to avoid paraphyletic taxa, *i.e.* taxa which give rise to other taxa of the same, or higher, level (Figure 2). For instance, according to our current understanding of coccolithophore phylogeny, the family Zygodiscaceae is paraphyletic since it is inferred to have given rise to the families Pontosphaeraceae and Helicosphaeraceae. Similarly, the genus *Lophodolichus* is paraphyletic if we accept the interpretation that it gave rise to the genus *Helicosphaera* and family Helicosphaeraceae. This is manifestly an unavoidable problem in nannofossil systematics since we have abundant evidence of ancestor-descendant relationships. To give an extreme example, the genera *Praeprinsius*, *Prinsius*, *Toweius*, *Reticulofenestra*, *Gephyrocapsa*, and *Emiliana* are widely inferred to constitute an evolutionary lineage (*e.g.* Romein, 1979; Gallagher, 1989) and so all these, except *Emiliana*, are paraphyletic.

On the other hand, it is clearly essential to eliminate polyphyletic taxa, *i.e.* all species included in a higher taxon must have a common ancestor within that taxon (Figure 2). This is an absolute necessity of a biologically meaningful classification - if available evidence suggests that a taxon contains unrelated sets of species then it must be revised. Of course, we often do not know for certain whether a group of more or less similar species is directly related or simply a set of convergent homeomorphs. All taxonomic groupings may be regarded as hypotheses which may be tested through analysis of morphology and direct evolutionary data. Our general approach has been to avoid giving taxonomic names to any subdivisions which we feel are likely to be polyphyletic, for instance we have followed Kleijne (1991) in dividing the large number of extant holococcolith-bearing genera into two groups based on whether they show dimorphism or not. However, since this character is very likely to have evolved repeatedly, it does not form a suitable basis for grouping the genera into formal taxa.

#### **Heterococcoliths, holococcoliths and nannoliths**

A special problem with nannofossil taxonomy is the uncertainty as to whether the structures we are examining are homologous. Indeed, we know that holococcoliths and heterococcoliths are not homologous, whilst we are uncertain as to the nature of nannoliths. This requires some discussion, and in addition there are separate taxonomic problems associated with each of these groupings.

### **Heterococcoliths**

This is the predominant group, usually defined as coccoliths formed of a limited number of complex and variably shaped crystal-units. The precise scope of the term heterococcolith is vague but there is no dispute that the term is based on typical extant coccoliths such as those of *Coccolithus*, *Emiliana*, *Pleurochrysis* and *Syracosphaera* (see also original description of Braarud *et al.*, 1955). These all share the basic morphology of a rim formed of a radial array of complex crystal-units surrounding a central-area, with variable structures in the central-area. This basic morphology characterises numerous living and fossil groups and forms an essential part of most workers' concept of an heterococcolith. There is also evidence that this is a natural, non-polyphyletic, grouping: (1) studies of evolution in the group tend to indicate a pattern of common origin and subsequent divergence, with no obvious indications of polyphyly (e.g. Bown, 1987; Romein, 1979; Bown *et al.*, 1992); (2) our ultrastructural research (Young & Bown, 1991; Young *et al.*, 1992; unpublished data) suggests that a widespread, and probably universal, feature of heterococcoliths is V/R mode biomineralisation, *i.e.* biomineralisation which commences with nucleation of a proto-coccolith ring of alternating subvertical and subradial crystal-units, which subsequently develop to form the rim. This type of biomineralisation is characteristic of all the heterococcolith families recognised here except possibly the Rhabdosphaeraceae (only V-units definitely identified), Hymenomonadaceae and Papposphaeraceae. V/R mode biomineralisation is a distinctive and sophisticated type of calcification and it seems reasonable to assume that it is a reliable synapomorphy (shared derived character state), and that the heterococcoliths as a whole form a non-polyphyletic group.

### **Holococcoliths**

Holococcoliths are plainly formed by a very different biomineralisation process to heterococcoliths. Nucleation must occur across the entire coccolith and the individual crystals retain simple euhedral morphologies. As a result, there is no clear distinction between the rim and central-area. Moreover, available evidence suggests that calcification occurs extra-cellularly (Rowson *et al.*, 1986), rather than intracellularly. Finally, there are now several well-established cases of holococcoliths and heterococcoliths occurring on alternate phases of the life-cycle of single species. Billard (1994) synthesises this evidence and suggests that it reflects a haplodiplontic life-cycle, with holococcoliths consistently occurring in the haploid phase. This rather suggests that biomineralisation may have evolved independently in the haploid and diploid phases, and that holococcoliths and heterococcoliths are not meaningfully homologous (Figure 3). Possibly we should consider holococcolith and heterococcolith taxonomy as independent, much as spore and whole-plant taxonomy are.

Holococcolith biomineralisation is distinctive and sophisticated. Crystallite faces are perfectly aligned across large zones, implying precise control of both *a*- and *c*-axis orientation, and the uniformity of crystallite size implies similarly precise control of nucleation spacing. Like V/R mode biomineralisation in heterococcoliths, it is unlikely that the holococcolith biomineralisation mode has evolved repeatedly, rather we can regard holococcolith formation as evidence for common descent of all taxa in which it is developed. Plainly though, both holococcolith formation and heterococcolith formation may have been lost repeatedly during the evolutionary history of haptophytes. So there is no reason for assuming that all

holococcoliths will have heterococcolith-bearing phases, or that all species which are known to have both holo- and heterococcolith-bearing phases will be particularly closely related. Future research will certainly help elucidate relationships. In the interim, it is entirely logical for all holococcolith bearing taxa, without known heterococcolith phases, to be classified together, in the family Calyptosphaeraceae.

Unlike heterococcoliths, holococcolith biomineralisation does not provide obvious characters for reliably subdividing the group. Homology is difficult to establish since the basic structure appears to consist of a simple mass of crystallites, gross morphology appears to be of limited value, and there are serious problems due to dimorphism. So at present, subclassification of the Calyptosphaeraceae is confined to a rather unsatisfactory, and probably partially artificial, generic classification. This applies particularly to extant holococcoliths for which crystallographic orientations are poorly known. In the larger fossil holococcoliths, subdivision into blocks with predictable crystallographic orientations appears to provide a reasonable basis for classification, but original morphology and possible dimorphism cause separate problems.

### **Nannoliths**

When Braarud *et al.* (1955) defined the terms heterococcolith and holococcolith, they explicitly described the pentaliths as a third category of similar status. This was a logical proposal since pentaliths show different structures to any heterococcoliths and it is reasonable to infer they have formed by a significantly different growth/biomineralisation process, and therefore are not directly homologous. The same applies to numerous other groups, particularly amongst the extinct nannofossils, *e.g.* sphenoliths, nannoconids and discoasters. The term nannoliths has been widely used as a collective term for this group (*e.g.* Perch-Nielsen, 1985a, b; Bown, 1987; Aubry, 1984 *et seq.*; Young *et al.*, in press). The most common definition is calcareous nannofossils of uncertain affinity, but probably related to coccolithophores, *i.e.* formed by haptophytes.

Although nannoliths are highly variable, several features are repeatedly shown: (1) most nannoliths have morphologies which are at least suggestive of having been part of a composite exoskeleton; (2) most nannoliths are formed of morphologically-complex crystal-units analogous to those of heterococcoliths, although in some cases with evidence of additional ultrastructure (*e.g.* laminae within pentalith crystal-units); (3) for all known nannoliths there are consistent relationships between morphology and crystallographic orientation; (4) most nannoliths definitely show consistent handedness or chirality (deviation from radial symmetry), *e.g.* nannoconids always show clockwise imbrication, *Braarudosphaera* sutures are always offset clockwise from the median point of the pentalith edge; (5) nannoliths typically have biogeographic patterns suggesting planktonic origin and as a group are only known from the Triassic to Recent.

These features all suggest close affinities with coccolithophores. Moreover, haptophytes are the only plankton group known to produce calcareous scales. Dinoflagellates also calcify but they form calcispheres rather than discrete scales. Various other phytoplankton produce scales, *e.g.* Prasinophytes and Chrysophytes, but these are either unmineralised or siliceous. Hence, an assumption that nannoliths are produced by haptophytes has seemed reasonable to phycologists and has been supported by independent evidence in several cases, *e.g.* association of ceratoliths and coccoliths (Norris, 1965; Alcober & Jordan, 1997), observation of haptonema on *Polycrater* (Thomsen *et al.*, 1994), LM observations of typical haptophyte cell-features for *Braarudosphaera* (J. Green, pers. comm., 1996).

Nannoliths as a whole are, however, almost certainly polyphyletic, probably including: (1) modified heterococcoliths (?*Florisphaera*, ?polycycloliths, ?helioliths, ?fasciculiths, ?sphenoliths); (2) modified holococcoliths (?ceratoliths, ?Lithostromationaceae); (3) and nannoliths formed by entirely different biomineralisation mechanisms (?pentaliths, ?*Polycrater*, ?nannoconids). So they cannot be regarded as a formal taxonomic group, even though it is extremely useful to distinguish them from the more rigorously definable holo- and heterococcoliths. Further research will probably allow some to be reclassified as aberrant heterococcoliths or holococcoliths, whilst others may prove to be discrete groups.

### Formal higher classification

The haptophytes were traditionally included in the phylum Chrysophyta along with a range of other golden-brown, scale-bearing algae. However, Parke *et al.* (1955) recognised the haptonema as a unique structure, and following this they were recognised as a distinct class by Christensen (1962) and division by Hibberd (1972). Rather unfortunately, Hibberd (1976) argued that the name Haptophyta was unsuitable since it was not based on a generic root. He proposed the alternative name Prymnesiophyta, and this name was widely used in the literature until recently. However, as noted by Green & Jordan (1994), under the *International Code of Botanical Nomenclature*, division-level names do not need to be typified and the name Haptophyta has priority. Following from this, the common term haptophyte is preferable to prymnesiophyte; it is also a less forbidding term so we expect it to rapidly regain universal currency.

Notwithstanding this nomenclatural confusion, the separation of the haptophytes on the grounds of flagellar character has been well supported by much other evidence from cytology, biochemistry and molecular genetics. There is no dispute that they form a discrete algal protist group separable at division/phylum level. Chloroplast colour, however, reflects rather fundamental aspects of pigment biochemistry, *e.g.* green algae and land plants all have chlorophyll *a* and *b*. By contrast, golden-brown algae, including haptophytes, have chlorophyll *a* and *c*. This unites them with a range of other non-green algae, including the diatoms and silicoflagellates. Another common feature of this group is that the chloroplasts are surrounded by four membranes, which is interpreted as the result of a complex endosymbiosis history. Finally, most of these groups have two flagella, one short and smooth, the other long and bearing tubular hairs (heterokont). On the basis of this set of shared characters, Cavalier-Smith (1981, 1994) has proposed removing the group from the Protista to form a separate kingdom, Chromista, also including various protozoa which show the same heterokont flagellation. The haptophytes, as noted above, have two smooth flagella, and so do not show heterokont flagellation, hence their position in this group is somewhat uncertain, but the general interpretation is that they are a primitive group that diverged prior to the evolution of heterokont flagellation (*e.g.* Cavalier-Smith, 1994).

Within the haptophytes, only the single class Prymnesiophyceae is now recognised, divided into two subclasses, the Prymnesiophycidae and Pavlovophycidae (see Green & Jordan, 1994). All coccolithophores belong to the Prymnesiophycidae, and so to:

Kingdom **CHROMISTA** Cavalier-Smith, 1981

Division (Phylum) **HAPTOPHYTA** Hibberd *ex* Cavalier-Smith, 1986

Class **PRYMNESIOPHYCEAE** Hibberd, 1976

Subclass **PRYMNESIOPHYCIDAE** Cavalier-Smith, 1986

### **Layout**

The same format has been adopted for both of the following papers. For each genus, the original authorship is given, followed by important synonyms in brackets (). There are then short notes outlining the basis for distinguishing the genus. Terminology used in these descriptions follows Young *et al.* (in press). In some places we have included genera which are arguably redundant, and these are placed in square brackets [].

The formal systematic classification is supplemented, as seems useful, by informal groupings. These are numbered and given in bold. In most cases, these subdivisions are arbitrary and are likely to prove artificial/polyphyletic, hence they are not proposed as the bases for future formal classification.

Constraints of space meant it was not practical herein to provide a complete bibliography of taxonomic references. The references can, however, be found in Perch-Nielsen (1985a, b), and/or the INA Bibliographies.

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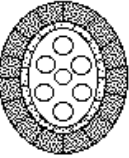

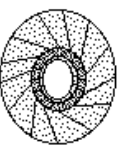

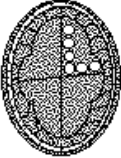



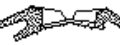


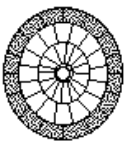


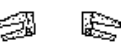




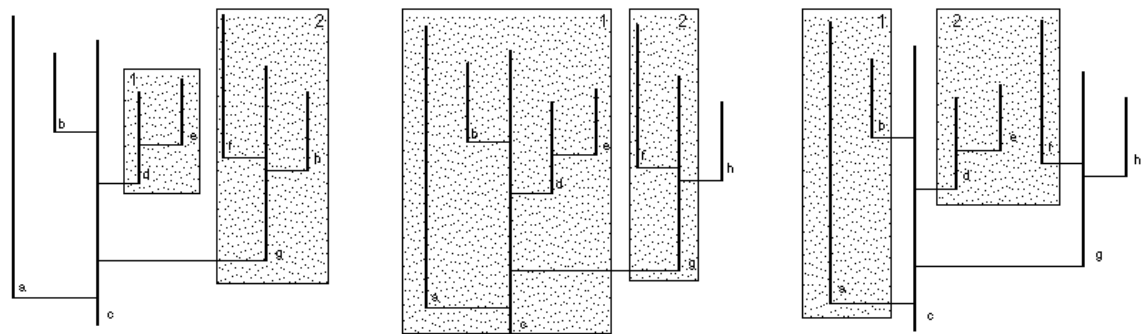
MAINLY MESOZOIC ORDERS	<b>EIFFELLITHALES</b>   Chiastozygaceae Eiffellithaceae Rhagodiscaceae	<b>STEPHANOLITHIALES</b>   Parhabdolothaceae Stephanolithaceae ?Calciosoleniaceae	<b>PODORHABDALES</b>   Axopodorhabdaceae Biscutaceae Calyculaceae Prediscosphaeraceae - STRUCTURE UNCERTAIN - Cretarhabdaceae Mazaganellaceae Tubodiscaceae	<b>WATZNAURIALES</b>   Watznaueriaceae	<b>ARKHANGELSKIALES</b>   Kamptneriaceae - STRUCTURE UNCERTAIN - Arkhangelskiellaceae	<b>NANNOLITHS</b> Braarudosphaeraceae Eoconusphaeraceae Goniolithaceae Lapideacassaceae Microrhabdulaceae Nannoconaceae Polycyclolithaceae Schizosphaerellaceae + <i>Ceratalithoides</i> <i>Ceratalithina</i>
	<b>ZYGODISCALES</b>   Pontosphaeraceae Zygodiscaceae  Helicosphaeraceae	<b>SYRACOSPHAERALES</b>   Syracosphaeraceae <div style="border: 1px solid black; padding: 5px; margin-top: 10px;"> <b>FAMILIES INCISED</b>            Hymenomonadaceae            Papposphaeraceae         </div>	<b>RHABDOSPHAERALES</b>   Rhabdosphaeraceae	<b>PRINSIALES</b>   Noelaerhabdaceae  Prinsiaceae	<b>COCCOSPHAERALES</b>   Coccolithaceae ?Pleurochrysidaceae  Calcidiscaceae	<b>NANNOLITHS</b> Braarudosphaeraceae Goniolithaceae Lapideacassaceae Discoasteraceae Fasciculithaceae Heliolithaceae Sphenolithaceae Lithostromationaceae Ceratolithaceae Triquetrorhabdulaceae

Fig. 1 HETEROCOCCOLITH ORDERS

 R-units
  V-units
  Other

Figure 1: Proposed heterococcolith orders. Sketches illustrate distal views, and side-views with interpreted cut-away cross-sections. Vertical thickness of cycles is sometimes exaggerated to clarify structure.



#### HOLOPHYLETIC TAXA

Grouping including a common ancestor and *all* its inferred descendants. This is an ideal type of taxon in any classification system, but note that it is not possible to subdivide a tree into a set of non-overlapping holophyletic taxa - if genera 1, 2 are defined as above, then any genus containing species c will be paraphyletic.

#### PARAPHYLETIC TAXA

Grouping including a common ancestor but *not* including *all* descendants of that ancestor. Taxa of this type are not recognised in cladistic classifications but are essential for Linnean classification, especially of groups in which inferred ancestor-descendant relationships form part of the phylogenetic evidence.

#### POLYPHYLETIC "TAXA"

Groupings which do not include a common ancestor within the taxon. Any features which distinguish e.g. spp. a and b from c must be the result of convergence rather than common ancestry. Such taxa are inadmissible.

NATURAL GROUP

**MONOPHYLETIC TAXA** - the term monophyletic is used in two quite distinct senses. (1) In cladistics, it is used as a preferred alternative to holophyletic. (2) In traditional systematics, it is used as a term meaning non-polyphyletic and so including both holophyletic and paraphyletic taxa. To avoid ambiguity the term is best avoided.

Figure 2 - Holophyletic, paraphyletic and polyphyletic taxa.

Figure 2: Holophyletic, paraphyletic and polyphyletic taxa.

