Calcareous Nannofossil Biostratigraphy

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Calcareous Nannofossil Biostratigraphy

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Preface

This book was primarily written as a practical guide to the use of calcareous nannofossils in biostratigraphy. Calcareous nannofossils are an exceptional microfossil group, with living counterparts, coccolithophores, representing one of the major components of the phytoplankton in present oceans, and an inconceivably abundant fossil record being the primary component of many marine sediments laid down in the last 220 million years. Although the smallest of all routinely studied fossils, they are conspicuously visible, both in the present surface-waters, as white-water producers, and in the rock record as the major components of 'chalky' sediments worldwide. This abundant fossil record and widespread distribution has led to their rapid acceptance as one of the most important index-fossil groups in both field geology and, perhaps most significantly, in subsurface research, such as the Ocean Drilling Program, and commercial hydrocarbon exploration. Although primarily concerned with biostratigraphic applications, we hope that the book also provides an insight into the broader aspects of the group, as their application expands into the fields of palaeoceanography and palaeobiology.

The first two chapters of the book provide general information concerning calcareous nannofossils, specifically, introductory and (palaeo)biologic material in the first chapter, and techniques of study in the second. Chapters 3 to 9 are ordered stratigraphically and provide state-of-the-art summaries of calcareous nannofossil biostratigraphy for each time period, with comprehensive illustrations of all taxa within a standardized classification based on our latest research on nannofossil structure and biomineralization. The practical application of these biostratigraphic schemes is discussed, including comments on zones, biogeography, taxonomy and evolution. For the most part, the stratigraphic information has a broad geographic relevance and global correlation is discussed. Chapter 7 is more narrowly focused, presenting a high-resolution scheme for the North Sea Basin.

The synthesis of illustrated material is an invaluable resource in our field and we have made every effort to make this component as comprehensive as possible, and to present them in a unified style. The Mesozoic chapters (3–6) include electron microscope illustrations as well as light micrographs, and the latter are enlarged equally to aid comparison through this time interval. There are 66 full-page plates, including over 2000 individual photographs, and as such we believe this to be the most comprehensive atlas of calcareous nannofossils ever produced.

As well as providing a practical handbook for biostratigraphers, we hope that the book will be valuable to other earth scientists who need to apply or interpret calcareous nannofossil data and that the comprehensive illustrations and more general information will be of interest to others who may not yet be familiar with arguably the most abundant fossil group in the history of life.

Acknowledgements

I would like to thank the Department of Geological Sciences, University College London, for the continuing support of nannofossil research and, specifically, Alan Lord, for giving most of the authors included here our start in life, and James Davy and Toby Stiles for the immense amount of photographic work on display. Much of the research presented was supported by studentships and research grants provided by The Natural Environment Research Council, for which we are eternally grateful. Sample material has come from many different sources including individuals too numerous to mention, but thanks to them, and also to the Ocean Drilling Program, whose material has transformed our science, the British Geological Survey, and EKU. Finally, I'd like to dedicate the book to Jackie, who 'lived through this' and contributed far more than just her chapter, and to Don Jacobsen whose teaching inspired me all those years ago in Liverpool.

Technical note

While every effort has been made to provide accurate calculations of magnifications, e.g. all LM photographs for Chapters 4, 5 and 6 are enlarged by the same factor, there is inherently a margin of error involved in the photographic processing, particularly of such a large number of specimens, therefore dimensions calculated from the photographs should be used with some caution.

Abbreviations used in the text

AP – austral province (Chapter 6)
AsZ – Ammonite Subzone
AZ – Ammonite Zone
BC – Boreal Cretaceous (nannofossil zones - Chapter 5)
Bel. Z – Belemnite Zone
BF – bright field (illumination)
BP – boreal province (Chapter 6)
DSDP – Deep Sea Drilling Project
EM – electron microscope
FCO – first common occurrence
FO – first occurrence
FOV – field(s) of view
LCO – last common occurrence
LM – light microscope
LO – last occurrence
MFZ – macrofossil zone (Chapter 6)
MFsZ – macrofossil subzone (Chapter 6)
NJ – Nannofossils Jurassic (nannofossil zones - Chapter 4)
NT – Nannofossils Triassic (nannofossil zones - Chapter 3)
ODP – Ocean Drilling Program
PC – phase contrast (illumination)
QAZ – Quaternary Acme Zone (nannofossils)
SEM – scanning electron microscope
SZ – subzone
TEM – transmission electron microscope
TP – intermediate-tethyan province (Chapter 6)
UC – Upper Cretaceous (nannofossil zones - Chapter 6)
XPL – cross polarized light

1

Introduction

P.R. Bown and J.R. Young

1.1 WHAT ARE CALCAREOUS NANNOFOSSILS?

The term 'calcareous nannofossil' is usually defined as including all calcareous fossils smaller than 30 microns (µm). It is based on the term nannoplankton which was defined by Lohmann (1909) as including the plankton which pass through the finest plankton nets, that is, <63µm. As might be expected, a diverse range of organisms can occur as calcareous nannofossils, including ascidian spicules, calcispheres (calcareous dinoflagellates) and juvenile foraminifera. The overwhelmingly predominant group, however, are the remains and probable remains of haptophyte algae, the dominant group of calcareous nannoplankton. Calcareous nannofossils are generally disc-like in form and clearly analogous to the calcite plates, coccoliths, produced by living haptophyte algae, more specifically the coccolith-bearing sub-group known as coccolithophores. However, there are also a significant number of variously-shaped nannofossils, nannoliths, whose biological affinities are less certain due to the lack of obvious living analogues. Despite this, it is generally assumed that nannoliths had algal origins as they show closely-comparable distributions to coccoliths and many display only slight morphological modifications to the basic coccolith plan. We do not include as nannoliths, groups which are known to have been formed by non-haptophytes, for instance calcispheres, which are produced by dinoflagellates. It should be noted that the term nannolith has been used in varying senses by different authors, and is not used at all by some workers.

The living coccolithophores are marine, unicellular, flagellate phytoplankton, belonging to the phylum Haptophyta and division Prymnesiophyceae. They are characterized by the possession of a cell-wall covering, a coccosphere, of coccoliths which are readily preserved as fossils, either as complete coccospheres or, more commonly, in a disaggregated state as individual coccoliths. Coccoliths are phenomenally abundant in sea-floor sediments above the calcite compensation depth, and preserve the composition of the overlying photic-zone communities due to protected and accelerated sedimentation in the faecal pellets of zooplankton or in marine snow. As a result, haptophyte algae have one of the most abundant fossil records of any phylum and, moreover, this fossil record is continuous from their first occurrence in the Late Triassic to the present day. It is a fascinating paradox that, despite their small size, nannofossils/nannoplankton are strikingly visible both in the geological record, as nannofossil sediments such as chalk, and in the present oceans as evidenced by satellite images of extensive coccolithophore blooms.

Due to their great abundance, photosynthesis and calcification, haptophyte algae are significant components of the earth's biogeochemical cycles. The evolution of nannoplankton resulted in a major shift in the locus of global calcification from the continental shelves toward deep oceans, with accompanying effects on deep-ocean CO_2 budgets, calcite compensation depths and geological carbonate turnover rates. Nonetheless, the prime geological interest in the group has been their application to biostratigraphy.

1.2 HAPTOPHYTE ALGAE

The following section discusses a range of topics related to coccolithophore biology. It is based mainly on the study of extant organisms but is intended to provide basic background information for understanding calcareous nannofossils. The primary literature on the biology of coccolithophores and other haptophytes is now quite large but there are several useful syntheses, including two recent edited volumes, by Winter and Siesser (1994) and Green and Leadbeater (1994). This section also introduces key terminology but for more extended discussions of terminology applied to nannofossils and haptophytes see Jordan *et al.* (1995) and Young *et al.* (1997).

1.2.1 Haptophyte cytology (cell structure)

Haptophyte algae are primarily characterized by the possession of golden-brown chloroplasts, an exoskeleton of scales and a unique flagella-like structure, the haptonema. The cell structure of haptophytes has been extensively studied, primarily by transmission electron microscope (TEM) examination of ultrathin sections, combined with light microscope (LM) studies of live cells. Approachable examples of such work include Manton and Leedale (1969), Outka and Williams (1971) and Inouye and Pienaar (1984, 1988); useful syntheses are given by Haq (1978), Tappan (1982), Pienaar (1994) and Jordan *et al.* (1995).

A generalized haptophyte cell is illustrated in Fig. 1.1. The cell is dominated by large chloroplasts and a nucleus, the sites respectively of photosynthesis and genetic material. Mitochondria (energy storage bodies) are also normally easily identifiable. The Golgi body is a set of interlinked vesicles which are the site of important biosynthesis processes and, in particular, the site where scales and coccoliths are formed. Typically there is a stack of Golgi vesicles in which scales and coccoliths, at various stages of formation, can be seen.

The cell is bounded by a multi-layered cell membrane, also known as the plasmalemma or plasma membrane. The flagella protrude through this membrane and have a complex root structure below it. The two flagella are of equal length and smooth, that is, they lack hairs. In addition, there is a third, flagellum-like structure called the haptonema. This has a unique ultrastructure of a few, usually seven, microtubules, in contrast to the 9+2 microtubular structure universally present in flagella. The haptonema is also unique in showing coiling, and appears to have a range of functional adaptations in swimming, attachment and particle capture (Inouye and Kawachi, 1994).

The cell wall outside the membrane is made up of an inner layer of organic body-scales and an outer layer of coccoliths. The scales and coccoliths are closely related structures, both formed in the Golgi body, and the coccoliths typically have an organic base-plate scale. The scales have a microfibrillar ultrastructure showing a fine radiating pattern on the proximal face and a more or less regular concentric pattern on the distal face.

The haptophyte algae were originally included in the division Chrysophyceae along with silicoflagellates and other algae with golden-brown chloroplasts. They were separated after recognition of the unique structure of the haptonema (Parke *et al.*, 1955; Christensen, 1962; Hibberd, 1972, 1976). This separation has since been strongly supported by additional evidence from cytology, biochemistry and molecular genetics (Green and Jordan, 1994). They are now well established as a discrete phylum including both the coccolithophores and a range of non-calcifying groups, e.g. *Prymnesium*, *Chrysochromulina* and *Phaeocystis*.

1.2.2 Calcareous scales as diagnostic features

Many flagellates have exoskeletons of organic, calcareous or siliceous scales formed in the Golgi body, including both chromists, such as haptophytes and chrysophytes, and green algae, such as prasinophytes. However, the organic scales of haptophytes are distinctive, and calcareous scales appear to be unique to the haptophytes. Calcification also occurs in some dinoflagellates but in the form of continuous cell-wall coverings, not scales, and with less precise control of crystal form. There is the possibility of circular reasoning here, since some genera have been assigned to the haptophytes almost solely on the grounds that they produce calcareous scales, e.g. *Florisphaera*. An interesting example of the success of this type of prediction is provided by *Polycrater*

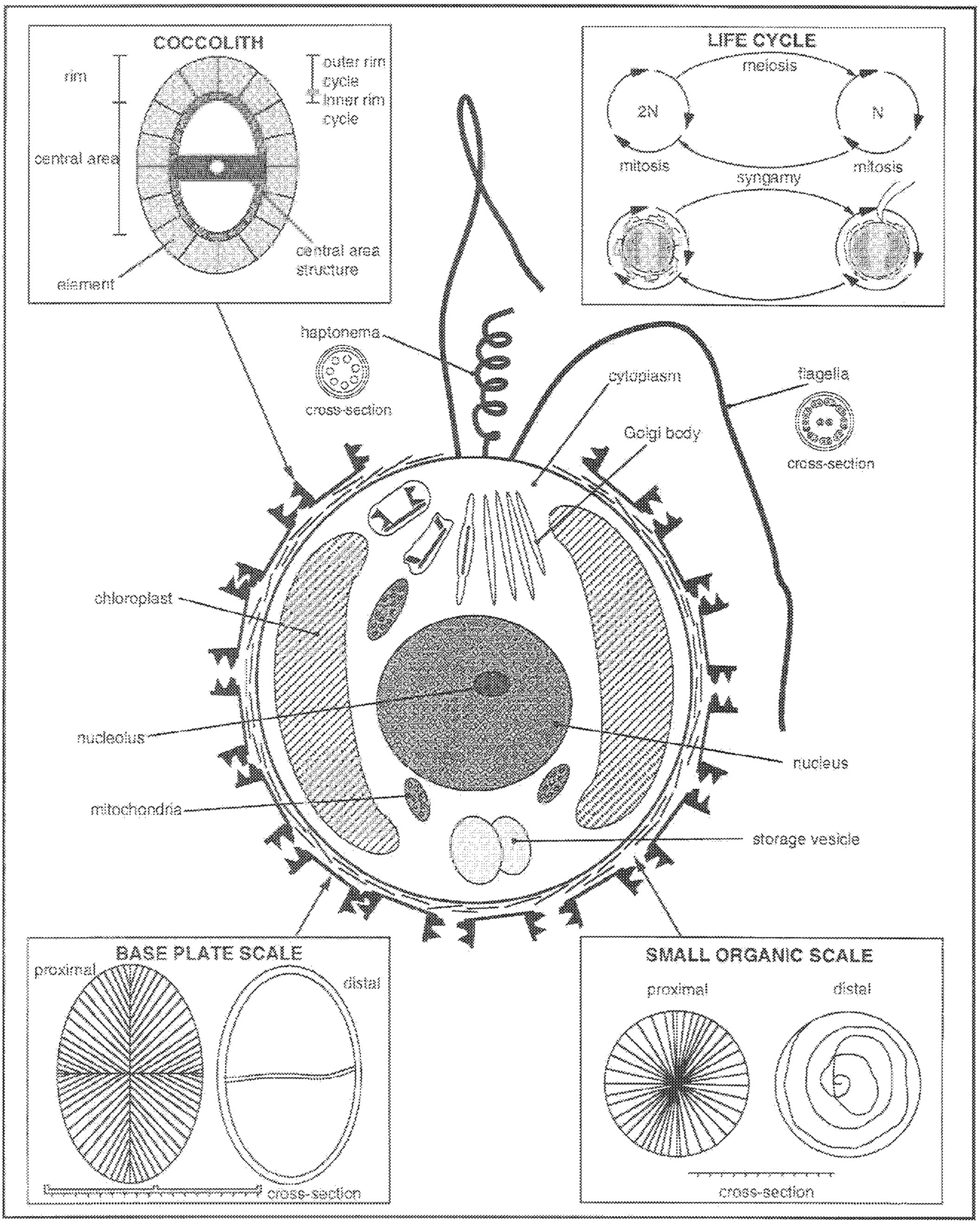


Fig. 1.1 Diagrammatic representation of a coccolithophore cell and cell-wall coverings.

galapagensis. This species produces square, cup-shaped, aragonitic nannoliths which appear quite different to normal coccoliths, so its original assignment to the haptophytes was speculative (Manton and Oates, 1980). However, it has recently been shown to possess a haptonema (Thomsen *et al.*, 1994), thus confirming its identity as a haptophyte. Overall, the evidence from modern algae strongly supports the palaeontologists' assumption that fossil nannolith groups are *a priori* likely to be related to coccoliths.

1.2.3 Coccolith morphology and formation

This discussion of morphology will deal mainly with coccoliths, as they show relatively consistent morphological plans to which a coherent terminology can be applied. Nannoliths are morphologically diverse, and require group by group descriptions and terminology. Basic terminology for the description of coccoliths is given in Fig. 1.2. A selection of coccolith and nannolith morphologies is illustrated in Plate 1.1.

Coccolithophore cells may produce two types of coccoliths, heterococcoliths and holococcoliths, which are distinguished by their morphology, mode of formation, and the life-cycle stage during which they are produced.

(a) Heterococcoliths

Heterococcoliths are circular to elliptical, more rarely polygonal, discs or rings constructed from one or more radial arrays (cycles) of elaborate and variably-shaped crystal units. This disc or ring is termed the rim and encloses a central area, which may be open, virtually closed or spanned by a variety of structures. There are considerable variations in rim form. The most common types are muroliths, which have a wall-like, sub-vertical rim, and placoliths, which have two sub-horizontal shields separated by a tube. Central-area structures are even more variable, including grills, plates, bridges and spines.

Heterococcoliths are formed intracellularly but are then extruded to form a composite exoskeleton, the coccosphere. A reasonable number of heterococcolith-bearing species have been cultured, and for these there is quite detailed information on coccolith formation. In all cases coccolith growth occurs in Golgi vesicles or, in the case of *Emiliania huxleyi*, in a separate but almost certainly Golgi-derived vesicle. Data comes from TEM observation of intracellular coccoliths, SEM, LM and TEM examination of isolated coccoliths, and biochemical investigations. Syntheses of the work include Westbroek *et al.* (1989), Young (1989) and Pienaar (1994).

Observation of rim morphology using electron microscopy, together with crystallographic observations using light-microscopy, reveals complex, multicyclic rim-architectures. However, in many cases the structural relationship between the rim cycles is not known or is uncertain, due to the superimposition, and often complex intergrowth, of cycles of elements. The intricate relationships between these intergrown cycles has only recently been established in detail, for a limited number of taxa, following the discovery of growth stages which preserve the step-by-step construction of coccoliths which occurs within the cell. These stages are most easily observed in monocultures of living species (Young *et al.*, 1992) but they have also been seen in exceptionally preserved fossil assemblages (Young and Bown, 1991).

These discoveries show that coccolith growth can be divided into three stages:

- formation of an organic baseplate;
- initial nucleation, which forms a cycle of simple crystals around the margin of the organic baseplate (the proto-coccolith ring);
- crystal growth in three dimensions, forming the complex, fully-formed coccolith.

In a limited number of examples, we have been able to identify how the numerous cycles of rim elements are interconnected, identify the locus of the proto-coccolith ring, and reconstruct growth of the crystal units. In each case, it appears that the heterococcolith rims are formed from only two crystal units, e.g. *Watznaueria* (Bown, 1987; Young and Bown, 1991), *Parhabdolithus* (Bown, 1987), *Emiliania* (Young *et al.*, 1992), *Coccolithus* (Young, 1992) and *Biscutum* (Ehrendorfer *et al.*, in prep.). These crystal units may form clearly separate parts of the rim or may be complexly intergrown, but they always originate as alternating crystal nuclei in the proto-coccolith ring. Typically, one set of crystal units has sub-vertical c-axes (and so appears dark in cross polarised light (XPL)) whilst the other has sub-radial c-axes (and so appears bright in XPL).

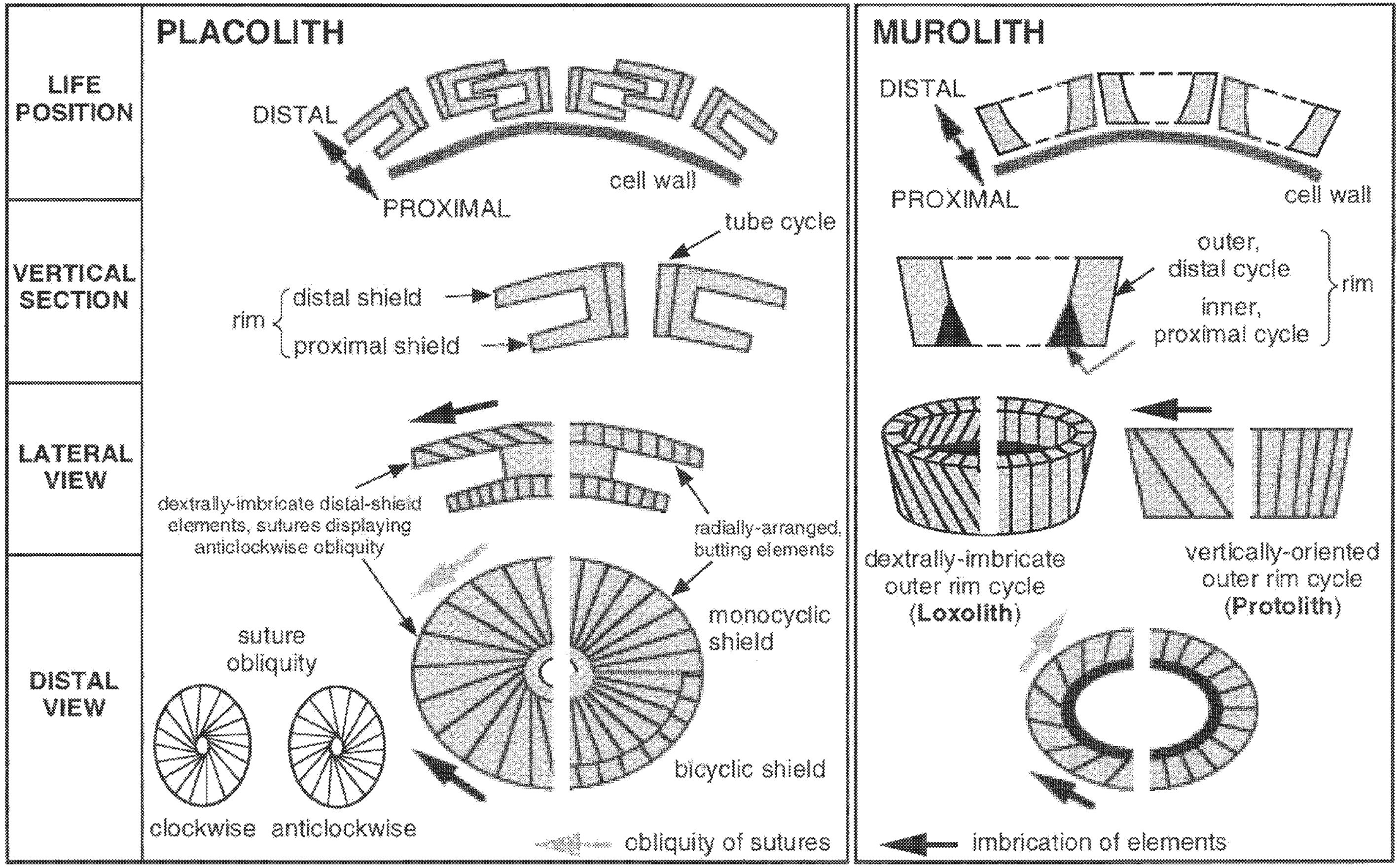


Fig. 1.2 Coccolith rim morphologies.

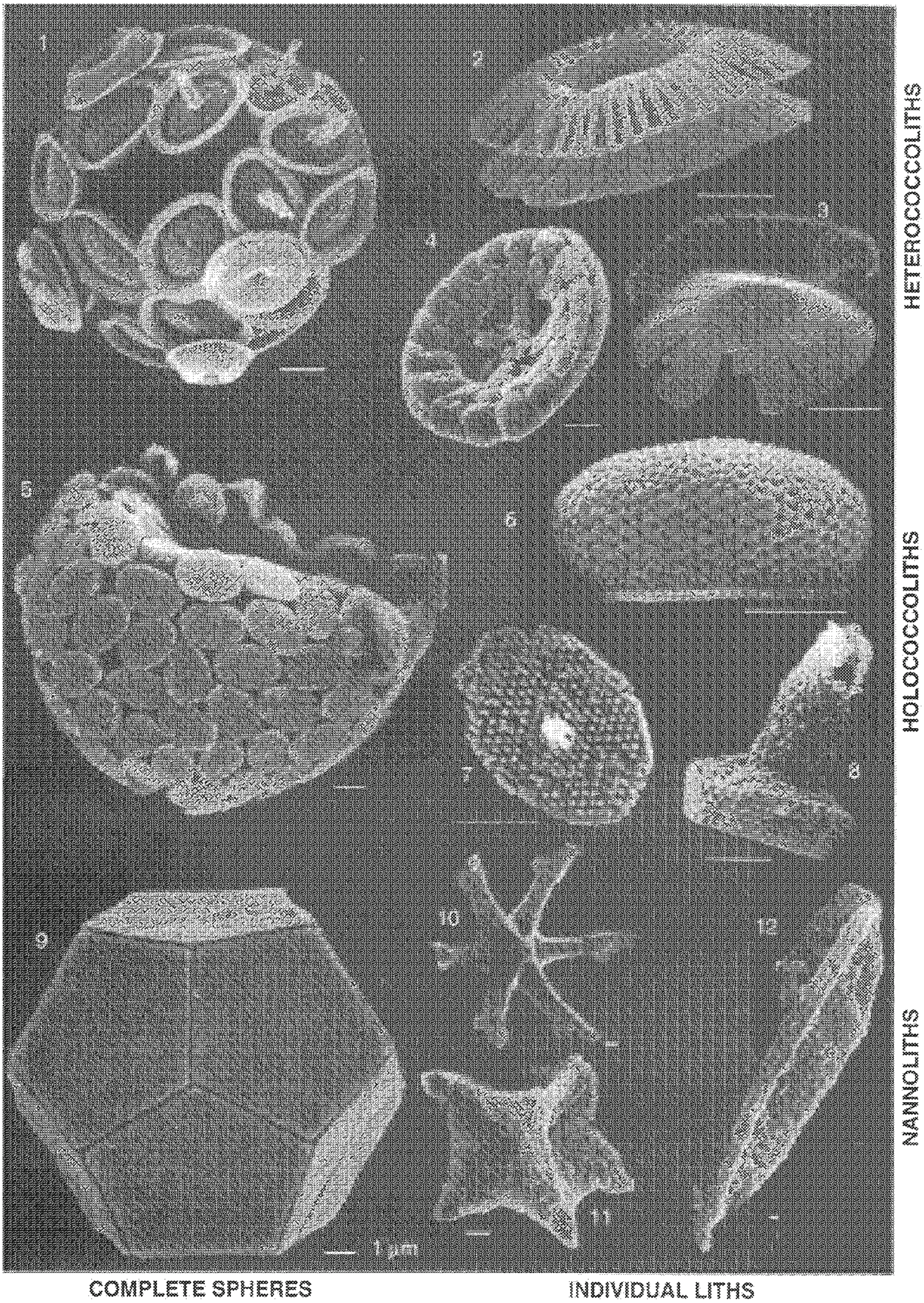


Plate 1.1 Calcareous nannofossil morphology: (1) *Syracosphaera pulchra* polymorphic coccosphere with distinctive endothecal, exothecal and circumflagellar (spinose) coccoliths; (2, 3) *Emiliania huxleyi* showing placolith structure; (4) *Prediscosphaera ponticula* in proximal view illustrating alternating V/R biomineralization; (5) *Calyptrolithophora papillifera* weakly dimorphic holococcosphere; (6) *Calyptrosphaera oblonga* with hexagonal crystallite arrangement; (7) *Syracolithus catilliferus* showing rhombohedral crystallite arrangement; (8) *Anfractus youngii*, Early Jurassic; (9) *Braarudosphaera bigelowii* 'sphere'; (10) *Discoaster surculus*; (11) *Micula concava*; and (12) *Triquetrorhabdulus rugosus*.

