

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

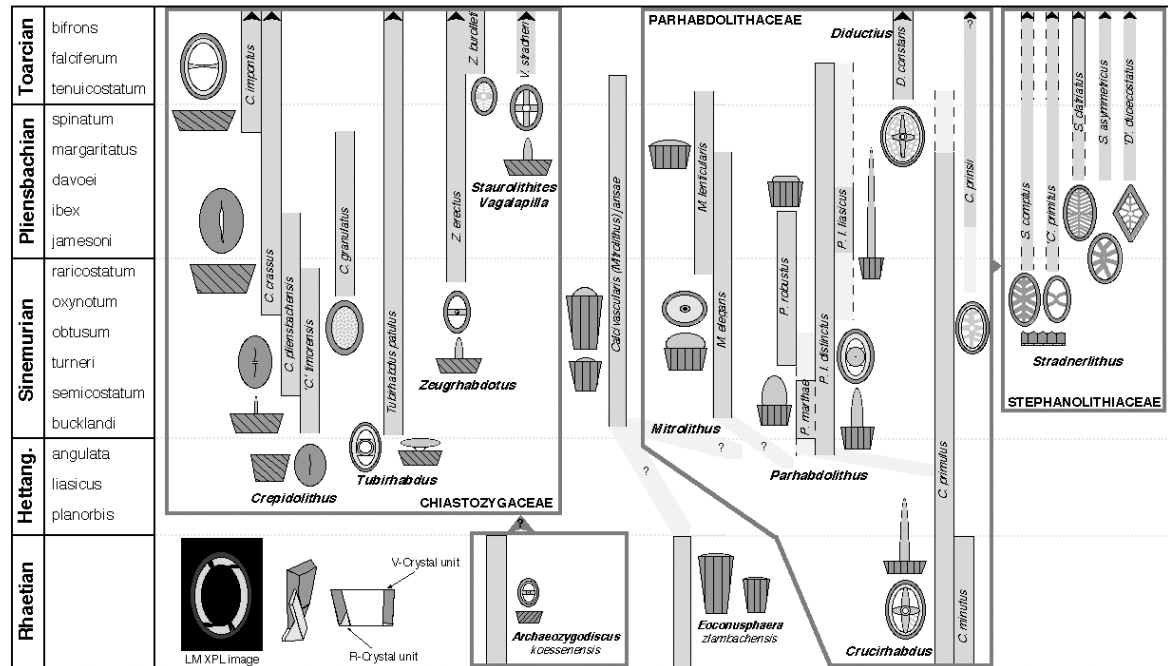


Figure 1 - Initial development of the Eiffellithales. Range-bar conventions as follows: darker shading denotes well-documented range, lighter shading denotes inconsistent or uncertain range; close-spacing indicates likely evolutionary relationships, and when adjacent these relationships are thought to 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.