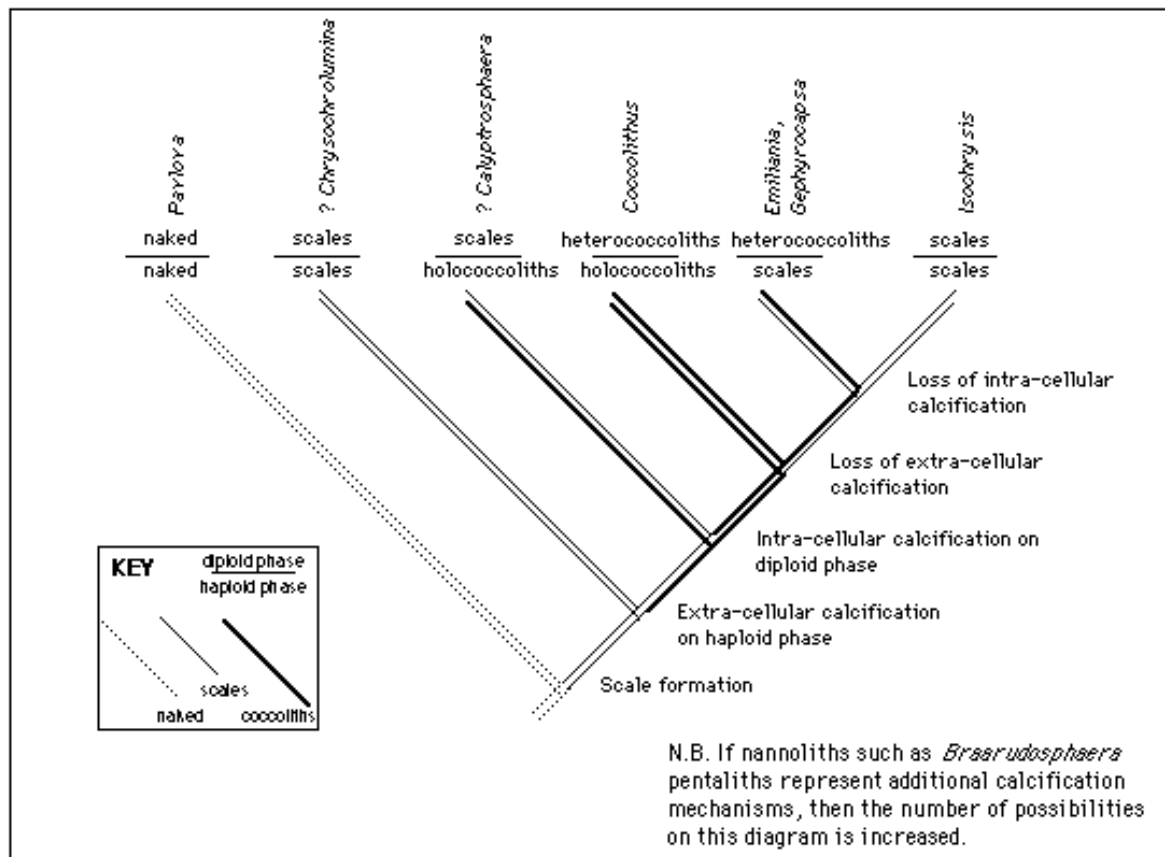


Figure 3 - Diagram showing how current observations on haptophyte life-cycles can be resolved into a consistent phylogeny.

Figure 3: Diagram showing how current observations on haptophyte life-cycles can be resolved into a consistent phylogeny.

# MESOZOIC CALCAREOUS NANNOPLANKTON CLASSIFICATION

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## Abstract

We present herein a revised three-level order-family-genus classification for Mesozoic calcareous nannoplankton. Two new orders (Arkhangelskiales, Stephanolithiales), five new families (Axopodorhabdaceae, Kamptneriaceae, Lapideacassaceae, Tubodiscaceae) and one new combination (*Zeugrhabdotus sigmoides* (Bramlette & Sullivan, 1961)), are introduced.

## Introduction

The purpose and philosophy of this contribution are explained in the introductory section (Young & Bown, above). A three-level order-family-genus classification is used, as far as seems reasonable, based on current knowledge. In addition, a set of numbered groupings (1. Heterococcoliths to 3. Nannoliths) are used to provide a logical, but very possibly artificial, organisation, particularly of families and genera *incertae sedis*. Question marks preceding generic names indicate tentative inclusion in the family.

## 1. HETEROCOCCOLITHS

### 1.1. Murolith coccoliths

**Description:** Wall-like rim, typically higher than it is wide, composed of two crystal-units: the distal/outer cycle (V-unit), which is commonly dominant; and the proximal/inner cycle (R-unit), which is subordinate and sometimes vestigial. The light microscope (LM) cross-polarised light (XPL) image is either bicyclic, with a dark outer cycle and a bright inner cycle, or unicyclic and relatively dark. This image variability is dependent upon the size of the proximal/inner cycle and the orientation of the rim, *i.e.* whether it is vertical or flaring.

**Remarks:** The division between the two murolith orders proposed herein, is based upon orientation of the elements in the distal/outer cycle, *i.e.* imbricating or non-imbricating. This distinction is apparent and stable through most of the Mesozoic but may be less clear amongst some Upper Triassic and Lower Jurassic muroliths, which represent the products of the initial diversification of this group (Figure 1).

#### 1.1a. Imbricating muroliths (loxoliths)

Order **EIFFELLITHALES** Rood, Hay & Barnard, 1971

**Description:** Murolith coccoliths with a distal/outer cycle composed of imbricating elements, *i.e.* in side-view, the sutures are not vertical. This feature is not distinguishable from non-imbrication in the LM. The distal/outer cycle imbrication is clockwise. The term loxolith is applied to this rim structure (Bown, 1987).

Family **CHIASTOZYGACEAE** Rood, Hay & Barnard, 1973 emend. Varol & Girgis, 1994

**Description:** Loxoliths with variably-developed proximal/inner-cycles and a central-area spanned by axial, non-axial or diagonal crossbars or a single transverse bar which is, however, usually formed from four, fused bars. LM image includes both unicyclic and bicyclic types.

**Comments:** This broad taxonomic group includes numerous simple loxolith forms. This simple model of coccolith construction was repeatedly modified through the Mesozoic and these subtle and numerous morphological variations are reflected in a taxonomy which is virtually unworkable. Very few distinctive and well-constrained species exist, and most commonly-used species names are virtually meaningless form-taxa. Even at the generic level there is no consensus on nomenclature, illustrated by the following list of names applied to forms with axial crosses: *Bownia* Varol & Girgis, 1994, *Rothia* Varol & Girgis, 1994, *Staurolithites* Caratini, 1963, *Staurorhabdus* Noël, 1973, *Vekshinella* Loeblich & Tappan, 1963, *Vagalapilla* Bukry, 1969.

A new classification of the group was recently proposed by Varol & Girgis (1994), however, their subdivision is based upon whether the LM rim image is unicyclic or bicyclic, a feature which appears to be of dubious taxonomic significance and is probably homoeomorphic within this group. An informal subdivision is applied below.

#### Central-area axial cross

Genus *Ahmuellerella* Reinhardt, 1964 (= *Actinozygus* Gartner, 1968)

{complex axial cross structure or plate, includes 8 axial or radial 'bars'}

?Genus *Bownia* Varol & Girgis, 1994

{type (and possibly only) species, *B. mutterlosei*, is bicyclic; both cycles highly birefringent}

Genus *Bukrylithus* Black, 1971

{unicyclic (LM) with broad, fibrous, tapering axial crossbars}

Genus *Diadorhombus* Worsley, 1971

{type species, *D. rectus*, has a square-shaped loxolith rim and is probably not related to similarly-shaped Stephanolithiaceae coccoliths, e.g. *Rhombolithion*}

Genus *Heteromarginatus* Bukry, 1969

{bicyclic, additional small bars in the central-area}

Genus *Misceomarginatus* Wind & Wise in Wise & Wind, 1977 (?= *Monomarginatus* Wind & Wise in Wise & Wind, 1977)

{narrow, bicyclic rim; wide central-area with axial crossbars and perforate plate}

Genus *Monomarginatus* Wind & Wise in Wise & Wind, 1977

{narrow, unicyclic rim; wide central-area with axial, concentric and lateral bars}

Genus *Rhabdophidites* Manivit, 1971 emend. Lambert, 1987 (= *Rhabdolekiskus* Hill, 1976)

{small basal coccolith with axial cross supporting very tall spine}

Genus *Staurolithites* Caratini, 1963 (= *Staurorhabdus* Noël, 1973; *Vekshinella* Loeblich & Tappan, 1963; *Vagalapilla* Bukry, 1969; *Haslingfieldia* Black, 1973; ?*Pontilithus* Gartner, 1968)

{practically a form-genus/genera for loxoliths with a simple axial cross}

Genus *Vaucherauvillius* Goy, 1979

{axial, lateral and concentric bars, span the central-area}

#### Central-area transverse bar

?Genus *Archaeozygodiscus* Bown, 1985

{Triassic genus, bicyclic (LM) with a birefringent, spine-bearing bar. Distal/outer cycle displays anticlockwise imbrication, unlike all other Mesozoic loxoliths}

Genus *Amphizygus* Bukry, 1969 (= *Bipodorhabdus* Noël, 1970)

{bicyclic rim; transverse bar formed from laths which continue around the inner edge of the rim, delineating the two circular perforations. No spine}

Genus *Gorkaea* Varol & Girgis, 1994

{bicyclic (LM), bright inner cyclic is broad; robust, birefringent, transverse bar; ?junior synonym of *Zeugrhabdotus*}

?Genus *Placozygus* Hoffman, 1970

{distal/outer cycle shows little or no imbrication; rim exhibits spiral interference pattern. The common species, *P. sigmoides*, is best classified as *Zeugrhabdotus*}

Genus *Reinhardtites* Perch-Nielsen, 1968

{unicyclic, very broad rim, with narrow central-area spanned/filled by a bar}

Genus *Tranolithus* Stover, 1966 (?= *Pontilithus* Gartner, 1968)

{central-area spanned by 2-4 broad, disjunct platelets. In *T. orionatus*, 4 platelets constitute a transverse bar, and there is a proximal net of lateral bars}

Genus *Tubirhabdus* Prins ex Rood, Hay & Barnard, 1973

{central-area structure supports broad, hollow, flaring spine}

Genus *Zeugrhabdotus* Reinhardt, 1965 (= *Glaukolithus* Reinhardt, 1964; ?*Gorkaea* Varol & Girgis, 1994; *Lordia* Varol & Girgis, 1994; *Rectapontis* Varol & Jakubowski, 1989; *Zygothites* Black, 1972; *Barringtonella* Black, 1973)

{uni- and bicyclic forms, with variably constructed transverse bar}

*Zeugrhabdotus sigmoides* (Bramlette & Sullivan, 1961) Bown & Young comb. nov.

Basionym: *Zygodiscus sigmoides* Bramlette & Sullivan, 1961 (*Micropalaeontology*, 7, 129-188, p.149, pl.4, fig.11a-e)

#### **Central-area diagonal cross**

Genus *Chiastozygus* Gartner, 1968

{includes uni- and bicyclic forms with variably constructed diagonal crossbars}

#### **Central-area closed or open with variable bars/grills**

Genus *Crepidolithus* Noël, 1965 (?= *Millbrookia* Medd, 1979)

{broad, high rim with central-area vacant, closed or spanned by bars or grill}

Genus *Neocrepidolithus* Romein, 1979

{broad, high rim with narrow or closed central-area which may be spanned by bars}

#### **Central-area net or vacant**

Genus *Loxolithus* Noël, 1965

{broad, open central-area, probably spanned by a rarely preserved, finely perforate net, see Lambert, 1993, pl. 5, figs 1 and 2 (named *Millbrookia perforata* therein)}

Family **EIFFELLITHACEAE** Reinhardt, 1965

**Description:** Loxoliths with a well-developed proximal/inner cycle and typically a wide central-area spanned by axial, non-axial (asymmetric), or diagonal crossbars. The broad, proximal/inner cycle is conspicuous in LM, creating a strongly bicyclic image.

?Genus *Diloma* Wind & Cepek, 1979

{?tricyclic - dark, narrow, inner and outer cycles; bright, broad median cycle; central-area spanned by axial or near-axial cross, with or without lateral bars}

Genus *Eiffellithus* Reinhardt, 1965

{crossbars generally fibrous and spine-bearing; relationship between Neocomian forms, and Albian and younger representatives uncertain; see *Rothia*}

Genus *Helicolithus* Noël, 1970

{narrow central-area, filled by broad, lath-formed crossbars}

Genus *Rothia* Varol & Girgis, 1994

{alternative name for Neocomian *Eiffellithus* representatives}

Genus *Tegumentum* Thierstein in Roth & Thierstein, 1972

{similar to *Eiffellithus*, however, the inner rim cycle is strongly imbricate and the crossbars are lath- formed rather than fibrous}

#### Family RHAGODISCACEAE

**Description:** Loxoliths with a dominant distal/outer-cycle and a central-area typically filled by a plate of granular calcite.

The central structure may be spine-bearing, perforate or massive. The LM image is generally unicyclic.

Genus *Calcicalathina* Thierstein, 1971

{central-area filled by a large, domed, granular mass}

Genus *Percivalia* Bukry, 1969

{concentric multicyclic inner-rim construction with granular plate or bar}

Genus *Rhagodiscus* Reinhardt, 1967 (?= *Viminites* Black, 1975)

{central-area filled by a granular plate which may be perforate and spine-bearing}

#### 1.1b. Non-imbricating muroliths (protoliths)

Order STEPHANOLITHIALES Bown & Young ord. nov.

**Description:** Muroliths with a distal/outer-cycle composed of non-imbricating elements, *i.e.* in side-view, the sutures are vertical or near-vertical. This feature is not distinguishable from imbrication in the LM. The term protolith is applied to this rim structure (Bown, 1987). Figure 2 provides a schematic overview for this group.

?Family CALCIOSOLENIACEAE Kamptner, 1927

**Description:** Coccoliths are rhombic muroliths, usually termed scapholiths. The central-area is spanned by numerous transverse bars. See Young & Bown (below) for further discussion.

Genus *Calciosolenia* Gran, 1912 (= *Acanthosolenia* Bernard, 1939; *Scapholithus* Deflandre, 1954)

{small, rhombic muroliths with numerous, parallel transverse bars}

Family PARHABDOLITHACEAE Bown, 1987

**Description:** Protoliths with high rims and a central-area spanned by an axial cross or transverse bar but commonly filled by broad, often tall spines. The LM image is usually bicyclic, with the proximal/inner cycle well-developed. Commonly observed in side-view.

Genus *Bucanthus* Bown, 1987

{bicyclic (LM), with offset central cross}

Genus *Crucirhabdus* Prins ex Rood, Hay & Barnard, 1973 (= *Apertius* Goy, 1979)

{spine-bearing axial cross, with or without additional lateral bars}

Genus *Diductius* Goy, 1979

{bicyclic (LM), with central-area grill}

Genus *Mitrolithus* Deflandre, 1954



- {central-area filled by massive boss/spine}
- Genus *Parhabdolithus* Deflandre, 1952
- {central-area filled or part-filled by broad, often tall, spines}
- Genus *Saeptella* Goy, 1979
- {central-area axial cross and grill}
- ?Genus *Thurmannolithion* Grün & Zweili, 1980
- {axial cross, lateral bars, and minor longitudinal bars forming a grill}
- ?Genus *Timorella* Bown, 1987
- {modified protoliths, with tapering, cup-like rim and central-area plate}
- ?Genus *Umbria* Bralower & Thierstein in Bralower *et al.*, 1989
- {bicyclic (LM) with granular central-area plate}

#### Family STEPHANOLITHIACEAE Black, 1968

**Description:** Protoliths with low rims, weakly-developed or vestigial proximal/inner cycles, and a central-area spanned by one to numerous bars. Coccolith outline may be polygonal. LM image is usually unicyclic and inconspicuous, although a number of genera do exhibit bicyclicity, *e.g.* *Rotelapillus*, *Stephanolithion* and *Stoverius* (Figure 2).

- Genus *Corollithion* Stradner, 1962
- {bicyclic, polygonal, usually hexagonal, rim with 4-6 radial bars in the central-area}
- [Genus *Cylindralithus* Bramlette & Martini, 1964]
- {see Watznaueriaceae}
- [Genus *Diadorhombus* Worsley, 1971]
- {type species, *D. rectus*, has a loxolith rim; see Chiastozygaceae}
- Genus *Rectilius* Goy, 1979
- {central-area grill}
- Genus *Rhombolithion* Black, 1973
- {diamond-shaped rim; arguably a junior synonym of *Stradnerlithus*}
- Genus *Rotelapillus* Noël, 1973
- {high, bicyclic (LM), circular rim with lateral rim spines and 8 radial central-area bars}
- Genus *Stephanolithion* Deflandre, 1939
- {bicyclic (LM), elliptical to geometric rim with lateral rim spines and 1-8 central-area bars}
- Genus *Stoverius* Perch-Nielsen, 1984
- {broadly-elliptical to circular, bicyclic (LM) rim with central-area cross}
- Genus *Stradnerlithus* Black, 1971 (= *Diadozygus* Rood, Hay & Barnard, 1971; *Nodosella* Rood, Hay & Barnard, 1973)
- {inconspicuous (LM), elliptical or polygonal rim with 4 or more central-area bars}
- Genus *Truncatoscapus* Rood, Hay & Barnard, 1971
- {elongate, subhexagonal rim with 6 or more central-area bars}

#### 1.2. Placolith coccoliths

**Description:** Broad and thin rim, usually constructed from two superimposed, appressed shields joined by a tube-cycle. Precise understanding of the relationship between rim-cycles is often lacking, but where known, the shields are constructed from two crystal-units which may be complexly intergrown and superimposed, leading to a multicyclic, surficial appearance. LM image is wholly dependent upon the relative development of the two crystal-units (V and R), which is extremely variable, but usually consistent within families. When V- and R-units are relatively equally developed, *i.e.* each

forming an entire shield, the LM image is predominantly dark but often bicyclic, the inner cycle being narrow and bright, *e.g.* Biscutaceae, Prediscosphaeraceae. When the V-unit is weakly developed, and it is often reduced to peg cycles or is vestigial, then both shields are almost wholly constructed from R-unit crystals and the LM image is bright, *e.g.* Watznaueriaceae. Mesozoic placoliths generally have simple, monocyclic proximal shields, which vary little from family to family. Cenozoic placoliths have more-complexly constructed proximal shields which are often bicyclic.

