

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 Zygodiscaeae 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; *Zygoilithus* 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 muraliths 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 muraliths 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 μm }

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 caneoliths. 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 **RHABDOSPHERALES** Ostenfeld, 1899

Family **RHABDOSPHERACEAE** 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

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

Genus *Rhabdolithus* 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 **NOELAE RHABDACEAE** 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 cirlet 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*}

[*Crenalithus* 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 **COCCOSPHAERALES** 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

{*Cruciplacolithus*-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 *Cruciplacolithus* 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 & Prievalder, 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 *Umblicosphaera** 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 muraliths 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 muralith 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

{muroolith 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 *Iselithina* 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 *Pedinocychus* 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.* *Calyptrosphaera 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 *Calyptrosphaera** Lohmann, 1902
 - {dome-shaped coccoliths - calyptroliths}
- Genus *Flosculosphaera*** 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 *Zygosphaera* 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) nanofossils, 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 *Rhombaster* 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 *Trochastrites* 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 TRIQUETRRORHABDULACEAE 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 120⁰ 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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