STEPHANOLITHIALES

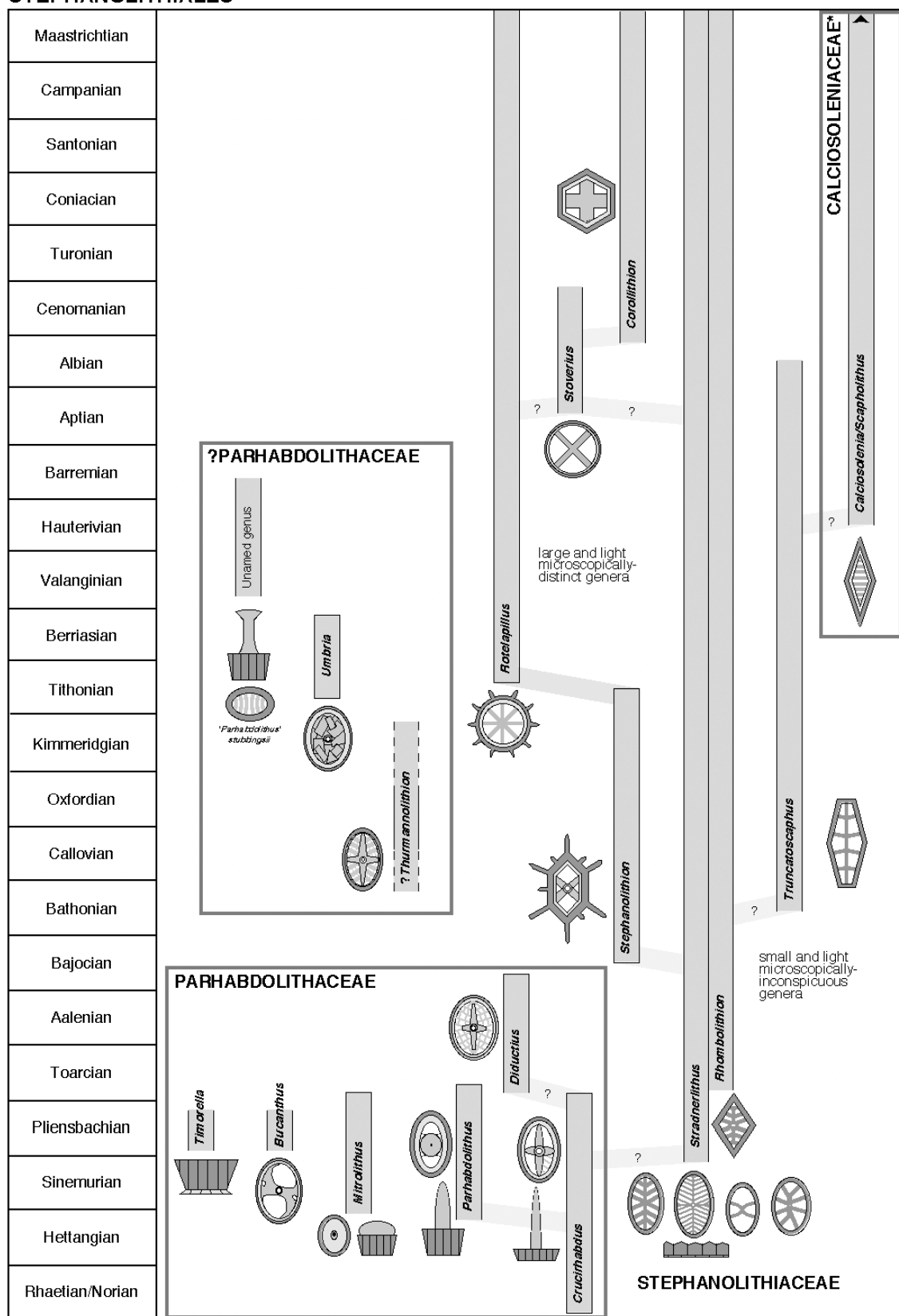


Figure 2 - Phylogeny of the Mesozoic Stephanolithiales. Range-bar and sketch shading conventions as for Figure 1.
 * indicates extant taxon.