### 1.2a. Non-imbricating (or radial) placoliths and related taxa

Order **PODORHABDALES** Rood *et al.*, 1971 emend. Bown, 1987

**Remarks:** This order includes the Biscutaceae and other closely related forms, which have placolith (or modified placolith) coccoliths with shields formed from elements which display little or no imbrication and, typically, equal development of V and R crystal-units, *i.e.* one shield (distal) formed from V-units, the other from R-units (proximal). The V/R development is reflected in consistent LM images which are of low birefringence but high relief in phase contrast. Shield elements are typically joined along radial sutures, but these may often curve or kink. Element curvature is consistently dextrogyre (veeing anticlockwise) and obliquity is broadly dextral (clockwise) in the distal shield, and the same in the proximal shield when viewed proximally.

The rim constructions of the Cretarhabdaceae, Tubodiscaceae and Mazaganellaceae are not well understood, and these families are only tentatively assigned to this order.

Family **AXOPODORHABDACEAE** Bown & Young fam. nov.

**Type genus:** *Axopodorhabdus* Wind & Wise in Wise & Wind, 1977.

**Description:** Placoliths with two narrow shields and a wide central-area, spanned by axial crossbars or granular plates with variable numbers of perforations; the central structure generally supports tall, hollow spines. The distal shield is formed from V-unit elements joined along radial or near-radial sutures which show little or no imbrication. The proximal shield and inner cycle (if present) are formed from R-units. LM image is generally dark, but bright inner-cycles may be developed. The image is characterised by clearly visible shield elements, often giving a 'beaded' appearance around the inner edge of the shields.

**Comments:** We have abandoned the name Podorhabdaceae in favour of Axopodorhabdaceae due to problems associated with the type genus of the former family (*Podorhabdus*, type species *P. grassei* Noël, 1965). Many authors believe that the holotype illustrations of *P. grassei* represent a species of *Discorhabdus*, which should then be classified in the Family Biscutaceae. It would be extremely undesirable to use *Podorhabdus* for those coccoliths presently within *Discorhabdus*, or to use Podorhabdaceae to replace Biscutaceae; the informal term podorhabdid is useful, and widely used, to describe the coccoliths classified together in the Axopodorhabdaceae.

The Axopodorhabdaceae has been dramatically overdivided, with numerous, monospecific genera distinguished only by the number of central-area perforations (Figure 3). The family requires a species-level review, and revision is not attempted here.

Genus *Axopodorhabdus* Wind & Wise in Wise & Wind, 1977

{tall-spine-bearing axial cross}

Genus *Cleistorhabdus* Black, 1972

{central-area plate with one large perforation/spine base}

- ?Genus *Cribrosphaerella* Deflandre in Piveteau, 1952 (= *Psyktosphaera* Pospichal & Wise, 1990)  
 {elliptical to subrectangular rim; multiperforate central-area net}
- ?Genus *Cribracorona* Perch-Nielsen, 1973  
 {high, subcircular rim; narrow central-area with grill}
- Genus *Dekapodorhabdus* Medd, 1979  
 {10 central-area perforations}
- Genus *Dodekapodorhabdus* Perch-Nielsen, 1968  
 {12 central-area perforations}
- Genus *Ethmorhabdus* Noël, 1965  
 {multiperforate central-area net with or without axial cross and spine}
- Genus *Hemipodorhabdus* Black, 1971  
 {spine-bearing transverse bar}
- Genus *Hexapodorhabdus* Noël, 1965  
 {bars delineate 6 large perforations, including one at each end of the central area}
- ?Genus *Nephrolithus* Górka, 1957  
 {reniform rim; central-area net with 2 to numerous pores}
- Genus *Octopodorhabdus* Noël, 1965  
 {bars delineate 8 large perforations, including one at each end of the central-area}
- Genus *Octocyclus* Black, 1972  
 {bars delineate 8 large perforations, lying at the sides of a longitudinal bar}
- Genus *Perrisocyclus* Black, 1971 (= *Teichorhabdus* Wind & Wise in Wise & Wind, 1977; *Duplexipodorhabdus* Varol & Girgis, 1992)  
 {one or two cycles of central-area perforations}
- [?Genus *Podorhabdus* Noël, 1965]  
 {granular central structure with two marginal perforations, supports tall, hollow, flaring spine; see discussion of family}
- Genus *Teichorhabdus* Wind & Wise in Wise & Wind, 1977  
 {two cycles of small central-area pores}
- Genus *Tetrapodorhabdus* Black, 1971  
 {diagonal or four offset cross bars}

#### Family **BISCUTACEAE** Black, 1971

**Description:** Placoliths with two broad shields, which may or may not include a distal innercycle (tube-cycle), and a small central-area which may be vacant, filled with granular calcite or spanned by variably-oriented bars or axial crossbars. The distal shield is formed from V-units and the proximal shield and tube-cycle are formed from R-units; the distal shield elements are joined along radial or near-radial sutures (+/- kinks) and show little or no imbrication. LM image is generally dark, but bright inner-cycles are common. Coccospheres are well known and usually spherical or cylindrical. A diagrammatic overview of the family is shown in Figure 4.

**Remarks:** The taxonomic significance of conspicuous tube-cycles has led to a variety of classification schemes within this family. In a study of the oldest (Early Jurassic) biscutaceans, de Kaenel & Bergen (1993) proposed considerable revision to this family. These authors distinguish *Palaeopontosphaera* (widely regarded as a junior synonym of *Biscutum*) from *Biscutum* by the presence of a birefringent, distal inner cycle. However, the type species holotype (EM) of *Biscutum* was a proximal view and thus the presence or absence of a tube-cycle cannot be determined. Moreover, they argue that the

aforementioned holotype is very nearly circular and emend the genus in such a way as to render it equivalent to *Bidiscus* Bukry, 1969 (= *Discorhabdus* Noël, 1965) (*i.e.* circular to subcircular, unicyclic placoliths), a drastic change compared to its normal and widespread usage.

The holotype in question is badly damaged (around 40% is missing) and most probably not lying flat, and it is therefore very difficult to prove that this specimen is circular. In fact, Black (*in* Black & Barnes, 1959) clearly states that the holotype is composed of "two unequal *elliptical* discs" (p.325), and discusses at some length the geometrical changes in the shape of the rim elements around the ellipse (p.326). We therefore propose that the traditional usage of *Biscutum* is retained, *i.e.* subcircular to elliptical biscutatean coccoliths which typically have a distal, inner tube-cycle. This causes least disruption in the relatively stable Biscutaceae taxonomy and is as justifiable as the case presented by de Kaenel & Bergen (1993), given the available evidence. The inclusion of the earliest biscutateans in the genus *Similiscutum* is, however, followed here.

The genus *Discorhabdus* (= *Bidiscus*) is distinguished on its circular outline. In many coccolith groups, outline is not a stable, taxonomically significant feature, however *Discorhabdus* represents a coherent, long-lived group in which outline is consistently circular. There are also additional morphological features which distinguish them from the rest of the family, *e.g.* most species lack an inner distal tube-cycle and many Jurassic representatives have large spines.

Genus *Biscutum* Black *in* Black & Barnes, 1959 (= *Palaeopontosphaera* Noël, 1965)

{broadly elliptical-elliptical shields with or without a tube-cycle; the central-area may be imperforate or narrow and vacant or spanned by a simple structure (cross or bar)}

Genus *Boletuvelum* Wind & Wise *in* Wise & Wind, 1977

{*Biscutum*-like coccoliths with large, hollow, flaring spines, closed distally by a domed covering; may simply represent well-preserved *Biscutum* coccoliths (see Hattner & Wise, 1980, pl.4, fig.6; Lambert, 1993, pl.13, fig.1)}

Genus *Crucibiscutum* Jakubowski, 1986

{*Biscutum*-like coccoliths with prominent, birefringent, axial cross}

Genus *Discorhabdus* Noël, 1965 (= *Bidiscus* Bukry, 1969)

{circular rim, generally no central-area structure, but may (Jurassic forms) or may not (Cretaceous forms) bear a spine}

Genus *Gaarderella* Black, 1973

{broad shields with wide granular central-area plate; rarely reported}

Genus *Gephyrobiscutum* Wise, 1988

{bicyclic rim; narrow central-area spanned by an oblique transverse bar; rarely reported}

Genus *Seribiscutum* Filewicz *et al.* *in* Wise & Wind, 1977

{central-area spanned by broad platelets}

Genus *Similiscutum* de Kaenel & Bergen, 1993

{subcircular-elliptical shields with smooth, grey appearance in LM and a narrow, bright inner-cycle (not a tube cycle); central-area narrow and may be empty or spanned by an axial cross}

Genus *Sollasites* Black, 1967 (= *Costacentrum* Bukry, 1969; *Noellithina* Grün & Zweili, 1974 *in* Grün *et al.*, 1974)

{elliptical, usually bicyclic rim; distinct central-area structure composed of axial cross, multiple longitudinal bars and/or concentric bars. Classified in a separate family or subfamily by some authors}

Family **CALYCULACEAE** Noël, 1973

**Description:** Modified placoliths constructed from a high, broad, flaring distal-shield composed of radial, non-imbricating elements, and a proximal-shield which is often reduced to a simple, narrow cycle of elements; central-area structures are highly variable, including numerous bars, concentric structures, nets and grills. The distal shield is formed from V-units and the proximal shield is formed from R-units. LM image is generally dark, but the high distal shield often shows some birefringence, reflecting the thickness of the crystals; commonly observed in side-view. There is some evidence of coccosphere dimorphism (Goy, 1981).

Genus *Calyculus* Noël, 1973 (= *Proculithus* Medd, 1979; *Incerniculum*, *Vikosphaera*, *Catillus* Goy, 1979)

{see description of family}

Genus *Carinolithus* Prins in Grün, Prins & Zweili, 1974

{extremely modified; trumpet-shaped coccoliths}

Family **PREDISCOSPHAERACEAE** Rood, Hay & Barnard, 1971

**Description:** Elliptical to circular placoliths with two shields and a central-area spanned by crossbars which support tall, complexly-constructed spines. The distal shield is typically bicyclic, with a broad outer cycle, usually constructed from 16 non-imbricating elements (V-units) and a narrow inner cycle (tube-cycle) (R-units). The proximal shield is formed from R-units. The LM image is bicyclic, with the outer cycle dark, and inner cycle bright.

?Genus *Petrarhabdus* Wind & Wise in Wise, 1983

{massive, short, blocky spine}

Genus *Prediscosphaera* Vekshina, 1959 (= *Deflandrius* Bramlette & Martini, 1964)

{see description of family}

#### **Rim structure uncertain but tentatively placed within the Podorhabdales**

Family **CRETARHABDACEAE** Thierstein, 1973

**Description:** Placoliths with two shields and a central-area spanned by a variety of structures, most commonly fibrous axial crossbars with subsidiary lateral bars and a solid central spine or process (Figure 5). The distal shield is generally bicyclic, with a narrow outer cycle and a dominant, broad inner cycle; the elements are usually radial or near radial and do not appear to imbricate. The relationship between these cycles and the coccolith crystallography is presently uncertain. LM image is moderately birefringent.

Genus *Cretarhabdus* Bramlette & Martini, 1964 (= *Allemannites* Grün in Grün & Allemann, 1975)

{axial cross and net}

Genus *Cruciellipsis* Thierstein, 1971 (= *Miravetesina* Grün in Grün & Allemann, 1975)

{broad shields with broad, tapering, birefringent axial cross bars; lateral bars have been reported}

?Genus *Flabellites* Thierstein, 1973

{central-area spanned by small, blocky diagonal cross; outline may be asymmetric}

Genus *Grantarhabdus* Black, 1971 (= *Gephyrorhabdus* Hill, 1976)

{diagonal cross bars}

Genus *Helenea* Worsley, 1971 (= *Microstaurus* Black, 1971)

{distal shield inner cycle displays distinct suture obliquity and ?imbrication; narrow central-area spanned by crossbars which may bifurcate at their ends and usually support a short, blocky spine}

[Genus *Microstaurus* Black, 1971]

{commonly used genus, but a junior synonym of *Helenea*}

Genus *Mirevetesina* Grün in Grün & Allemann, 1975

{broad shields, weak axial cross, net; ?early *Cruciellipsis*}

?Genus *Pickelhaube* Applegate, Covington & Wise, 1987

{large, broad, strongly concavo-convex ?proximal shield; narrow ?distal shield; central-area axial cross and lateral bars}

Genus *Polypodorhabdus* Noël, 1965

{distal shield slopes in to the central-area; axial cross and numerous lateral bars}

Genus *Retecapsa* Black, 1971 (= *Allemannites* Grün in Grün & Allemann, 1975)

{axial cross with lateral bars; some authors include these forms within *Cretarhabdus*}

Genus *Speetonia* Black, 1971

{single transverse bar}

[Genus *Stradneria* Reinhardt, 1964]

{holotype drawing shows a weak axial cross and a solid intergrowth of radial laths; name not commonly used}

Family **MAZAGANELLACEAE** Bown, 1987

**Description:** Three-shielded placoliths with a wide central-area spanned by a variety of bars, grills, nets or plates. The distal shield may be high and flaring. The distal shield is formed from one cycle of non-imbricating elements, joined along radial sutures; the exact structural relationship between the different shields is unknown at present. LM image is generally dark, but birefringence increases when the distal shield is high.

Genus *Mazaganella* Bown, 1987

{low to moderately high rim, dark shields (bright inner cycle in *M. protensa*); central-area axial cross, which is broad and plate-like in *M. pulla*}

Genus *Triscutum* Dockerill, 1987

{distal shield is elevated; variable central-area structures, mainly grills and nets}

Family **TUBODISCACEAE** Bown & Rutledge fam. nov.

**Type genus:** *Tubodiscus* Thierstein, 1973.

**Description:** Elliptical placoliths composed of two narrow shields and a third, narrow, proximally-situated collar-cycle which is variable in height. The central-area is broad and open; no central structures have yet been observed. The LM image is dark, although the collar-cycle is brighter. Element curvature is dextrogyre in the distal shield and suture obliquity is broadly dextral (clockwise). In the proximal shield these orientations are the same when viewed proximally. Suture curvature in the collar-cycle is laevogyre when viewed proximally; element imbrication is anticlockwise (for *T. verenae*).

The crystallography of these coccoliths has not yet been determined.

Genus *Manivitella* Thierstein, 1971

{low proximal collar-cycle; large rim and wide ?vacant central-area}

Genus *Tubodiscus* Thierstein, 1973

{high and birefringent proximal collar-cycle; wide ?vacant central-area}

### **1.2b. Imbricating placoliths (R-unit dominated)**

Order **WATZNAUERIALES** Bown, 1987

**Remarks:** Includes placoliths (or modified placoliths) with shields formed from elements which display imbrication and in which the V-unit is usually reduced or vestigial, resulting in a high birefringence LM image. Element curvature is laevogyre in the distal shield with broadly sinistral obliquity, and the same in the proximal shield when viewed proximally. Imbrication

is clockwise in the distal shield, anticlockwise in the proximal shield, and clockwise in the V-unit cycle when developed (e.g. *Bussonius*).

Family **WATZNAUERACEAE** Rood, Hay & Barnard, 1971

**Description:** Imbricating placoliths with two shields and a central-area which is usually closed or narrow and devoid of central structures; or filled by a plug, spanned by bars, axial cross, or grill. The distal shield is superficially tricyclic, composed of a broad outer-cycle of imbricating elements (R-unit) joined along kinked sutures; a narrow, median-cycle of peg-like elements (V-unit) and a narrow inner cycle (R-units). The two shields are actually formed from single R-unit elements into which fit the narrow cycle of peg-like V-units (Young & Bown, 1991). The dominance of the R-units creates a highly-birefringent LM image, in which the V-unit cycle appears only as a thin, dark line. The typical rim morphology is modified in a number of genera, listed below (see also Figure 6).

Genus *Cyclagelosphaera* Noël, 1965

{circular shields; narrow or closed central-area}

Genus *Lotharingius* Noël, 1973 (= *Bennocyclus* Zweili & Grün, 1974 in Grün *et al.*, 1974)

{central-area axial cross, with or without additional lateral bars}

Genus *Watznaueria* Reinhardt, 1964 (= *Ellipsagelosphaera* Noël, 1965; *Caterella* Black, 1971; *Calolithus* Noël, 1965; *Coptolithus* Black, 1973; *Margolatus* Forchheimer, 1972; *Actinosphaera* Noël, 1965)

{central-area closed or narrow but may be spanned by transverse bar, bars or grill}

#### **Modified *Watznaueria*-type rim**

Genus *Ansulasphaera* Grün & Zweili, 1980

{high, narrow, cylindrical proximal shield (anticlockwise imbrication); narrow, vacant central-area}

?Genus *Bibreviconus* Rahman & Roth, 1991

{high, cylindrical morphology with a peg-like distal cycle; possibly the isolated central part of *Cyclagelosphaera deflandrei* specimens which have lost the shields}

Genus *Bussonius* Goy, 1979

{V-unit cycle high and broad, forms a third, uppermost shield; central-area axial cross and lateral bars}

?Genus *Cylindralithus* Bramlette & Martini, 1964

{earliest species, *C. nudus*, has watznaueriacean construction, but the shields are high (*cf. Ansulasphaera*) and differentiation between them is reduced (clockwise distal shield imbrication, anticlockwise proximal shield imbrication; central-area vacant or with cross bars)}

?Genus *Diazomatolithus* Noël, 1965

{subcircular-circular with broad, vacant central-area; distal shield is monocyclic with radial sutures, proximal shield may be high and tapering with laevogyre element curvature, broadly sinistral obliquity and anticlockwise imbrication; low birefringence due to the expanded V-unit which forms the distal shield}

[Genus *Darwinilithus* Watkins in Watkins & Bowdler, 1984]

{possible junior synonym of *Cylindralithus* but tube-cycle elements protrude distally}

#### **1.2c. Other placolith-like groups**

Order **ARKHANGELSKIALES** Bown & Hampton ord. nov.