These crystal units are termed V-units (vertical) and R-units (radial) (Young *et al.*, 1992). As the appearance of coccoliths in the LM is largely a reflection of the c-axis orientation of the individual elements, many coccoliths have XPL images of concentric, low- and high-birefringence zones. In other coccoliths, one of the units may be suppressed, resulting in a wholly low- or high-birefringence image. These observations are incorporated into a model of coccolith assembly, called the V/R model, which predicts that only two crystallographic units constitute coccolith rims, these units originating from a common nucleation site in the proto-coccolith ring (Young *et al.*, 1992).

It should be noted that the actual orientations often depart significantly from radial and vertical, considerably more so than was initially suggested in Young *et al.* (1992). Another important limitation of the model is that many central-area structures are not derived from rim units, that is, separate nucleation occurs in the central area away from the proto-coccolith ring. Nonetheless, identifying the rim V- and R-units provides an essential basis for understanding homology, and so evolution, in heterococcoliths.

The number of crystal units in a coccolith is determined at the nucleation stage and since the V- and R-nuclei alternate around the proto-coccolith ring there is the same number of each type of unit. By contrast the number of crystal units per coccolith of a species is usually highly variable, and typically linearly related to coccolith size. For instance in *Emiliania huxleyi* there are 20 to 50 crystal units, corresponding to a size range of 2.0 to 5.0μm (Young and Westbroek, 1991). The nucleation stage also fixes the orientation of the crystal units; whilst the orientations are broadly radial and vertical in detail they depart from these orthogonal directions and this gives a chirality to the coccolith structures. This chirality is expressed in terms of imbrication and obliquity directions of individual elements and details of element shape (Didymus *et al.*, 1994). Virtually all coccoliths show chiral features and the sense of chirality appears to be absolutely consistent within species providing valuable phylogenetic characters.

(b) Holococcoliths

Holococcoliths are typically disc- or dome-shaped and formed of numerous, minute (typically 0.1μm), equidimensional calcite crystallites of simple shape. Compared to heterococcoliths, holococcolith morphologies are more conservative through time, and there is a less well-defined division between rim and central-area structures (reflecting the consistent use of identical building blocks).

Holococcolith formation has been less well studied, only two holococcolith-bearing species having been cultured. *Coccolithus pelagicus* produces *Crystallolithus hyalinus* holococcoliths in an alternate, motile, life-cycle stage (Parke and Adams, 1960; Manton and Leedale, 1969; Rowson *et al.*, 1986), whereas *Calyptrosphaera sphaeroidea* is only known to produce holococcoliths (Klaveness, 1973; Pienaar, 1994). In both species, the holococcoliths have well-developed organic base-plate scales and separate body-scales. These scales can be observed forming in Golgi vesicles but the holococcoliths themselves have never been observed inside the cell. It has been inferred from this that calcification in holococcoliths is extracellular, and Rowson *et al.* (1986) produced some experimental results supporting this. Holococcoliths do not obviously display growth sequences and it is quite possible that calcification occurs across the entire surface simultaneously. The very different formation mechanisms of holococcoliths and heterococcoliths suggest that there may be only limited homology between them.

Holococcolith crystallites are arranged in precise geometric arrays clearly showing that the location of nucleation is precisely controlled (Plate 1.1). Equally, individual crystallite faces are aligned, so crystal orientation must also be precisely regulated. Holococcolith surfaces often show hexagonal arrays of crystals with rhombohedral faces developed on the crystallites (Plate 1.1), and LM observations show that this is due to their c-axes being orientated perpendicular to the surface. Other surfaces, however, are covered by crystallites lying with a rhombohedral face parallel to the surface, and so with their c-axes oblique to the surface (Plate 1.1). It is difficult to envisage a simple model of calcite nucleation to accommodate both nucleation patterns.

Neighbouring crystallites often have closely orientated c-axes and during diagenesis, large zones of crystallites overgrow as single crystal blocks which extend to fill any internal spaces. Many fossil holococcoliths (e.g. *Calculites*) display a proximal or distal surface formed of a few such blocks surrounded by a narrow rim with smaller radial elements. The general appearance of holococcoliths in the LM is distinctive but electron micrograph studies of well-preserved material, in which individual crystallites are visible, provide the best proof of holococcolith nature (Gartner and Bukry, 1969; Kleijne, 1991; Bown, 1993; Farhan *et al.*, 1994).

The fossil record of holococcoliths is sporadic and sparse, reflecting their low preservation potential despite their diversity in modern assemblages. The holococcolith taxa which are preserved as fossils tend to be larger, possibly atypical forms.

(c) Nannoliths

Nannoliths are a heterogeneous group including a wide range of shapes (Plate 1.1). Most of them show some of the features of heterococcoliths, such as rotational symmetry, complex crystal-unit shape, chirality or broadly plate-like shape. They are all, however, sufficiently different to make their relationship with coccolithophores uncertain. It is almost certainly an artificial grouping, and many nannoliths may prove to be modified heterococcoliths evolved from a range of ancestors (e.g. *Nannotetrina*, *Discoaster*, *Florisphaera*). Others may perhaps be modified holococcoliths (e.g. *Ceratolithus*), still others may prove to have been formed by haptophytes with calcification mechanisms unrelated to either mode (e.g. *Braarudosphaera*, *Nannoconus*), or even by non-haptophytes (e.g. *Schizosphaerella*).

1.2.4 Life cycles

Our knowledge of life cycles in haptophytes is inevitably limited to the few species which have been maintained in culture regularly, and even for these, observations are often incomplete. There is also a confusing diversity of patterns in terms of motile *vs* non-motile stages and development of different cell coverings, occurrence of pseudo-filamentous benthic stages, etc. Billard (1994) has synthesized available data and suggests, following the work of Gayral and Fresnel (1983) and Fresnel and Billard (1991), that a fairly clear general pattern can be discerned. Diploid stages (complete DNA compliment) may be motile or non-motile but if they calcify they produce heterococcoliths, and innermost organic body-scales (if present) that are rimmed and patterned with concentric plus radial microfibrils on both faces. Haploid stages (half the normal DNA compliment) are predominantly motile but may produce benthic pseudo-filamentous cells; if they calcify they produce holococcoliths and rimless body-scales with distinctly different proximal and distal faces. This elegant synthesis is by no means proven but is a convincing rationalization of existing data and provides a useful model for future research. A key feature of the model is that cell coverings in haploid and diploid phases of the life cycle are distinctive and probably have had separate evolutionary histories. Hence classifications based exclusively on the products of one stage, e.g. heterococcoliths, should be rigorous even though inferences of relationships between stages will always be difficult. This supports our confidence in the basic validity of fossil heterococcolith classification.

As an example, Fig. 1.1 illustrates the life cycle of *Emiliania huxleyi*, as currently understood. The predominant stage consists of diploid, heterococcolith-forming, non-motile 'C' cells. These are capable of reproducing indefinitely by asexual binary fission (simple mitosis). During this process naked 'N' cells can be created, indeed strains can virtually lose their ability to calcify. 'N' cells are essentially similar to the 'C' cells, and their development is not now thought to have any relevance to life cycles. The significant transition comes with formation of haploid, scale-bearing, motile 'S' cells, presumably through meiotic division. These stages can also reproduce by asexual binary fission but can give rise to new diploid 'C' cells, presumably by syngamy.

Key observations on this cycle were made by Klaveness (1972) who identified the three basic cell types and speculated on the likelihood of a sexual cycle, but was unclear as to the significance of naked, scale-bearing and coccolith-bearing cells. Subsequent work demonstrated that the 'N' and 'C' cells were essentially identical, and more recently flow cytometry has demonstrated that the 'C' (and 'N') cells do have double the DNA content of the 'S' cells (Green *et al.*, 1996). In addition, genetic fingerprinting type studies have demonstrated that within individual populations of

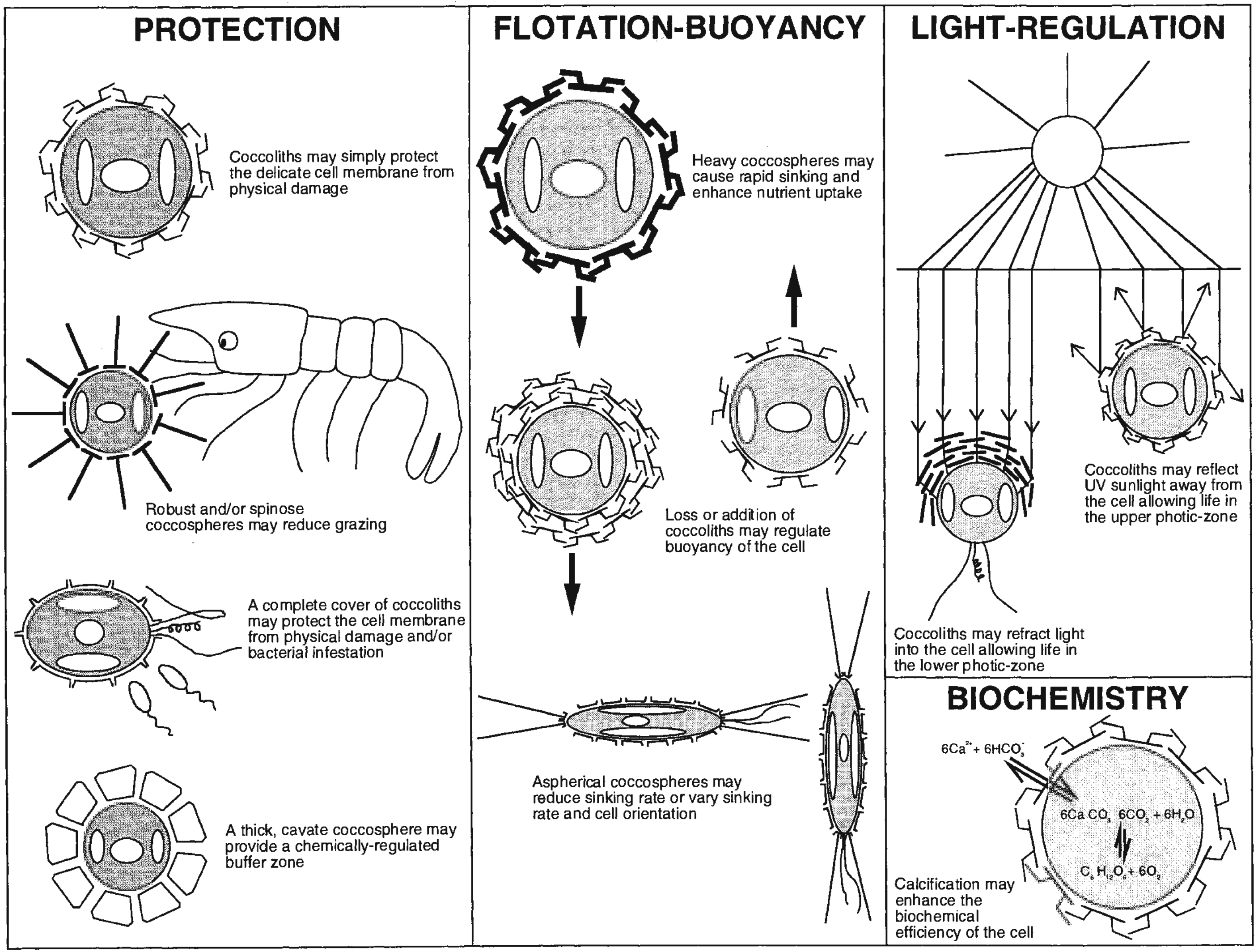


Fig. 1.3 Cartoon of possible functions for coccoliths (after Young, 1994).

Emiliania huxleyi there is great genetic diversity and so genetic recombination must be occurring (Medlin *et al.,* 1996). Nonetheless, the conditions which trigger transition between life cycle stages are still unclear, so observations are still difficult and the actual processes of syngamy and meiosis have yet to be observed.

1.2.5 Coccolith function

Although there has been abundant speculation on the function of coccoliths (Fig. 1.3), no definitive explanation has as yet been forthcoming (Young, 1987, 1994). Coccolithophores are only one of a number of algal phytoplankton groups which possess mineralized cell-wall covers, e.g. diatoms have silica frustules and dinophytes have organic thecae, and this perhaps suggests a common function for such coverings, the most obvious being protection of the delicate cell wall, whether it be from mechanical damage, bacterial/viral attack or chemical shock. However, there is no clear evidence that the presence of coccoliths is an effective defence against predation, which is usually in the form of herbivorous zooplankton.

Another common explanation is related to flotation and buoyancy of the cell, critical to phytoplankton which need to maintain a position within the photic zone while escaping nutrient-depleted water. Heavy coccospheres may produce rapid sinking, allowing more effective nutrient uptake, while turbulent mixing will maintain their position in the photic zone. Varying the number of coccoliths on a coccosphere may lead to greater control over sinking and flotation, whilst aspherical coccospheres and long coccolith spines may both facilitate orientation and vary sinking rates.

A number of elegant explanations have suggested that coccolith function is related to light-regulation, either reflecting light from the cell, allowing a life-position high in the photic zone where UV radiation is high, or refracting light into the cell allowing life deep in the photic zone where light-levels are low but nutrients are plentiful. There is evidence to support both cases, e.g. *Florisphaera profunda* is an extant species with an atypical, asymmetric coccosphere for which the light-concentration function has been proposed, and recent research has shown that indeed this species occupies an unusually deep photic-zone niche where few other algae can grow. In contrast, *Emiliania huxleyi* is an upper photic-zone, bloom species, which produces huge numbers of coccoliths many of which are shed into the water column. Reflection of sunlight results in high albedo, 'white-water' conditions and increased water temperatures (Holligan *et al.*, 1993). This production of numerous coccoliths per cell may benefit *Emiliania huxleyi* in this high-light, near-surface niche.

Evidence that coccoliths have opposing functions in different species suggests that diversification of morphology has led to adaptation for different functions which may be reflected in the size, shape and number of coccoliths, and the resultant coccosphere morphology, although there may have been an original common function, e.g. protection.

Finally, there are also biochemical explanations for coccolith formation, mainly hypothesizing that coccolith formation is a by-product of the cell's biochemical functions, or that their formation enhances the energy efficiency of these biochemical processes. None of these hypotheses have been definitively proven but they remain possibilities which may explain, at least in part, why coccoliths were initially produced.

1.2.6 Coccolithophore ecology and distribution

Extant coccolithophores have a widespread oceanic distribution, living in the photic zone and being most diverse at low latitudes. Generally speaking, they are not found at latitudes higher than 70° and flourish in warm, stratified, oligotrophic, mid-ocean environments. However, a number of species have very broad ecological tolerances, e.g. the living species *Emiliania huxleyi* thrives in a wide range of temperatures and salinities (1 to 31°C and 11 to 41ppt (Brand, 1994)). Only one freshwater coccolithophore has been well documented (e.g. Braarud, 1954; Manton and Peterfi, 1969).

Coccolithophores show distinct biogeographic distribution patterns, defining broad, latitudinal belts or zones (Winter *et al.*, 1994). These zones are generally distinguished by variations in assemblage composition rather than high endemicity, the great majority of coccolithophore species being virtually cosmopolitan. These distribution patterns have been interpreted in terms of surface-water temperature but are increasingly seen as a reflection of both temperature and nutrient distributions, which themselves are linked to the large-scale features of oceanic circulation such as divergence zones, ocean gyres and seasonal mixing. The major limiting nutrients are nitrate and phosphate, but the abundance of other trace elements and vitamins, such as Fe, Zn, Mn and thiamine, are also thought to be significant. There is also evidence that some coccolithophores may supplement their nutrient requirements by heterotrophy or phagotrophy, using the haptonema to capture food particles. Seasonally stable, oligotrophic, tropical and subtropical mid-ocean gyre environments support the highest diversities, but standing crops are low, reflecting low reproduction rates. Eutrophic conditions, due to upwelling or deep seasonal mixing, often support high standing crops dominated by one or a few species, however diatoms are the most effective eutrophic phytoplankton in present oceans and coccolithophores generally bloom following depletion of silica in the surface waters. Continental shelf environments also tend to be unstable and eutrophic in nature and support distinctive assemblages, including taxa which do not live in open-ocean environments, e.g. *Pleurochrysis carterae*. The partitioning of species between nutrient-differentiated environments is a good indication that contrasting r- and K-selection life strategies have been developed (Aubry, 1992; Brand, 1994; Young, 1994).

There is also good evidence that coccolithophore communities show limited vertical stratification, with distinctive deep photic-zone assemblages occurring in or below the thermocline/nutricline, exploiting a less-competitive low-light, low-temperature, high-nutrient niche, in particular, *Florisphaera profunda* and *Thorosphaera flabellata* (Winter *et al.*, 1994).

Evidence from the fossil record suggests that coccolithophores have always displayed broadly similar ecological tolerances, and certainly palaeobiogeographic distributions are generally comparable with those of the present.

1.3 CALCAREOUS NANNOFOSSIL TAXONOMY/CLASSIFICATION

The systematics of calcareous nannofossils/nannoplankton are based entirely on phenetic data and largely confined to the structure and shape of the coccoliths and nannoliths. Cytological information has been used by phycologists but only to develop higher taxonomy of the haptophytes. In living coccolithophores, calcareous scales are highly reliable indicators of haptophyte affinity, and isolated heterococcolith and holococcolith morphology is a robust taxonomic criterion down to species level. There are obvious taxonomic pitfalls as coccolith morphology may be variable through life cycle stages, across the same coccosphere (polymorphism), through ecological factors (ecophenotypic), and preservational factors (conspecific preservational morphotypes). However, these are generally fairly easily overcome and benefit from careful consideration of the study of natural populations or culture studies. In the case of polymorphism, this appears to be restricted to more exotic taxa, both in the Recent and in the fossil record. The probable lack of homology between heterococcoliths and holococcoliths is discussed above, and in practice, the taxonomy of these two coccolith types is treated separately. The classification of nannoliths is also problematical, as we can now demonstrate that some living haptophytes produce very un-coccolith-looking structures, but may in fact be coccolithophores, e.g. *Ceratolithus* and *Florisphaera*. The phylogeny of this non-V/R-type biomineralization is presently unknown, and for fossil representatives at least, we retain a high-level, bipartite division, separating coccoliths from nannoliths.

The present taxonomy of nannofossils has been greatly influenced by progressive technological advances which have, in some cases, dramatically improved our ability to resolve morphology. For over a century, light microscopy was the only method of observation, and for much of that time only bright field illumination, a relatively unrevealing technique at best, was employed. It could be argued that, until the advent of electron microscopy, in the great majority of cases, the species-level taxonomy was suspect, and the generic-level taxonomy virtually meaningless, with many species grouped into form genera, such as *Coccolithus, Discolithus* and *Zygolithus*. To illustrate this, of the 190 Mesozoic genera recognized by the authors herein, only the highly distinctive nannolith taxa *Nannoconus, Schizosphaerella* and *Braarudosphaera,* and the coccolith genus *Stephanolithion,* were described before 1950. There has subsequently been an avalanche of taxonomic descriptions which has been based upon a variety of taxonomic concepts, observational techniques and morphological understanding.

This taxonomic revolution has not proceeded particularly smoothly, and inconsistencies remain firmly embedded in the classification. Common problems include the variable weighting given to morphological features seen in the LM as opposed to the EM; the taxonomic significance of rim *vs* central-area structures; and the use of fine central-area details only observed in EM when preservation is exceptional. We have attempted a uniformity of approach in the taxonomy presented in the following chapters, but this is weighed against a desire to retain stability in the taxonomy, and thus some inconsistency must be endured in order to achieve this goal.

1.3.1 Taxonomic rationale

The most fundamental differentiation in nannofossil classification is arguably the bipartite division between coccoliths and nannoliths, although we also acknowledge the importance of the heterococcolith/holococcolith division. Coccoliths are clearly the remains of haptophyte algae, and have displayed relatively uniform morphological features throughout their geological history, allowing a consistent and standard approach to their taxonomy. This is not always well-reflected in the existing taxonomy due to the historical factors discussed above. The morphological variability of nannoliths generally prevents any standardized taxonomic approach, and they are best treated on a group-by-group basis.

Most authors agree that coccolith rim structure is the most significant and conserved morphological feature and thus the most appropriate for familial and higher-level classification. Fine details of rim construction, central-area size and central-area structure should be reserved for generic- and specific-level classification. The major problem in applying this taxonomic rationale is the difficulty in elucidating the true structure of coccolith rims. However, in most cases, sufficient information has been made available from routine, non-analytical light microscopy and electron microscopy of vast numbers of specimens, and this has allowed the development of a relatively stable higher taxonomy.

At family level there is general agreement between living and fossil workers, with coccolith morphology the major criterion for classification. The family groupings applied herein are described in Bown and Young (1997) and Young and Bown (1997b), and are broadly comparable to the schemes of Hay (1977) and Perch-Nielsen (1985a, b).

At order-level, however, there is no such consensus and indeed there is a significant gulf between the way in which they are applied in fossil and living material. Phycologists, at present, maintain an order-level classification based largely on flagella number and length, with four orders in common use (Green and Jordan, 1994):

- Isochrysidales Pascher, 1910 – two more or less equal flagella;
- Prymnesiales Papenfuss, 1955 – two equal flagella and a third 'flagellum';
- Coccosphaerales Haeckel, 1894 (= Coccolithophorales Schiller, 1926) – coccolith-bearing; and
- Pavlovales Green, 1976 – significantly different cells, including haptonema size, flagella length, coverings and root structure, no body scales, etc.

Of these four, only the Pavlovales are now considered to be a well characterized group, and modern classifications make less use of the orders.

Palaeontologists have developed a coccolith-based order-level classification, clearly representing a level of classification beneath that currently employed by phycologists, although these orders are not in common use. The ordinal level classification applied herein is described in Bown and Young (1997) and Young and Bown (1997b), and summarized in Fig. 1.4. We believe the introduction of a stable supra-family classification, based on heterococcolith morphology, is of significant benefit to our understanding and communication of phylogeny. The use of coccoliths at this taxonomic level is comparable to the classification of

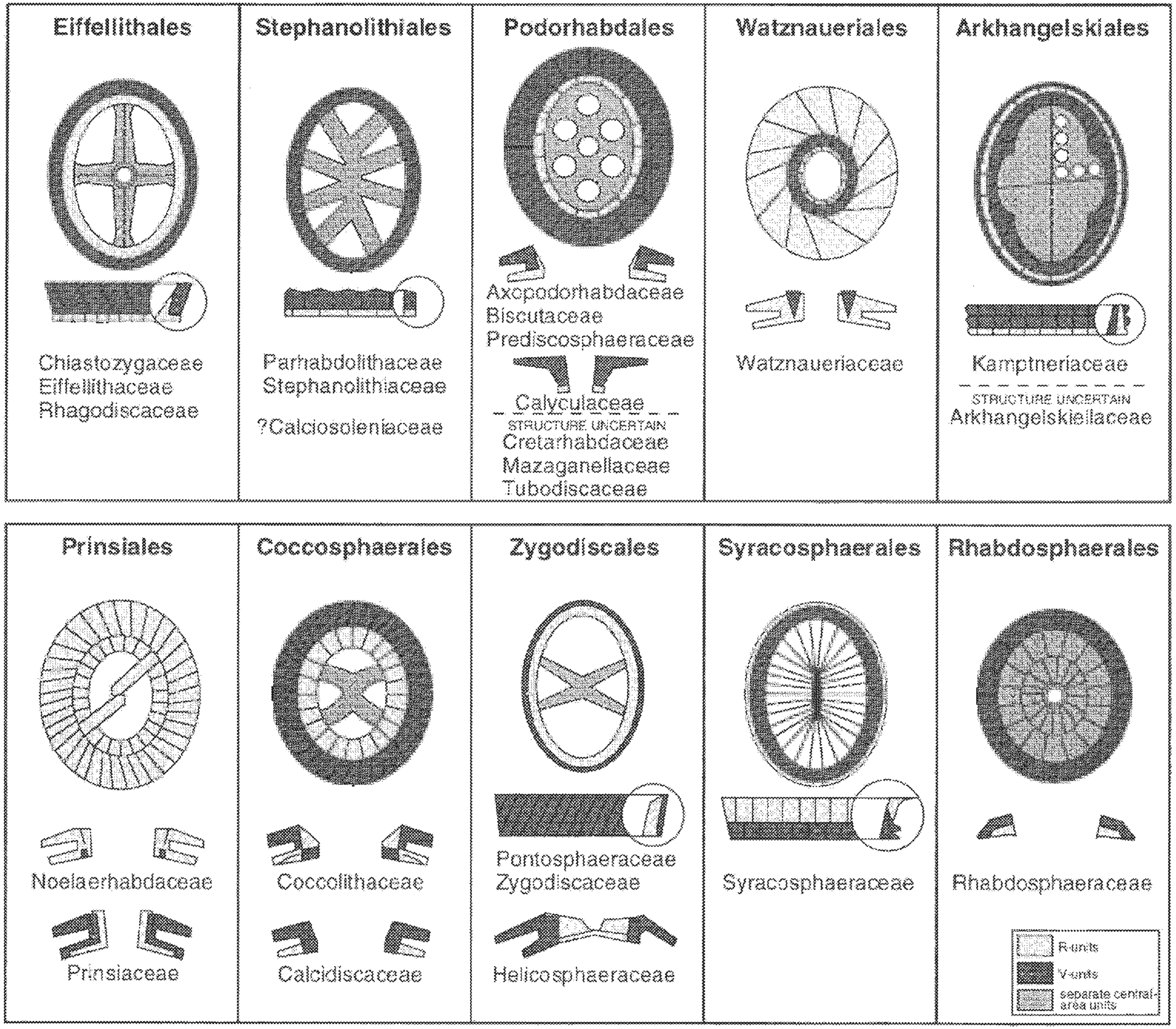


Fig. 1.4 Ordinal-level classification of heterococcoliths (after Bown and Young, 1997; Young and Bown, 1997a, b).