AXOPODORHABDACEAE

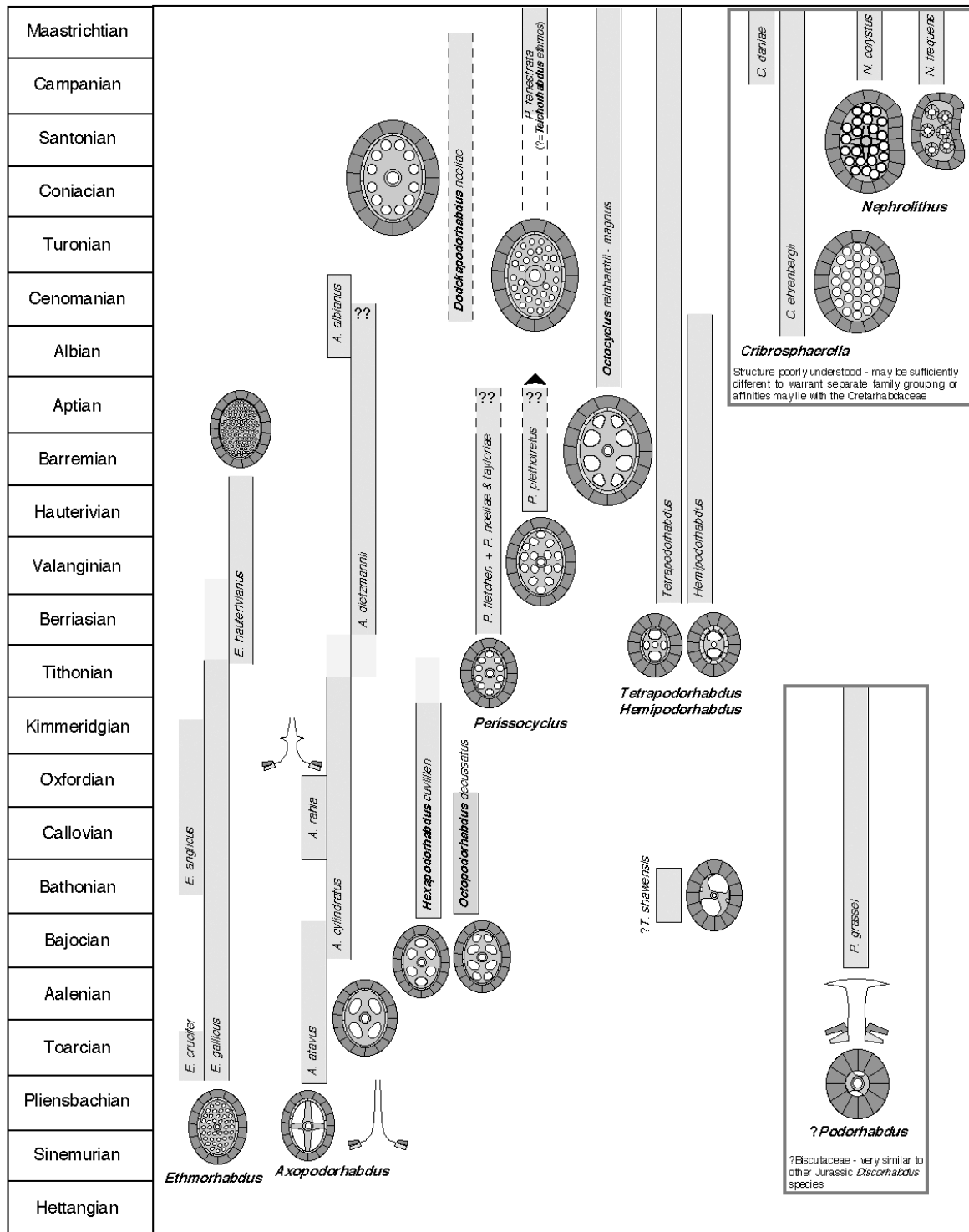


Figure 3 - Phylogeny of the Axopodorhabdaceae. Conventions as for Figure 1.