**Description:** Tiered 'placoliths' (see comments), with 3-5 closely appressed 'shields'. Central-area structures include transverse bars with proximal net; axial or near-axial crosses with proximal net; and perforate plates crossed by axial or near-axial sutures. LM images vary significantly, from predominantly dark in the Kamptneriaceae, to predominantly bright

in the Arkhangelskiellaceae.

**Comments:** The Kamptneriaceae appears to have originated from loxolith coccoliths, and the tiered placolith rim structure is actually a modified loxolith construction (Hampton *et al.*, in prep.). The earliest representatives of the family are only slightly modified loxolith coccoliths. Such an evolutionary history has not yet been established for the Arkhangelskiellaceae.

Family **ARKHANGELSKIELLACEAE** Bukry, 1969 emend. Bown & Hampton

**Description:** Tiered 'placolith' coccoliths with central-areas spanned by axial crosses and grills, or filled by a perforate plate divided by axial sutures. The 'shields' are typically bright in cross polarised light (rim dominated by R-unit) but bicyclic images are also observed.

Genus *Acaenolithus* Black, 1973

{2-3 cycles form the distal shield, the inner cycle is broadest; bicyclic LM image, broad, bright inner cycle and narrow, dark outer cycle; broad central-area axial cross and grills, support boss or spine}

Genus *Arkhangelskiella* Vekshina, 1959

{1-2 distal shield cycles; bright, unicyclic LM image although darker towards outer edge; central-area perforate plate with axial sutures}

Genus *Aspidolithus* Noël, 1969

{2-3 cycles form the distal shield, the inner cycle is broadest; indistinct bicyclic LM image, broad, bright inner cycle and narrow, darker outer cycle; central-area perforate plate with axial sutures, with no boss or spine. Considered a junior synonym of *Broinsonia* by some}

Genus *Broinsonia* Bukry, 1969 (?= *Aspidolithus* Noël, 1969)

{as for *Aspidolithus* but if both genera are used, it is restricted to forms with broad central-area axial crosses and grills}

Genus *Thiersteinia* Wise & Watkins in Wise, 1983

{as for *Aspidolithus* with perforate plate, axial struts and spine}

Family **KAMPTNERIACEAE** Bown & Hampton fam. nov.

**Type genus:** *Kamptnerius* Deflandre, 1959.

**Description:** Modified loxolith coccoliths, with distinctive LM images consisting of a narrow to moderately-broad rim with a narrow, dark outer cycle; a diagnostic, bright median cycle; and a dark, inner cycle. Central-area structures are generally dark in LM, and may be a transverse bar, crossbars or plate, usually perforate; proximally-situated fine nets may be seen when preservation is good. Rim structure varies from apparently typical loxolith (*e.g.* Thierstein, 1974: pl.4, figs 1, 9, 12) to placolith-like, with at least three (pseudo) 'shields' (*e.g.* Thierstein, 1974: pl.7, figs 6, 8). The tiered nature is produced by lateral protrusions from the outer cycle of the loxolith wall. The V-unit cycle dominates the wall, but is penetrated by a thin cycle of R-units, seen as a peg-like cycle in proximal view, and a median cycle in distal view, and it is this cycle which creates the distinctive LM image.

[Genus *Cribricatillus* Black, 1973]

{modified loxolith rim with *Gartnerago*-like LM image, central-area axial cross and net or bars; ?junior synonym of *Gartnerago*}

?Genus *Crucicribrum* Black, 1973

{small ?tiered placoliths, with perforate central-area plate and axial cross and/or sutures}

Genus *Gartnerago* Bukry, 1969 (= ?*Cribricatillus* Black, 1973; *Laffittius* Noël, 1969)

{see family description. Central area structures - transverse bar, broad axial cross, or perforate plate with axial or near axial sutures; additional proximal nets or grills}



Genus *Kamptnerius* Deflandre, 1959

{as for *Gartnerago* with an asymmetric rim flange forming a wing; reduced central-area plate}

### 1.3. Heterococcoliths of uncertain affinities

#### 1.3a. Muroliths

Genus *Clepsilithus* Crux, 1987

{loxolith with 8 or more broad bars in the central-area}

Genus *Laguncula* Black, 1971

{?loxoliths with bulbous/spherical, hollow 'spines'}

Genus *Paralithella* Lambert, 1993

{protoliths with central-area axial cross and longitudinal bars}

Genus *Rectocorona* Lambert, 1987

{protoliths with short, flaring distal-process}

Genus *Tortolithus* Crux, 1982

{muroliths with central-area closed by overlapping plates}

?Genus *Angulofenestrellithus* Bukry, 1969

{narrow, bicyclic rim with broad perforate central-area plate (?3 cycles of holes)}

#### 1.3b. Placoliths

Genus *Boletuvelum* Wind & Wise in Wise & Wind, 1977

{large, hollow, closed, flaring distal spine - see Biscutaceae}

Genus *Chiastella* Lambert, 1993

{?tricyclic distal shield, diagonal cross}

Genus *Diazomatolithus* Noël, 1965

{subcircular-circular with broad, vacant central-area; distal shield is monocyclic with radial sutures, proximal shield may be high with dextrally imbricating elements; low birefringence - see Watznaueriaceae}

Genus *Haqius* Roth, 1978

{(?elliptical)-circular with monocyclic distal shield formed from numerous dextrally imbricate elements, low birefringence LM image; narrow or closed central-area}

Genus *Markalius* Bramlette & Martini, 1964

{moderately birefringent interference figure with a bright tube-cycle; central-area narrow or closed}

Genus *Prolatipatella* Gartner, 1968

{narrow, ?tiered rim; thin, imperforate plate across wide central-area}

Genus *Repagulum* Forchheimer, 1972

{imbricating placoliths; monocyclic distal shield with numerous imbricate elements, distinctive but inconspicuous, low birefringence, 'flaring' LM image; central-area spanned by ~16 radial bars}

## 2. HOLOCOCCOLITHS

Family **CALYPTROSPHAERACEAE** Boudreaux & Hay, 1969

**Remarks:** A strictly morphological taxonomic grouping which embraces coccolithophores which secrete holococcoliths. Almost certainly includes taxa which also secrete heterococcoliths during non-motile phases and are then included in other families.

The list below is probably overdivided, particularly the small forms which have rims formed from numerous blocks and have only rarely been observed in the LM. However, a number of taxa are consistently recorded and applied in biostratigraphy, e.g. *Anfractus*, *Calculites* and *Lucianorhabdus*.

## **2a. Cavate, *Anfractus*-like holococcoliths**

*Anfractus* holococcoliths have been recorded inconsistently from Early Jurassic to mid-Cretaceous sediments (see Bown, 1993; Lambert, 1987).

Genus *Anfractus* Medd, 1979 emend. Bown, 1993

{elliptical, cavate (and usually septate), often bearing hollow spines; distal surface may be perforate; may have internal buttresses}

Genus *Stereorhabdus* Lambert, 1987

{spine terminates in a stellate process}

## **2b. Cavate with three to four proximal blocks, *Lucianorhabdus*-like**

These forms are large and robust, and have been recorded consistently from Late Cretaceous sediments. They are typically cavate but diagenesis commonly produces infilled cavities/spines and overgrown blocks.

Genus *Acuturris* Wind & Wise in Wise & Wind, 1977

{proximal plate of 3 blocks; tall, tapering spine}

Genus *Calculites* Prins & Sissingh in Sissingh, 1977

{proximal plate of 4 blocks; ridged and pitted distal surface; short, narrow, hollow spines}

Genus *Isocrystallithus* Verbeek, 1976 (= *Owenia* Crux, 1992)

{?cavate holococcoliths bearing moderately tall spines}

Genus *Lucianorhabdus* Deflandre, 1959

{proximal plate of four blocks; tall, hollow spine, often ridged or pitted; may be bulbous or curved}

?Genus *Orastrum* Wind & Wise in Wise & Wind, 1977

{narrow rim surrounds central-area formed of 2-4 blocks; ?non-cavate, ?no spine}

[Genus *Owenia* Crux, 1992]

{bicyclic; narrow central-area spanned by arched bar. Junior synonym of *Isocrystallithus*}

[Genus *Semihololithus* Perch-Nielsen, 1971]

{the genus is probably a junior synonym of *Daktylethra* (Cenozoic). The Mesozoic species should probably be assigned to *Calculites* or *Lucianorhabdus*}

## **2c. Rim formed from numerous small blocks with variable central structures**

These forms are small and, in most cases, have only been described in the LM from a limited number of sites/samples; mainly Late Cretaceous.

Genus *Bifidalithus* Varol, 1991

{narrow rim with central-area filled by two blocks divided by a transverse suture}

Genus *Multipartis* Risatti, 1973

{rim formed from ~7 triangular blocks; irregular blocks in the central-area}

Genus *Munarinus* Risatti, 1973

{rim formed from 4-12 blocks; central-area filled or spanned by disjunct bar/block}

Genus *Octolithus* Romein, 1979

{rim formed of 8 blocks, 4 large and 4 small}

Genus *Okkolithus* Wind & Wise in Wise & Wind, 1977

{rim of ~20 blocks; central-area filled by 2 or more disjunct blocks}

Genus *Ottavianus* Risatti, 1973

{rim of 10-15 blocks, central-area spanned by ?conjunct bar/block}

Genus *Pharus* Wind & Wise in Wise & Wind, 1977

{elliptical, comprising one or two blocks, pierced by two round holes}

Genus *Ramsaya* Risatti, 1973

{rim of 12-14 blocks, central-area spanned by a narrow, dark bar}

Genus *Russellia* Risatti, 1973

{rim of 10-26 blocks; central perforation}

Genus *Saepiovirgata* Varol, 1991

{rim of 8-12 elements, with 2 longitudinally-oriented elongate blocks in the central-area}

## 2d. Others with recognisable coccolith morphology

Genus *Coccosphaerida* Lambert, 1987

{high rim, formed from 3 layers of crystallites, ?distal surface covering}

Genus *Lacunolithus* Bown, 1993

{cavate, open proximal ring, flaring collar, domed distal covering}

## 2e. Non-coccolith morphology

[Genus *Athenagalea* Hattner & Wise, 1980]

{junior synonym of *Petrobrasiella*}

Genus *Metadoga* Wind & Cepek, 1979

{conical-flask-shaped, with lid and internal partition}

Genus *Petrobrasiella* Troelsen & Quadros, 1971

{domed-shaped, pierced by holes/cavities}

Genus *Pseudoconus* Bown & Cooper, 1989

{solid, truncated-cone-shaped ?holococcolith with rectangular cross-section}

Genus *Zebrashapka* Covington & Wise, 1987

{solid, truncated-cone-shaped ?holococcolith, with distinct outer rim and banded core}

## 3. NANNOLITHS

**Comments:** The groups included here are mostly extinct taxa which had calcite tests within the size limits of calcareous nannofossils but with morphologies which are distinct from either hetero- or holococcoliths.

Family **BRAARUDOSPHAERACEAE** Deflandre, 1947

**Description:** The extant species *Braarudosphaera bigelowii* has not been cultured but observations on live specimens suggest that it is a haptophyte (J. Green, pers. comm., 1996). It has a cell-wall covering of twelve pentaliths, which form an imperforate dodecahedron. The nannoliths are constructed from five segments which form a pentalith (a five-sided plate), although stellate outlines are also common. C-axes are tangential to pentalith outline in plan view and individual crystal units show laminar ultrastructure.

Genus *Braarudosphaera* Deflandre, 1947

{elements trapezoidal, sutures go to edges of the pentagon}

?Genus *Bukryaster* Prins, 1971

{stellate; sutures go to edges of the pentagon; ornament of 5 ridges and depressions}

Genus *Micrantholithus* Deflandre in Deflandre & Fert, 1954

{sutures go to points of the pentagon; relationship between Neocomian and Cenozoic representatives uncertain}

Genus *Trapezopentus* Wind & Cepek, 1979

{pentalith formed from 5 subrectangular elements surrounding a large central opening}

Family **EOCONUSPHAERACEAE** Kristan-Tollmann, 1988

**Description:** Nannoliths with a truncated-cone-like morphology constructed from an outer rim of thin, elements joined along vertical sutures, and an inner core of numerous radial lamellae which protrude distally.

**Comments:** The three genera listed below have non-concurrent stratigraphic ranges but very closely comparable morphologies and biogeographies (Bown & Cooper, 1989). The taxonomic validity of this grouping is thus uncertain. These forms may prove to be modified heterococcoliths.

**Genus** *Calcivascularis* Wiegand, 1984 (= *Mitrolithus jansae*)

{inner core differentiated into proximal and distal parts, Early Jurassic}

Genus *Conusphaera* Trejo, 1969

{inner core differentiated longitudinally into 2 concentric cycles, L. Jurassic-E. Cretaceous}

Genus *Eoconusphaera* Jafar, 1983

{inner core formed from a single cycle of radial laths, Late Triassic}

Family **GONIOLITHACEAE** Deflandre, 1957

**Description:** Pentagonal plates with a thin rim and granular central-area plate.

**Comments:** Rare and sporadic stratigraphical distribution; K/T boundary survivor.

**Genus** *Goniolithus* Deflandre, 1957

{pentagonal plate with a distinct rim surrounding a mesh-like array of small crystals}

Family **LAPIDEACASSACEAE** Bown & Young fam. nov.

**Type genus:** *Lapideacassis* Black, 1971.

**Description:** Hemispherical to cylindrical nannoliths, with walls constructed from one to several cycles of thin elements, enclosing a hollow central space; the nannolith tapers ?distally, and may have ?apical spines or processes.

**Comments:** Rare and sporadic stratigraphic distribution, but K/T boundary survivor.

Genus *Lapideacassis* Black, 1971 (= *Scampanella* Forchheimer & Stradner, 1973; *Pervilithus* Crux, 1981)

{see family description}

[Genus *Scampanella* Forchheimer & Stradner, 1973]

{has been used for forms with a single wall cycle; regarded here as a junior synonym of *Lapideacassis*}

Family **MICRORHABDULACEAE** Deflandre, 1963

**Description:** Elongate, rod-like nannoliths with a cruciform or circular cross-section, which generally taper at both ends.

**Comments:** The relationship between the four genera listed below is uncertain and this family may prove to be polyphyletic.

Genus *Lithraphidites* Deflandre, 1963

{narrow rods with cruciform cross-section; may have expanded lateral blades}

Genus *Microrhabdulus* Deflandre, 1959

{~circular cross-section; complex construction from systematically arranged laths commonly creating a 'chequered' LM image}

Genus *Pseudolithraphidites* Keupp, 1976

{nannoliths formed from 4-6 fused, circular rods; parallel sided}

Genus *Pseudomicula* Perch-Nielsen in Perch-Nielsen *et al.*, 1978

{rod with massive, expanded mid-section}

Family **NANNOCONACEAE** Deflandre, 1959

**Description:** Conical, globular or cylindrical nannoliths composed entirely of spirally-arranged platelets, enclosing an axial cavity or canal. C-axes arranged tangentially to central axis.

?Genus *Faviconus* Bralower in Bralower *et al.*, 1989

{elongate, single or multiple columns of stacked platelets with thin axial canals}

Genus *Nannoconus* Kamptner, 1931

{see description of family}

Family **POLYCYCLOLITHACEAE** Forchheimer, 1972 emend. Varol, 1992

**Description:** Nannoliths composed of two vertically-appressed wall cycles and a central-area which may be closed, open and vacant, or spanned by a diaphragm-like structure. Elements have tangential c-axis orientation.

**Comments:** This family has previously been used for a wide variety of nannoliths with radial, petaloid morphologies (*e.g.* Perch-Nielsen, 1985). Varol (1992) redefined the family to include only those forms which appear to represent a clear phylogenetic grouping, and this is followed below. Those forms which do not fall into this category are listed separately as uncertain 'polycycloliths'.

Genus *Eprolithus* Stover, 1966 (= *Polycyclolithus* Forchheimer, 1968)

{5-9 petal-like, wall-cycle elements, moderately large median diaphragm}

Genus *Farhania* Varol, 1992

{16-24 rectangular, imbricating, wall-cycle elements, moderately large median diaphragm}

Genus *Lithastrinus* Stradner, 1962

{5-7 ray-like, strongly curved, wall-cycle elements, small median diaphragm}

?Genus *Micula* Vekshina, 1959

{4 blocky, strongly twisted, wall-cycle elements, joined along sutures which go out to the points of the cube; no central opening or diaphragm}

Genus *Quadrum* Prins & Perch-Nielsen in Manivit *et al.* 1977

{4-9 ray-like, wall-cycle elements. When cubiform, the elements are joined along sutures which go out to the mid-point of the cube edges; no central opening or diaphragm}

Genus *Radiolithus* Stover, 1966 (= *Rhombogyrus* Black, 1973)

{9-16 brick-like, wall-cycle elements, large median diaphragm}

Genus *Uniplanarius* Hattner & Wise, 1980

{3 or 4 ray-like, wall-cycle elements, small median diaphragm}

#### **Uncertain 'polycycloliths'**

Genus *Assipetra* Thierstein, 1973

{solid, subrectangular-globular nannoliths formed from intergrown crystals}

Genus *Hayesites* Manivit, 1971 emend. Applegate *et al.* in Covington & Wise, 1987

{stellate, with 6-11 dextrally imbricate rays; small subsidiary cycles and spines may be present; include only *H. albiensis* and *H. irregularis*}

Genus *Hexalithus* Gardet, 1955

{form-taxon applied to 'hexaliths', *i.e.* hexagonal nannoliths formed from 6 elements}

Genus *Perchnielsenella* Watkins *in* Watkins & Bowdler, 1984

{high, robust wall of ~30 imbricating elements, moderately large median diaphragm}

Genus *Polycostella* Thierstein, 1971

{circular to stellate, which may exhibit 6-8 radial ridges}

Genus *Rucinolithus* Stover, 1966

{stellate, formed from 5 or more ?sinistrally imbricating elements; small additional cycles may be present}

Genus *Tegulalithus* Crux, 1986

{single cycle of ~16 elements forms the wall; each end of the nannolith is covered by overlapping, concentric cycles of diamond-shaped elements, becoming smaller in diameter towards the centre, thus forming a depression}

Family **SCHIZOSPHAERELLACEAE** Deflandre, 1959

**Description:** Hollow, spheroidal, bivalved nannoliths with walls constructed from a systematic geometric arrangement of small, equidimensional crystallites.