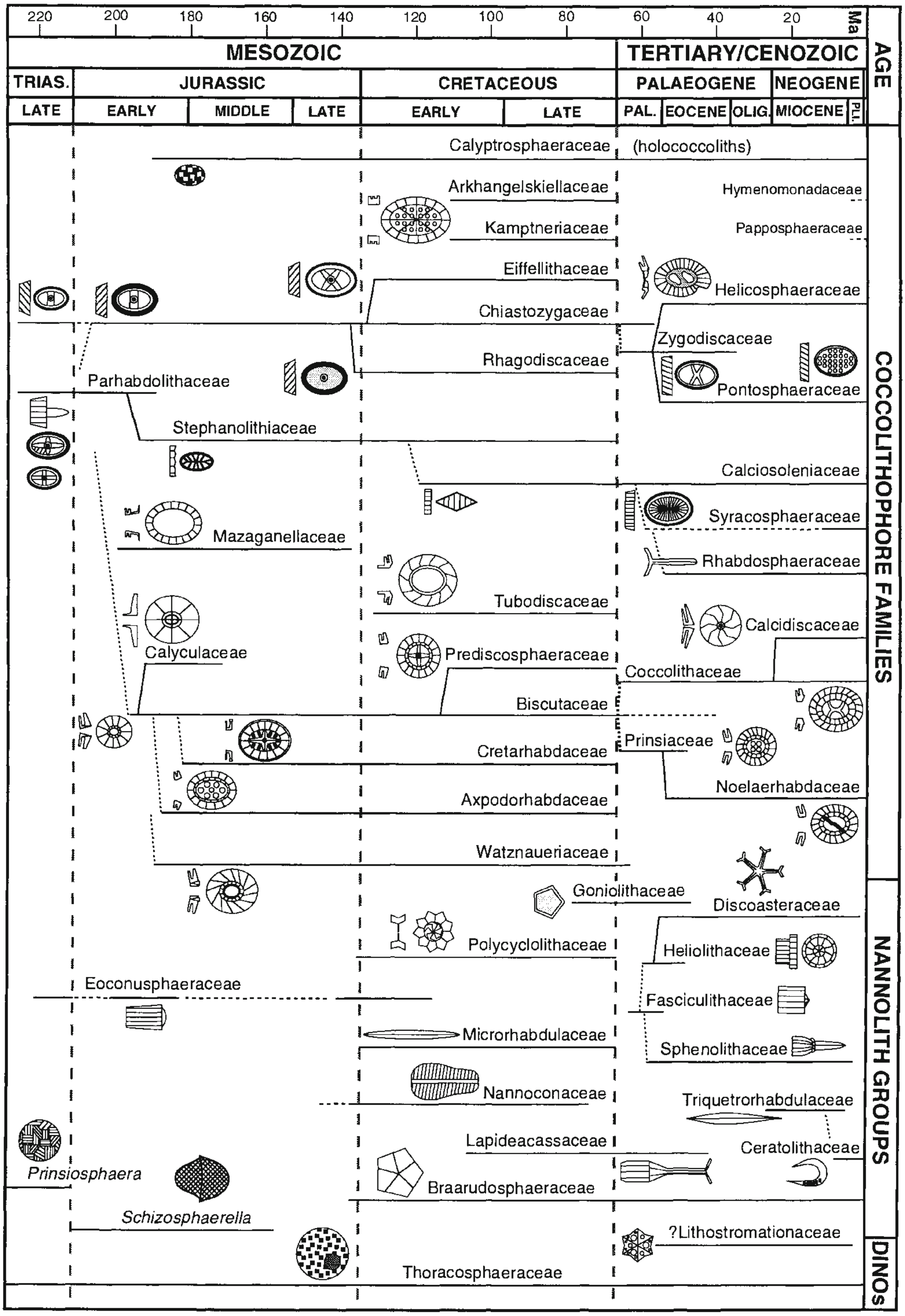


Fig. 1.5 Phylogenetic model for calcareous nannofossils (after Bown *et al.*, 1991). Abbreviations: Dinos - dinoflagellates, Pli. - Pliocene, Olig. - Oligocene, Pal. - Paleocene.

dinoflagellates and diatoms, which utilize exoskeleton morphology to define orders and suborders (e.g. Fensome *et al.*, 1993; Round *et al.*, 1990). However, the integration of the order-level classification between living and fossil material is a problem which needs to be addressed.

1.4 OUTLINE OF GEOLOGICAL HISTORY

Calcareous nannofossils first appeared in the Late Triassic as abundant but low-diversity assemblages apparently restricted to low latitudes. All but one species of coccolith disappeared during an extinction event at the Triassic/Jurassic boundary. Nannofossils were rapidly re-established in the earliest Jurassic and appear to have colonized all marine environments during this time. Most major coccolith families were established during the Early Jurassic radiation (Fig. 1.5). Diversity increased steadily through the Jurassic and Cretaceous, reaching a diversity-peak in the Late Cretaceous. High abundances are reflected by nannofossil-generated carbonate sediments from at least the Late Jurassic. Nannofossils were severely affected by the Cretaceous/Tertiary boundary mass-extinction event when around 90% of species became extinct, apparently abruptly, including virtually all common species. Subsequently, nannofloras recovered rapidly in the Early Paleocene, reaching a second diversity peak in the mid Eocene, comparable to that of the Late Cretaceous. The Paleocene radiation was more rapid and diverse than the Mesozoic radiations, and established significantly different coccolith families accompanied by numerous new nannolith groups. There followed a significant decline into the Oligocene, increased diversity in the Miocene and a general decrease into the Pleistocene. Additional details are given in the following chapters.

1.5 BIOSTRATIGRAPHY

Nannofossils are exceptionally good for biostratigraphy since they are abundant, planktonic, rapidly evolving and largely cosmopolitan. Also, their small size means they can be studied from minute rock chips which is of particular value in hydrocarbon exploration and development, and scientific drilling. Their biostratigraphic potential was first realized in the 1950s and was initially applied in Cenozoic studies (Bramlette and Riedel, 1954) leading to the standard zonation of Martini (1971). Their biostratigraphic value was consolidated by their use as primary reference fossils on most DSDP (1968–1983) and ODP (1985–present) cruises. Nannofossil zonations now provide one of the standard biochronological references for the Cenozoic, with biostratigraphic resolution of between one million and 60 000 years.

Mesozoic nannopalaeontology has developed at a slower pace, primarily due to there being less material forthcoming from the DSDP/ODP, although Cretaceous work has benefited from a large number of favourable sites. Jurassic nannofossil work has essentially been limited to onshore outcrop studies (although there are a limited number of invaluable oceanic exceptions), with most work having taken place in the last 15 years.

The huge volume of data on the stratigraphic distribution of nannofossils is synthesized in a number of relatively stable biostratigraphic zonation schemes covering the range of nannofossils (notably Martini, 1971; Sissingh, 1977; Okada and Bukry, 1980; Bown *et al.*, 1988). These are primarily based on evolutionary first and last occurrences of species, supplemented by some abundance based events. The current schemes for all geological periods are presented in the following chapters, with comments on their application, execution and correlation. Other general reviews and syntheses of nannofossil biostratigraphy are given by Lord (1982), Haq (1983a), Perch-Nielsen (1985a, b) and Siesser (1993), but the large volume of subsequent work means that the comprehensive reviews and new data presented here should be of great value, for both nannofossil specialists and end users of nannofossil data.

2

Techniques

P.R. Bown and J.R. Young

Nannofossils are generally straightforward to study, they occur in a wide range of lithologies and preparation is simple and fast. Their small size means that only very small samples are required, but also that contamination and reworking can be significant problems which need careful attention. It also means that nannofossil work requires high quality microscopes which is the one significant equipment constraint. The following notes are intended to be a guide to good practice. Other reviews of techniques are given by Hay (1977), Taylor and Hamilton (1982) and Perch-Nielsen (1985a).

2.1 SAMPLE COLLECTION

Micropalaeontological sample collection is not a complex type of fieldwork but it does benefit from a degree of organisation and preparation. It is also quite time and labour intensive: the various tasks of section measuring, sample collection and bagging-up, and information logging, take time to do properly. As a result, it is usually much better for micropalaeontologists to carry out the fieldwork, rather than leaving it to a geologist with other priorities.

2.1.1 Sample size and number

Nannofossils are typically present at abundances of billions of specimens per gram so samples for nannofossil work can be very small. For core sampling, toothpick samples of a few mm^3 are often used. A sample of about 3cm^3 gives a comfortable excess of material, even allowing for careful cleaning before preparation, repeated preparation and sub-sampling. The main advantage of collecting larger samples is that samples collected for nannofossil work will also usually be ideal for other microfossil work and geochemical analyses, such as stable isotope measurements, calcimetry and organic carbon content.

2.1.2 Sample type

Nannofossils can occur in virtually any Mesozoic or Cenozoic marine sediment with a fine carbonate fraction which has not undergone metamorphism, severe diagenesis or weathering. The most favourable lithologies are marls and chalks, but muddy sands and silts, including glauconitic sands, can often contain good assemblages. Poor preservation or complete absence is common in coarse clastic sediments, where the fine calcite fraction has been etched or leached, or in micritic limestones, where calcite has been recrystallized or heavily overgrown. Encouraging signs include the presence of aragonite-preserved macrofossils, especially ammonites, or any marine microfossils, especially planktonic foraminifera. An acid reaction is a safe indication that the rock does have a carbonate content. Discouraging signs include evidence of dolomitisation, winnowing, dissolution of aragonitic fossils, decalcification or original shallow-water deposition. Surface weathering can badly affect assemblages, particularly in tropical climates, so it is worth excavating sections to obtain fresh material. It is also important to ensure that samples are free of any contamination since nannofossils can easily be introduced via surface downwash, rootlets and percolation along fine fractures. Crystals of selenite (gypsum, $CaSO_4.2H_2O$) are a particularly bad sign since they are produced by reaction of calcium carbonate with sulphuric acid, usually from pyrite decay. Since the best lithologies are usually the finest grained and softest, it is essential to search for outcrops of the less prominent units. Hay (1977) discusses field sampling in some detail.

2.2 PREPARATION TECHNIQUES

The small size of nannofossils prevents individual specimen extraction from sediments and they are generally viewed in sediment smear or strew slides. The liberation of nannofossils from sediments/sedimentary rocks is a relatively simple process, in theory, involving mechanical breakdown of the rock, dispersal in water, and mounting of the resultant suspension onto a microscope slide. However a number of special problems require particular attention.

Due to the small size of nannofossils, the chances of contamination are higher than for most other fossils. To prevent this, special care is needed in order to keep rock dust to a minimum and to see that all equipment, bench surfaces and hands, that come into contact with the sample are spotlessly clean. Wherever possible this is best effected by using disposable laboratory ware, but when equipment is reusable then cleaning is best achieved by washing, soaking in dilute hydrochloric acid and, finally, thorough rinsing. Bench tops should be covered in clean paper towel. The sediment sample itself should also be cleaned before processing begins, by trimming away all outer surfaces.

The calcareous nature of nannofossils makes them prone to etching, dissolution or overgrowth, and such processes can occur rapidly. This can be avoided by keeping sample soaking time to a minimum, or avoiding this step altogether, and by using buffered distilled water (this is critical in soft-water areas).

2.2.1 Standard preparation techniques

(a) Simple smear slide

1. Trim all outer surfaces of the sample.
2. Scrape a small portion of sediment onto a glass cover-slip.
3. Add a drop of distilled water and make a thick sediment suspension using a flat-sided toothpick.
4. Smear the suspension thinly across the surface of the coverslip with a toothpick, and dry rapidly on a hotplate.
5. Label a glass microscope slide, and affix the coverslip (smear-side down) using an optical mounting medium (section 2.2.5c).

Notes This technique is fast and effective but does require a certain amount of practice and experimentation to achieve good results. Areas of variable grain density can be produced with a rippling motion of the toothpick. Coarse grains can be dragged to the edge of the slide and discarded. Repeated drying and resuspension can aid breakdown of the sediment. The technique is especially well suited to marls and chalks which disaggregate easily, but can be applied to all but the hardest sediments.

Preparations of this kind are suitable for biostratigraphic studies but can also be used for relative abundance count analysis. Although the ratio between nannofossils is not affected during preparation there is some size fractionation caused by the action of the toothpick across the slide.

Variation on the simple smear may be required when sediments are particularly indurated or if concentration or cleaning of the sample is required to enhance poor recovery, to prepare for electron microscope observation, or to remove sand- or clay-sized particles. In addition, more controlled techniques have been developed to allow quantitative analysis of nannofossil abundances. These alternative techniques are described below.

(b) Pipette strew slide

1. Trim all outer surfaces of the sample.
2. Crush the sample, avoiding contamination by wrapping in a paper towel.
3. Place the powdered sediment into a beaker and add distilled water.
4. Stir and leave to disintegrate as required (several hours maximum, but pH should be monitored and controlled). A deflocculant (e.g. *Calgon*) can be added at this stage or ultrasonication can be performed in order to aid disintegration.
5. Decant a small amount of the suspension into a vial and dilute with distilled water.
6. Flood a glass slide or coverslip with the suspension (~0.2 to 1.0ml) and dry on a hotplate

(alternatively, the dried residue can be resuspended and smeared with a toothpick as described above).
7. Label the glass slide, and affix the coverslip (smear-side down) using an optical mounting medium.

Notes The suspension can be concentrated or cleaned following step 4, by either gravity settling or centrifuging. The use of sieves as a first step in preparation has been advocated by some workers, but we have avoided this step due to the difficulty in ensuring thorough cleaning between each preparation. Disposable filters are perhaps the best option if this step is thought to be necessary.

(c) Gravity settling

1. Prepare a sediment suspension in a beaker as described above (section 2.2.1b: 1–4).
2. Stir the suspension and allow to settle for 1–2 minutes.
3. Decant the supernatant into a second beaker and allow to settle for 10–15 minutes.
4. Discard the supernatant and use the settled fraction to make a slide.

Notes Settling techniques have been described by, e.g., Moshkovitz and Ehrlich (1976) and Hay (1977). More precise settling fractionation is provided by elutriation (Hay, 1977) but this technique is time consuming, requires special apparatus and has consequently been little used.

(d) Short centrifuging

1. Prepare a sediment suspension in a beaker as described above (section 2.2.1b: 1–4).
2. Decant into a labelled test-tube and load into centrifuge.
3. Spin at 350r.p.m. for 15 seconds, and decant supernatant into a second labelled test-tube, discarding spun pellet containing particles >~30μm (alternatively this step may be achieved by gravity settling).
4. Spin at 1000r.p.m. for 30 seconds and discard supernatant containing particles <~2 μm.
5. Resuspend the pellet using distilled water and repeat process 4 until the supernatant is clear.
6. Mount the diluted suspension onto a coverslip or microscope slide as described above.

Notes Centrifuge speeds and times will depend on the centrifuge geometry (Katz, 1978) but also the sediment type and age. The technique is described by Edwards (1963), Pienaar (1966), Katz (1978) and Taylor and Hamilton (1982). The main value of the technique is to prepare clean samples for SEM work. Since there is inevitably some concentration of the larger nannofossils it should not be used for any quantitative work.

(e) SEM preparation

1. Prepare a suspension, preferably using the centrifuge method (section 2.2.1d).
2. Dilute the solution using distilled water.
3. Using a pipette, carefully flood a 13mm round coverslip with suspension and dry in an oven. The slides may be placed on an overturned petri dish or beaker which can be labelled. Alternatively the coverslip can be labelled using a fine *Rotring* pen.
4. When dry, attach the coverslip to a labelled aluminium EM stub using colloidal silver.
5. Coat the slide with gold or palladium (thickness ~500Å).

Notes SEM observation generally benefits from cleaning of the sample using the centrifuge technique described above. Alternatively, the surfaces of sediment chips may be directly viewed in the SEM, and in exceptional circumstances, particularly in organic-rich, laminated sediments where faecal pellets or 'bloom' laminae are undisturbed, spectacular nannofossil assemblages can be observed, including intact placolith coccospheres, collapsed murolith coccospheres, delicate heterococcoliths and holococcoliths (e.g. Goy, 1981; Thomsen, 1989a, b; Lambert, 1987, 1993; Bown, 1993).

The appearance of nannofossils in the SEM is often very much worse than might be expected from their appearance in the LM. This is commonly due to fine organic matter or clay particles obscuring specimens. In addition, nannofossils are always harder to spot in the SEM, and slight overgrowth and etching, which is almost unnoticeable in the LM, can seriously affect their appearance in the SEM. For these reasons SEM work is only really worthwhile on the best preserved samples.

Transmission electron microscopes are now rarely used in routine nannofossil observation. Preparation techniques are described in Hay (1977).

2.2.2 Special preparation techniques

(a) Preparations for quantitative analysis
The increasing use of quantitative assemblage data in both biostratigraphy and palaeoceanographic studies has led to the development of more rigorous preparation methods which allow an approximation of the absolute number of nannofossils, or a particular species of nannofossil, per unit of sediment. Backman and Shackleton (1983) made counts on standard smear slides and proposed that the number of specimens counted by unit area (mm^2) is approximately proportional to the abundance of the selected species per gram of sediment, assuming that the grain density is constant over the slide and that it is representative of the sample. They compared this method with a dilution/filtering technique developed by McIntyre (*in* Backman and Shackleton, 1983) for preparing SEM samples, and found the two techniques compared favourably. Henriksson (1993) proposed a similar method with the additional step of weighing the amount of sediment on the slide following preparation, although this requires an extremely precise microbalance. Beaufort (1991) argued that smear slides could not provide representative or even grain-density distributions across the surface of the slide, and used a modified random-settling technique to improve evenness on the slide. His technique used weighed sample fractions diluted to a given volume, and allowed reproducible calculation of the number of specimens per gram of sediment. Variations on his technique were described by Williams and Bralower (1995) and Su (1996). An alternative to these methods was proposed by Okada (1992) who 'seeded' nannofossil preparations with a measured amount of microbeads. The ratio of counted beads to nannofossil specimens provides a comparable proxy for absolute abundance.

(b) Mobile mounts
For taxonomic research it is useful to be able to turn over specimens and see them in side view. Temporary mounts which allow rotation of nannofossil specimens can be produced by replacing the normal, fixed mounting medium with a viscous medium such as immersion oil, castor oil or silicone oil (Bramlette and Sullivan, 1961; Gartner, 1968; Romein, 1979). Movement of the coverslip over the glass slide then allows controlled rotation of the nannofossil specimens. The process may be aided by scraping the nannofossils loose with the edge of a coverslip, before adding the viscous medium and dropping a coverslip on top.

(c) LM/SEM same-specimen interchange
Viewing of the same specimen in LM and SEM is useful for confirming the identifications of problematic specimens, allows LM location of rare specimens and is desirable for illustration of type specimens. Numerous authors have described systems for doing this (e.g. Moshkovitz, 1974; Greig, 1983; Varol, 1989c). These vary somewhat in detail, but all employ the use of a grid which allows re-identification of specimens. Gallagher (1988) described a simple same-specimen method and also reviewed several older techniques. The basic procedure is:

1. Prepare specimens on a circular SEM coverslip with a grid system and temporarily mount for LM observation.
2. Using an LM, find and photograph specimens and record their location using the grid system.
3. If necessary, clean the coverslip using a suitable chemical solvent.
4. Mount the coverslip on an SEM stub, coat it, relocate the specimens, and photograph them.

Notes The most problematic stage is cleaning of the slide (step 3), since nannofossils can easily be lost. Greig (1983) and Varol (1989c) recommend normal immersion oil as the temporary mounting medium which is then removed using xylene. An alternative is to use a volatile viewing medium instead of immersion oil and then simply allow it to evaporate: Gallagher (1988) used methanol, Moshkovitz (1978) used xylene or anisole.

Methods of location recording (step 2) include use of special TEM grids (Moshkovitz, 1978), photographic mapping, or a grid drawn by hand with a drafting pen (Gallagher, 1988).

SEM to LM transfer can be achieved more easily (Thierstein *et al.*, 1971; Smith, 1975). The basic technique is:

1. Prepare sample on a circular SEM coverslip with a grid system.
2. Temporarily mount on a stub and apply a thin metal coating.
3. View in the SEM, record locations using the grid.

4. Remove the coverslip from the SEM stub and permanently mount on a microscope slide.

LM to TEM techniques have also been described (Perch-Nielsen, 1967) and even techniques for viewing both sides of a specimen in the SEM (Mai, 1988, 1995).

(d) Thin sections

In rare cases, thin sections of highly indurated carbonate-rich sediments may allow observation of nannofossils, but sections need to be cut thinly (~0.01mm), and generally only large and abundant nannofossils are observed, e.g. calcispheres, *Schizosphaerella* and nannoconids.

2.2.3 Industrial samples

(a) Sample degradation

Any sample recovered during drilling will undergo drastic change in physico-chemical conditions as it is brought to the surface. This can cause rapid diagenetic change and loss of nannofossils. In scientific drilling, special precautions are normally taken to minimise this problem, and in any case it is only a slight problem in the chemically inert oozes which are often the primary drilling target. In industrial contexts, sample degradation can cause great problems since the sediments are often organic-rich mudrocks, will be mixed with drilling muds, and exposed to the worst indignities of life on drilling rigs (Jutson, 1995). In these circumstances samples can deteriorate rapidly and slides should be prepared at the wellhead if possible.

(b) Drilling mud samples

The most common samples provided by industrial drilling are drill muds containing rock chips. With such samples the best option is to pick out soft rock chips by hand and prepare slides from them individually. Washed rock chips are also often available but washing may remove the softest chips with the best nannofloras. Such chips often contain detergents and other chemicals from the drill muds and these can produce some strange crystals but do not generally seem to harm the nannofloras. Styzen and Reugger (1994) discuss problems with polymer muds, which caused severe coagulation, and they recommend use of 100% bleach to remove the polymers.

Clearly the contamination of cuttings samples by downhole caving cannot be avoided and biostratigraphy is achieved using last occurrences (extinction datums) almost exclusively. However, standard biostratigraphic methods can be applied to core and side wall core (SWC) samples.

2.2.4 Live nannoplankton

A wide range of techniques is required for preparation of live nannoplankton samples. These notes are only a brief synopsis; see also Winter *et al.* (1994).

(a) Oceanic samples

Nannoplankton are only present at concentrations of a few thousand to a few million cells per litre in natural populations. These concentrations are several orders of magnitude lower than the final concentrations needed and are too low for normal centrifuge concentration, hence filtration is the routine means of concentration. Typically, one to ten litres of sea water are filtered through a 0.2 μm filter using a filter holder and a vacuum pump. The volume of water filtered should be carefully logged so that cell concentrations can be calculated. The filter is then rinsed with buffered distilled water to remove salts. A wide range of filters and filtration equipment can be purchased from companies such as *Millipore*. An economical solution for small scale work is to use inline filters connected to a syringe, and to force the sample through under pressure rather than to pump it under vacuum. Filters are then air dried and stored in plastic petri dishes, with care taken to keep the sample-side uppermost and in an acid-free environment.

The resultant filters can readily be mounted on SEM stubs, or they can be embedded in slide mounting medium and examined by light microscopy. Two main types of filter are available. Cellulose acetate filters (also called *Nucleopore* filters), which are thin plastic sheets with etched holes, are ideal for SEM work since they have a smooth surface against which nannofossils show high contrast. They cannot, however, be used for light microscopy since they are virtually opaque (most makes), or have very poor optical properties (*Isopore* filters). Fibrous cellulose nitrate filters are virtually transparent when mounted, and can readily be used for light microscopy. However, they are unsatisfactory for

SEM work since the fibres show high contrast and make it difficult to locate isolated nannofossils. There is no satisfactory compromise and the best solution is to make two preparations per sample.

To mount filters for SEM work, double-sided tape or nail varnish is commonly used. Both of these, however, are volatile at high vacuums and so should not be used in field emission SEMs, whilst epoxy resins such as *Araldite* may pass through the filter and contaminate the sample. An effective solution to this dilemma is to use photographic film. The film is glued to the SEM stub with epoxy resin, matt surface upward. Moistening the film surface mobilises the emulsion and filter samples will stick to it.

(b) Culture samples

Coccolithophore cultures are typically maintained at concentrations of around one billion cells per litre. At these concentrations, live cells can be viewed in simple water mounts. To prepare permanent mounts the cells need to be harvested to remove the salt water. For this, high-speed microcentrifuges (*Eppendorf* centrifuges) are ideal. Culture techniques are described in Guillard (1973) and Green *et al.* (1989). Cultures of the most common coccolithophores, such as *Emiliania huxleyi* and *Pleurochrysis carterae*, can be purchased at low cost from culture collection centres such as the Plymouth Marine Laboratory (UK) or Bigelow Laboratory (USA).