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

BISCUTACEAE

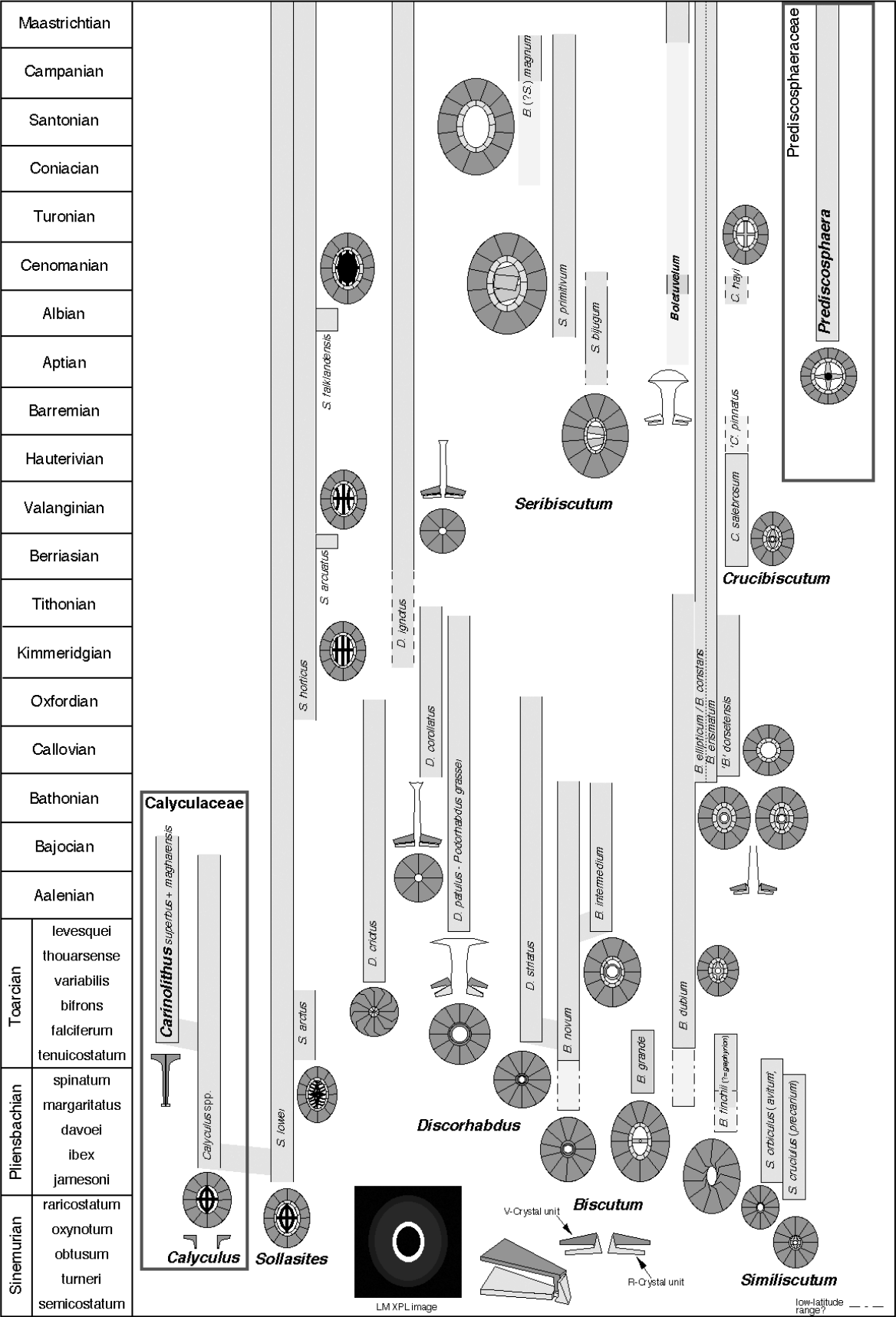


Figure 4 - Phylogeny of the Biscutaceae. Range-bar conventions as for Figure 1.

CRETARHABDACEAE

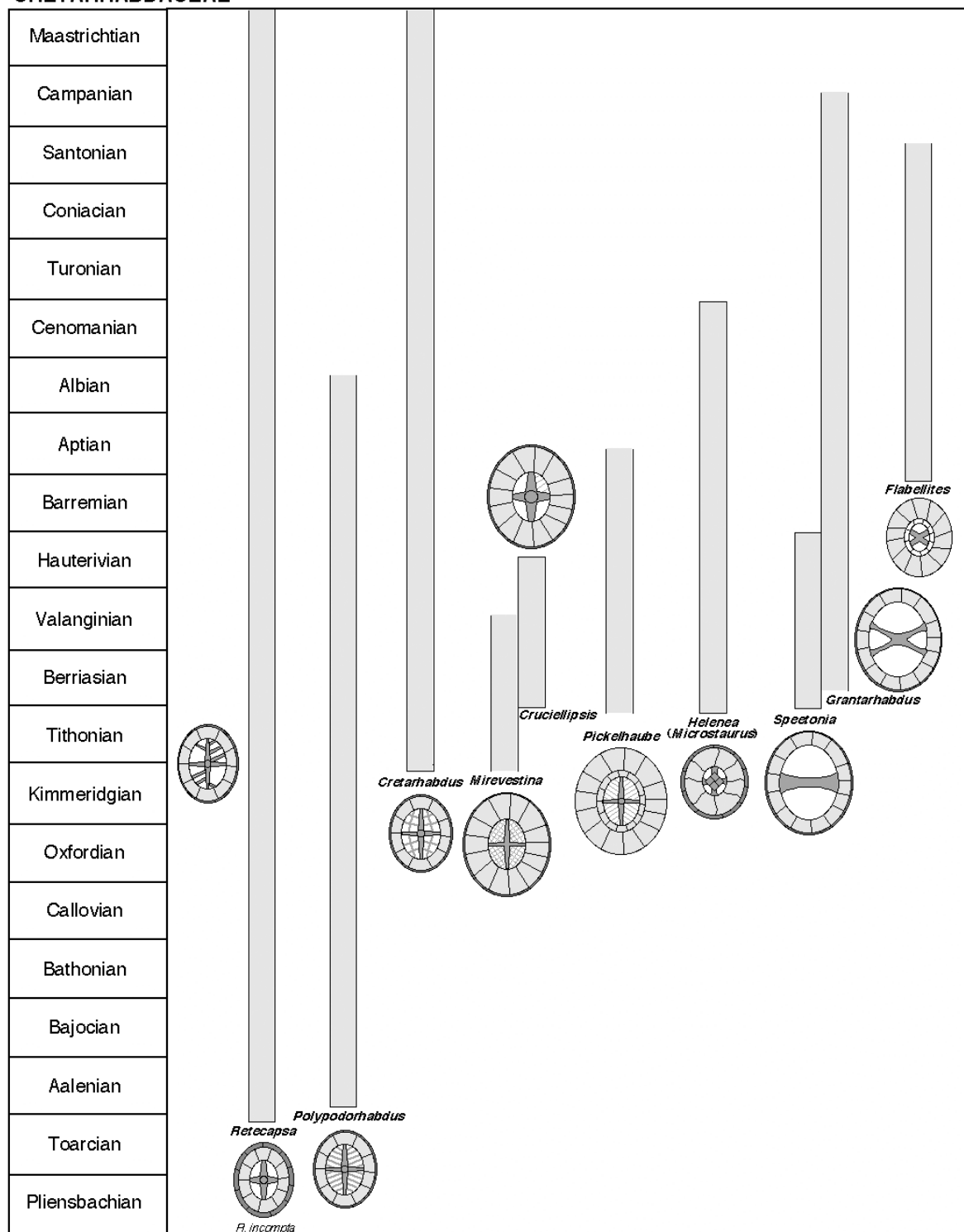


Figure 5 - Stratigraphic distribution of the Cretarhabdaceae. The rim structure and phylogeny of this group are not well understood. Shading of the rim does not indicate V or R unit.