Genus *Schizosphaerella* Deflandre & Dangeard, 1938

{see family description}

#### **Unclassified Mesozoic nannoliths**

Genus *Centosphaera* Wind & Wise *in* Wise & Wind, 1977

{keeled sphere, constructed from hour glass-shaped crystallites. Considered a calcareous dinoflagellate by Fütterer, 1990}

Genus *Ceratolithina* Martini, 1967

{straight or hooked rods with lateral spurs and/or blades}

Genus *Ceratolithoides* Bramlette & Martini, 1964

{conical, arrowhead- or horseshoe-shaped nannoliths}

Genus *Kokia* Perch-Nielsen, 1988

{rosette-shaped with 6 (8-10) or more rays (tangential *c*-axes); low birefringence}

Genus *Liliasterites* Stradner & Steinmetz, 1984

{3-rayed; long bifurcations give a 6-rayed appearance}

Genus *Marthasterites* Deflandre, 1959

{3-rayed; ray tips may bifurcate}

Genus *Orthogonoides* Wiegand, 1984

{orthogonally arranged 6-rayed nannolith}

Genus *Prinsiosphaera* Jafar, 1983

{solid, spherical nannolith formed from blocks of calcite laths}

?Genus *Watkinsia* Covington, 1994

{large, narrowly elliptical, structureless base from which a broad, flat blade emerges}

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## FIGURES

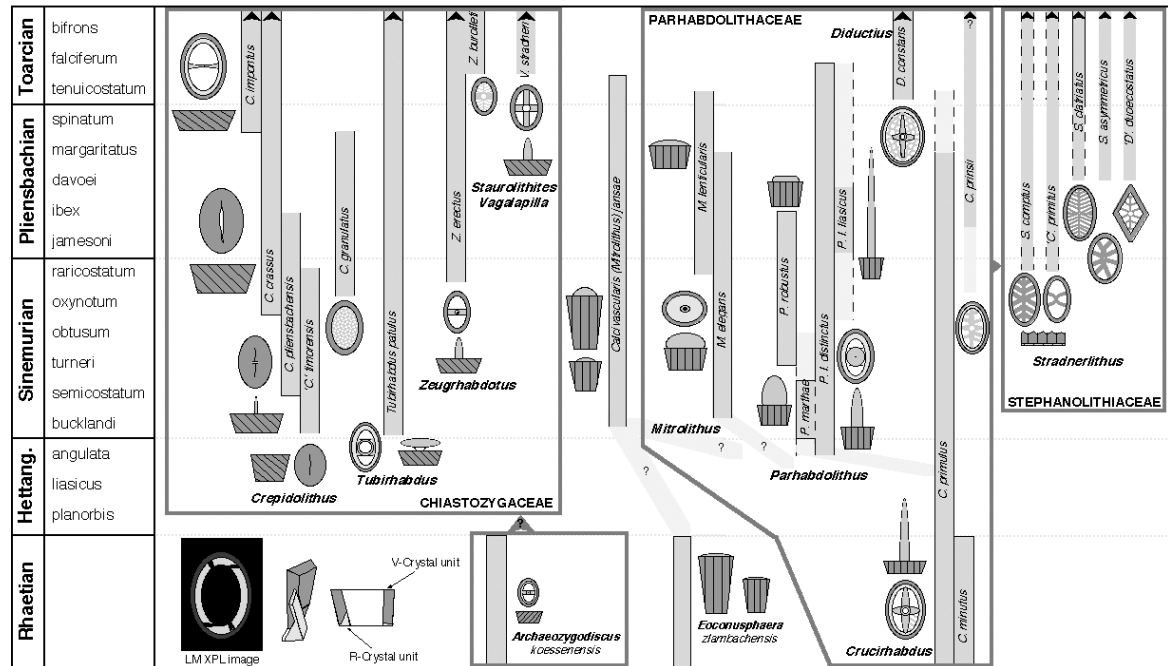


Figure 1 - Initial development of the Eiffellithales. Range-bar conventions as follows: darker shading denotes well-documented range, lighter shading denotes inconsistent or uncertain range; close-spacing indicates likely evolutionary relationships, and when adjacent these relationships are thought to be intergradational. Coccolith sketches are distal and side views, darker-shaded rim cycles indicate V-units, and lighter-shaded cycles R-units; central area structures are given a different shade.

Figure 1: Initial development of the Eiffellithales. Range-bar conventions as follows: darker shading denotes well-documented range, lighter shading denotes inconsistent or uncertain range; close-spacing indicates likely evolutionary relationships and, when adjacent, these relationships are thought to be intergradational. Coccolith sketches are distal and side-views, darker-shaded rim-cycles indicate V-units, and lighter-shaded cycles R-units; central-area structures are given a different shade.



Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Tithonian
Kimmeridgian
Oxfordian
Calloviaan
Bathonian
Bajocian
Aalenian
Toarcian
Pliensbachian
Sinemurian
Hettangian
Rhaetian/Norian

**?PARHABDOLITHACEAE**

Unamed genus  
*Umbria*  
*'Parhabdolites' stubbingii*  
*? Thaumannolithon*

**PARHABDOLITHACEAE**

*Timorella*  
*Bucanodus*  
*Nitroclitellus*  
*Parhabdolites*  
*Diductius*  
*Crucinhabdus*

**STEPHANOLITHIACEAE**

*Rotelapillus*  
*Stoverius*  
*Stephanolithon*

**CALCIOSOLENIACEAE\***

*Calciosolenia*  
*Scapholithus*  
*Truncatoscapheus*

\*Note: The original image contains several misspellings and corrections. The corrected names are used here: *Calciosoleniaceae*, *Calciosolenia*, *Scapholithus*, *Truncatoscapheus*.

\* indicates extant taxon.

# AXOPODORHABDACEAE

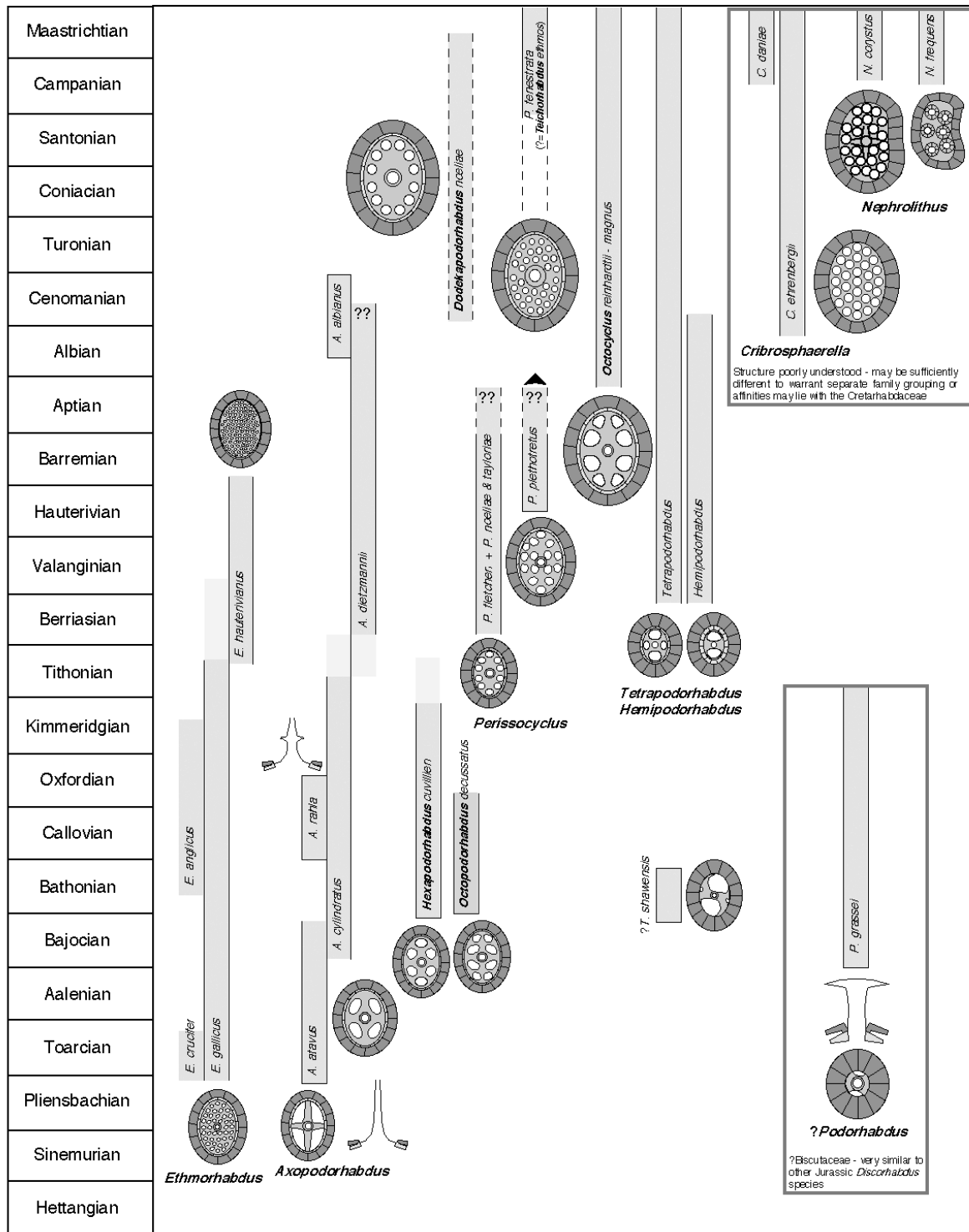


Figure 3 - Phylogeny of the Axopodorhabdaceae. Conventions as for Figure 1.

Figure 3: Phylogeny of the Axopodorhabdaceae. Conventions as for Figure 1.

BISCUTACEAE

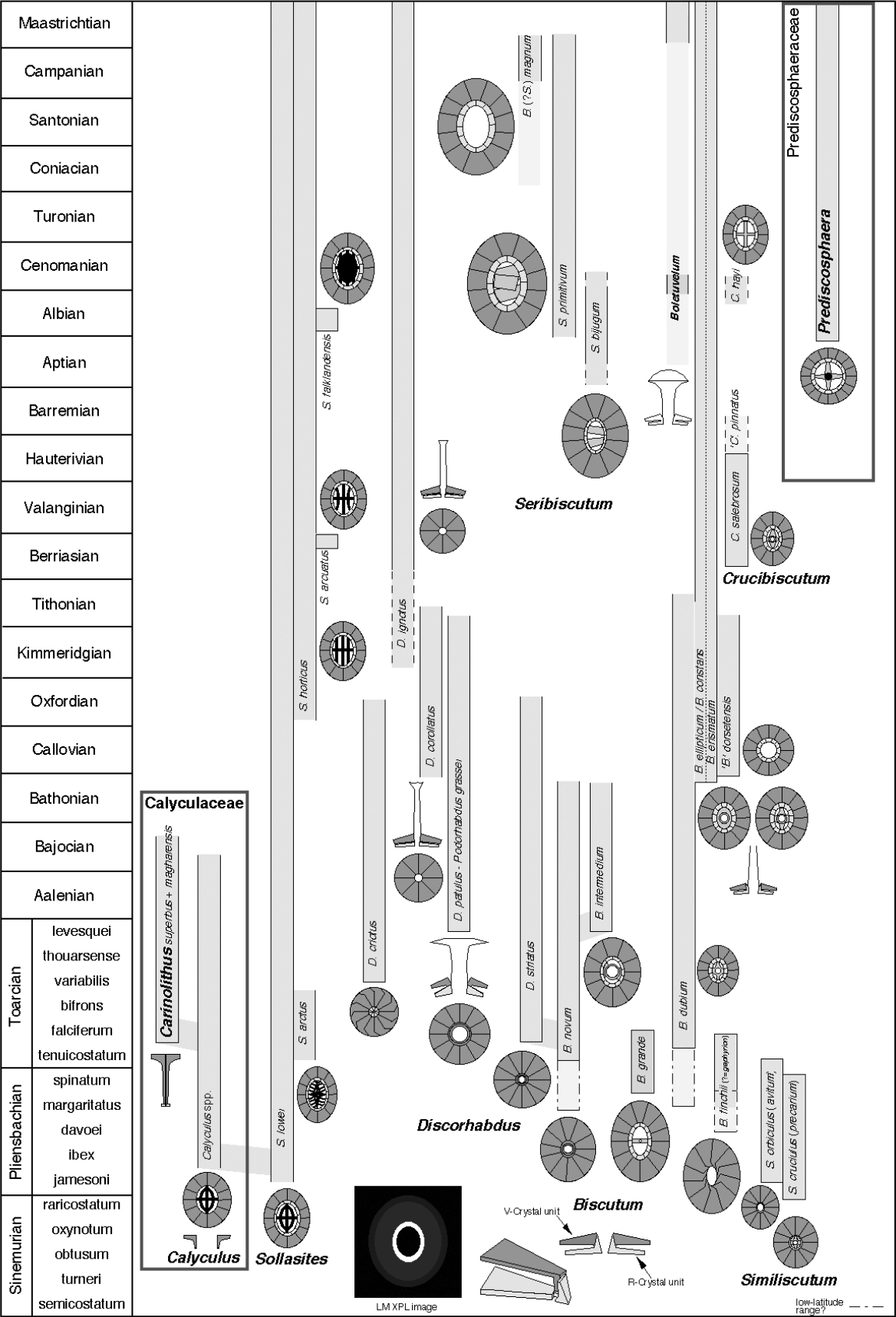


Figure 4 - Phylogeny of the Biscutaceae. Range-bar conventions as for Figure 1.

# CRETARHABDACEAE

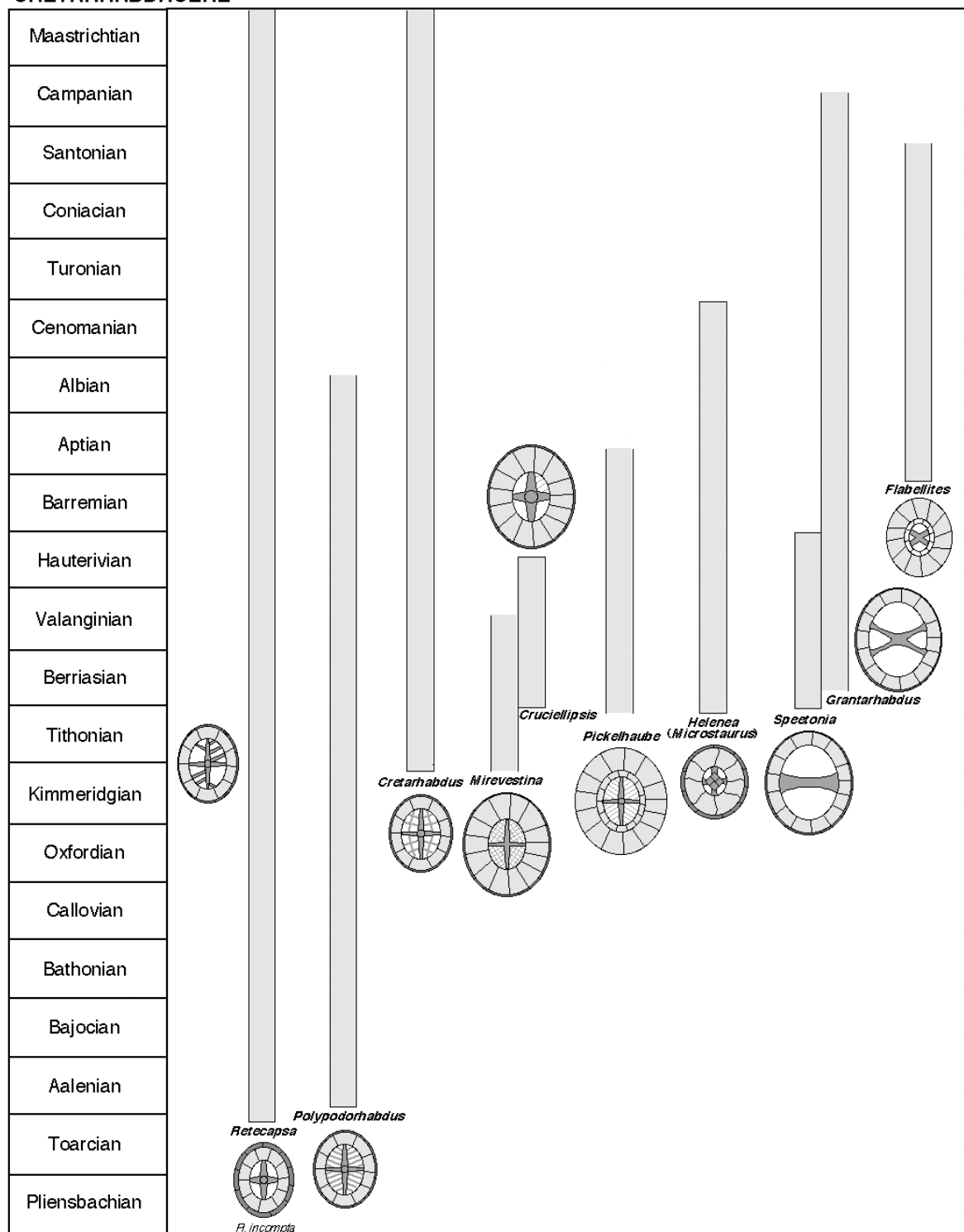


Figure 5 - Stratigraphic distribution of the Cretarhabdaceae. The rim structure and phylogeny of this group are not well understood. Shading of the rim does not indicate V or R unit.