2.2.5 Preparation equipment and chemicals

(a) Essential basics

The essential equipment needed for nannofossil preparation is very simple. An electric hotplate is required for drying slides, and curing some mountants. Microscope slides and coverslips are obviously needed. Etched slide ends are convenient for writing on directly but paper labels stick better to smooth surfaces. Surface properties of slides and cover-slips are highly variable: on some slides pipetted liquid will concentrate in droplets whilst on others it will disperse in thin films. The latter are much easier to use. Saliva (i.e. licking) can be used to produce the desirable properties but it is preferable to find a source of suitable slides. It is important to use the thinnest grade of coverslips available (usually 'No.1'), since high-magnification lenses have very low depths of field.

(b) Useful extra equipment

Most nannofossil workers use only simple equipment but there are a number of additional items which can be invaluable.

Centrifuge: as discussed above centrifuging can be useful for removing clay from samples. Small bench centrifuges taking 10ml tubes are ideal. High speeds are not needed, but the speed should be regulatable, ideally with a braking device.

Micro-centrifuge: *Eppendorf* micro-centrifuges are almost essential for work with cultures and can be put to use in other contexts.

Ulrasonicator: Ultrasound can be used to disaggregate samples.

Balance: For quantitative techniques a micro-balance is useful. Balances capable of measuring in micrograms and below are, however, very expensive.

Pipettors: Unless smear slides are used exclusively then it is necessary to pipette sample suspensions onto slides. Disposable plastic pipettes are adequate, but pipettors with disposable plastic tips allow precise measurement of the volume of liquid being dispensed. The precision is not routinely necessary but is invaluable for quantitative techniques. The most useful pipettors have a 100–1000ml range, 10–100ml pipettors are the next most useful.

Filtration equipment: Basic filtration equipment consists of microfilter disks, which are expensive, a filter holder and a vacuum pump of some kind.

UV lamp: This is needed for curing *Norland Optical Adhesive* if this is used for slide mounts.

(c) Optical mounting media

Numerous mounting media have been used for preparing nannofossil slides, as surveyed by van Heck (1996). They should be permanent, solid, chemically inert and possess a refractive index which falls below or between those of calcite (1.658–1.486) in order to allow good resolution in transmitted light and to avoid the effects of inverted relief (Edwards, 1963). Many media present problems of toxicity, impermanence, expense, bubble formation or inconvenience. A widely used medium which appears free of all these problems is *Norland Optical Adhesive*. This is applied to the slide as a drop of liquid, and is cured by exposure to UV light, using either daylight or a UV lamp. Canada balsam has also been used extensively and has a proven record of longevity. One medium which should definitely be avoided with calcareous nannofossils is *Petropoxy*, since it etches and dissolves specimens. Any medium containing xylene is carcinogenic and should only be used in a fume cupboard.

Whatever medium is used it is essential that it is used sparingly since a thick layer can make it impossible to focus on the specimens.

(d) Chemicals

Various chemical techniques can be used to help with difficult samples. However, all chemical techniques present possibilities of sample degradation. Good practice is to use a very simple technique for routine use and reconnaissance work and only adopt more complex techniques to solve special problems.

Buffers To avoid contaminants, most workers use distilled water, but this is usually slightly acidic and should be buffered if the sample is kept in suspension for any length of time. The addition of NH_4OH, $NaHCO_3$, NH_3 and Na_2CO_3 have all been suggested for this purpose. A pH of 9.4 prevents dissolution and provides the best dispersion of clays (Hay, 1977). In some areas it is possible to use tap water instead of buffered distilled water, but it should first be checked for pH and to ensure it does not contain suspended nannofossils.

Deflocculants Clay flocculation can cause clumping of grains and adhesion of clay flakes to individual nannofossils. Deflocculants such as *Calgon* (sodium hexametaphosphate) can solve these problems but can also cause sample dissolution. They should only be used at low dilutions (~0.1%). Ammonia (NH_3) is a less effective deflocculant but avoids the problem of dissolution.

Oxidising agents Amorphous organic matter can cause sample clumping and thus obscure nannofossils. Oxidising agents, such as bleach (NaOCl, sodium hypochlorite) and hydrogen peroxide (H_2O_2), can be used to remove this organic matter and are also widely used to clean coccoliths grown in culture. These oxidising agents will not cause dissolution of calcite on their own, but if pyrite is present they can lead to formation of sulphuric acid.

Eshet (1996) added 10% NaOCl to sediment suspensions and soaked for 10 hours in order to oxidise organic material. Herold-Vieuxblé (1979) removed organic material using benzene in a Soxhlet apparatus. Girgis (1986) developed a more complicated series of steps in order to liberate nannofossils from kerogen-rich shales, which involved sieving (to remove particles >10µm), centrifuging (to remove particles <3µm), flotation in TBE/acetone of 2.2 specific gravity (to remove kerogen) and then centrifuge-accelerated settling in TBE/acetone of 2.9 specific gravity (to remove heavy minerals).

2.3 OBSERVATION

For over 100 years, the light microscope was the only instrument with which nannofossils could be viewed and due to the ease of preparation and speed of observation it has remained the primary observational tool, particularly in biostratigraphic applications. The advent of electron microscopes in the 1950s provided high-resolution images of nannofossils for the first time, and revolutionised our ideas and knowledge of nannofossil structure and consequently classification. However, it is through a combination of the two observational techniques that the maximum amount of information on nannofossils can be gathered: structural and crystallographic information in the LM and detailed surficial morphology from the SEM.

2.3.1 Light microscopy

For routine studies of nannofossils, and invariably in industrial work, the LM remains the most useful observational instrument. It allows accurate determination of the crystallographic assembly and, with some acclimatisation, reveals many features of morphology which allow identification down to species level. The observation of significant morphological features is also less dependent on good preservation, in contrast to the SEM, where clay and secondary calcite overgrowth may completely obscure the nannofossils.

Nannofossil size is close to the limit of LM resolution and therefore high quality optics are essential. Petrographic research microscopes will produce acceptable results, but the low grade microscopes available in typical undergraduate geology laboratories will not. The principal suppliers are Leitz, Nikon, Olympus and Zeiss. The essential requirements are a x100 oil-immersion objective lens with a good condenser and XPL illumination. A binocular head is preferable for extended work.

(a) Lenses

A high quality x100 oil-immersion objective lens is essential. Lower powered objectives (e.g. x40) may be used to ascertain whether slides are productive or to log particularly large forms, such as discoasters and nannoconids, but are not adequate for routine observation of assemblages. If purchasing a system it is probably better to get strain free lenses for optimum XPL work, rather than phase lenses, although an ideal system has both.

(b) Stage

Stage design is important. Working with a x100 lens means that a mechanical stage is needed, that is, a stage with slide movement controlled mechanically rather than directly by hand. In addition, XPL illumination really requires a rotating stage. The combined requirement for a rotating stage and mechanical control is difficult to meet well.

(c) Condenser and illumination modes

A high quality condenser lens matched to the objective is essential, and to get good results the condenser should be carefully set up. Phase contrast (PC) illumination is useful but not essential. Reflected light illumination is never used.

(d) Accessories

The most important accessories are an eyepiece graticule and a gypsum plate.

(e) Illumination techniques

The principle transmitted light techniques applied are plane-polarised light, XPL, PC and XPL with accessory (gypsum) plate. XPL is now most commonly used but was not applied until Kamptner's work in the 1950s. Plane-polarised light or PC is required when low birefringence nannofossils are present. The gypsum plate provides further crystallographic orientation information and is routinely used by some workers.

Using careful observation techniques, a great deal of information concerning nannofossil structure can be provided by light microscopy. Reviews of microscopical theory and techniques are provided by Romein (1979), Moshkovitz and Osmond (1989) and Young (1992).

Bright field (BF) This is plain light viewing, with or without a single polariser, and is available on all microscopes. Nannofossils show low contrast in BF but by careful use of the condenser diaphragm, useful contrast can be obtained. In BF the depth of focus is very narrow, which can be useful for making careful observations at different focal depths through specimens.

Phase contrast (PC) Phase contrast illumination requires special lenses and condenser, and produces a grey/blue background field on which objects may appear bright or dark. Contrast, optical relief and depth of field are all enhanced relative to BF and it is a useful general purpose mode of illumination. The contrast shown by nannofossils is strongly dependent on their optical orientation. Specimens with sub-vertical c-axes which can be nearly invisible in XPL show up as very distinct dark objects in PC, hence it can be very valuable for locating such specimens.

Cross polarised light (XPL) As a result of their size, composition and structure, coccoliths show very distinct pseudo-extinction crosses in XPL. XPL is essential for identifying many nannofossils and for finding them in low abundance samples. The key principle is that brightness of a crystal is a non-linear function of thickness and orientation. Calcite crystals oriented with their c-axes vertical will show zero birefringence and be dark in all orientations. With horizontal c-axes, crystals will be dark when they are oriented parallel to one of the polars (i.e. N-S or E-W), and show maximum birefringence at the 45° position. The maximum birefringence value is dependent on thickness, hence very thin calcite crystals ($<0.1\mu m$) will be dark whatever their orientation.

Gypsum plate In XPL, a crystal will show maximum birefringence when its c-axis is oriented either NE–SW or NW–SE. Accessory plates have their crystallographic axis oriented diagonally and when they are inserted a birefringent mineral will show either constructive or destructive interference (i.e. increase or decrease in birefringence colours, respectively). This can be used to determine the sense of orientation of the c-axis, e.g. a rod-shaped nannolith showing straight extinction may have the c-axis parallel to the length of the rod (e.g. *Triquetrorhabdulus carinatus*) or perpendicular to it (e.g. *Orthorhabdus serratus*). Most coccoliths show sub-radial c-axis distributions, and inserting an accessory plate provides little additional information. However, many nannoliths with radial structure show tangential c-axis orientations, e.g. *Nannoconus*, most Polycyclolithaceae and all Braarudosphaeraceae. Use of an accessory plate can be invaluable in confirming identification of these. For very simple nannoliths, such as *Quadrum gartneri, Minylitha convallis* and *Florisphaera profunda,* consistency of optical orientation is a key criterion in distinguishing them from inorganic debris.

The most widely used accessory plate is the gypsum plate, also known as a 1λ or sensitive tint plate. This causes a retardation of one wavelength of red light (1λ = 590nm) and so produces first-order red (~purple) interference colours. Constructive interference of this plate with first order greys produces blue interference colours, whilst destructive interference produces yellows and oranges. In most microscopes the gypsum plate is inserted with its slow/fast ray orientated NE/SW, but this is not universal so any published colour distributions from one microscope may be exactly inverted in another microscope. For this reason, and many others, it is far better to report c-axis orientations than colour distribution patterns.

2.3.2 Scanning electron microscopy

As with light microscopy, nannofossils push the limits of SEM resolution and for good results a good quality, well-maintained and adjusted SEM is needed. If it is possible to influence purchase of an SEM, the prime criterion should be image quality in secondary electron mode. Analytical facilities are rarely needed. Field emission microscopes give excellent results. Useful features include a stage capable of high angle tilting (to 90°) and able to take several stubs.

2.3.3 Transmission electron microscopy

The high resolution and rapid exposure time of the TEM make it a useful tool for nannofossil work but it is now rarely used, mainly because of the need for elaborate preparation, including carbon replication, and the difficulty in interpreting 'shadowed' images. The technique is worth considering if extended study of individual samples in the EM is needed, e.g. counting of Quaternary nannofossils (Matsuoka and Okada, 1989).

2.3.4 Illustration

(a) Photography

Photography of nannofossils is necessary for reports, publications, etc. Fine grain film should be used but the main limits are imposed by the specimens, not the film. In XPL, metering is unreliable unless the microscope has spot metering. A convenient solution is to insert the gypsum plate, record the metering reading, then revert to XPL for the actual photography. For presentations, colour transparencies taken directly on the microscope give far better results than photographs of assembled plates.

(b) Digital image capture

It is now entirely practical and economical to set up a system which will capture LM images direct to a desktop computer with quality close to conventional film. The equipment needed for this is a computer equipped to accept a video signal and a CCD video camera. The total cost of such equipment will usually be a fraction of the cost of the microscope. A well documented use of such images is in biometric work (e.g. Backman and Hermelin, 1986; Young *et al.*, 1996), but other applications include rapid assembly of plates for reports, investigation of morphological features using through focal series, summary of c-axis orientations, and query to remote experts by sending images through the internet. The system we use is based on an Apple Macintosh computer and the excellent public domain program NIH-

Image, and macro programs developed for this system are available from us (Young *et al.*, 1996). Plates produced using this system illustrate the Neogene chapter (Plates 8.1–10).

2.4 DATA COLLECTION

While the simple recording of presence or absence of particular nannofossil species is the most basic method of collecting and presenting data, most nannofossil studies, whether they be biostratigraphic or palaeoceanographic, attempt some quantification of abundances. Much of this data is semi-quantitative, recording the abundance of particular species as abundant, common, few or rare, with each of these categories being loosely defined in terms of a number of specimens per number of fields of view (FOV). The definition of these categories has varied considerably between authors, making comparison difficult (e.g. Hay, 1970).

Recent years have seen something of a quantitative revolution, with a profusion of different counting techniques being applied, and much statistical analysis of the results. These quantitative studies have generally been palaeoceanographic, seeking to identify fluctuations in the abundance of key species in response to varying climatic or oceanographic conditions. However, the accurate quantification of nannofossil abundance is also of biostratigraphic value, since it can provide a rigorous definition of datum levels and a measure of bioevent reliability. In addition, it allows the recognition of 'influx' or 'acme' events which are often correlatable at least regionally. Such acmes are often more easily recognisable than the discrete first or last occurrence datums of rare marker species.

2.4.1 Semi-quantitative counting

The simplest technique is to record the approximate abundance of each species in terms of specimens per FOV using a logarithmic scale. The following categories are standard; R-Rare, F-Frequent/Few, C-Common, A-Abundant. There is no universal agreement on categories but a typical set of values is given in section 5.4. Additional categories sometimes used include D-Dominant (although semantically there can only ever be one dominant species in a sample); VR–Very Rare; X–present but only one specimen seen.

2.4.2 Simple relative abundance counting

The simplest way to quantify relative abundances is to count a fixed number of specimens. Three hundred specimens is generally regarded as a sensible compromise between time spent and precision required. At the 95% confidence level, 300 counts assures the presence of a taxon whose relative abundance was 1% in the total population (Thierstein *et al.*, 1977). Performing a 300 specimen count is also a valuable discipline, since it forces identification of every specimen encountered, and frequently reveals species which are overlooked in simple reconnaissance. In addition, the number of FOV required to count 300 specimens gives an approximate measure of nannofossil abundance in the sample.

This method is independent of terrigenous or other biogenic dilution but may not pick up rare taxa, and difficulties are encountered when interpreting percentage figures gathered in this way, due to the interdependency of the figures (closed sum effects).

For accurate counting it is best to have slides with concentrations of about 20–30 specimens per FOV. It is an unsatisfactory technique if there are great variations in size and/or preservation potential between species.

Another alternative is to count a fixed number of FOV but for statistical analysis it is preferable to keep the number of specimens counted uniform.

2.4.3 Extended counting

To quantify the abundances of rarer species, more complex counting procedures may be used, e.g. counting all species for the first 300 specimens, then a further 100 specimens of the rarer species. Alternatively, all species may be counted in 10 FOV then rare species in a further 30 FOV.

The measurement of particular marker species' abundance has been achieved by counting the number of specimens of a given species relative to all specimens of the same genus or family (Backman and Shackleton, 1983; Fornaciari and Rio, 1996). Assuming the taxonomic group had similar preservational and ecological prerequisites, the data gathered in this way can be considered independent of preservation state, dilution and palaeoecological exclusion.

Many variations on these methods have been used, especially for analysis of Quaternary assemblages which typically are dominated by small genera (e.g. *Emiliania, Gephyrocapsa, Florisphaera*) but also include rarer, large coccoliths (e.g. *Coccolithus, Calcidiscus*) which may give useful palaeoceanographic signals (e.g. Rio *et al.*, 1990b; Okada, 1992).

2.4.4 Unit area counting

Backman and Shackleton (1983) noted that if smear slides are made up at consistent concentrations, then the number of specimens per standard FOV (or per unit area of slide) can be used to compare the abundance of single species between slides. The technique involves the counting of all specimens of a selected taxon in a predetermined number of FOV at a specified magnification. The abundance data are then expressed relative to the unit area of slide examined (number of specimens per mm^2). Although the technique is strictly semi-quantitative, Backman and Shackleton (1983) demonstrated a close approximation to abundances generated by more rigorous absolute preparation and counting methods. However, the technique is influenced by preparation technique (grain density), dissolution and dilution.

The technique allows fast quantification of distribution patterns of individual species and has been widely used, especially in the Cenozoic, for researching biostratigraphic events (e.g. Rio *et al.*, 1990b; Fornaciari *et al.*, 1990) and palaeoceanography (Chepstow-Lusty *et al.*, 1989).

2.4.5 Absolute abundance calculation

It is obviously tempting to convert counts per unit area of slide into counts per gram of sediment. Moreover if the sedimentation rate is known then this data can be converted into accumulation rates of specimens per unit area per year. Unfortunately it is not easy to do this and the preparation techniques must be modified accordingly. These generally involve preparing slides from a known weight of sample, diluted to a given volume and settled and dried to give an even slide coverage (e.g. Wei, 1988; Beaufort, 1991); see also discussion of preparation techniques (section 2.2.2). As a result of the difficulties posed by these time-consuming preparation techniques, few workers have produced estimates of absolute abundances of nannofossils but examples of this approach include Williams and Bralower (1995) and Su (1996).

2.4.6 Sediment trap counting

Absolute abundance estimates are of particular importance in sediment trap work, and special attention has been applied to them. Most workers however admit that there are severe problems posed by specimens locked within micro-zooplankton pellets so that most flux estimates are underestimates (Steinmetz, 1994).

(a) Lith to cell conversion

Workers counting living nannoplankton predominantly count complete coccospheres but for increased rigour may also count dispersed coccoliths and convert these loose liths into equivalent numbers of coccospheres. Since the number of coccoliths per coccosphere is highly variable a separate estimate needs to be made for each species. Various workers have applied this technique to analysis of sediment trap samples and Late Quaternary nannofossils on the grounds that conversion to cells should give more meaningful palaeoceanographic results.

(b) Lith to mass conversion

For sediment trap work a prime objective is to calculate fluxes, that is, unit weights of different components being transported toward the seabed per unit area per unit time (e.g. grams Coccolith $CaCO_3/m^2/year$). To achieve this, counts of coccoliths need to be converted into weights of $CaCO_3$ which in turn requires estimates of the mass of individual coccoliths. The mass of a coccolith can be calculated from basic dimensions and cross-sectional shape, and estimates of the average mass of most common Quaternary coccoliths have been made by Beaufort and Heussner (in press) and Young and Ziveri (in press). It should be noted that mass is proportional to the cube of linear dimensions and so most species will produce coccoliths varying in mass by about an order of magnitude.

2.4.7 Preservation analysis

Nannofossil preservation is highly variable. The principal processes are dissolution and overgrowth, both of which may occur in varying degrees in a single sample. It is good practice to provide a measure of nannofossil preservation, as this gives some indication of the integrity of the data. The descriptive scheme of Roth and Thierstein (1972), with modifications by Roth (1983), is relatively widely used, relying on the LM identification of etching and overgrowth effects, allowing the categorisation of nannofossil preservation as follows:

- E-3 – heavily etched (much fragmented material, only solution-resistant species left)
- E-2 – moderately etched (irregular outlines, delicate structures and species dissolved)
- E-1 – slightly etched (serrate outlines, partial dissolution of delicate structures)
- X – excellent (coccoliths appear pristine)
- O-1 – slightly overgrown (extended coccolith elements, thickened cross-bars, etc.)
- O-2 – moderately overgrown (delicate central structures obscured)
- O-3 – heavily overgrown (coccoliths so overgrown that identification is difficult)

An alternative is to simply record the general preservation state as X-Excellent, G-Good, M-Moderate or P-Poor.

A few quantitative indices of preservation have been proposed, e.g. Matsuoka (1990), using percentage of *Calcidiscus* specimens with detached shield, and Roth and Krumbach (1986), using percentage of *Watznaueria.*

2.5 DATA PRESENTATION

Nannofossil research is a well defined specialization and results of work usually need to be presented so that they are accessible to less-specialized end users. In addition, results need to be adequately documented to allow other specialists to verify them or to use the data in different ways.

2.5.1 Biostratigraphic data presentation

Distribution charts are tables documenting the occurrence of each species in each sample. They are normally the most effective and efficient way to present primary biostratigraphic data. Ideally they should include data on relative abundances of species, total abundance of nannofossils per sample, preservation, inferred zonal assignment, sample height in the section or core, and lithostratigraphy. Quite complex charts can be produced using a spreadsheet program (e.g. Wei, 1990). There are also a limited number of specialist programs available to produce good graphic output and to allow intelligent integration and databasing of different types of stratigraphic data.

Given a good distribution chart there is no need for detailed text description of assemblages, instead this part of a report can concentrate on outlining general results, problems and areas of uncertainty. Additional diagrams are normally needed to explain the zonation used, and summarise correlations inferred.

Biostratigraphic results should virtually always be presented with reference to the standard nannofossil zonations. These are an excellent communication device and should not be abandoned simply because one or two events cannot be recognised locally or the author disagrees with a few details. If appropriate, nannofossil results may then be extrapolated to chronostratigraphic units or Ma ages.

2.5.2 Taxonomic documentation

Most nannofossil taxa are well documented and do not require description in a routine report. It is good practice, however, to include an appendix giving the full combinations of all taxa cited. These citations should include author and date, e.g. *Coccolithus pelagicus* (Wallich 1877) Schiller 1930, but it is not necessary to include bibliographic references; readers can instead be referred to standard references (e.g. Perch-Nielsen, 1985a, b; this volume). A plate or two of light micrographs illustrating marker species can be useful supporting documentation, particularly if the markers are rare or the biostratigraphic interpretation is likely to be controversial.

If new taxa are described this should be done thoroughly, with first class illustration, and in full accordance with the latest edition of the International Code of Botanical Nomenclature. Type material should be deposited in a professionally curated collection, ideally a university department or national museum. Deposited material should include the slide containing the type specimen or negative, together with a sub-sample of the material from which it was prepared.

2.5.3 Journals and societies

Papers containing information on nannofossils appear in a wide range of journals reflecting the wide use of nannofossils in modern geological research. Nannofossils studies have played a key role in Ocean Drilling Program research and its predecessor, the Deep Sea Drilling Project, and most report volumes contain important chapters on nannofossils.

The International Nannoplankton Association (INA) includes most workers studying living or fossil nannoplankton. It publishes the *Journal of Nannoplankton Research* (formerly the *INA Newsletter*) which includes a comprehensive bibliography of publications on nannoplankton as well as short research articles. The INA also holds international conferences every two or three years, usually with published proceedings.

Finally, it is worth mentioning a number of world wide web sites which provide valuable information and/or images of calcareous nannofossils: The Calcite Palace (www.nannos.com), The Nannofossil Lab (wwei.ucsd.edu), the *Emiliania huxleyi* Home Page (www.soc.soton.ac.uk/SUDO/tt/eh/) and the INA site (www.nhm.ac.uk/hosted_sites/ina or gs.ucsd.edu/ina).

3

Triassic

P.R. Bown
(with contributions from D. Janofske)

3.1 INTRODUCTION

The discovery of Triassic nannofossils is one of the major advances which has been made since the previous incarnation of this book (Lord, 1982). The first substantiated report of Triassic calcareous nannofossils *sensu stricto* was published by Moshkovitz in 1982, although there had been many claims for pre-Jurassic nannofossils prior to this. The literature relating to pre-Jurassic nannofossils thus falls into two groups: those published mainly before 1982, reporting objects interpreted as nannofossils, but which are either dubious at best or single records of nannofossil-like objects which have remained unconfirmed; and those published since 1982, which have recorded unequivocal nannofossils, including coccoliths, calcispheres and nannoliths.

The first group of papers includes unillustrated claims for Palaeozoic nannofossils (Gümbel, 1870), illustrations of Triassic and older objects which are highly dubious and probably of inorganic origin (Pirini Radrizzani, 1971; Di Nocera and Scandone, 1977), 'Palaeozoic' coccoliths which are clearly contamination sourced from younger sediments (Noël (1965) illustrated Jurassic *Watznaueria* coccoliths from Devonian- and Pennsylvanian-aged sediments), and cryptic Palaeozoic objects which are somewhat comparable to nannofossils but which differ in size, structure or composition and which remain unsubstantiated and in any case are unlikely to be ancestral to calcareous nannofossils *sensu stricto* (Deflandre, 1970; Gartner and Gentile, 1972).

The second group of reports have established beyond doubt the existence of Triassic nannofossils, including the earliest coccoliths, a relatively diverse calcisphere record, and numerically dominant *incertae sedis* nannoliths. Triassic nannofloras are typically of low diversity but abundant, and appear to be restricted to Late Triassic, low palaeolatitude sites. At present they have little biostratigraphic value, but an extinction event at the Triassic/Jurassic boundary provides a distinctive bioevent.