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WATZNAUERIAEAE

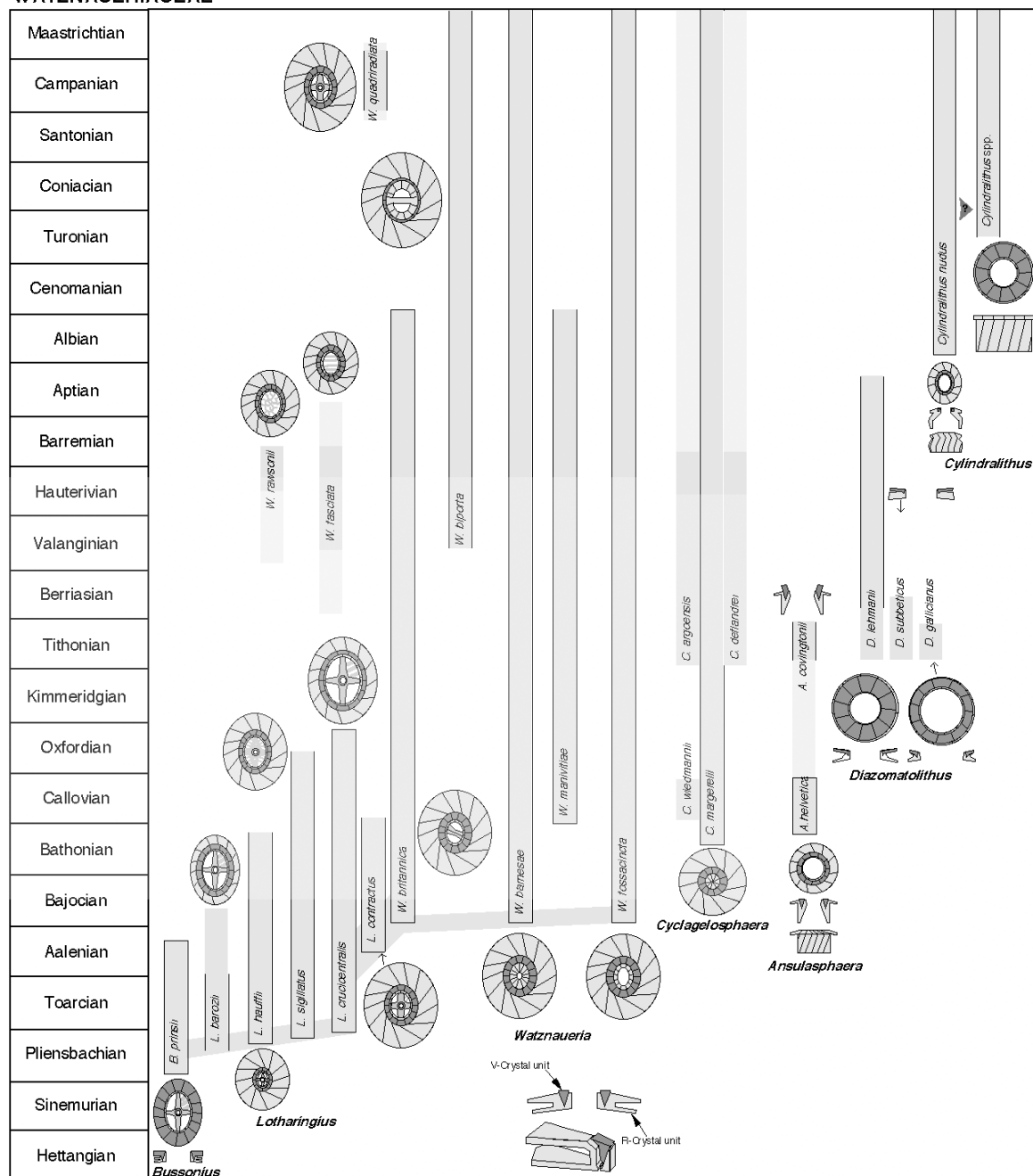


Figure 6 - Phylogeny of the Watznaueriaceae. Range-bar conventions as for Figure 1.

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