Figure 5: Stratigraphic distribution of the Cretarhabdaceae. The rim structure and phylogeny of this group are not well understood. Shading of the rim does not indicate V- or R-unit.

# WATZNAUERIAEAE

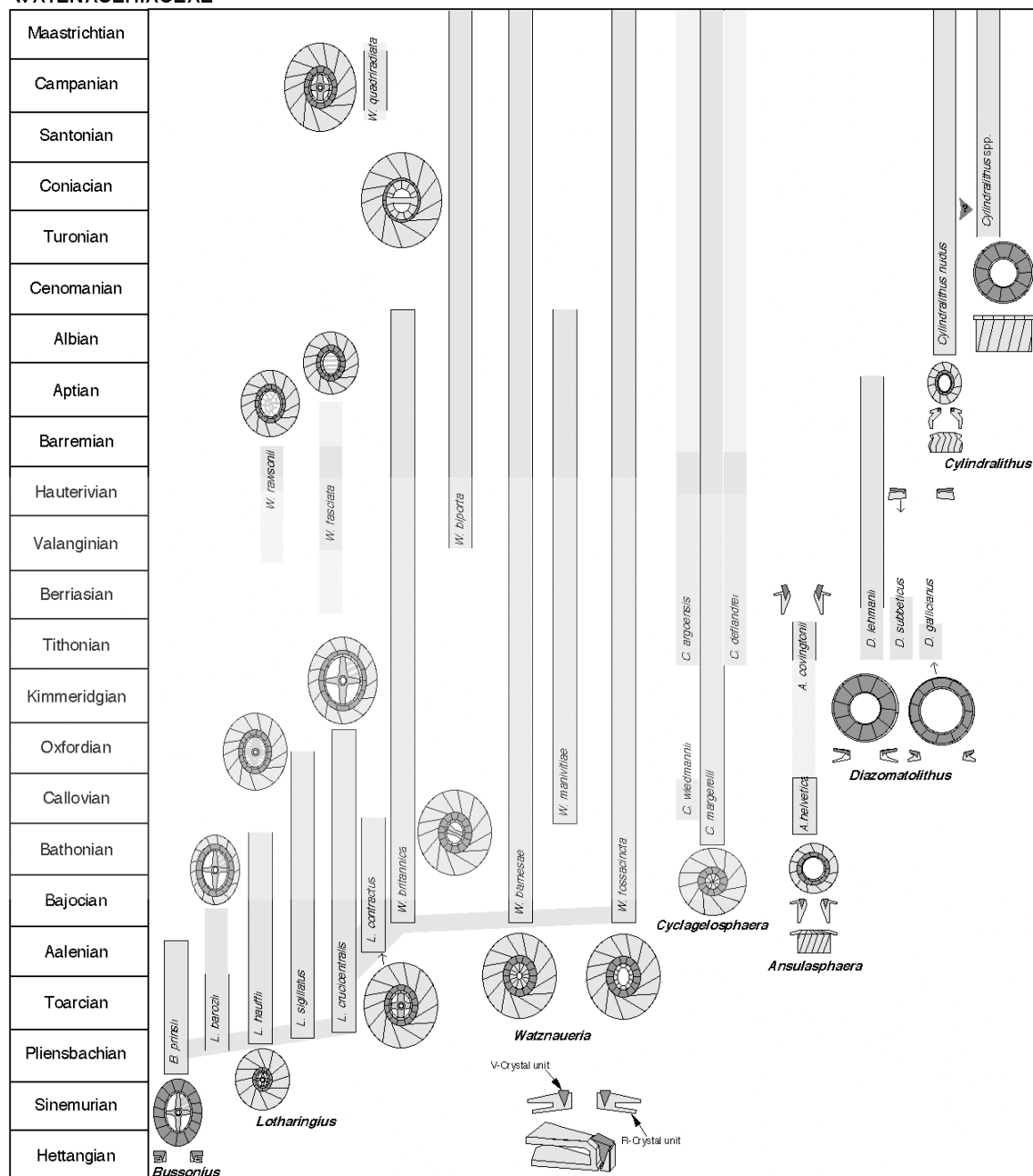


Figure 6 - Phylogeny of the Watznaueriaceae. Range-bar conventions as for Figure 1.

Figure 6: Phylogeny of the Watznaueriaceae. Range-bar conventions as for Figure 1.

# CENOZOIC CALCAREOUS NANNOPLANKTON CLASSIFICATION

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## Abstract

We present herein a revised three-level order-family-genus classification for Cenozoic calcareous nannoplankton. Two new orders (*Zygodiscales*, *Prinsiales*) and one new family (*Calcidiscaceae*) are introduced.

## Introduction

The purpose and philosophy of this contribution are explained in the introductory section (Young & Bown, above). As in the Mesozoic section (Bown & Young, above), a three-level order-family-genus classification is used, as far as seems reasonable, based on current knowledge. In addition, a set of informal numbered groupings (1. *Murolith* coccoliths to 5c. *Nannoliths* consisting of a single crystal-unit, and lacking radial symmetry) are used to provide a logical, but very possibly artificial, organisation, particularly of families and genera *incertae sedis*. For completeness, living coccolithophorids are included, even when they have no known fossil record, this part of the classification being largely derived from Jordan & Green (1994) and Jordan *et al.* (1995). Genera with extant species are indicated by an asterisk \*. If no fossil representatives are known, a second asterisk is added \*\*.

## 1. HETEROCOCCOLITHS

### 1.1. *Murolith heterococcoliths*

#### 1.1a. *Imbricating muroliths (loxoliths)*

Order **EIFFELLITHALES** Rood, Hay & Barnard, 1971

This order is predominantly Mesozoic, see Bown & Young (above) for discussion.

Family **CHIASTOZYGACEAE** Rood, Hay & Barnard, 1973 emend. Varol & Girgis, 1994

The following two genera are known from both the Palaeocene and Maastrichtian and display the typical *Zeugrhabdotus*-type rim-structure.

Genus *Zeugrhabdotus* Reinhardt, 1965

{The only Tertiary species, *Z. sigmoides*, has previously been included in *Placozygus* but shows typical *Zeugrhabdotus* rim and central-area structure}

Genus *Neocrepidolithus* Romein, 1979

{broad, high rim with narrow or closed central-area which may be spanned by bars}

Order **ZYGODISCALES** Young & Bown ord. nov.

**Description:** Muroliths, and modified descendants, with an outer rim-cycle of V-units showing anticlockwise imbrication and an inner rim-cycle showing clockwise imbrication - the opposite imbrication sense to Eiffellithales. This is a diverse group but with clear evolutionary relationships (*e.g.* Romein, 1979; Aubry, 1989). Central-area structures include disjunct transverse bars, diagonal crosses and perforate plates but no spines.

**Comments:** Often assumed to have evolved from the Eiffellithales, via *Chiastozygus*, *Zeugrhabdotus* or *Placozygus*.

However, this is not based upon any directly observable transitions and the opposite imbrication directions of the rim-cycles in the two orders makes this questionable. It is equally likely that the first member of the family, *Neochiastozygus*, evolved from a quite different Cretaceous ancestor.

*N.B.* Regroupings - a conventional subdivision into three families is followed here, however:

1. The Pontosphaeraceae vs Zygodiscaceae subdivision is not obviously logical.
2. The *Neococcolithes* group arguably should be a separate group from the rest.
3. Grouping could be done via a new suborder or by making them all subfamilies of Pontosphaeraceae (this would have to be used since it has priority).

#### Family **HELICOSPHAERACEAE** Black, 1971

**Description:** Extant species are motile, forming ellipsoidal coccospheres with a prominent flagellar opening. Coccoliths are arranged spirally round the coccosphere and may vary slightly in size and shape from the antapex to the flagellar pole. Outer rim (V-units) of the coccolith is modified into a helical flange, ending in a wing or spike. R-units form the baseplate and ?extend to form a blanket of small elements. Central-area bars are conjunct, disjunct or absent.

Genus *Helicosphaera*\* Kamptner, 1954 (= *Helicopontosphaera* Hay & Mohler, 1967)

{coccoliths with helical flange, subgroups can be recognised based on presence/absence of a disjunct bar, bar orientation, flange shape, etc.}

#### Family **PONTOSPHAERACEAE** Lemmermann, 1908

**Description:** Extant species apparently non-motile, coccospheres subspherical and may possess strongly-modified equatorial coccoliths (*Scyphosphaera*). V-units form narrow outer rim-cycle. R-units form inner rim, baseplate and ?blanket. No disjunct structures.

Genus *Pontosphaera*\* Lohmann, 1902 (= *Crassapontosphaera* Boudreaux & Hay, 1969; *Discolithina* Loeblich & Tappan, 1963; *Discolithus* Huxley, 1868; *Koczyia* Boudreaux & Hay, 1969)

{central-area solid or with a variable number of pores}

Genus *Scyphosphaera*\* Lohmann, 1902

{like *Pontosphaera* but with elevated equatorial coccoliths - lopadoliths [*N.B.* *Calciopilleus* and *Tintinnabuliformis* are lopadolith-like coccoliths with apparently different ultrastructures, see *incertae sedis* heterococcoliths]}

Genus *Transversopontis* Hay, Mohler & Wade, 1966

{central-area spanned by a conjunct bar, usually oblique}

#### Family **ZYGODISCACEAE** Hay & Mohler, 1967

##### **A. Rim formed from well-developed V- and R-units, with opposite imbrication directions**

Genus *Jakubowskiella* Varol, 1989

{open central-area}

Genus *Lophodolithus* Deflandre in Deflandre & Fert, 1954

{asymmetrical, often with disjunct bar}

Genus *Neochiastozygus* Perch-Nielsen, 1971

{with diagonal or asymmetric cross in central-area}

Genus *Zygodiscus* Bramlette & Sullivan, 1961

{symmetrical, with disjunct bar}

## B. Rim formed from V-units; R-units vestigial or absent

Assignment of these genera to the Zygodiscaceae is based on imbrication direction of V-units, and putative evolutionary link from *Neochiastozygus* to *Neococcolithes*.

Genus *Neococcolithes* Sujkowski, 1931 (= *Heliorthus* Bronnimann & Stradner, 1960; *Indumentalithus* Vekshina, 1959; *Zygodolithus* Kamptner ex Matthes, 1956){H-shaped cross in central-area}

Genus *Chiphragmalithus* Bramlette & Sullivan, 1961

{High wall and well-developed central-area cross}

? Genus *Isthmolithus* Deflandre, 1954

{parallelogram-shape, affinities to Zygodiscaceae uncertain, see Aubry (1988)}

Genus *Nannotetrina* Achuthan & Stradner, 1969 (= *Nannotetraster* Martini & Stradner 1960)

{X-shaped cross with no rim, probably derived from *Chiphragmalithus* or *Neococcolithes* by loss of rim (Perch-Nielsen, 1985). *N.B.* Species were assigned to *Nannotetraster* until Achuthan & Stradner (1969) showed that it is a junior synonym of *Micula*}

### 1.1b. Other muraloliths and planoliths

**Comments:** The structure of the three groups included here has not been fully worked out, and there is no direct fossil evidence as to their phylogenetic relationships. Affinities between them have been inferred on the basis of central-area structures which are characteristically composed of numerous concentric cycles of apparently disjunct elements, with tangential *c*-axis orientations (T-units). The outermost of these central-area cycles usually consists of radial lath-shaped elements which alternate around the rim with rim elements. This type of structure is shown by the three families included here and so it has been inferred that they have a common ancestry. However the rim structures are markedly different in the three so the apparent central-area similarities maybe misleading. All these groups are well known from the modern plankton where they typically have medium-sized coccospheres covered with large numbers of small coccoliths (often <3 µm). Many species show polymorphism. In the fossil record the small size of the coccoliths makes identification problematic.

Order **STEPHANOLITHIALES** Bown & Young ord. nov.

Family **CALCIOSOLENIACEAE** Kamptner, 1927

**Description:** Extant species are motile with elongate fusiform coccospheres and spine-bearing polar coccoliths. Coccoliths are rhombic muraloliths without flanges, usually termed scapholiths. The rim is predominantly formed of V-units, with small R-units at the base. The central-area has a single lath-cycle, *i.e.* bars are formed of two laths, one from each side of the central-area.

**Comments:** This family is not recognised in many classifications of the extant coccolithophores, with the genera instead being included in the Syracosphaeraceae, mainly due to similarities between central-area structures. We prefer to maintain it as a separate family since the rim structure is not like that of typical Syracosphaeraceae. The group certainly extends into the Mesozoic and may have evolved from the Stephanolithiaceae. In the LM, the rhombic shape makes it easy to recognise these coccoliths but they are too small to be identified to a lower level and many palaeontologists assign all scapholiths to the somewhat artificial species *Scapholithus fossilis*.

Genus *Anoplosolenia*\* Deflandre, 1952

{no polar spines, coccoliths medium-sized - 4-7 µm}

Genus *Calciosolenia*\* Gran, 1912 (= *Acanthosolenia* Bernard, 1939; ?= *Scapholithus* Deflandre, 1954)



{with polar spines, coccoliths small - 2.5-3.5  $\mu\text{m}$ }

Order **SYRACOSPHAERALES** Ostenfeld, 1899

Family **SYRACOSPHAERACEAE** Hay, 1977

**Description:** Extant species are motile, typically with elaborate coccospheres, often showing dithecatism (development of distinct inner and outer layers of coccoliths) and/or modified polar coccoliths. The endothecal (inner layer) coccoliths are normally relatively conservative in form, typically muraliths with the rim-structure described above, a well-developed central-area lath-cycle and variable inner central-area; they are often termed caneloliths. Exothecal coccoliths are much more variable, including discoidal and dome-shaped forms (cyrtoliths).

**Comments:** These coccoliths are typically delicate and only rarely preserved. The recent tendency (*e.g.* Jordan *et al.*, 1995), pending a detailed revision, has been to combine the whole range of forms into the single genus *Syracosphaera*. Polar coccoliths are often only mildly dimorphic, slightly smaller, more angular in shape and bear larger spines. In other cases they are highly-modified, forming elaborate whorl structures. These forms are recognised as separate genera, as are a few other distinctive forms. The fossil record of the family is poor but extends back into the Paleogene; fossil specimens are normally assigned to *Syracosphaera*.

#### **A. Genera with appendages**

These genera have a whorl of appendages formed from highly modified coccoliths around either the apical (flagellar) or antapical pole. They are all monothecate and the body coccoliths are muraliths with a single, weak, proximal flange. This grouping is convenient but probably artificial and so we do not recommend describing a taxon based on it.

Genus *Calciopappus*\*\* Gaarder & Ramsfjell, 1954 emend. Manton & Oates, 1983

{monothecate, with flangeless muraliths, apical coccoliths modified into elongate spines}

Genus *Michaelsarsia*\*\* Gran, 1912 emend. Manton *et al.*, 1984 (= *Halopappus* Lohmann, 1912)

{monothecate, with flangeless muraliths, apical appendages formed from a string of three highly- modified coccoliths - osteoliths}

Genus *Ophiaster*\*\* Gran, 1912 emend. Manton *et al.*, 1984

{monothecate, with flangeless muraliths, antapical appendages formed from a string of several highly modified coccoliths - osteoliths}

#### **B. Genera without appendages**

Genus *Alisphaera*\*\* Heimdal, 1973

{monothecate, coccoliths are placolith-like, with asymmetrical flange bearing a spike or protrusion}

Genus *Alveosphaera*\*\* Jordan & Young, 1990

{monothecate, coccoliths are elongate oblong muraliths, scapholith-like}

Genus *Canistrolithus*\*\* Jordan & Chamberlain, 1993

{monothecate, coccoliths are elongate oblong muraliths, wall/rim weakly imbricate (anticlockwise) with distal flange}

Genus *Coronosphaera*\* Gaarder in Gaarder & Heimdal, 1977

{monothecate, coccoliths are flangeless muraliths, with strongly imbricate (anticlockwise) rims; placement within this family is conventional but rim structure is anomalous}

Genus *Syracosphaera*\* Lohmann, 1902

{usually dithecate, exothecal coccoliths highly variable, endothecal coccoliths include muroliths with 1, 2 or 3 flanges and placolith-like form, apical coccoliths often have spines}

[Genus *Caneosphaera*\*\* Gaarder in Gaarder & Heimdal, 1977]

{monothecate, coccoliths placolith-like, with asymmetrical flange; the included species are now usually recombined in *Syracosphaera*}

[Genus *Deutschlandia*\* Lohmann, 1912]

{exothecal coccoliths disc-shaped, the included species are now usually recombined in *Syracosphaera*}

Order **RHABDOSPHAERALES** Ostenfeld, 1899

Family **RHABDOSPHAERACEAE** Lemmermann, 1908

**Description:** Coccospheres may be motile or non-motile, typically they have spine-bearing and non-spine-bearing coccoliths with similar shields. The spine-bearing coccoliths may be confined to the poles or distributed around the coccosphere, greatly increasing its outer diameter. The coccoliths are disc-shaped (planoliths, see Young *et al.*, in press) with a distinct, slightly elevated rim. In modern species, this is formed of two cycles of elements: a lower/inner cycle showing strong obliquity and an upper/outer cycle of simple non-imbricate elements (Kleijne, 1992). The upper/outer cycle is formed of V-units, the orientation of the inner/lower cycle is unclear. Central-area T-unit cycles are well developed, including both radial laths and usually a central spine or protrusion formed of numerous small elements with a spiral arrangement.

**Comments:** The spinose coccoliths are easy to spot in the LM and can usually be identified. In the Eocene, the Rhabdosphaeraceae form a diverse and abundant group (Perch-Nielsen, 1985; Varol, 1989; Shafik, 1989).