3.2 IMPORTANT REFERENCES

The earliest references to true Late Triassic nannofossil occurrences are Fischer *et al.* (1967) and Wiedmann *et al.* (1979), who illustrated *Prinsiosphaera* as unknown objects from Alpine limestone thin-sections, and Prins (1969) who recorded the coccolith *Crucirhabdus* (line-drawings only) from undisclosed Rhaetian sediments. Moshkovitz (1982) provided the first well-documented account, but found only nannoliths. This discovery, and the majority of later reports, are from Norian and Rhaetian sediments of the Northern Calcareous Alps in southern Germany and Austria (e.g. Jafar, 1983; Bown, 1985, 1987; Posch and Stradner, 1987; Bown and Lord, 1990; Janofske, 1987, 1992). Jafar (1983) recorded a relatively high-diversity assemblage, including coccoliths, some of which are now thought to have been contaminants, and other more dubious objects which may be of inorganic origin. Bown (1985) provided the first SEM micrographs of Triassic coccoliths. Since 1985, Triassic nannofossils have been recorded from a number of different localities: Northern Calcareous Alps, Timor and British Columbia (Bown, 1987, 1992a); NW Australian continental shelf (Bralower *et al.*, 1991); and the Southern Alps, where new calcispheres and nannoliths have been found in older, Lower Carnian sediments (Janofske, 1990, 1992).

3.3 TRIASSIC NANNOFOSSIL SUCCESSION

The earliest Triassic nannofossils are calcispheres and nannoliths of Early Carnian age which have only been found in the Southern Alps (Janofske, 1990, 1992). The calcispheres are almost certainly calcareous dinoflagellates, belonging to the genera *Orthopithonella* and *Obliquipithonella*, and appeared at approximately the same time as the closely-related, organic-walled dinocysts. The nannofossil record from the Upper Carnian and Lower Norian is, at present, poorly known.

In the Norian, two dominant nannoliths appeared, along with subordinate calcispheres and the first, very small coccoliths (~2μm). This assemblage is often abundant and has been found consistently throughout the range of productive Triassic sites. All but one of these nannofossils, a coccolith species, became extinct at the Triassic/Jurassic boundary (Fig. 3.1).

The most common nannolith is *Prinsiosphaera triassica*, a solid sphere constructed from equidimensional calcite crystallites, whose biological affinities are unknown. The species was subdivided by Jafar (1983) but this appears to be an artefact of preservation, as demonstrated by Bralower *et al.* (1991). Also common is *Eoconusphaera zlambachensis*, a conical nannolith with a central core of radiating calcite laths. This morphology is similar to the Early Jurassic *Mitrolithus* (=*Calcivascularis*) *jansae*, however, any link between the two remains unproven due to the poor records from the Hettangian interval (Bown and Cooper, 1989b).

Three coccolith species appeared in the Norian, all small and possessing simple murolith morphologies. *Crucirhabdus primulus* is the only species known to have survived the terminal Triassic extinction event, and clearly gave rise to the Early Jurassic protolith lineage (Parhabdolithaceae). *Archaeozygodiscus koessenensis* has a loxolith rim but the direction of element imbrication is opposite to that of all other, later, Mesozoic loxoliths, and its relationship to them is uncertain.

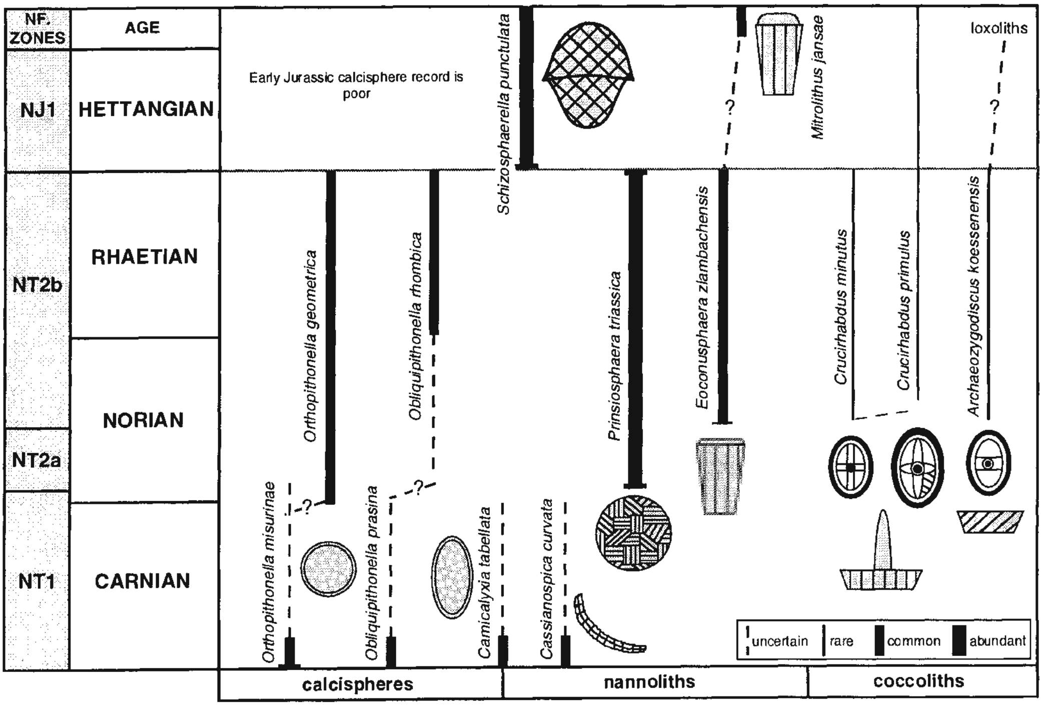


Fig. 3.1 Nannofossil succession through the Late Triassic and earliest Jurassic.

3.4 BIOSTRATIGRAPHY

At present, Triassic nannofossils have little biostratigraphic value, although the extinction of species at the top of the Triassic is a dramatic and widespread bioevent, and *Prinsiosphaera*-dominated assemblages are characteristic of the Norian and Rhaetian. Further subdivision is limited by the small number of documented sites, many of which have poorly-constrained stratigraphy (e.g. ODP Site 761 and Timor). Bralower *et al.* (1991) defined two zones (presented in modified form, below) and also suggested that finer subdivision may be possible based on systematic morphometric variations in *Prinsiosphaera triassica.*

Triassic nannofossils are illustrated in Plate 3.1 and biostratigraphy summarised in Fig. 3.1.

NT1 Orthopithonella misurinae Zone

Author. Bown, herein.
Definition. FO of *Orthopithonella misurinae* to the FO of *Prinsiosphaera triassica.*
Range. Lower Carnian to Lower Norian.
Remarks. Assemblages of the Carnian and Norian-Rhaetian appear to be readily distinguishable, the former being dominated by calcispheres (*Orthopithonella misurinae, Obliquipithonella prasina*) and *incertae sedis* forms (*Carnicalyxia tabellata, Cassianospica curvata*), the latter dominated by *P. triassica,* along with rarer calcispheres, *Eoconusphaera zlambachensis* and small coccoliths.

NT2 Prinsiosphaera triassica Zone

Author. Bralower *et al.* (1991).
Definition. Total range of *Prinsiosphaera triassica.*
Range. Lower Norian to the Triassic/Jurassic boundary.
Remarks. The first appearance of *P. triassica* has yet to be confidently established, but it is common and dominant in Upper Norian and Rhaetian sediments (Bralower *et al.,* 1991), and has also been recorded from the Lower Norian (Bown, 1992a). The Carnian records of Jafar (1983) are thought to represent inorganic spheres (Janofske, 1992). A preliminary morphometric study by Bralower *et al.* (1991) shows an increase in size in *P. triassica,* from 6µm in the Lower Norian to 9µm in the Rhaetian.

NT2a Orthopithonella geometrica Subzone

Author. Bralower *et al.* (1991).
Definition. FO of *Prinsiosphaera triassica* to the FO of *Eoconusphaera zlambachensis.*
Range. Lower Norian to Upper Norian.

NT2b Eoconusphaera zlambachensis Subzone

Author. Bralower *et al.* (1991).
Definition. FO of *Eoconusphaera zlambachensis* to the LO of *Prinsiosphaera triassica.*
Range. Upper Norian to the Triassic/Jurassic boundary.

3.5 BIOGEOGRAPHY

With the exception of the Carnian calcisphere assemblages, presently only known from the Southern Alps, Triassic nannofossil assemblages are remarkably consistent and widespread but apparently restricted to low-latitude sites. The only biogeographic variation so far observed is a possible abundance gradient in *Eoconusphaera zlambachensis,* from western to eastern Tethys (becoming rarer to the east) and a complete absence in the eastern Pacific (Bown, 1992a).

Perhaps more significant is the absence of Triassic nannofossils from high-latitude sections, although this conclusion is so far supported by relatively few studies. A number of early studies of Rhaetian sections from Britain recorded *Schizosphaerella punctulata* (a Jurassic nannolith) and *Annulithus arkellii* (considered here to be inorganic in origin) (Rood *et al.,* 1973; Hamilton, 1982; Crux, 1987a). However, these sections (Penarth Group, southern Dorset, northern Somerset and South Wales) and others have been restudied by the author and yielded no recognisable nannofossils. A particularly good section, Hampstead Farm (Wiltshire), has yielded the only Rhaetian ammonite from Britain (Donovan *et al.,* 1989) and has other indications of good marine connections, however, no nannofossils were recovered (*pers obs.*). The opinion of the author is that migration of nannoplankton into high latitudes did not occur until the earliest Jurassic, although our present knowledge is severely restricted by the lack of productive sections.

Plate 3.1

All Triassic calcareous nannofossils, except *C. primulus* (illustrated in Chapter 4), are listed and illustrated here. Magnifications are given in the plate caption. The photographs come from the research of Drs Paul Bown and Dorothea Janofske.

COCCOLITHS

Family CHIASTOZYGACEAE Rood *et al.*, 1973 emend. Varol and Girgis, 1994
Figs 1–3. ***Archaeozygodiscus koessenensis*** Bown, 1985. 1, SEM distal view, Weissloferbach (S Germany), Rhaetian (marshi), UCL-2040-33, x18560. 2-3, LM XPL (2) and PC (3), Fischerwiese (Austria), Rhaetian (marshi), 5630-36/5631-2, x2300. Range: Norian – Rhaetian.

Family PARHABDOLITHACEAE Bown, 1987
Figs 4–7. ***Crucirhabdus minutus*** Jafar, 1983. SEM distal views (4, 5) and LM XPL (6) and PC (7). 4, Weissloferbach (S Germany), Rhaetian (marshi), UCL-2025-23, x14450; 5, Site 761 (Wombat Plateau, NW Australian shelf), Rhaetian, UCL-2966-20, x14090; 6-7, Fischerwiese (Austria), Rhaetian (marshi), UCL-5630-32/33, x2300. Range: Norian – Rhaetian.

NANNOLITHS

Incertae sedis
Figs 8–9. ***Prinsiosphaera triassica*** Jafar, 1983. SEM (8) and LM XPL (9). 8, Site 761 (Wombat Plateau, NW Australian shelf), Rhaetian, UCL-2968-3, x3600; 9, Weissloferbach (S Germany), Rhaetian (marshi), UCL-5630-20, x2300. Range: Norian – Rhaetian.

Family EOCONUSPHAERACEAE Krystan-Tollmann, 1988a
Figs 10–11. ***Eoconusphaera zlambachensis*** (Moshkovitz, 1982) Kristan-Tollmann, 1988a. SEM distal oblique view (10) and LM XPL (inset PC image) (11), Weissloferbach, S Germany, Rhaetian (marshi), UCL-UCL-2036-36, x7680 and UCL-5630-25, x2300. Range: Norian – Rhaetian.

Incertae sedis
Figs 12–13. ***Cassianospica curvata*** Janofske, 1992. SEM (12) and LM XPL (13), Picolbach, L. Carnian (Cordevolian), DJ-9868/DJ66-36, x3200/2000. Range: ?L. Carnian.

Figs 14–15. ***Carnicalyxia tabellata*** Janofske, 1990. SEM (14) and LM XPL (15), Picolbach, L. Carnian (Cordevolian), DJ-89997/DJ6832, x1350/1000. Range: ?L. Carnian.

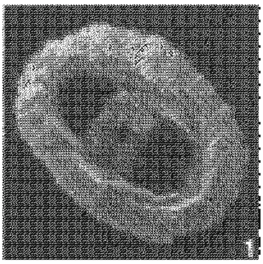
CALCAREOUS DINOFLAGELLATES

Division DINOFLAGELLATA Butschli, 1885
Class Dinophyceae Fritsch, 1929
Order Peridinales Haeckel, 1894
Family CALCIODINELLACEAE Deflandre, 1947b emend. Bujak and Davies, 1983
Figs 16–17. ***Obliquipithonella prasina*** Janofske, 1992. SEM (16) and LM XPL (17), Picolbach, L. Carnian (Cordevolian), DJ-91047/DJ89123, x1900/1500. Range: ?L. Carnian.

Figs 18–19. ***Obliquipithonella rhombica*** Janofske, 1987. SEM (18) and LM XPL (19), Rossmoosgraben, Rhaetian, DJ89389/DJ-643, x3600/2000. Range: ?Rhaetian.

Figs 20–21. ***Orthopithonella geometrica*** (Jafar, 1983) Janofske, 1987. SEM (20) and LM XPL (21). 20, Site 761 (Wombat Plateau, NW Australian shelf), Norian, UCL-2966-27, x3720; 21, Fischerwiese (Austria), Rhaetian (marshi), UCL-5630-34, x2300. Range: Norian? – Rhaetian.

Figs 22–23. ***Orthopithonella misurinae*** Janofske, 1992. SEM (22) and LM XPL (23), Misurina, L. Carnian (Cordevolian), DJ-90370/DJ-7415, x3000/x2000. Range: ?L. Carnian.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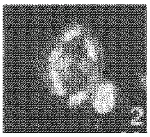
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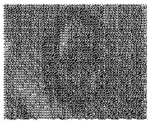

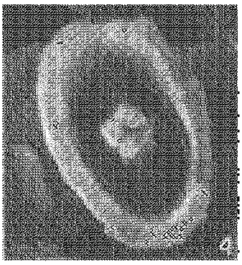
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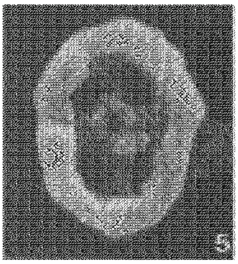
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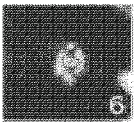
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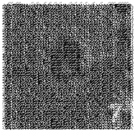
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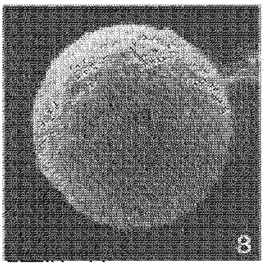
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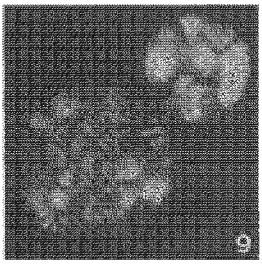
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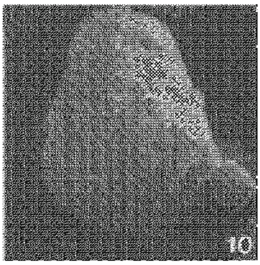
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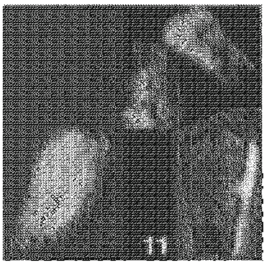
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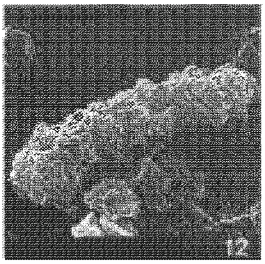
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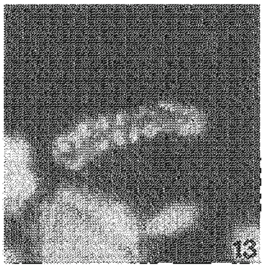
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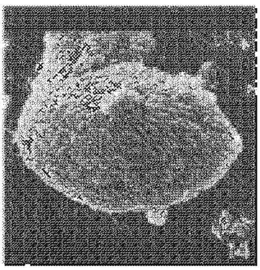
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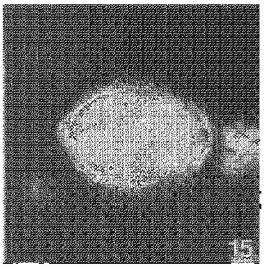
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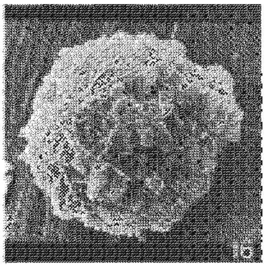
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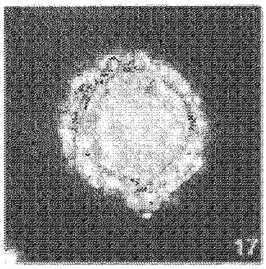
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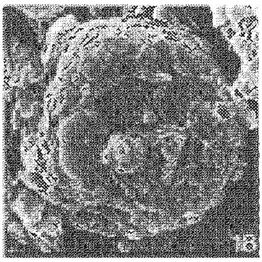
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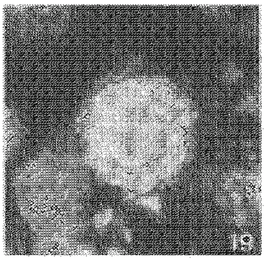
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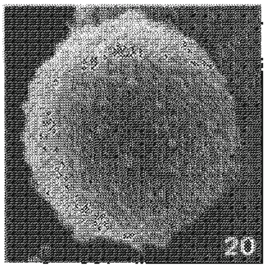
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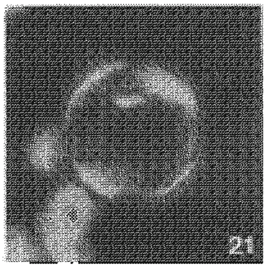
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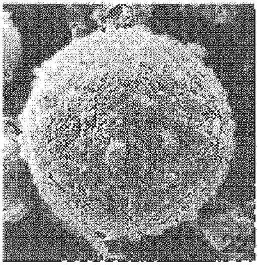

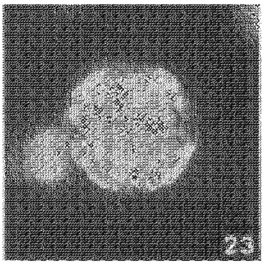
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4

Jurassic

P.R. Bown and M.K.E. Cooper

4.1 INTRODUCTION

> *For the stratigrapher the Jurassic is the very well and fountain of his subject. It was on the Jurassic rocks that William Smith, Father of Historical Geology, founded the science of stratigraphy, enunciated the law of superposition, identified fossils with particular strata, and named the classic formations. It was on Jurassic rocks that Oppel founded modern zonal stratigraphy and named the classic zones. It was for Jurassic rocks that d'Orbigny introduced the first scheme of stages. All these concepts became part of the fabric of stratigraphical geology the world over.*
>
> Arkell, 1956

The study of calcareous nannofossils has come relatively late to the Jurassic system (the first Jurassic nannofossil was described by Deflandre and Dangeard in 1938) and, as the quotation above reveals, we are following a prestigious and lengthy history of stratigraphic research. Jurassic strata (Calcaires de Jura) were first recognized by von Humboldt in 1795 in the Jura Mountains of France and Switzerland, although the term 'Jurassique' was not introduced until 1829 by Brongniart. In Britain, William Smith, working as a canal company surveyor, published lists of Jurassic stratal successions, fossil contents, and a geological map, between 1797 and 1817. The grouping of Jurassic strata into stages, and the correlation of these units using assemblages of fossils, was demonstrated by d'Orbigny in 1842, and in 1858 Oppel divided the Jurassic into 33 'biostratigraphic' zones. Since these basic principles of stratigraphy were established, there has been an immense amount of data published on Jurassic strata. This has included the development of a standard biochronologic scale based upon ammonites, which provide a finer biostratigraphic resolution than any other fossil group. It is against this background that the study of Jurassic calcareous nannofossils is proceeding. While we have not yet achieved (and may never do so) the biostratigraphic resolution that ammonites can provide (albeit after 150 years of work!) the last two decades have seen the introduction of successively improved nannofossil biozonations.

This chapter aims to summarize work carried out in the NW European area and the biozonation scheme that has resulted from it, together with comments on the wider application of this zonation scheme and the nature of Jurassic nannofossil provincialism.

4.2 IMPORTANT REFERENCES

The first taxonomic descriptions of Jurassic nannofossils were published by Deflandre (1938, 1939, 1952, 1954) and Noël (1956, 1958, 1965, 1973). More recent contributions include Prins (1969), Rood *et al.* (1971, 1973), Grün *et al.* (1974), Medd (1979), Grün and Zweili (1980), Goy (1981), Bown (1987), Bralower *et al.* (1989), de Kaenel and Bergen (1993) and Bergen (in press).

The utility of Jurassic nannofossils in biostratigraphy was first demonstrated by Stradner (1963), followed by a succession of new or revised biozonation schemes including Prins (1969), Amezieux (1972), Barnard and Hay (1974), van Hinte (1976a), Thierstein (1976), Hamilton (1977, 1979, 1982), Medd (1982), Roth *et al.* (1983), Haq (1983a), Crux (1984, 1987a), Bown (1987), Lord *et al.* (1987), Bown *et al.* (1988) and Bralower *et al.* (1989). Comprehensive reviews of the current biostratigraphic literature are presented in Bown (1996) and de Kaenel *et al.* (1996).

Most early biostratigraphic work was based on sections from northern Europe, and first Barnard and Hay (1974) and then Bown *et al.* (1988) presented zonation schemes which were established as 'standards' for the Jurassic. In the last two decades, the focus has shifted from northern Europe to Jurassic studies elsewhere, with particular impetus being provided by a number of DSDP sites in the Atlantic Ocean and new onshore studies in Italy (e.g. Baldanza and Mattioli, 1992; Cobianchi, 1992; Reale *et al.*, 1992), Portugal (Bergen, in press), North Africa (de Kaenel, in press), Timor (Bown, 1987, 1992a; Kristan-Tollmann, 1988a, b) and western Canada (Bown, 1992a). The Atlantic Ocean DSDP sites have provided valuable material for the Bathonian to Tithonian time-interval and have prompted new zonation schemes (Roth *et al.*, 1983; Bralower *et al.*, 1989) reflecting the recognition of increased provincialism through this interval.

4.3 JURASSIC NANNOFOSSIL SUCCESSION

The Jurassic period was extremely significant in the early evolutionary history of calcareous nannofossils. Nannofossils first appeared in the Late Triassic and were initially restricted to low latitudes (Bown, 1992a). Triassic nannofloras consisted of nannolith (*incertae sedis*) forms, together with rarer and very small (~2µm) coccoliths. A significant extinction event at the Triassic/Jurassic boundary was followed by the expansion of nannoplankton into all open-marine environments and the establishment of coccolithophores as the dominant nannofossil group. Coccolithophores diversified rapidly in the Early Jurassic (Hettangian–Early Toarcian) and latest Jurassic (Tithonian) by which time nannoplankton were producing biogenic carbonate in rock-forming proportions (Bown *et al.*, 1992).

Earliest Jurassic (Hettangian) nannofloras were dominated by the nannolith, *Schizosphaerella punctulata*, along with rare coccoliths of *Crucirhabdus primulus*, the only coccolith species known to have survived the earlier extinction event. In the late Hettangian and Sinemurian, simple, murolith coccoliths (e.g. *Parhabdolithus* and *Crepidolithus*) diversified but were soon joined by coccoliths with radically new morphologies (placoliths) which evolved rapidly and began to dominate numerically. In the Early Pliensbachian, the placolith genus, *Similiscutum* (early forms, formerly included within *Biscutum*), appeared and diversified rapidly through the remaining Early Jurassic, giving rise to *Biscutum*, *Sollasites*, *Calyculus*, *Carinolithus* and *Discorhabdus*. The Sinemurian appearance of another placolith group, represented by the genus *Mazaganella*, is not recorded in NW Europe. Representatives of the Mazaganellaceae did not occur here until the appearance of *Triscutum* in the latest Toarcian. In the Late Pliensbachian, a third placolith family, the Watznaueriaceae (represented by the genus *Lotharingius*), appeared and almost immediately began to numerically dominate assemblages.

A nannofloral turnover event occurred through the Pliensbachian/Toarcian boundary-interval, as placolith coccoliths diversified, seemingly at the expense of the earlier murolith species. Thus, *Biscutum* and *Lotharingius* became important assemblage components, whilst *Parhabdolithus*, *Crucirhabdus* and *Mitrolithus* became extinct.

The Late Toarcian was a period of relative stasis, although the family Cretarhabdaceae and genus *Triscutum* first appeared at the Toarcian/Aalenian boundary. By the end of the Toarcian, nine coccolith families were established, forming lineages which gave rise to the majority of remaining Middle and Late Jurassic taxa (Fig. 1.5).

The Aalenian to Early Bajocian saw the evolutionary transition from *Lotharingius* to *Watznaueria*. These two genera dominated nannofloras through the Bajocian and Bathonian. By Callovian times, *Watznaueria* had become the dominant genus. This trend continued through the Late Jurassic and into the Cretaceous. The Middle Jurassic was also characterized by diversification of the families Stephanolithiaceae and Axopodorhabdaceae. The former family includes the distinctive genus, *Stephanolithion*, which is utilized extensively for biostratigraphy through the Middle and Late Jurassic.

The Callovian and Early Oxfordian were intervals of high diversity, including many delicate species of Stephanolithiaceae. The remaining Jurassic saw a progressive reduction of diversity in the boreal area, with extinctions outnumbering inceptions through the Oxfordian, Kimmeridgian and Volgian. Throughout this time, however, nannofossil abundance remained high, with *Watznaueria* (particularly *W. britannica*) constituting the principal component of all assemblages.

This evolutionary succession is essentially observed worldwide for the Hettangian to Kimmeridgian interval, however, in the Volgian (= Tithonian), a diversification event occurred which was initially restricted to western Tethys and the proto-Atlantic Ocean. Diversity increased significantly in the tethyan area and introduced new nannolith groups, such as *Conusphaera* and *Nannoconus*. A number of boreal endemic species, e.g. *Stephanolithion atmetos*, also appeared at this time. This interval saw the maximum degree of Jurassic biogeographic differentiation, and also coincided with the first occurrence of significant thicknesses of nannofossil-generated, pelagic carbonates, as represented by, e.g., the Maiolica Formation in Italy.

This pattern of distributions continued into the Early Cretaceous, although many of the new tethyan forms became more widely distributed. Provincialism, however, remained significant through much of the Neocomian.

4.4 BIOSTRATIGRAPHY

The Bown *et al.* (1988) biozonation scheme was an attempt to stabilize biostratigraphic nomenclature for the Jurassic, utilizing many of the well-established nannofossil bioevents which had been successfully introduced in previous zonations, e.g. Prins (1969), Barnard and Hay (1974), Thierstein (1976), Medd (1982) and Crux (1984). The Bown *et al.* (1988) scheme has been used as the basis for comparison and correlation in this chapter. The biostratigraphic framework and regional biostratigraphic zonations and events are presented in Figs 4.1–4.2 with zonal markers directly correlated with the standard boreal ammonite zonation, where possible. The stratigraphic distribution of selected Jurassic nannofossil taxa is shown in Fig. 4.3. Marker-species and principle assemblage components are illustrated in Plates 4.1–4.16.

A number of the Upper Jurassic boreal zones have been modified here following a detailed study of the Kimmeridgian–Upper Volgian section at Gorodische (Russia): the Gorodische data is provided in the Appendix (section 4.9).

NJ1 Schizosphaerella punctulata Zone

Author. Bown (1987).

Definition. FO of *Schizosphaerella punctulata* to the FO of *Parhabdolithus liasicus distinctus*.

Range. Triassic/Jurassic boundary to upper Hettangian (angulata AZ).

Remarks. Assemblages are generally low in abundance although 'floods' of *S. punctulata* have been recorded. Generally, only two species are recorded, *S. punctulata* and *Crucirhabdus primulus*. The record of Triassic nannofossils in NW Europe is at present limited to reports of *S. punctulata* from the Rhaetian of southern England (Hamilton, 1982; Crux, 1987a) which has not been confirmed by our research (PRB, pers obs.). In sections from the Austrian Alps, where Triassic nannofossils are well-represented, *S. punctulata* is not present in the Rhaetian and does not occur until the Hettangian. *Prinsiosphaera triassica* and *Eoconusphaera zlambachensis*, which characterize the Upper Triassic, both became extinct at the Triassic/Jurassic boundary, also approximating the base of this zone (Bown and Lord, 1990; Bralower *et al.*, 1991).

NJ2 Parhabdolithus liasicus Zone

Author. Bown (1987).

Definition. FO of *Parhabdolithus liasicus distinctus* to the FO of *Crepidolithus crassus*.

Range. Upper Hettangian (angulata AZ) to Upper Sinemurian (oxynotum AZ).

Remarks. Characterized by increased abundance and diversity in murolith coccoliths, and continued abundance of *S. punctulata*.

NJ2a Parhabdolithus marthae Subzone

Author. Prins (1969).

Definition. FO of *Parhabdolithus liasicus distinctus* to the LO of *Parhabdolithus marthae*.

Range. Upper Hettangian (angulata AZ) to Lower Sinemurian (semicostatum AZ).

Remarks. *Parhabdolithus* coccoliths are abundant and display a plexus of variable morphologies. The genera *Mitrolithus* and *Crepidolithus* have FOs within the subzone. *S. punctulata* and *C. primulus* are both common.

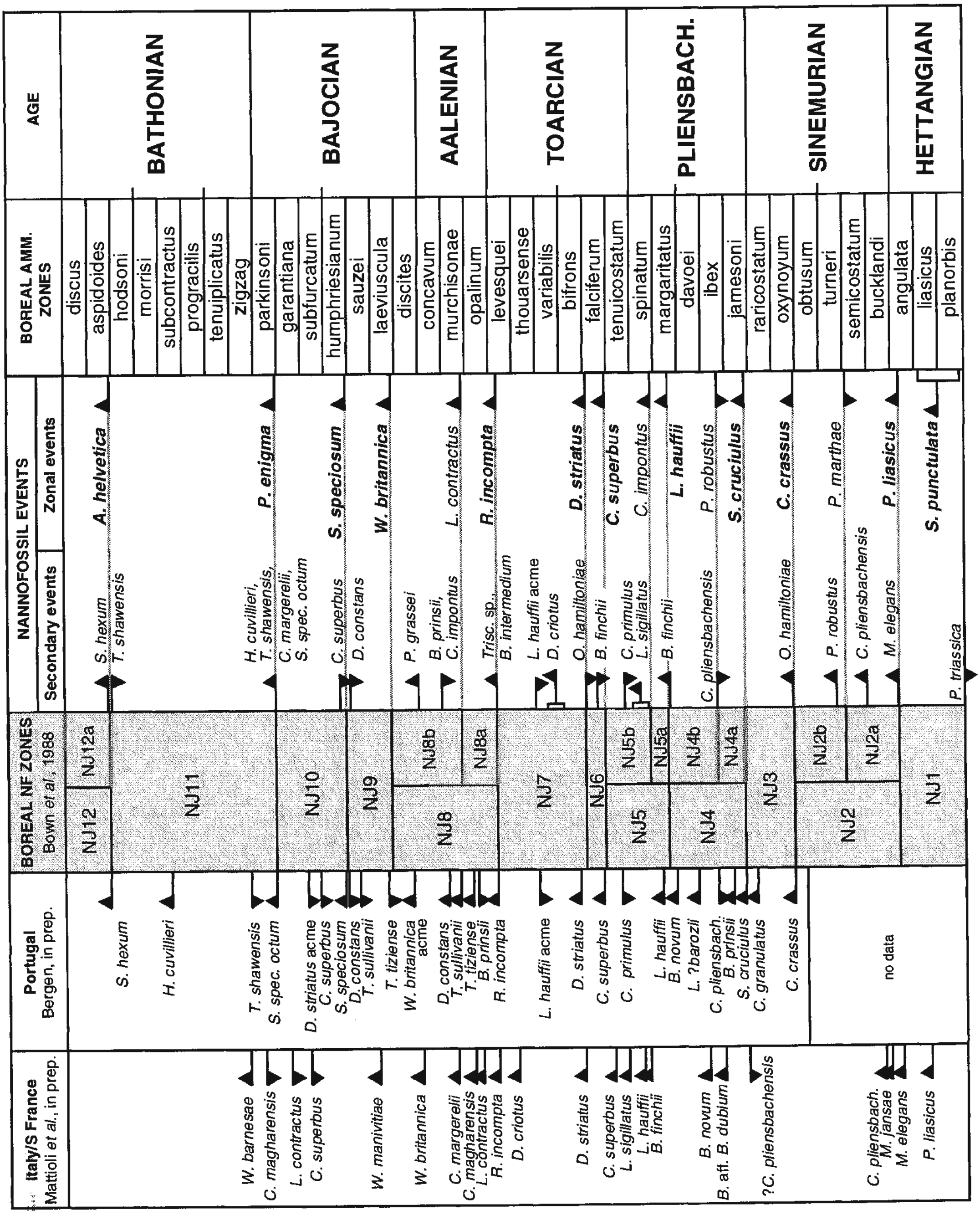


Fig. 4.1 Hettangian to Bathonian biostratigraphic zones and events.

NJ2b Mitrolithus elegans Subzone
Author. Bown (1987).
Definition. LO of *Parhabdolithus marthae* to the FO of *Crepidolithus crassus*.
Range. Lower Sinemurian (semicostatum AZ) to Upper Sinemurian (oxynotum AZ).

NJ3 Crepidolithus crassus Zone
Author. Bown (1987).
Definition. FO of *Crepidolithus crassus* to the FO of *Similiscutum cruciulus*.
Range. Upper Sinemurian (oxynotum AZ) to Lower Pliensbachian (jamesoni AZ).
Remarks. The FO of *C. crassus* has been variably recorded in the literature (e.g. Crux, 1987a), reflecting the presence of intermediate forms between *C. crassus* and its ancestor, which is probably *Crepidolithus pliensbachensis* or *Crepidolithus timorensis*. The assemblages are composed of murolith coccoliths, together with the nannoliths *S. punctulata* and *Orthogonoides hamiltoniae*.

NJ4 Similiscutum cruciulus Zone
Author. Bown (1987), emended herein.
Definition. FO of *Similiscutum cruciulus* to the FO of *Lotharingius hauffii*.
Range. Lower Pliensbachian (jamesoni AZ) to Upper Pliensbachian (margaritatus AZ).
Remarks. The FO of the Biscutaceae is a notable and distinctive bioevent. These placolith-coccoliths are very different in appearance to the murolith coccoliths which characterize the lower Lower Jurassic assemblages. The naming of the first radiating placolith-coccolith has varied from author to author, e.g. *Palaeopontosphaera veterna* in Prins (1969), *Biscutum dubium* in Crux (1987a), *Biscutum novum* in Bown (1987) and, most recently, *Similiscutum cruciulus* (de Kaenel and Bergen, 1993), but the stratigraphic level has been consistently recorded as Lower Pliensbachian. The distinctive nature of these first Biscutaceae warrants taxonomic separation and therefore the zone name has been modified according to the new taxonomy of de Kaenel and Bergen (1993). The species *S. cruciulus* is applied here in a slightly broader sense than that of de Kaenel and Bergen (1993), to include all sub-circular to elliptical forms with variable central-area widths which may or may not reveal a central-area axial cross; this probably includes the species *S. praecarium*, *S. avitum* and *S. orbiculus*, as defined by de Kaenel and Bergen (1993).

Sollasites and *Calyculus* also have their FOs in the NJ4 Zone (Crux, 1987a; Bown *et al.*, 1988) but they are rare and sporadic.

NJ4a Crepidolithus pliensbachensis Subzone
Author. Bown (1987).
Definition. FO of *Similiscutum cruciulus* to the LO of *Parhabdolithus robustus*.
Range. Lower Pliensbachian (jamesoni to ibex AZs).

NJ4b Crepidolithus granulatus Subzone
Author. Bown (1987).
Definition. LO of *Parhabdolithus robustus* to the FO of *Lotharingius hauffii*.
Range. Lower Pliensbachian (ibex AZ) to Upper Pliensbachian (margaritatus AZ).
Remarks. The LO of *C. pliensbachensis* also approximates the base of NJ4b.

NJ5 Lotharingius hauffii Zone
Author. Bown (1987).
Definition. FO of *Lotharingius hauffii* to the FO of *Carinolithus superbus*.
Range. Upper Pliensbachian (margaritatus AZ) to Lower Toarcian (falciferum AZ).
Remarks. The NJ5 Zone sees an important nannofloral turnover, with many murolith-coccoliths becoming extinct and new placolith groups diversifying and becoming more abundant. The *Lotharingius* group, particularly, begins to dominate the assemblages numerically. The zone is also characterized by the near-total range of *Biscutum finchii*.

NJ5a Biscutum finchii Subzone
Author. Bown (1987).
Definition. FO of *Lotharingius hauffii* to the FO of *Crepidolithus impontus*.
Range. Upper Pliensbachian (margaritatus to spinatum AZs).
Remarks. The FO of *B. finchii* also approximates the base of this zone.

NJ5b Crepidolithus impontus Subzone
Author. Bown (1987), emended herein.
Definition. FO of *Crepidolithus impontus* to the FO of *Carinolithus superbus*.
Range. Upper Pliensbachian (spinatum AZ) to

Lower Toarcian (falciferum AZ).
Remarks. The nominate taxon (previously called *Crepidolithus cavus*) is given an alternative name, *C. impontus*, to avoid the confusion which has arisen over the identification of earlier *Crepidolithus* coccoliths which have a central-area bar. *C. impontus* has a wide central-area spanned by a delicate, narrow bar, and is quite distinct from *C. cavus* which was described by Rood *et al.* (1973) from the Lower Pliensbachian.

Many new species have FOs, or first occur consistently, in this subzone, e.g. *Axopodorhabdus atavus, Biscutum grande, Bussonius prinsii, Calyculus* spp., *Sollasites arctus* and *Zeugrhabdotus erectus*.

The LOs of murolith taxa, such as *P. liasicus, C. primulus* and *M. elegans*, have been variably reported in the literature. This may be due to increasing rarity in the highest parts of their ranges.

The evolutionary transition from *Calyculus* to *Carinolithus* is observed through this subzone.

NJ6 Carinolithus superbus Zone

Author. Bown (1987).
Definition. FO of *Carinolithus superbus* to the FO of *Discorhabdus striatus*.
Range. Lower Toarcian (falciferum AZ).
Remarks. The LOs of *B. finchii, B. grande* and *O. hamiltoniae* are recorded in this zone.

NJ7 Discorhabdus striatus Zone

Author. Bown (1987).
Definition. FO of *Discorhabdus striatus* to the FO of *Retecapsa incompta*.
Range. Lower Toarcian (falciferum AZ) to Upper Toarcian (levesquei AZ).
Remarks. Few FOs and LOs are observed through this interval. The FO of *Discorhabdus criotus* may prove to be useful in dividing the zone. Assemblages are dominated by *Lotharingius*.

NJ8 Biscutum intermedium Zone

Author. (Bown, 1987) Bown *et al.* (1988).
Definition. FO of *Retecapsa incompta* to the FO of *Watznaueria britannica*.
Range. Upper Toarcian (levesquei AZ) to Lower Bajocian (laeviuscula AZ).
Remarks. The FOs of *Biscutum intermedium* and *Triscutum* sp. also approximate the base of the zone. NJ8 includes the evolutionary transition from *Lotharingius* to *Watznaueria* and many intermediate morphologies occur. All younger Jurassic zones are characterized by assemblages dominated by species of *Watznaueria*, particularly *W. britannica*.

NJ8a Retecapsa incompta Subzone

Author. Bown *et al.* (1988).
Definition. FO of *Retecapsa incompta* to the FO of *Lotharingius contractus*.
Range. Upper Toarcian (levesquei AZ) to Aalenian (murchisonae AZ).

NJ8b Lotharingius contractus Subzone

Author. Bown *et al.* (1988).
Definition. FO of *Lotharingius contractus* to the FO of *Watznaueria britannica*.
Range. Aalenian (murchisonae AZ) to Lower Bajocian (laeviuscula AZ).
Remarks. The evolutionary plexus which occurs at the *Lotharingius–Watznaueria* transition, may hinder the correct identification of the nominate species but the base of this subzone is also approximated by the LOs of *B. prinsii* and *C. impontus*.

NJ9 Watznaueria britannica Zone

Author. Bown *et al.* (1988).
Definition. FO of *Watznaueria britannica* to the FO of *Stephanolithion speciosum*.
Range. Lower Bajocian (laeviuscula to humphriesianum AZs).
Remarks. The abundant co-occurrence of *L. contractus* and *W. britannica* is characteristic of this zone. The application of the FO of *W. britannica* has proven somewhat problematical as it has been recorded earlier by other authors, and in southern Europe. However, at present, we believe this is a taxonomic problem related to the *Lotharingius–Watznaueria* plexus, which may be alleviated by the application of more restricted taxonomic concepts.

NJ10 Stephanolithion speciosum Zone

Author. Bown *et al.* (1988).
Definition. FO of *Stephanolithion speciosum* to the FO of *Pseudoconus enigma*.
Range. Lower Bajocian (humphriesianum AZ) to Upper Bajocian (parkinsoni AZ).

NJ11 Pseudoconus enigma Zone

Author. Bown *et al.* (1988).
Definition. FO of *Pseudoconus enigma* to the

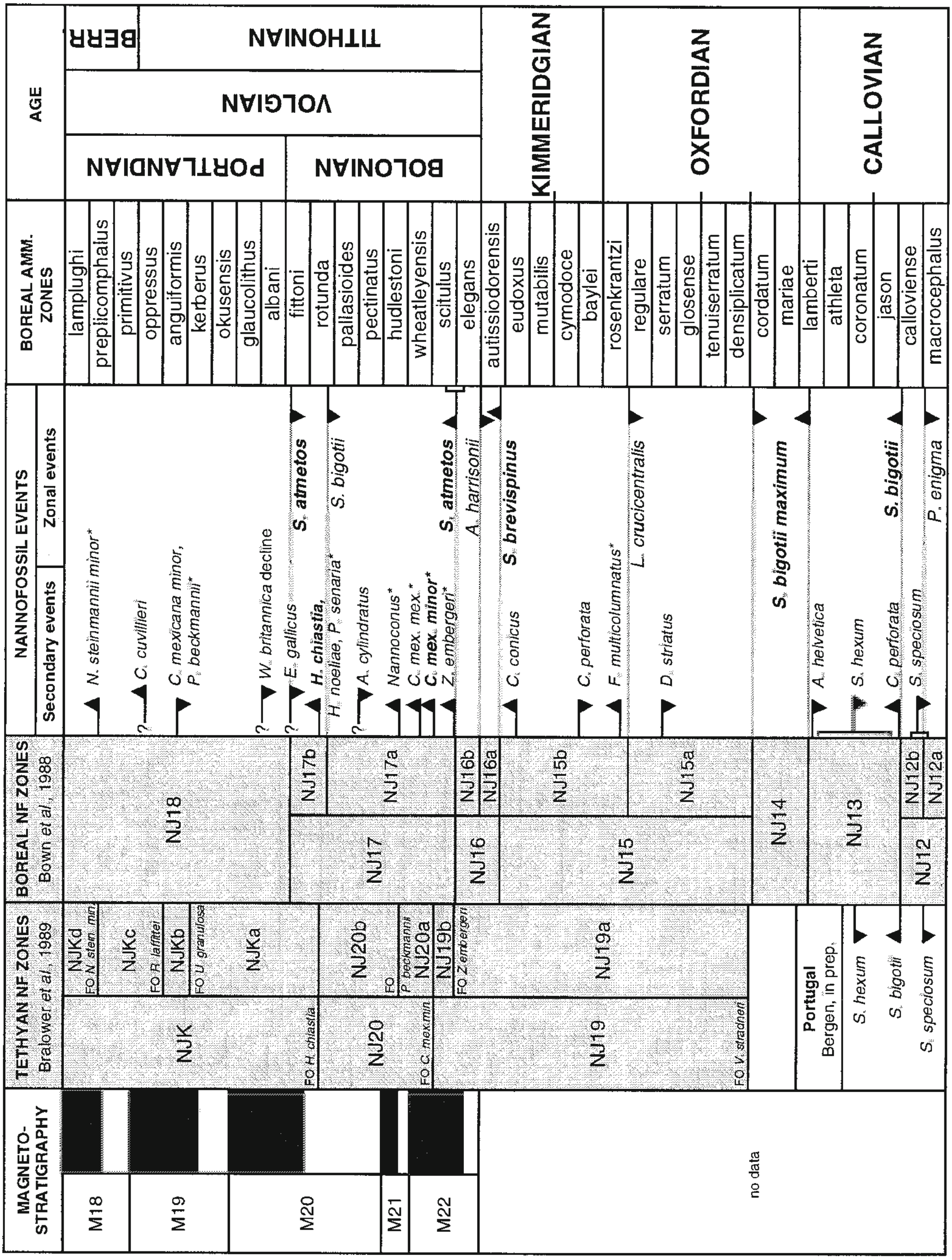


Fig. 4.2 Callovian to Volgian/Tithonian biostratigraphic zones and events (those with an asterix have only been reported from the tethyan area).

FO of *Ansulasphaera helvetica.*
Range. Upper Bajocian (parkinsoni AZ) to Upper Bathonian (aspidoides AZ).
Remarks. The base is also marked by the FOs of *Cyclagelosphaera tubulata, Hexapodorhabdus cuvillieri, Tetrapodorhabdus shawensis* and *Staurolithites stradneri* (small variety). *T. shawensis* has a total range within NJ11. The small, distinctive holococcolith, *Anfractus harrisonii,* has its first consistent occurrence towards the base of the zone; it is virtually never found below this level, except where preservation is exceptional (Bown, 1993).

NJ12 Ansulasphaera helvetica Zone

Author. Bown *et al.* (1988).
Definition. FO of *Ansulasphaera helvetica* to the FO of *Stephanolithion bigotii bigotii.*
Range. Upper Bathonian (aspidoides AZ) to Callovian (calloviense AZ).
Remarks. The base of this zone is also approximated by the FO of *Stephanolithion hexum.*

NJ12a Stephanolithion hexum Subzone

Author. Bown *et al.* (1988).
Definition. FO of *Ansulasphaera helvetica* to the LO of *Pseudoconus enigma.*
Range. Upper Bathonian (aspidoides AZ) to the Callovian (macrocephalus AZ).

NJ12b Watznaueria manivitiae Subzone

Author. Bown *et al.* (1988).
Definition. LO of *Pseudoconus enigma* to the FO of *Stephanolithion bigotii bigotii.*
Range. Callovian (macrocephalus to calloviense AZs).

NJ13 Stephanolithion bigotii bigotii Zone

Author. Stradner (1963).
Definition. FO of *Stephanolithion bigotii bigotii* to the FO of *Stephanolithion bigotii maximum.*
Range. Callovian (calloviense to lamberti AZ).
Remarks. The base of this zone is also approximated by the FO of *Crepidolithus perforata.*

NJ14 Stephanolithion bigotii maximum Zone

Author. Medd (1982).
Definition. Total range of *Stephanolithion bigotii maximum.*
Range. Callovian (lamberti AZ) to Lower Oxfordian (cordatum AZ).
Remarks. Reworked Lower and Middle Jurassic nannofossils are common in sections from England and France. The highest diversities of Jurassic nannofossils from northern Europe are recorded from this interval.

NJ15 Cyclagelosphaera margerelii Zone

Author. Bown *et al.* (1988).
Definition. LO of *Stephanolithion bigotii maximum* to the FO of *Stephanolithion brevispinus* (= *helotatus* of Cooper, 1987).
Range. Lower Oxfordian (cordatum AZ) to Upper Kimmeridgian (autissiodorensis AZ).
Remarks. NJ15 is a long zone, reflecting a period of evolutionary stasis. This, and all younger, boreal Jurassic zones record steadily declining nannofloral diversity as extinctions outweigh inceptions. Assemblages are typically dominated by *W. britannica* and also include *Axopodorhabdus cylindratus, B. dubium, C. margerelii, Ethmorhabdus gallicus, Polypodorhabdus escaigii, S. bigotii bigotii, S. stradneri* and *Z. erectus.*

NJ15a Lotharingius crucicentralis Subzone

Author. Bown *et al.* (1988).
Definition. LO of *Stephanolithion bigotii maximum* to the LO of *Lotharingius crucicentralis.*
Range. Lower Oxfordian (cordatum AZ) to Upper Oxfordian (regulare AZ).
Remarks. The LO of *L. crucicentralis* has been recorded at this level in a number of sections but it is rare towards the top of its range. This datum has been reported from the Middle Oxfordian in SE France and Portugal (de Kaenel *et al.,* 1996). Other, potentially-useful LOs include *C. perforata* (baylei AZ - NJ15b) and *D. striatus* (glosense AZ).

NJ15b Hexapodorhabdus cuvillieri Subzone

Author. Bown *et al.* (1988).
Definition. LO of *Lotharingius crucicentralis* to the FO of *Stephanolithion brevispinus.*
Range. Upper Oxfordian (regulare AZ) to Upper Kimmeridgian (autissiodorensis AZ).
Range. The FO of *Faviconus multicolumnatus* has been reported from the Upper Oxfordian in de Kaenel *et al.* (1996).

NJ16 Stephanolithion brevispinus Zone

Author. Bown *et al.* (1988), emended herein.
Definition. FO of *Stephanolithion brevispinus* to the FO of *Stephanolithion atmetos*.
Range. Upper Kimmeridgian (autissiodorensis AZ) to Lower Volgian (klimovi AZ, equivalent to ?elegans/scitulus AZs in England).
Reference section. Gorodische, Russia; Beds 3 through 6.
Remarks. The name of this zone has been changed in order to satisfy taxonomic criteria, which are discussed in the Appendix (section 4.9). The concept of the zone as defined in Bown *et al.* (1988) remains the same. The range of the zone is somewhat reduced due to the extended lower range of *S. atmetos*, reported herein, which defines the base of the overlying zone. The zone is divided into two subzones based on the LO of *Anfractus harrisonii*.

NJ16a Anfractus harrisonii Subzone

Author. Defined herein.
Definition. FO of *Stephanolithion brevispinus* to the LO of *Anfractus harrisonii*.
Range. Upper Kimmeridgian (autissiodorensis AZ).
Reference section. Gorodische, Russia; Beds 3 and 4.
Remarks. See Appendix (section 4.9).

NJ16b Zeugrhabdotus erectus Subzone

Author. Defined herein.
Definition. LO of *Anfractus harrisonii* to the FO of *Stephanolithion atmetos*.
Range. Lower Volgian (klimovi AZ).
Reference section. Gorodische, Russia; Beds 5 and 6.