### **Eocene genera**

Rhabdololiths are common in the Eocene and show broadly similar structures and morphologies to modern forms but detailed homologies with the extant genera are not clear. They are characterised by complex multicyclic shields and often multi-tiered central-structures. In addition, the outermost shield-cycle has far fewer elements than the inner shield-cycle. Forms with cap-shaped protrusions appear particularly complex and Shafik (1989) differentiated numerous genera on structural details, although these may prove to be oversplit (*N.B.* Shafik (1989) has priority over Varol (1989); official publication dates are March 1989 vs May 1989, NHM library accession dates are August 1989 vs June 1990).

Genus *Blackites* Hay & Towe, 1962 emend Stradner & Edwards, 1968; Varol, 1989

{multicyclic rhabdololith with hollow spine and flaring collar}

Genera *Cepkiella* Roth, 1970; *Discoturbella* Roth, 1970; *Naninfula* Perch-Nielsen, 1968 emend Perch-Nielsen, 1971; *Amitha* Shafik, 1989; *Notiocyrtolithus* Shafik, 1989; *Ommatolithus* Shafik, 1989; *Cruxia* Varol, 1989

{multicyclic rhabdololiths with cap-shaped protrusions. Differential preservation and illustration modes (LM, TEM, SEM) makes it impossible to rationalise the taxonomy on current data}

Genus *Rhabdololithus* Kamptner ex Deflandre in Grassé 1952

{with hollow spine, without flaring collar. Shield includes outer cycle with approximately half the number of elements of the inner cycle. *N.B.* Many authors assign Eocene species to *Rhabdosphaera* but the structure of these forms appears significantly different to that of modern *Rhabdosphaera*}

### **Extant genera**

Many species are too small to be readily identified by LM as isolated coccoliths and are rarely recorded as fossils. See

Kleijne (1992) for review and detailed descriptions.

Genus *Acanthoica*\* Lohmann, 1903 emend. Schiller, 1913 and Kleijne, 1992

{spines at poles only, coccoliths with radial T-cycle}

Genus *Algirosphaera*\*\* Schlauder, 1945 emend. Norris, 1984

{spines modified into elongate domal or double-lipped (labiatiform) protrusion}

Genus *Anacanthoica*\*\* Deflandre, 1952

{monomorphic, no spines, otherwise similar to *Acanthoica*}

Genus *Cyrtosphaera*\* Kleijne, 1992

{vari-monomorphic, with domal or conical protrusions on all coccoliths, some species are strikingly similar to the Eocene genera, but with simple shields}

Genus *Discosphaera*\* Haeckel, 1894

{monomorphic, spines trumpet-like (salpingiform)}

Genus *Palusphaera*\*\* Lecal, 1965 emend. Norris, 1984

{monomorphic, long spines}

Genus *Rhabdosphaera*\* Haeckel, 1894 (= *Rhabdolithus* Kamptner ex Deflandre in Grassé, 1952)

{dimorphic with spine and non-spine bearing coccoliths, distributed around coccosphere. Used for many fossil rhabdoliths}

## 1.2. Placolith heterococcoliths

Order **PRINSIALES** Young & Bown ord. nov.

**Description:** Extant species are based on non-motile heterococcolith-bearing stages. In addition, at least *Emiliana huxleyi* and *Gephyrocapsa oceanica* have a motile scale-bearing stage. Coccospheres are subspherical and monomorphic. Coccoliths are placoliths but unlike the Coccolithaceae, growth does not occur downward from the proto-coccolith ring. The R-unit is always well developed, forming a proximal shield-element, two tube-elements with opposite senses of imbrication, and usually a central-area element. The V-unit is well developed in early forms, the *Toweius*-type structure, forming an upper layer to the proximal shield, an outermost tube and the distal shield. In the *Reticulofenestra*-type structure, the V-unit is virtually absent and the outer of the two R-unit tube-cycles is extended to form the distal shield. In both structure types, the locus of the proto-coccolith ring is usually marked by a ring of slits. Central-area structures are always conjunct, being formed from either the central-area element or the inner tube-element of the proximal shield.

**Comment:** The major difference between the *Reticulofenestra*-type structure and the *Toweius*-type structure forms a useful basis for subdividing this group (see Young & Bown, above, Figure 1), which was previously considered of family level and has been variously referred to as the Noelaerhabdaceae and Prinsiaceae. Both family names are valid and so are used for the two emended families.

Family **PRINSIACEAE** Hay & Mohler, 1967 emend. (V-unit prominent)

**Description:** Genera with a prominent V-unit, and so a dark distal shield in LM (*Toweius*-type structure - see description of order).

**Comments:** Confined to the Paleogene. They can be difficult to separate from small *Coccolithus* species in the LM, despite the great structural differences; details of central-area structure and the extinction figure need to be used.

Genus *Futyania* Varol, 1989

{tube-elements extended to form a flower-like distal structure}

Genus *Girgisia* Varol, 1989

{modified *Toweius*-type structure - central-area open, proximal shield shows low birefringence and appears to be monocyclic but visible cycle must be an R-unit. Monospecific, *G. gammation*}

?Genus *Hornibrookina* Edwards, 1973

{narrowly elliptical placoliths with central-area filled by large bars; proximal shield monocyclic; distal shield bicyclic with inner cycle forming crown-like structure}

Genus *Neobiscutum* Varol, 1989

{earliest Danian forms, possibly with a simpler structure}

Genus *Praeprinsius* Varol & Jakubowski, 1989

{small early *Prinsius*/*Neobiscutum* intermediates}

Genus *Prinsius* Hay & Mohler, 1967

{elliptical, central-area closed by plate}

Genus *Toweius* Hay & Mohler, 1967

{circular to subcircular, central-area with variable number of pores}

Family **NOELAERHABDACEAE** Jerkovic, 1970 emend. (V-unit vestigial)

**Description:** Coccoliths with *Reticulofenestra*-type structure, *i.e.* V-unit vestigial, R-unit forms proximal shield, distal shield, inner and outer tube-cycles, grill and any central-area structures; strongly birefringent (see also description of order Young (1989)).

Genus *Bekelithella* Bona & Gal, 1985

{with flaring circlet of spines, formed from inner tube-elements, only recorded from Paratethys}

?Genus *Craterolithus* Firth, 1988

{distal shield large and flaring upwards with 10-12 spines projecting down from it}

Genus *Cribrocentrum* Perch-Nielsen, 1971

{central-area partially closed by extensions of the inner tube-elements}

Genus *Cyclicargolithus* Bukry, 1971

{(sub)circular with narrow central opening, often regarded as a junior synonym of *Reticulofenestra*}

Genus *Dictyococcites* Black, 1967

{central-area closed by plates formed from inner tube-cycle. *N.B.* Paleogene species such as *D. scissura* appear distinct, but Neogene forms sometimes assigned to *Dictyococcites* are probably heavily calcified varieties of *Reticulofenestra*}

Genus *Emiliana*\* Hay & Mohler in Hay *et al.*, 1967

{slits between all distal shield, and some proximal shield, elements}

Genus *Gephyrocapsa*\* Kamptner, 1943

{with conjunct bar, formed from inner tube-elements}

Genus *Noelaerhabdus* Jerkovic, 1970

{with spine, formed from inner tube-elements, only recorded from Paratethys}

Genus *Pseudoemiliana* Gartner, 1969

{slits between some distal shield elements}

Genus *Reticulofenestra*\* Hay, Mohler & Wade, 1966 (= *Apertapetra* Hay, Mohler & Wade, 1966)

{lacking distinctive features, or with central-area partially closed by extensions of the inner tube- elements}

[*Bicolumnus* Wei & Wise, 1990]

{this morphotype is very similar to *Pyrocyclus*; it probably represents the isolated central-area and tube-cycles of *Dictyococcites*}

[*Crenolithus* Roth, 1973]

{often used for small *Reticulofenestra* species, but the holotype is a junior synonym of *Gephyrocapsa oceanica*}

[*Pyrocyclus* Hay & Towe, 1962]

{used for small 'species' with open central-area and no real shield development; these are probably early growth stages and broken specimens of other reticulofenestrids, Young (in press)}.

Order **COCCOSPHERALES** Haeckel, 1894 emend.

**Comments:** Extant species form non-motile heterococcolith-bearing stages. In *Coccolithus* and *Calcidiscus*, these are known to alternate with motile holococcolith-bearing stages. The family Coccolithaceae is often used for all placoliths not placed in the Prinsiales. Nonetheless, typical members of the family have a very characteristic rim-structure whilst many other members have modified versions of this structure with sufficient similarity to strongly suggest a common origin. In particular, growth occurs downward from the proto-coccolith ring which consequently becomes embedded within the rim. Hence, on intact specimens, there is no obvious belt of alternating V- and R-elements, but such a belt is seen on specimens where the proximal shield has been partially detached.

Family **COCCOLITHACEAE** Poche, 1913 emend. (*Coccolithus*-type rim)

**Description:** These have the *Coccolithus*-type rim-structure, as described in Young (1992). The V-unit forms both the distal shield and the proximal layer of the central-area (= centro-proximal cycle). The R-unit forms the proximal shield and the distal layer of the central-area (= centro-distal cycle). The proximal shield itself is bicyclic with distinct upper and lower layers but these are both formed from the R-unit, unlike the *Toweius*-type structure. The central-area is often spanned by disjunct structures and these are used to define genera.

Genus *Bramletteius* Gartner, 1969

{*Crucioplacolithus*-like base with very large monocrystalline 'paddle' or spine}

Genus *Campylosphaera* Kamptner, 1963

{strongly convex shield giving subrectangular outline, axial cross in central-area}

Genus *Chiasmolithus* Hay, Mohler & Wade, 1966

{diagonal, usually offset, cross in central-area, the bars of which show a median extinction line in XPL; the centro-distal cycle forms a distinct collar around contact with V-units}

Genus *Clausicoccus* Prins, 1979

{typical Coccolithaceae rim (see SEMs in Varol (1989)), central-area wide, filled by disjunct plate with variable number of perforations}

Genus *Coccolithus*\* Schwartz, 1894 (= *Coccosphaera* Wallich, 1877; *Ericsonia* Black, 1964; *Cyclolithus* Kamptner, 1948)

{Central-area open or with a disjunct transverse bar}

Genus *Crucioplacolithus* Hay & Mohler in Hay *et al.*, 1967

{axial or near-axial cross in central-area}

Genus *Sullivania* Varol, 1992

{diagonal, usually offset, cross in central-area, bars undivided in XPL. Centro-distal cycle does not form a distinct collar}

#### **?Slightly modified *Coccolithus*-type rim**

The following genera show strong similarities to the typical Coccolithaceae but probably have somewhat modified rims.

[Genus *Birkelundia* Perch-Nielsen, 1971]

{Perch-Nielsen (1971) placed three Eocene species in this genus on grounds that they had a monocyclic proximal shield, however, none of them are unambiguous}

Genus *Coronocyclus* Hay, Mohler & Wade, 1966

{open ring-like coccolith without shields, elements of rim complexly intergrown, apparently with outer V-unit and inner R-unit. Included here in Coccolithaceae as structure suggests it is a neomorphic *Coccolithus* derivative}

Genus *Crassidiscus* Okada, 1990

{monospecific, *C. backmanii*, large form with indistinct XPL image; SEM shows 3 tiers which may be equivalent to the three shield cycles of *Coccolithus*}

Genus *Hughesius* Varol, 1989

{like *Clausicoccus* but no inner bright cycle, so centro-distal R-unit element probably missing; ?proximal shield also formed from V-unit}

Genus *Solidopons* Theodoridis, 1984

{narrow rimmed ?placolith with prominent arched bridge; extinction figure suggests affinities to *Coccolithus*}

Family **CALCIDISCACEAE** Young & Bown fam. nov. (*Calcidiscus*-type rim)

**Diagnosis:** *Coccosphaerales constans ex coccolithis cum R-unitis no nisi in proximo scuto*. Coccosphaerales consisting of coccoliths with R-units only in the proximal shield.

**Description:** Dominant phase of life-cycle, non-motile with placolith heterococcoliths. V-unit forms the distal shield and tube, extending to the proximal surface. R-unit forms the proximal shield. As in the Coccolithaceae, growth occurs downward from the proto-coccolith ring which becomes embedded within the structure so that alternating V- and R-units are only visible on specimens where the proximal shield has broken off. Distal shield sutures typically show laevogyral curvature. The proximal shield is usually monocyclic with radial sutures; sometimes it is bicyclic due to the development of a lower layer, with elements showing strong dextral obliquity (in proximal view). The connection between the proximal and distal shields is weak and they frequently separate.

**Comments:** These genera have previously been included within the Coccolithaceae but the distinctively different structure appears to warrant classification in a separate family. The cytology of *Umbilicosphaera* is described by Inouye & Pienaar (1984).

Genus *Calcidiscus*\* Kamptner, 1950 (= *Cyclococcolithus*, *Cyclococcolithina*, *Cycloplacolithella*, *Cycloplacolithus*, *Tiarolithus*, *Striatococcolithus* Bukry, 1971)

{{(sub)circular, central-area closed or narrow. Proximal shield elements often kinked, sometimes becoming bicyclic}}

Genus *Cryptococcolithus* Gartner, 1992

{elliptical, proximal shield thin so coccolith is dark in XPL, central-area with non-birefringent perforate plate}

Genus *Cycloperfolithus* Lehotayova & Priewalder, 1978

{sub-circular, central-area with non-birefringent perforate plate. Often regarded as a junior synonym of *Calcidiscus* but proximal shield is described as bicyclic}

Genus *Geminilithella* Backman, 1980

{wide central-area and narrow rim (see Young (in press)) better regarded as a junior synonym of *Umbilicosphaera*}

Genus *Hayaster*\* Bukry, 1973

- {proximal shield diminutive, distal shield with straight radial sutures and angular ray ends, 9-13 elements}
- Genus *Oolithotus*\* Reinhardt in Cohen & Reinhardt, 1968
  - {asymmetrical, proximal shield elements show complex kinking, nearly becoming bicyclic, otherwise very like *Calcidiscus*}
- Genus *Umbilicosphaera*\* Lohmann, 1902
  - {open central-area, distal shield elements show complex kinked sutures. Proximal shield monocyclic or bicyclic}
- [Genus *Striatococcolithus* Bukry, 1971]
  - {the only species, *S. pacificanus*, should probably be included in *Calcidiscus*}

Family **PLEUROCHRYSIDACEAE** Fresnel & Billard, 1991

This family is here included in the Cocco-sphaerales since the rim structure appears to be a simplified version of that of the Coccolithaceae. It is monogeneric and possibly should be subsumed into the Coccolithaceae.

- Genus *Pleurochrysis*\*\* Pringsheim, 1955 (= *Cricosphaera* Braarud, 1960)
  - {Coccolithophore motile, neritic, coccosphere monomorphic. Coccoliths are narrow-shielded placoliths. Tightly interlocked crystal-units, V-unit forms distal shield and tube. R-unit forms proximal shield and small element on inside of tube - cricoliths}

Order **WATZNAUERIALES** Bown, 1987

Family **WATZNAUERIACEAE** Rood, Hay & Barnard, 1971

- Genus *Cyclagelosphaera* Noël, 1965
  - {this predominantly Mesozoic genus persisted into the Danian; see Bown & Young (above)}

**1.3. Heterococcoliths of uncertain affinities**

Family **HYMENOMONADACEAE** Senn, 1900

**Description:** Small littoral and fresh-water coccolithophores. Coccoliths are goblet-shaped muroliths with open central-area, well-developed proximal flange, and a narrow distal flange or flaring end, entirely formed of a single cycle of <15 crystal-units (tremaliths). In *Ochrosphaera*, crystal-units have sub-vertical orientations. They differ from *Pleurochrysidaceae* by the absence of a second cycle of units (*i.e.* R-units). References include Manton & Peterfi (1969), Braarud (1954) and Fresnel (1994).

- Genus *Hymenomonas*\*\* Stein, 1878
  - {freshwater and marine species, coccoliths with distal part flaring, elements have pointed ends}
- Genus *Ochrosphaera*\*\* Schussnig, 1930
  - {littoral, coccoliths with distinct distal flange}

Family **PAPPOSPHAERACEAE** Jordan & Young, 1990

**Description:** Family of minute, lightly-calcified coccolithophores, mainly known from high-latitudes, with holo- and heterococcolith phases (Thomsen *et al.*, 1991). Heterococcoliths have a narrow murolith rim; +/- open central-area; tall, delicate spine supporting calyx of four plates (pappoliths). Holococcoliths tower-like, crystallites arranged in hexagonal or triangular groups.

- Genus *Pappomonas*\*\* Manton & Oates, 1975
  - {heterococcospheres dimorphic, only circum-flagellar coccoliths have spines}

Genus *Papposphaera*\*\* Tangen, 1972

{heterococcospheres monomorphic, all bear spines}

Genus *Trigonaspsis*\*\* Thomsen, 1980

{tower-like holococcoliths with triangular crystallite groups}

[Genus *Turrisphaera*\*\* Manton, Sutherland & Oates, 1976]

{tower-like holococcoliths with hexagonal crystallite groups, = holococcolith phases of *Pappomonas* and *Papposphaera* spp.}

#### **Possibly related weakly-calcified holococcoliths**

Genus *Balaniger*\*\* Thomson & Oates, 1978

{coccoliths are organic scales with a few pyramidal ?crystallites}

Genus *Calciarcus*\*\* Manton, Sutherland & Oates, 1977

{rhombohedral crystallites forming 4 struts ?with calcareous rim}

Genus *Quaternariella*\*\* Thomsen, 1980

{coccoliths are organic scales with a few rhombohedral crystallites}

#### **Possibly related weakly-calcified heterococcoliths**

Genus *Jomonolithus*\*\* Inouye & Chihara, 1983

{mural coccoliths with *Wigwamma*-like rim, no central-area structures; partially calcified specimens show beaded ultrastructure}

Genus *Wigwamma*\*\* Manton, Sutherland & Oates, 1977

{simple rim and 'wigwam' of 3 or 4 struts}

#### **Genera *incertae sedis***

##### **A. Forms with a fossil record**

This is a diverse group but all show typical heterococcolith structure, only *Umbellosphaera* and *Neosphaera* are extant.