NJ17 Stephanolithion atmetos Zone

Author. Bown *et al.* (1988), emended herein.
Definition. Total range of *Stephanolithion atmetos*.
Range. Lower Volgian (upper klimovi AZ) to Middle Volgian (upper panderi AZ).
Reference section. Gorodische, Russia; Beds 6 through 11.
Remarks. The modified range of this zone reflects new observations of the range of the nominate taxon, and the zonal definition is emended to include the total range of *S. atmetos*. The zone is divided into two subzones using the LO of *Stephanolithion bigotii*. The upper limit of the zone is constrained by the LO of *S. atmetos* but the exact level of this datum is uncertain due to the scarcity of nannofossil-bearing boreal sediments at this level. However, the species has not been recorded above the panderi AZ (zarasjkensis AsZ), and the base of the overlying zone is thus tentatively placed at this level. The base of NJ17 is also approximated by the LO of *Staurolithites lumina*. The zone is characterized by the successive LOs of S. *lumina*, *S. brevispinus*, *A. cylindratus* and *S. bigotii*. The top of the zone may also be marked by the LO of *E. gallicus*.

NJ17a Axopodorhabdus cylindratus Subzone

Author. Defined herein.
Definition. FO of *Stephanolithion atmetos* to the LO of *Stephanolithion bigotii bigotii*.
Range. Lower Volgian (upper klimovi AZ) to Middle Volgian (lowermost zarasjkensis AsZ).
Reference section. Gorodische, Russia; Beds 6 through 10.
Remarks. The reliability of this subzonal boundary is uncertain due to the rarity of *S. bigotii bigotii* towards the top of its range.

NJ17b Ethmorhabdus gallicus Subzone

Author. Defined herein.
Definition. LO of *Stephanolithion bigotii bigotii* to the LO of *Stephanolithion atmetos*.
Range. Middle Volgian (zarasjkensis AsZ).
Reference section. Gorodische, Russia; Beds 10 and 11.

NJ18 Watznaueria fossacincta Zone

Author. Defined herein.
Definition. LO of *Stephanolithion atmetos* to ?
Range. Middle Volgian (?virgatus AZ) to ~Jurassic/Cretaceous boundary.
Remarks. The present scarcity of boreal Upper Volgian material has so far precluded the definition of well-defined nannofossil biozones for this interval, and the Gorodische observations do not provide sufficient data to apply nannofossil datums with any confidence. However, it is almost certain that *S. atmetos* and *E. gallicus* disappear before the virgatus/nikitini AZs, and that relatively depauperate, *Watznaueria*-dominated assemblages are characteristic of the Upper Volgian. It is presumed that new 'typically Cretaceous' taxa must

have reached the boreal area during this interval, as many new species are recorded in the lowest boreal (Upper) Ryazanian samples from Speeton and the North Sea. However, the data from Gorodische does not provide a suitable index-species candidate, although the questionable FO of *Rhagodiscus asper* is recorded in the nodiger AZ of the Kashpir section and may prove to be useful if found at this level elsewhere. Other bioevents which are recognised worldwide and occur close to the Jurassic/Cretaceous boundary include FO *C. cuvillieri,* FO *Rotelapillus laffitei,* FO *Micrantholithus* and FO *Lithraphidites carniolensis.*

Upper Jurassic Tethyan Nannofossil Zones (after Bralower *et al.*, 1989)

The following zones are stratigraphically equivalent to the preceding NJ16 to NJ18 zones, but are required and desirable due to the restricted geographic distributions of many Upper Jurassic taxa and the enhanced biostratigraphic resolution provided by exclusively tethyan taxa. The letter 'T' is placed in brackets after the zonal number in order to distinguish the zones from their boreal counterparts.

NJ19(T) Staurolithites stradneri Zone

Author. (Barnard and Hay, 1974) Bralower *et al.* (1989).
Definition. FO of *Staurolithites stradneri* to the FO of *Conusphaera mexicana minor.*
Range. Upper Oxfordian to Lower Tithonian (CM22n).
Remarks. Rigorous species concepts are difficult to apply within the *Staurolithites* group, and this factor may compromise the biostratigraphic integrity of this zone; in any case Bralower *et al.* (1989) believe the zone cannot be recognized in southern Europe.

NJ19a(T) Unnamed Subzone

Author. Bralower *et al.* (1989).
Definition. FO of *Staurolithites stradneri* to the FO of *Zeugrhabdotus embergeri*.
Range. Upper Oxfordian to Upper Kimmeridgian.

NJ19b(T) Zeugrhabdotus embergeri Subzone

Author. (Worsley, 1971) Bralower *et al.* (1989).
Definition. FO of *Zeugrhabdotus embergeri* to the FO of *Conusphaera mexicana minor.*
Range. Kimmeridgian/Tithonian boundary interval (within CM22n).
Remarks. The problems associated with the taxonomic definition and identification of *Z. embergeri* are well known (e.g. Roth, 1983; Bralower *et al.*, 1989), and rigorous taxonomic concepts must be strictly applied. The time of entry of this species into the boreal area is also uncertain, and is discussed further in the Appendix (section 4.9).

NJ20(T) Conusphaera mexicana Zone

Author. (Thierstein, 1975) Bralower *et al.* (1989).
Definition. FO of *Conusphaera mexicana minor* to the FO of *Helenea chiastia.*
Range. Lower to middle Tithonian (CM22n-CM20).
Remarks. The appearance of *C. mexicana minor*, followed by *C. mexicana mexicana* and the earliest nannoconids (*Nannoconus compressus*), provide a distinctive series of bioevents through this zone. The decline in *W. britannica* abundance occurs in this zone at DSDP Site 534 (North Atlantic Ocean) (pers. obs.). Although this event is well known, it is poorly constrained stratigraphically. *W. britannica* remains abundant in boreal sections into the uppermost Bolonian at least (i.e. Upper Tithonian).

NJ20a(T) Hexapodorhabdus cuvillieri Subzone

Author. (Roth *et al.*,1983) Bralower *et al.* (1989).
Definition. FO of *Conusphaera mexicana minor* to the FO of *Polycostella beckmannii.*
Range. Lower Tithonian (CM22n–CM21n).

NJ20b(T) Polycostella beckmannii Subzone

Author. (Roth *et al.*, 1983) Bralower *et al.* (1989).
Definition. FO of *Polycostella beckmannii* to the FO of *Helenea chiastia.*
Range. Middle Tithonian (CM21n–CM20).

NJK Helenea chiastia Zone

Author. Bralower *et al.* (1989).
Definition. FO of *Helenea chiastia* to the FO *Nannoconus steinmannii steinmannii.*

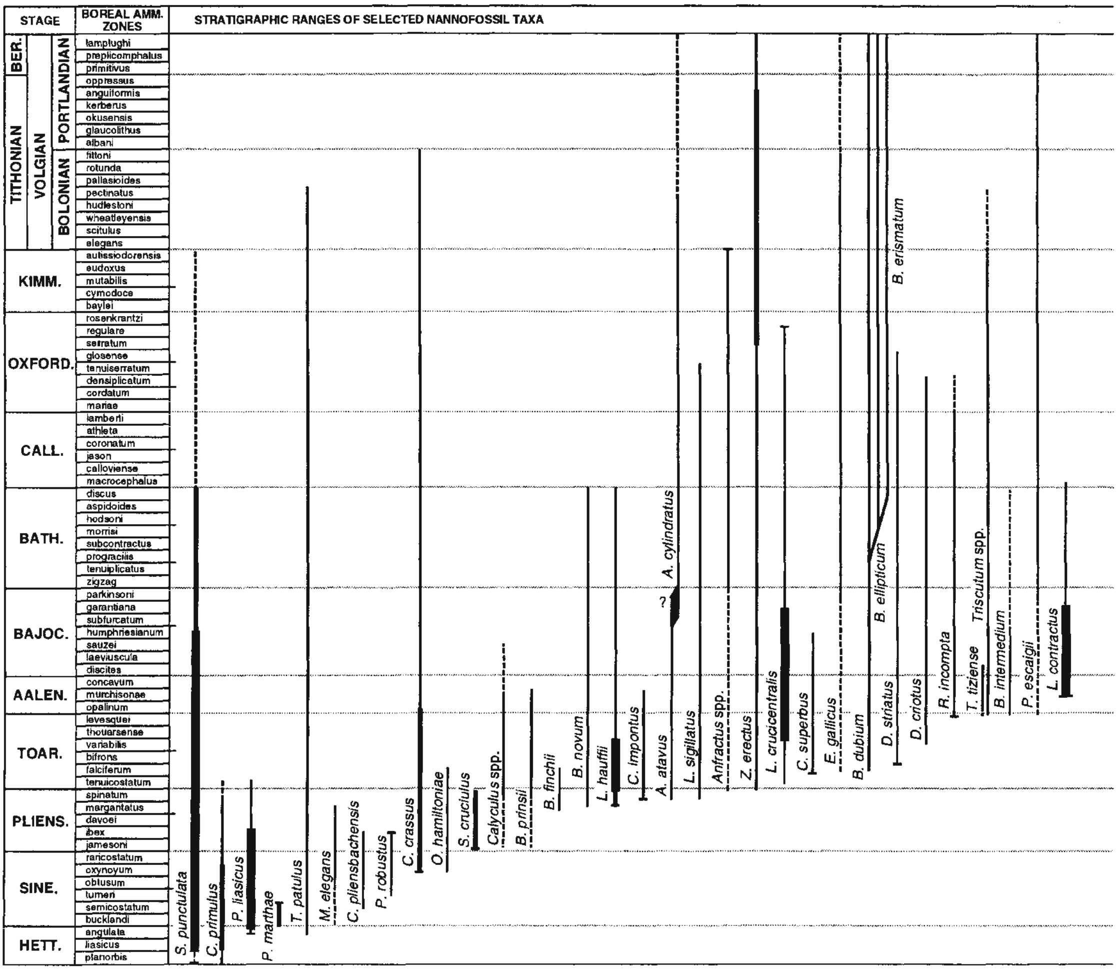
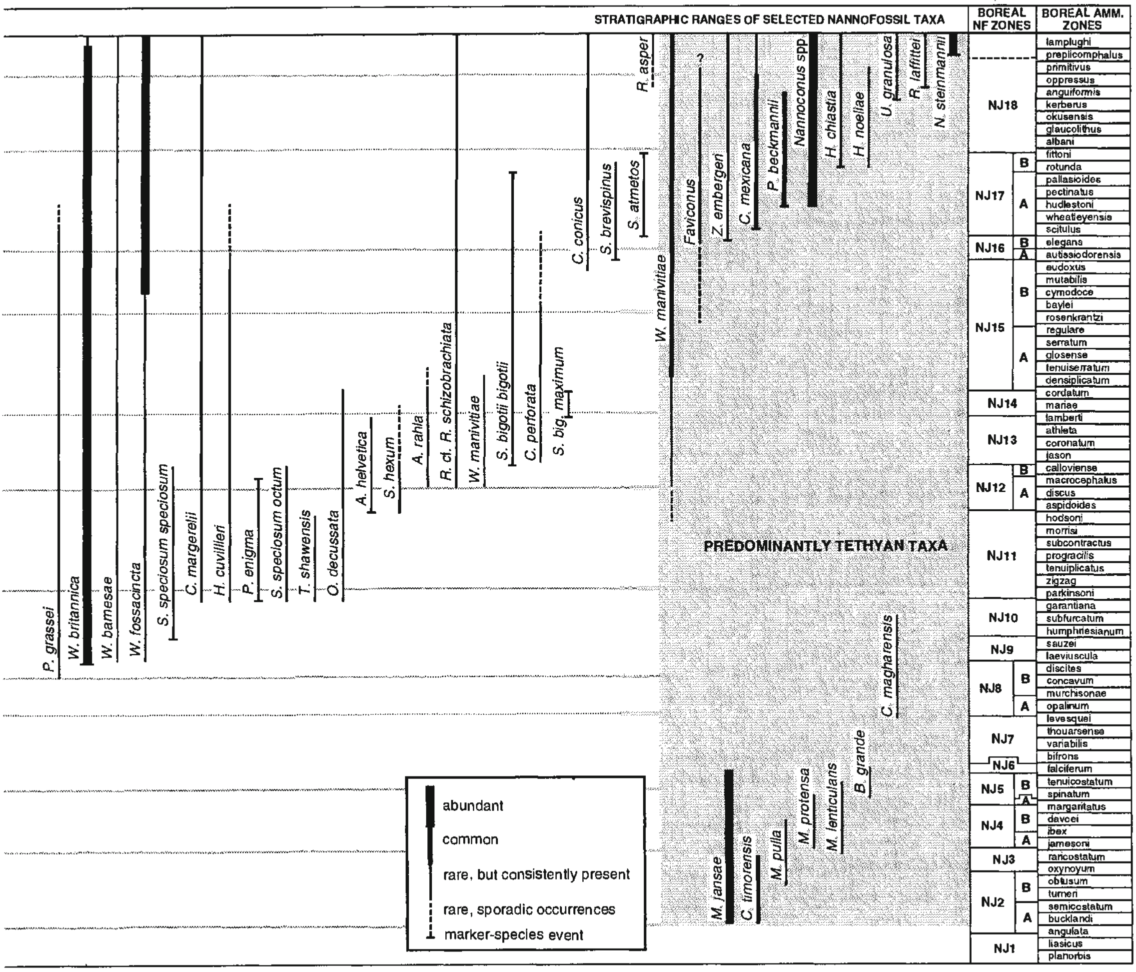


Fig. 4.3 Stratigraphic ranges of selected Jurassic taxa.


STRATIGRAPHIC RANGES OF SELECTED NANNOFOSSIL TAXA
BOREAL NF ZONES
BOREAL AMM. ZONES
P. grassei
W. britannica
W. barnesae
W. fossacincta
S. speciosum speciosum
C. margerelii
H. cuvillieri
P. enigma
S. speciosum octum
T. shawensis
O. decussata
A. helvetica
S. hexum
A. rahla
R. cf. R. schizobrachiata
W. manivitiae
S. bigotii bigotii
C. perforata
S. big. maximum
C. conicus
S. brevispinus
S. atmetos
R. asper
W. manivitiae
Faviconus
?
Z. embergeri
C. mexicana
P. beckmannii
Nannoconus spp.
H. chiastia
H. noeliae
U. granulosa
R. laffittei
N. steinmannii
PREDOMINANTLY TETHYAN TAXA
C. magharensis
B. grande
M. lenticularis
M. protensa
M. pulla
C. tiimorensis
M. jansae
abundant
common
rare, but consistently present
rare, sporadic occurrences
marker-species event
NJ18
NJ17
B
A
NJ16
B
A
NJ15
B
A
NJ14
NJ13
NJ12
B
A
NJ11
NJ10
NJ9
NJ8
B
A
NJ7
NJ6
NJ5
B
A
NJ4
B
A
NJ3
NJ2
B
A
NJ1
lamplughi
preplicomphalus
primitivus
oppressus
anguiformis
kerberus
okusensis
glaucolithus
albani
fittoni
rotunda
pallasioides
pectinatus
hudlestoni
wheatleyensis
scitulus
elegans
autissiodorensis
eudoxus
mutabilis
cymodoce
baylei
rosenkrantzi
regulare
serratum
glosense
tenuiserratum
densiplicatum
cordatum
mariae
lamberti
athleta
coronatum
jason
calloviense
macrocephalus
discus
aspidoides
hodsoni
morrisi
subcontractus
progracilis
tenuiplicatus
zigzag
parkinsoni
garantiana
subfurcatum
humphriesianum
sauzei
laeviuscula
discites
concavum
murchisonae
opalinum
levesquei
thouarsense
variabilis
bifrons
falciferum
tenuicostatum
spinatum
margaritatus
davoei
ibex
jamesoni
raricostatum
oxynoyum
obtusum
turneri
semicostatum
bucklandi
angulata
liasicus
planorbis

Range. Upper Tithonian to Lower Berriasian (CM20–CM17).
Remarks. This zone encapsulates much of the late Tithonian evolutionary radiation, which occurred in the western Tethys/proto-Atlantic Ocean region, and saw the introduction of many new coccolith (*Helenea, Umbria, Speetonia, Cruciellipsis, Manivitella* and *Rhagodiscus*) and nannolith (*Lithraphidites, Nannoconus globulus, N. winteri, N. kamptneri* and *N. steinmannii*) taxa. The FO of *H. chiastia* is coincident with the FOs of *Hexalithus noeliae* and *Polycostella senaria.*

NJKa Hexalithus noeliae Subzone
Author. Bralower *et al.* (1989).
Definition. FO of *Helenea chiastia* to the FO of *Umbria granulosa granulosa.*
Range. Upper Tithonian (CM20–CM19n).

NJKb Umbria granulosa granulosa Subzone
Author. Bralower *et al.* (1989).
Definition. FO of *Umbria granulosa granulosa* to the FO of *Rotelapillus laffittei.*
Range. Uppermost Tithonian (CM19n).

NJKc Rotelapillus laffittei Subzone
Author. Bralower *et al.* (1989).
Definition. FO of *Rotelapillus laffittei* to the FO of *Nannoconus steinmannii minor.*
Range. Tithonian/Berriasian boundary interval (CM19n–CM18n).

NJKd Nannoconus steinmannii minor Subzone
Author. Bralower *et al.* (1989).
Definition. FO of *Nannoconus steinmannii minor* to *Nannoconus steinmannii steinmannii*
Range. Lowermost Berriasian (CM18n–CM17).

4.5 GLOBAL CORRELATION

Two Jurassic nannofloral realms are presently well-known: the northern-high-latitude Boreal Realm and the low-latitude Tethyan Realm. A third, southern-high-latitude Austral Realm has been postulated but very little information is available at present.

The realms are defined by endemic species distributions and contrasting assemblage compositions. It has also been suggested that species ranges may vary between the realms but this has yet to be conclusively proven and may simply reflect taxonomic and preservational problems.

Currently, only the Upper Jurassic interval has required the development of separate biozonation schemes for the northern-high-latitude and low-latitude regions.

4.5.1 Lower Jurassic

The Bown *et al.* (1988) zonation has been successfully applied worldwide, including northern Europe (Bown, 1987), British Columbia, Timor, Argentina (Bown, 1992a), India, eastern Africa, northwestern Australian shelf (Bown, pers. obs.), Mazagan Plateau (offshore Morocco) (Wiegand, 1984; Bown, 1987) and Portugal (Bown, 1987; Bergen, in press). Despite relatively high percentages of endemic taxa, all of those species which are utilized as zonal fossils have virtually cosmopolitan distributions.

4.5.2 Middle Jurassic

Compared to the Lower Jurassic, much less work has been carried out on Middle Jurassic sections outside the European area. For the most part, the zonation of Bown *et al.* (1988) can be applied, although further subdivision has been achieved in the excellent sections of Portugal (Bergen, in press) (Figs 4.1–4.2). Correlation of the Aalenian and Bajocian zones has been problematical, due to the apparent diachroneity of a number of *Lotharingius* and *Watznaueria* species, although this most probably reflects differing species concepts applied to a difficult lineage. However, these zones (NJ8b, NJ9) may require subsequent modification.

4.5.3 Upper Jurassic

The restricted biogeographic distributions of a high proportion of Upper Jurassic taxa, particularly in the Tithonian, has necessitated the development of separate biozonations for the tethyan and boreal areas (Fig. 4.2), with far greater refinement currently achieved in the former region. This currently achieved in the former region. This interval presents the most problems for correlation of the boreal and tethyan regions for the following reasons:

- declining nannofossil diversity in the boreal area (Middle Volgian = Bolonian);
- unfavourable facies and incomplete sections in the boreal area (Upper Volgian = Portlandian);
- absence of new and biostratigraphically-valuable tethyan taxa in the boreal area;
- poor nannofossil preservation in carbonate-rich, tethyan facies; and
- tethyan nannofossil events poorly-constrained and mainly defined in DSDP cores.

The development of tethyan biostratigraphy has relied almost completely on one DSDP site in the western Atlantic Ocean (Site 534) which has yielded an excellent succession of nannofossil events, which are correlated with magnetostratigraphic chronozones (Roth *et al.*, 1983; Bralower *et al.*, 1989). Further refinement of the scheme has been hampered by poor preservation in onshore tethyan sections and a lack of direct correlation with ammonite data.

The few potentially correlatable marker-species found in both realms are beset with problems: *S. bigotii bigotii* appears to have a diachronous LO, *Z. embergeri* is poorly-constrained taxonomically, and *S. brevispinus* (= *helotatus*) is a small and rare species which is easily overlooked.

A number of workers are presently addressing the problems listed above but good sections of this age, particularly those which yield co-occurring boreal and tethyan markers, are few and far between. Recent work from Bulgaria and the Czech Republic (pers. obs.) has confirmed the co-occurrence of boreal and tethyan species, e.g. *S. brevispinus* with *C. mexicana minor* and *S. atmetos* with *C. mexicana mexicana* underlining the great potential nannofossils have for providing correlation through this problematical interval.

4.6 MAGNETOBIOCHRONOLOGY

The lack of magnetostratigraphic data for the Jurassic has meant that few studies have correlated nannofossil datums and the geomagnetic timescale. Ogg and Steiner (1988) and Bralower *et al.* (1989) present data for the Upper Jurassic of the tethyan area. No data are available at present for boreal areas.

4.7 BIOGEOGRAPHY

The biogeographic differentiation of Jurassic marine invertebrate faunas has long been recognised (Neumayr, 1883), and similar patterns are also seen in many other fossil groups. Arkell (1956) distinguished three faunal realms on the basis of ammonite distributions, the Boreal, Tethyan and Pacific. In contrast, Hallam (1975) distinguished only the former two. The Boreal Realm corresponded to the northern part of the Northern Hemisphere, the Tethyan Realm to the rest of the globe. The limit between the two realms, while variable through time, corresponded approximately with a gradational zone through southern Europe and, in the North Pacific region, with a zone through northern California and between Japan and eastern Siberia (Hallam, 1975). The Jurassic Boreal Realm is well-defined by ammonites and belemnites but for other groups it is defined by an absence of tethyan forms rather than by a distinct fauna/flora of its own. Ammonite distributions reveal a temporal variability in the degree of provincialism, with differentiation in the Pliensbachian and Bathonian, and extreme endemism in the Tithonian and Volgian. In general, the faunas of the Tethyan Realm have a greater diversity than those of the Boreal Realm (Hallam, 1975).

The cause of Jurassic provincialism has been the subject of much debate, and explanations have included temperature gradients, land barriers, water depth and salinity. Arguments for and against these explanations are set out in Hallam (1975). More recently, the concept of environmental stability has been proposed as a possible explanation, with the Tethyan Realm reflecting a region of high stability with oceanic influence, and the Boreal Realm the product of variable and stressful environments in widespread epeiric seas (Hallam, 1975).

The global distribution of Jurassic nannofloras is still poorly known and information remains heavily weighted towards Europe. Several DSDP and ODP sites have provided information from the Atlantic and Indian Ocean regions but these generally penetrate only Middle and Upper Jurassic strata. Despite a somewhat limited data set, nannofossil distribution is seen to exhibit variable degrees of provincialism through the Jurassic, with nannofloras from the tethyan region distinguishable from those of northern Europe.

In the Lower Jurassic, nannofloras from western Tethys and the proto-Atlantic area are characterized by the abundant occurrence of *Mitrolithus jansae. M. jansae* ranges from Sinemurian to Lower Toarcian and is often the principal component of assemblages. This species has been reported from certain stratigraphic intervals in NW European sections but is always rare (Bown, 1987). There are a number of other essentially endemic tethyan forms which also occur in Timor (further to the east in the Tethys Ocean), e.g. *Mitrolithus lenticularis, Biscutum grande, Timorella cypella*, and the Family Mazaganellaceae (*Mazaganella pulla* and *M. protensa*).

The Late Jurassic (Middle Oxfordian and younger) saw the renewal of biogeographic distinctness in nannofloral distribution, which increased in Tithonian (= Volgian) times. This corresponds with similar observations of ammonite distributions. Many new nannofossil groups which had their first occurrences in the Tithonian, e.g. the genera *Nannoconus* and *Conusphaera*, were initially restricted in distribution to the western Tethys and North Atlantic region. The tethyan nannofloras are thus distinguished by the presence of endemic taxa and by considerably higher diversities. The existence of endemic boreal taxa in the Late Jurassic is uncertain but a number of species have been suggested, e.g. *Stephanolithion atmetos* (Cooper, 1989), and distinct boreal species are clearly present by Early Cretaceous times (Cooper, 1989). Preliminary research in central Europe and the Balkans has provided evidence of a transitional zone between the Boreal and Tethyan realms (pers. obs.).

The occurrence of nannofossils in Upper Jurassic DSDP/ODP sections from the Argo Abyssal Plain (NW Australian shelf; palaeolatitude of ~35°S) (Bown, 1992b) and Falkland Plateau (palaeolatitude of ~60°S) (Wise and Wind, 1977) allows a limited assessment of Southern Hemisphere nannofossil distributions, and the results suggest the existence of an Austral Realm, a counterpart to the Boreal Realm, which was dominated by taxa with boreal (i.e. high-latitude) affinities, e.g. *Stephanolithion brevispinus*, and devoid of tethyan taxa such as *Conusphaera* and *Nannoconus*. The presence of common *Watznaueria manivitiae* on the Argo Abyssal Plain, however, also infers a degree of tethyan-austral mixing, inferring a transitional biogeographic zone in this region. Bipolar distributions, together with endemicity in northern and southern high-latitudes, has been well documented in the Cretaceous (Wise, 1988; Watkins *et al.*, 1996). These observations are presently at odds with interpretations of cephalopod distributions, which do not indicate a distinct Austral Realm.

4.8 ATLAS OF SPECIES

Most Jurassic calcareous nannofossils are listed and illustrated in Plates 4.1 to 4.16. Taxa are listed according to the classification of Bown and Young (1997), firstly by order and secondly by family. Electron micrographs are not uniformly enlarged but magnifications are given in the plate captions. Light micrographs are uniformly enlarged at x2300. Stratigraphic information is given as stages (L=Lower, M=Middle, U=Upper) and ammonite zones (in brackets), where possible; question marks indicate a degree of uncertainty. Photographs are identified by a UCL number (film and frame) and are stored in the Postgraduate Unit of Micropalaeontology, University College London. The majority of photographs come from the research of Drs Paul Bown, Kevin Cooper and Hilary Dockerill.