Genus *Calciopilleus* Müller, 1974

{bell-shaped with external ridges}

Genus *Conococcolithus* Hay & Mohler, 1967

{poorly-documented conical placolith, one species, *C. minutus*, Palaeocene}

Genus *Ellipsolithus* Sullivan, 1964

{placolith morphology but structure anomalous}

Genus *Hayella* Gartner, 1969 (= *Nannocorbis* Müller, 1974, cf. Theodoridis, 1984)

{tube with two flanges, ?a modified placolith, formed of a single cycle of sub-vertical crystal-units}

Genus *Ilseolithina* Stradner in Stradner & Adamiker, 1966

{modified placolith, distal shield reduced to a cycle of spines, formed of single cycle of steeply inclined crystal-units}

Genus *Markalius* Bramlette & Martini, 1964

{moderately birefringent interference figure with a bright tube-cycle; central-area narrow or closed - details of structure uncertain}

Genus *Neosphaera*\* Lecal-Schlauder, 1950 (= *Craspedolithus* Kamptner, 1963)

{open ring-like coccolith with proximal shield only, formed of single cycle of sub-vertical crystal- units; possibly an alternate life-cycle stage of *Ceratolithus* (Alcober & Jordan, 1997)}

Genus *Pedinocyclus* Bukry & Bramlette, 1971 (*nom subst pro Leptodiscus* Bukry & Bramlette, 1969)

{poorly-documented circular placolith showing low birefringence}



Genus *Tintinnabuliformis* Varol, 1991

{bell-shaped with apical horns}

Genus *Umbellosphaera*\* Paasche in Markali & Paasche, 1955 (= *Ellipsodiscoaster* Boudreaux & Hay, 1969)

{? motile, placolith-like morphology with distal shield greatly extended, R-unit forms central-area, tube and distal shield. Diminutive V-unit forms very narrow proximal shield. Distal shield is thin, except in some *U. tenuis*, and so shows low birefringence; tube highly birefringent}

## B. Recent genera

This diverse group of genera all show basic heterococcolith features (except perhaps *Polycrater*) and are mostly small and poorly known. (*N.B. Florisphaera* is placed here among the nannoliths since it lacks any basal disc structure.)

Genus *Gladiolithus*\* Jordan & Chamberlain, 1993

{basal disk of two elements supporting a long hexagonal-section spine; in LM isolated spine fragments resemble long-thin *Florisphaera profunda* coccoliths}

Genus *Polycrater*\*\* Manton & Oates, 1980

{coccoliths are aragonitic square-section cones, c. 1 µm across, very numerous on coccosphere}

Genus *Turrilithus*\*\* Jordan *et al.*, 1991

{narrow-rimmed placolith base, square-section flaring spine}

Genus *Vexillarius*\*\* Jordan & Chamberlain, 1993

{small and rare, murolith base, square-section flaring spine}

[Genus *Thorosphaera*\*\* Ostenfeld, 1910]

{very poorly-documented large coccolithophore, with tube-like coccoliths, possibly *Scyphosphaera*. *N.B. Thorosphaera flabellata* is now placed in *Gladiolithus*}

## 2. HOLOCOCCOLITHS

Family **CALYPTROSPHAERACEAE** Boudreaux & Hay, 1969

**Comments:** Coccolithophores which are only known from a holococcolith-bearing stage are assigned to this family. Holococcolith formation must be a rather precise biomineralisation process so this is probably not a polyphyletic grouping. However, on present evidence it is likely that holo- and heterococcoliths are formed respectively during the haploid and diploid life-cycle phases (Manton & Leedale, 1969; Rowson *et al.* 1986; Billard, 1994). It is quite likely that many more holococcolith taxa will prove to have heterococcolith equivalents. So for the moment the holo- and heterococcolith classifications should be seen as independent.

Holococcoliths have a very poor fossil record in the Quaternary and Neogene, perhaps largely because most of them are too small (<2 µm) to be easily preserved or identified. In the Paleogene, however, there are a number of large, distinctive holococcolith taxa. It is therefore convenient to subdivide the holococcoliths into fossil (predominantly Paleogene) and extant groups. The Paleogene genera are divided into birefringent and non-birefringent groups, whilst the living group is subdivided into monomorphic and dimorphic genera, following Kleijne (1991) and Jordan *et al.* (1995).

### A. Non-birefringent fossil holococcoliths

Holococcoliths which are non-birefringent in plan view (*i.e.* all crystallites have vertical *c*-axes), predominantly Paleogene.

Genus *Clathrolithus* Deflandre, 1954

{large, discoidal with large perforations}

Genus *Holodiscolithus* Roth, 1970

- {discoidal with large perforations; one species *H. macroporus* occurs in the Neogene}
- Genus *Corannulus* Stradner, 1962 (= *Guttolithion* Stradner, 1962; *Diademopetra* Hay, Mohler & Wade, 1966)
- {discoidal with large central opening and marginal perforations or indentations}
- Genus *Peritrachelina* Deflandre, 1952
- {crescent-shaped in plan view}
- Genus *Orthozygus* Bramlette & Wilcoxon, 1967
- {basin shaped with a bridge (zygolith)}

## B. Birefringent fossil holococcoliths

Holococcoliths showing birefringence in plan view, typically composed of several blocks with a narrow rim showing radial crystallographic orientation.

- Genus *Dakylethra* Gartner in Gartner & Bukry, 1969
- {domal with exterior ridges and depressions. *N.B.* *Calypetrosphaera pirus*, a living species, is often assigned to *Dakylethra*, but has a quite different morphology}
- Genus *Lanternithus* Stradner, 1962
- {subhexagonal in plan view}
- Genus *Octolithus* Romein, 1979
- {discoidal, formed of 4 large and 4 small blocks}
- Genus *Zygrhablithus* Deflandre, 1959 (= *Pseudozygrhablithus* Haq, 1971; *Sujkowskiella* Hay, Mohler & Wade, 1966)
- {discoidal base extended into tall spine}
- Genus *Quadrilateralis* Varol, 1991
- {quadrilateral rim of four blocks plus bridge}
- [Genus *Semihololithus* Perch-Nielsen, 1971]
- {defined as showing combined holococcolith and heterococcolith parts. Included Cenozoic species are assignable to *Dakylethra* and *Zygrhablithus*}

## C. Extant monomorphic holococcoliths

Genera with monomorphic coccospheres, *i.e.* only one type of coccolith developed.

- Genus Kleijne, 1992
- {chalice-shaped coccoliths - calcicaliths}
- Genus *Calypetrosphaera*\* Lohmann, 1902
- {dome-shaped coccoliths - calyptroliths}
- Genus *Flosculusphaera*\*\* Jordan & Kleijne in Kleijne *et al.*, 1991
- {flaring tube-shaped coccoliths with distal cover - flosculoliths}
- Genus *Gliscolithus*\*\* Norris, 1985
- {bulb-shaped coccoliths - gliscoliths}
- Genus *Homozygosphaera*\* Deflandre, 1952
- {basin-shaped coccoliths with bridge - zygoliths}
- Genus *Periphyllophora*\*\* Kamptner, 1937
- {basin-shaped coccoliths with bridge extended into leaf-like process - helladoliths}
- Genus *Syracolithus*\*\* Deflandre, 1952
- {disk-like coccoliths with variable number of depressions - laminoliths}

#### D. Extant dimorphic holococcoliths

Genera with dimorphic coccospheres. These have body coccoliths of one type with a second type occurring apically, *i.e.* around the flagellar opening.

Genus *Anthosphaera* Kamptner, 1937 emend. Kleijne, 1991

{calyptrolith body coccoliths and apical coccoliths with narrow basal ring and leaf-like process - fragarioliths}

Genus *Calyptrolithina* Heimdal, 1982

{calyptrolith body coccoliths and apical zygoliths}

Genus *Calyptrolithophora* Heimdal in Heimdal & Gaarder, 1980

{calyptrolith body coccoliths and apical calyptroliths}

Genus *Corisphaera* Kamptner, 1937

{zygolith body coccoliths and apical zygoliths}

Genus *Helladosphaera* Kamptner, 1937

{zygolith body coccoliths and apical helladoliths}

Genus *Poricalyptra* Kleijne, 1991

{calyptrolith body coccoliths and apical helladoliths}

Genus *Poritectolithus* Kleijne, 1991

{zygolith body coccoliths and apical helladoliths}

Genus *Sphaerocalyptra* Deflandre, 1952

{calyptrolith body coccoliths and apical calyptroliths}

Genus *Zygospaera* Kamptner, 1936

{laminolith body coccoliths and apical laminoliths}

### 3. NANNOLITHS

As noted above (Young & Bown, above), the nannolith/heterococcolith divide is subjective. We include here all forms which lack a distinct rim. Since V/R mode calcification has not been identified in any of these taxa we cannot be certain that they are directly related to the coccoliths. However they share with heterococcoliths the characteristics of being formed from a relatively low number of calcite crystals each of which has both its crystallographic orientation and morphology strongly regulated. In addition, for all these, the distribution pattern suggests a planktonic origin.

#### 3a. Nannoliths consisting of several crystal units and showing radial symmetry

Family **BRAARUDOSPHAERACEAE** Deflandre, 1947

**Description:** See Bown & Young (above).

Genus *Braarudosphaera*\* Deflandre, 1947

{elements trapezoidal, sutures go to edges of the pentagon. Paleogene species are very diverse and include conical forms}

Genus *Micrantholithus* Deflandre in Deflandre & Fert, 1954

{elements triangular, sutures go to vertices of the pentagon}

Genus *Pemma* Klump, 1953

{elements triangular, with a central knob, hole or depression}

Genus *Pentaster* Bybell & Gartner, 1972

{elements elongated into free rays}

Genus *Quinquerhabdus* Bukry & Bramlette, 1971

{pentalith greatly elevated}

Family **GONIOLITHACEAE** Deflandre, 1957

Genus *Goniolithus* Deflandre, 1957

{pentagonal plate with a distinct rim surrounding a mesh-like array of small crystals. Rare and sporadic stratigraphic distribution}

Family **LAPIDEACASSACEAE** Bown & Young fam. nov.

Genus *Lapideacassis* Black, 1971 (? = *Scampanella* Forchheimer & Stradner, 1973; *Pervilithus* Crux, 1981)

{see Bown & Young, above}

### **Genera incertae sedis**

Genus *Biantholithus* Bramlette & Martini, 1964

{consist of 6-11 radial elements; LM birefringence is low and with an offset radial extinction cross; the nannoliths are concavo-convex and form spheres (Romein, 1979; Mai *et al.*, 1994)}

Genus *Nannoturba* Müller, 1979

{mass of radiating rods, uncertain affinities}

?Genus *Nannotetrina* Achuthan & Stradner, 1969 - see Zygodiscaceae

Genus *Pseudotriquetrorhabdulus* Wise in Wise & Constans, 1976

{rod-shaped with 6-12 laths; each lath is a separate crystal-unit with *c*-axis radial, relative to axis of the rod}

Order **DISCOASTERALES** Hay, 1977

We include in this order nannoliths with a structure of elements radiating from a common centre or axis. They all originate in the Paleocene and evolutionary relationships between them have been suggested by, for example, Romein (1979) and Perch-Nielsen (1985). Nonetheless, it may represent a polyphyletic grouping.

Family **DISCOASTERACEAE** Tan, 1927

**Description:** Discoidal nannoliths of 3-40 elements radiating from a common centre. *C*-axes vertical, so nannoliths appear dark in plane-polarised light. Some early forms also include a cycle of birefringent units.

Genus *Catinaster* Martini & Bramlette, 1963

{basket shaped, certainly derived from *Discoaster*, e.g. Peleo-Alampay *et al.* (in press)}

Genus *Discoaster* Tan, 1927 (= *Agalmatoaster*, *Clavodiscoaster*, *Discoasteroides*, *Eudiscoaster*, *Gyrodiscoaster*, *Heliodiscoaster*, *Hemidiscoaster*, *Radiodiscoaster*, *Truncodiscoaster*, *Turbodiscoaster*)

{includes >100 species. The most obvious subdivision is into rosette-shaped species with >8 rays and star-shaped species with <10 rays, and a number of other features parallel this subdivision. Formal classification as proposed by Theodoridis (1984) into the genera *Heliodiscoaster* and *Eudiscoaster* has not, however, proven popular}

Family **FASCICULITHACEAE** Hay & Mohler, 1967

**Description:** Conical- or top-shaped nannoliths consisting of 10-30 wedge-shaped, radially-arranged elements. Apparently distinct distal cycles are developed in some species but these probably are formed by kinking of the elements rather than being new crystal-units. Suggested to be ancestral to the Heliolithaceae (Romein, 1979).

Genus *Fasciculithus* Bramlette & Sullivan, 1961

{see family description}

Family **HELIOLITHACEAE** Hay & Mohler, 1967

**Description:** Discoidal nannoliths consisting of at least two superposed cycles of crystal units. Suggested to be ancestral to the Discoasteraceae (e.g. Romein, 1979).

Genus *Bomolithus* Roth, 1973

{in LM in plan view only the central column is bright}

Genus *Heliolithus* Bramlette & Sullivan, 1961 (= *Bomolithus* Roth, 1973)

{in LM in plan view the entire nannolith is bright}

Family **SPHENOLITHACEAE** Deflandre, 1952

**Description:** Conical-shaped nannoliths consisting of several superimposed cycles of elements all radiating from a common point of origin. C-axes of the elements run along their length.

Genus *Sphenolithus* Deflandre in Grassé, 1952 (= *Furcatolithus* Martini, 1965; *Sphenaster* Wilcoxon, 1970)

{see family description}

### **3b. Nannoliths consisting of a single crystal-unit, showing radial symmetry**

Family **LITHOSTROMATIONACEAE** Deflandre, 1959

**Description:** Relatively large (10-20µm) nannofossils, confined to epicontinental areas. Morphology is plate-like with rays and interconnecting ridges. Strongly reminiscent of the internal spicules in actiniscid dinoflagellates. Show low birefringence in plan view.

Genus *Lithostromation* Deflandre, 1942

{3-fold symmetry}

Genus *Martiniaster* Loeblich & Tappan, 1963 (= *Coronaster* Martini, 1961)

{12-rayed platelets}

Genus *Trochoaster* Klumpp, 1953

{6-fold symmetry}

?Genus *Isolithus* Lyul'eva, 1989

{3-fold symmetry}

Genus *Lacunolithus* Lyul'eva, 1989

{platelet with 8 pairs of rays}

### **Genera *incertae sedis***

Genus *Imperiaster* Martini, 1970

{flattened tetrahedron}

Genus *Rhomboaster* Bramlette & Sullivan, 1961

{+/- rhomboidal}

Genus *Tribrachiatus* Shamrai, 1963

{initially hexaradiate, formed by two superposed triplets of rays. Triplets rotate through evolution to become parallel giving triradiate nannolith with bifurcate ray tips}

Genus *Trochasterites* Stradner, 1961

{planar triradiate nannolith with bifurcate ray tips, ?a holococcolith}

[*Marthasterites* Deflandre, 1959]

{this genus is now only used for Cretaceous forms but many species of *Tribrachiatus* were previously included in it}

### 3c. Nannoliths consisting of a single crystal unit, and lacking radial symmetry

Family **CERATOLITHACEAE** Norris, 1965

**Description:** Horseshoe-shaped nannoliths (ceratoliths) composed of a single crystal unit.

**Comments:** The extant species, *Ceratolithus cristatus*, occurs as a single nannolith which is apparently wrapped around the cell. Some cells also bear hoop-shaped coccoliths. Alcober & Jordan (1997) observed *C. cristatus* hoop-shaped coccoliths inside *Neosphaera coccolithomorpha* coccospheres which suggests that ceratoliths may, like holococcoliths, be an alternate phase of the life-cycle.

Genus *Amaurolithus* Gartner & Bukry, 1975

{*c*-axis vertical, nannolith dark in LM}

Genus *Ceratolithus*\* Kamptner, 1950

{*c*-axis in plan of ceratolith, perpendicular to long axis, bright in LM}

[*Angulolithina* Bukry, 1973]

{angular V-shaped nannolith with *c*-axis parallel to length. These are of irregular morphology and distribution, and may well be fragments of a larger non-haptophyte fossil}

Family **TRIQUETRORHABDULACEAE** Lipps, 1969

**Description:** Rod-shaped nannoliths formed of three blades (these may bear subsidiary ridges). The entire nannolith behaves as one crystal-unit, crystallographic orientation varies between genera.

Genus *Orthorhabdus* Bramlette & Wilcoxon, 1967

{one blade wider than the other two, *c*-axis lies in plane of this blade, and perpendicular to the long- axis of the nannolith}

Genus *Triquetrorhabdulus* Martini, 1965

{blades arranged at 120° to each other, uncurved, *c*-axis parallel to length; always shows strong birefringence}

unnamed Genus

{*T. rugosus* and related species have structure distinct from *Triquetrorhabdulus sensu* Martini, 1965; one blade narrower than the other two, *c*-axis lies in plane of this blade, and perpendicular to the long- axis of the nannolith; birefringence usually low (depends on how the specimen is lying); often curved. New genus to be proposed (Varol & Young, in prep.)}

[*Pseudotriquetrorhabdulus* Wise in Wise & Constans, 1976]

{formed of a set of laths with radial *c*-axes and so included in radial nannoliths}

### Genera *incertae sedis*

Genus *Florisphaera*\* Okada & Honjo, 1973

{liths are small tapering plates which form artichoke-like coccospheres. *C*-axis parallel to the long axis of the plate but birefringence is low due to small size. Very abundant. A peg-like structure on the base of some specimens may indicate a second crystal-unit}

Genus *Minylitha* Bukry, 1973 emend. Theodoridis, 1984

{kite-shaped plate with raised rims on both sides, *c*-axis in plane of plate}

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