4.9 APPENDIX 1. CALCAREOUS NANNOFOSSILS FROM THE UPPER KIMMERIDGIAN-VOLGIAN OF GORODISCHE, RUSSIA (P.R. BOWN)

4.9.1 Introduction

A total of 44 samples from the Gorodische section in Russia (Kimmeridgian to Volgian; proposed Volgian lectostratotype) were examined for calcareous nannofossils. A previous study by Cooper (1987) reported well-preserved and diverse nannofossil assemblages from a stratigraphically shorter suite of fewer samples (10).

All but two of the samples yielded nannofossil assemblages which, in general, are well-preserved, abundant and diverse. These results show that the Gorodische section provides the finest nannofossil succession for this time interval in the boreal area, confirming Cooper's (1987a) preliminary findings. Other coeval boreal sections, notably the Kimmeridge Clay of southern England, are in part comparable but generally nannofossil assemblages are lower in diversity or through certain intervals, absent (Cooper, 1987b). Tethyan sections generally yield poorly-preserved nannofossils due to the predominance of micritic limestone lithologies, however, a number of DSDP sections from the Atlantic Ocean (e.g. Sites 391 and 534) have provided excellent results for this interval, revealing markedly different assemblage compositions from those seen in the boreal area (e.g. Roth, 1983; Bralower *et al.*, 1989).

The Gorodische nannofossil results are particularly valuable in confirming a sequence of extinction events which characterizes this interval, but more importantly it has allowed the testing of the Upper Jurassic zonal scheme of Cooper (1987a) and Bown *et al.* (1988) and revealed a number of problems which are discussed below.

4.9.2 Stratigraphic terminology

Kimmeridgian is used throughout in the restricted, *sensu gallico*, sense. The term Bolonian is adopted, as discussed by Cope (1993), for the Upper Kimmeridgian (*sensu anglico*). Ammonite correlations between England and Russia are based upon Cope (1993).

4.9.3 Nannofossil results

a. Kimmeridgian–Middle Volgian

Samples 1A–25, from the Upper Kimmeridgian to lower Middle Volgian (eudoxus AZ through panderi AZ, zarasjkensis AsZ), yielded well-preserved, abundant, and diverse nannofossil assemblages. Samples 26A–28, from the Middle and Upper Volgian (virgatus, fulgens, subditus and nodiger AZs), were either barren or depauperate (Fig. 4.4). The Upper Volgian results are discussed separately below.

The Upper Kimmeridgian to Volgian part of this section has yielded the best succession of nannofossil events yet seen in the boreal area. Diversity is highest in the Kimmeridgian (27–29 species) but falls to lower levels in the Lower and Middle Volgian (15–20 species). The assemblages are characterized by the numerical dominance of *Watznaueria*, and in particular *W. britannica.*

The stratigraphic distribution of nannofossils is presented in Fig. 4.4, along with ammonite and nannofossil zone designations. The Gorodische nannofossil succession is particularly notable for:

(i) **common *Zeugrhabdotus erectus*** – this distinctive species occurs commonly in most of the samples studied. Its increase in size through this interval is well documented (e.g. Roth, 1983; Bralower *et al.*, 1989) but its differentiation from *Zeugrhabdotus embergeri* has remained a source of much discussion, particularly as the latter species has been commonly used as a zonal marker around the Kimmeridgian–Volgian (= Tithonian) boundary (e.g. Barnard and Hay, 1974; Medd, 1982; Hamilton, 1982). First Stradner (1963) and later Bralower *et al.* (1989) attempted to differentiate these species by imposing morphometric limits, but the latter observed 'complete gradation between true *Z. erectus* and *Z. embergeri* and it is impossible to divide the two taxa morphometrically', underlining the difficulty encountered in this lineage. The present study did not recognize *Z. embergeri* in any of the Gorodische samples, although Roth (pers. comm.) recorded its first occurrence in the klimovi AZ (lowermost Volgian), and considers it a potentially valuable interregional marker-species. Its first occurrence in the tethyan area is better known, occurring in polarity chron CM22n (Site 534, Bralower *et al.*, 1989, but CM22r, pers. obs.), which is correlated to the middle hybonotum AZ (lowermost Tithonian). The opinion of the author is that *Z. embergeri* is not present, or only rarely present, in the Volgian of the boreal area, and did not move into this area until the earliest Cretaceous.

(ii) **the abundant occurrence of small, delicate coccoliths of the Family Stephanolithiaceae (*Stradnerlithus* and *Truncatoscaphus*)** – these coccoliths are rarely preserved but have often been described in vast numbers from sediments which are laminated and organic-rich, e.g. the Posidonienschiefer, Schistes Carton, Kimmeridge Clay and Munk Marl. It is uncertain whether their occurrence is a result of exceptional preservation in these unusual sediments, or a reflection of a particular, primary surface-water environment, e.g. high productivity.

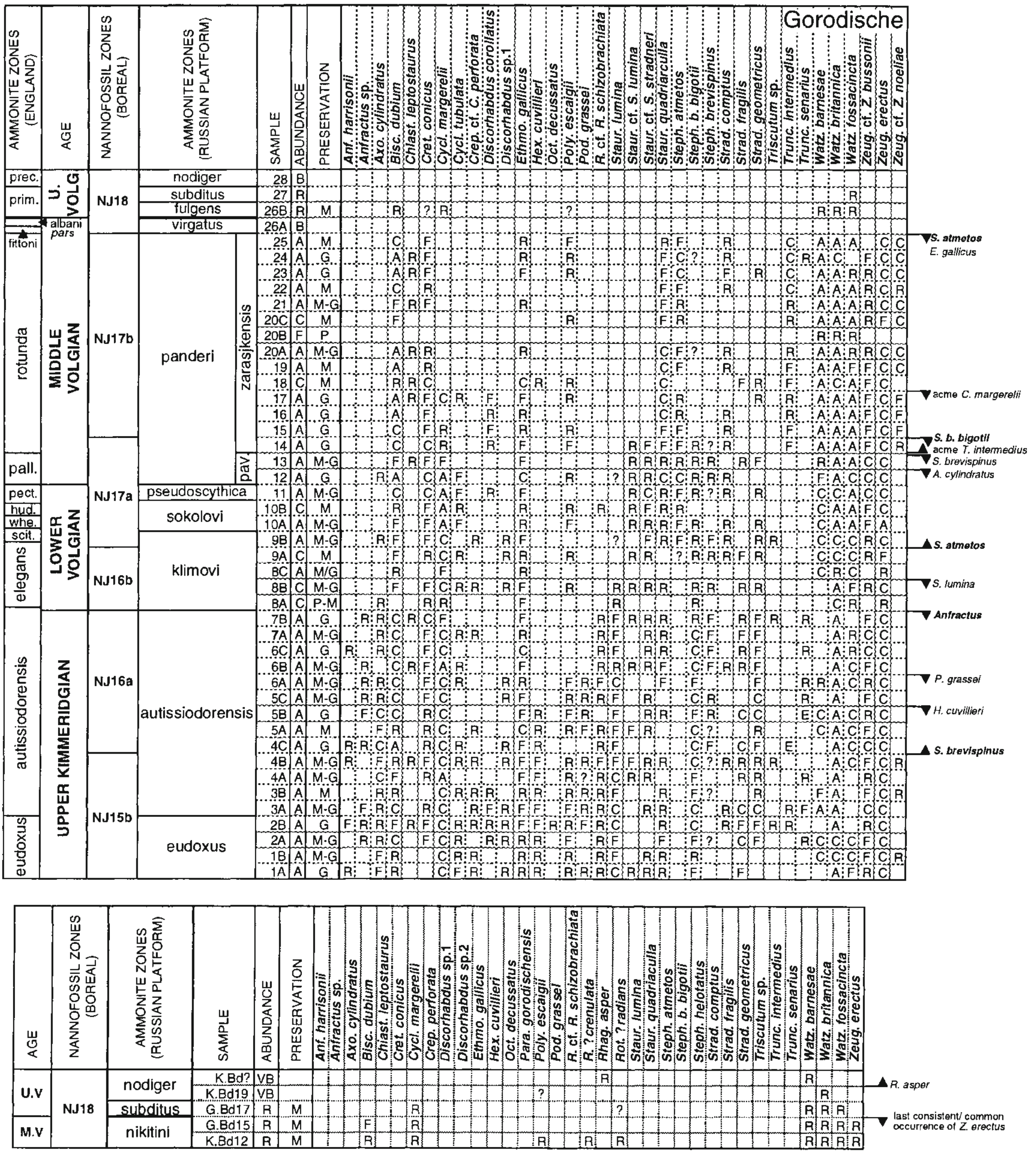


Fig. 4.4 Stratigraphic distribution of nannofossils for the Gorodische section, Russia. The lower chart includes additional spot samples from Gorodische and Kashpir. Species abundance: A >10/FOV, C 1-10/FOV, F 1/2-10 FOV, R 1/11-100 FOV. Nannofossil abundance: A >10%, C 1-10%, F 0.1-1%, R < 0.1%, VB virtually barren, B barren.

The species *S. fragilis* and *S. geometricus* are particularly common.

(iii) **the occurrence of holococcoliths** – due to the fragile nature of holococcolith construction, most Jurassic forms have only been found in assemblages which are exceptionally well-preserved (Bown, 1993). The exception is *Anfractus harrisonii*, which is relatively consistently recorded in Lower Bathonian through Upper Kimmeridgian sediments. *A. harrisonii* is recorded in the Gorodische section but its upper range is slightly extended here, into the autissiodorensis AZ. In addition, a number of other *Anfractus*-type holococcoliths have been seen in both LM and SEM observation.

(iv) **evolution and extinction of three *Stephanolithion* species** – three species of *Stephanolithion* are recorded in the Gorodische section, *S. atmetos, S. bigotii bigotii* and *S. brevispinus* (=*S. helotatum* of Cooper, 1987a), and all have previously been utilized as biostratigraphic marker-species. Cooper (*in* Lord *et al.*, 1987) proposed two new nannofossil zones based upon the successive first occurrences of *S. helotatum* and *S. atmetos*, and formally defined these zones in Bown *et al.* (1988), using Gorodische as a reference section. The present study has revealed a number of problems with these zones which have thus been emended herein.

b. Upper Volgian

These samples yielded low-abundance and -diversity nannofossil assemblages, were virtually barren (i.e. <10 specimens), or were barren. Preservation, however, is not particularly poor, which suggests that the rare occurrences reflect dilution by clastic material and/or unfavourable primary environmental conditions, rather than post-sedimentation destruction by etching. A number of supplementary spot samples from Gorodische and the nearby Kashpir section were provided by Prof. John Calloman.

Boreal nannofossil data from this time interval are virtually unknown. The Russian Upper Volgian correlates with the Purbeck Group of southern England which is in predominantly marginal and non-marine facies. The highest record of nannofossiliferous sediments for this interval in England are of fittoni and albani AZ age (Middle Volgian) (Cooper, 1987b; Bown *in* Lord and Bown, 1987). The oldest Ryazanian sediments with recorded nannofloras are from the albidum AZ (Upper Ryazanian) of the Speeton section (NE England). Rahman and Roth (1992) studied Ryazanian samples from central Russia but give no assemblage or stratigraphic information.

The significance of the Gorodische/Kashpir results is uncertain as the assemblages appear to be depauperate, for the reasons given above. However, they do show the continued range of all three *Watznaueria* species, and also include discontinuous ranges of *B. dubium, C. margerelii, P. escaigii,* and *Z. erectus* (all of which have Lower Cretaceous records). The absence of *S. atmetos* and *E. gallicus* is thought to be the result of extinctions in the Middle Volgian (?prior to the virgatus/nikitini AZs).

The decline in *W. britannica* abundance, which was shown by Cooper (1984) to approximate the Jurassic/Cretaceous boundary could not be assessed in these samples because of the low number of specimens involved.

4.9.4 Taxonomy

Family CHIASTOZYGACEAE Rood, Hay and Barnard, 1973 emend. Varol and Girgis, 1994
Genus *Staurolithites* Caratini, 1963
Staurolithites lumina Bown sp. nov.
Plate 4.1, fig. 20; Plate 4.9, figs 21–25

Derivation of name. From *lumino*, Latin for 'light up', and referring to the appearance of the coccolith's cross-bars in XPL.

Diagnosis. An elliptical, bicyclic (in distal view) murolith with broad, axial cross-bars which are highly birefringent in XPL (maximum birefringence is achieved in both cross-bars in the same orientation, although the c-axes are perpendicular as shown by the gypsum-plate).

Description (SEM). Outer, distal rim is composed of numerous, highly-inclined, i.e. imbricating, elements. In distal view, a second inner rim-cycle is seen but structural details are unclear (it is assumed that, like other murolith-coccoliths, this inner cycle is a distal extension of the proximal rim-cycle). The central-area is spanned by an axial cross which is attached to the inner rim-cycle. The bars are formed from elongate laths, and are bisected by a median suture. The cross supports a central spine-base/?spine.

Description (LM). The rim is bicyclic; both cycles are narrow. The outer cycle is slightly birefringent (dark, and high relief in PC) and the inner cycle is birefringent (bright in PC). The cross-bars show coincident maximum birefringence colours (white) when orientated approximately 25° anticlockwise from the N–S position. The junction of the four cross-bars is marked by distinct, dark suture-lines.

Remarks. The genus *Staurolithites* (= *Vagalapilla, Vekshinella*) is a taxonomic grouping which has become virtually unusable because of poor species-definition, somewhat reflecting almost infinite variety on a basic, and stratigraphically long-ranging, morphological theme. A variety of species names have been applied to Jurassic murolith coccoliths with axial cross-bars, including *stradneri, dibrachiata, quadriarculla, crux* and *magnus*, but the ill-defined species concepts have resulted in poorly-defined ranges. Barnard and Hay (1974) and later Roth *et al.* (1983) used the first occurrence of *'V. stradneri'* to define the base zone in the Lower Oxfordian, but this has rarely been recognized due to the presence of *stradneri*-type coccoliths throughout the Jurassic. The new species, *S. lumina*, is found in the Kimmeridgian and Lower Volgian samples from Gorodische, and is very distinctive in the LM. Its LO in the klimovi AZ is also recognized in English material, but this species has not yet been recognized in tethyan samples.

Holotype. Plate 4.9, fig. 21 (LM).

Paratype. Plate 4.1, fig. 20 (EM).

Type locality. Gorodische, Russia.

Type level. Upper Kimmeridgian (autissiodorensis AZ).

Range. Gorodische: eudoxus AZ (Upper Kimmeridgian) to klimovi AZ (Lower Volgian).

Family STEPHANOLITHIACEAE Black, 1969
Genus *Stephanolithion* Deflandre, 1939

Stephanolithion atmetos Cooper, 1987
Plate 4.3, fig. 8 and Plate 4.11, figs 8–10

Remarks. The stratigraphic range of this species is poorly defined, being reported as lower Middle Volgian (panderi AZ) from Gorodische by Cooper (1987) and Upper Kimmeridgian (autissiodorensis AZ) from Russia by Roth (pers. comm.). In the present study, the FO was observed in the klimovi AZ, considerably lower than Cooper's (1987a) record, which calls into question the position and validity of the S. atmetos Zone. This problem is a reflection of the gradualistic evolutionary development of *S. atmetos*, which is clearly an end-member descendant of the *S. bigotii bigotii–S. brevispinus* lineage/plexus.

Stephanolithion bigotii bigotii Deflandre, 1939
Plate 4.3, fig. 9–11; Plate 4.11, figs 11–13

Remarks. This distinctive taxon has been used extensively as a marker-species, particularly its FO which occurs in the Callovian. Its LO is less well-constrained, firstly because of the evolution of the two new species discussed above, and secondly because of its apparent rarity or total absence towards the top of its range in the classical Kimmeridgian sequences of England. This study found the LO in the lower Middle Volgian (panderi AZ, zarasjkensis AsZ). Considering the importance of this species, as one of the only cosmopolitan marker-species for this interval, it is suggested that this datum be upgraded to zonal status, although the synchroneity of this horizon requires testing in tethyan sections. It has been recorded within polarity chron CM20r in Site 534 (pers. obs.), near the Lower/Middle Tithonian boundary, which is probably equivalent to one ammonite zone lower than in the Gorodische section, although this is difficult to substantiate.

Stephanolithion brevispinus (Wind and Wise *in* Wise, 1988) Bown stat. nov.
Plate 4.3, figs 13–14; Plate 4.11, figs 16–20

1983	*Stephanolithion bigotii* Deflandre; Wise, pl. 34, figs 3 and 4.
1987	*Stephanolithion helotatum* (Wise and Wind); Cooper, p. 610, fig. 1 (13–15).
1988	*Stephanolithion bigotii brevispinus* Wind and Wise *in* Wise, p. 175.

Emended diagnosis. An elliptical species of *Stephanolithion* with short, ?irregular, lateral rim-spines and a central-area diagonal cross which supports a spine.

Remarks. The generic affinity and taxonomy of *S. helotatum* has been questioned by both Wise (1988) and Rahman and Roth (1992). Both rejected the inclusion of this species in *Stephanolithion* on the grounds that the holotype, and other recorded specimens, have no lateral rim spines. Wise (1988) recognized the existence of similar, and probably closely-related forms which possess the short spines that Cooper (1987a) illustrated, and proposed a new subspecies of *S. bigotii* (*S. bigotii brevispinus* Wind and Wise *in* Wise, 1988) to include them. It is thought best to conform to these suggestions, although the subspecies of Wise (1988) is here elevated to species level.

The stratigraphic range of *S. brevispinus* is still poorly defined, reflecting the gradualistic evolution of *S. brevispinus* from the ancestral species *S. bigotii*. In the present study, the first occurrence of *S. brevispinus* was observed in the autissiodorensis AZ, confirming the observation of Cooper (1987a) and the lower level of the NJ16 S. brevispinus Zone.

Differentiation. *S. bigotii* has long, lateral rim-spines, normally six in number, which are regularly arranged, and its outline is often angular rather than elliptical. *Stradnerlithus helotatus* is similar in shape, size and central-area configuration but lacks rim spines. *S. atmetos* has merged cross-bars and is narrowly elliptical in outline, with almost parallel sides.

Range. *Gorodische*: autissiodorensis AZ (Upper Kimmeridgian) to sokolovi AZ (Lower Volgian) (this study); *Gorodische*: autissiodorensis AZ (Upper Kimmeridgian) to zarasjkensis AsZ (Middle Volgian) (Lord *et al.*, 1987); *Falkland Plateau* (Site 511): ?Kimmeridgian-Lower Volgian (Wise, 1983) (the stratigraphy of these cores, Sites 330 and 511, is questionable and evidence from the range-charts of Wise and Wind (1977) and Wise (1983) suggests the range could be limited to the Upper Kimmeridgian-Volgian); *Dorset coast*: hudlestoni AZ to rotunda AZ (Bolonian = Lower Volgian) (Cooper, 1987b); *S England*: wheatleyensis AZ (Bolonian = Lower Volgian) (pers. obs.); *Central Russia*: Oxfordian (Rahman and Roth, 1992 – non-spinose forms, i.e. true *Stradnerlithus helotatus*).

Plate 4.1

Order EIFFELLITHALES Rood *et al.*, 1971
Family CHIASTOZYGACEAE Rood *et al.*, 1973 emend. Varol and Girgis, 1994
Fig. 1. ***Crepidolithus crassus*** (Deflandre *in* Deflandre and Fert, 1954) Noël, 1965. Distal (lower three specimens), side and proximal (upper specimen) views, Ilminster (UK), L. Toarcian, UCL-2615-8, x2400. Range: U. Sinemurian (oxynotum) – U. Tithonian (fittoni).

Figs 2–3. ***Crepidolithus granulatus*** Bown, 1987. Distal (2) and side (3) views of same specimen, Brenha (Portugal), L. Plienbachian (ibex), UCL-2170-3/4, x5450. Range: L. Pliensbachian (ibex) – U. Plienbachian (margaritatus).

Figs 4–5. ***Crepidolithus impontus*** (Grün *et al.*, 1974) Goy, 1979. Distal (4) and side (5) views of same specimen, Unterstürmig (Germany), L. Toarcian, UCL-2036-2/3, x6560. Range: U. Pliensbachian (spinatum) – Aalenian (murchisonae).

Figs 6–8. ***Crepidolithus perforata*** (Medd, 1979) Grün and Zweili, 1980. Distal (6), side (7) and proximal (8) views, Villers-sur-mer (France), L. Oxfordian (mariae), UCL-2032-17/7; UCL-2207-4, x6905/8095/6788. Range: L. Callovian (jason) – L. Volgian (klimovi).

Figs 9–10. ***Crepidolithus pliensbachensis*** Crux, 1985. Distal (9) and side (10) views of same specimen, Timor, L. Pliensbachian, UCL-2072-25/26, x4950. Range: L. Sinemurian (semicostatum) – L. Pliensbachian (ibex).

Figs 11–12. ***Crepidolithus timorensis*** (Kristan-Tollmann, 1988a) Bown comb. nov.. Distal (11) and proximal oblique (12) views, Timor, Sinemurian, UCL-2736-25/26, x7777. Range: ?Sinemurian.
Basionym: *Timorhabdus timorensis* Kristan-Tollmann, 1988a (*Geol. Paläont. Mitt. Innsbruck*, **15**, 71–83, p. 74–75, pl. 2, figs 1, 3, 5).

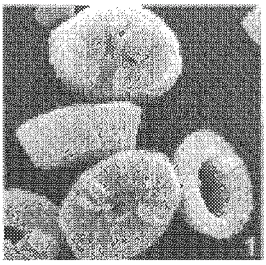
Figs 13–15. ***Tubirhabdus patulus*** Rood *et al.*, 1973. Distal (13), side (14) and distal oblique (15) views. 13, Mochras Borehole (UK), L. Toarcian (falciferum), UCL-1993-5, x8095. 14, Timor (L. Pliensbachian), UCL-2072-7, x7866; 15, modified Middle Jurassic morphotype, Dorset (UK), Bathonian (zigzag), UCL-1902-9, x4686. Range: L. Sinemurian (bucklandi) – L. Tithonian (pectinatus).

Fig. 16. ***Vacherauvillius implicatus*** Goy, 1979. Distal (upper specimen) and proximal (lower right specimen) views, Hambühren (Germany), L. Toarcian, UCL-3848-28, x11500. Range: ?L. Toarcian (tenuicostatum – falciferum).

Fig. 17. ***Staurolithites stradneri*** (Rood *et al.*, 1971) Bown comb. nov.. Distal view, Gorodische (Russia), U. Kimmeridgian (eudoxus), UCL-1502-3, x6975. Range: L. Pliensbachian? – ?Cretaceous.
Basionym: *Vekshinella stradneri* Rood *et al.*, 1971 (*Eclogae Geologicae Helvetiae*, **64**, 245–272, p. 249, pl. 1, fig. 2).

Figs 18–19. ***Staurolithites quadriarculla*** (Noël, 1965) Wilcoxon, 1972. 18, Distal and proximal views, Hambühren (Germany), L. Toarcian, UCL-3776-3, x4500; 19, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-1506-11, x10555. Range: U. Sinemurian – ?Cretaceous.

Fig. 20. ***Staurolithites lumina*** Bown sp. nov.. Distal view, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-1539-11, x7000. Range: U. Kimmeridgian (eudoxus) – L. Volgian (klimovi).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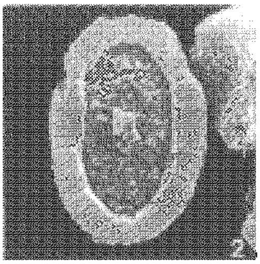
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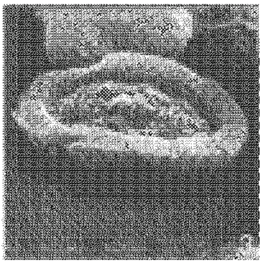
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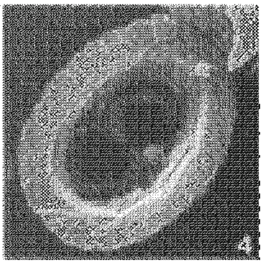
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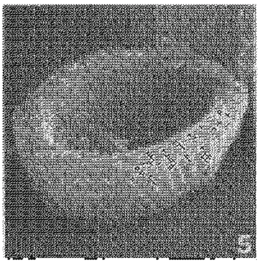
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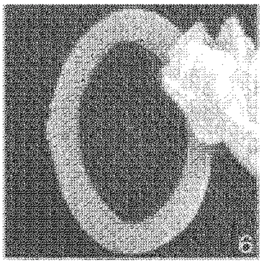
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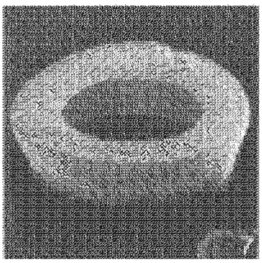
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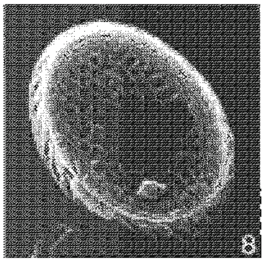
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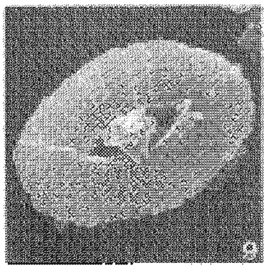
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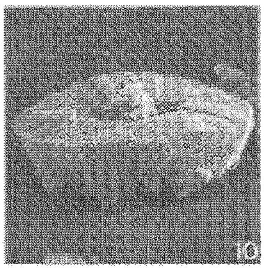
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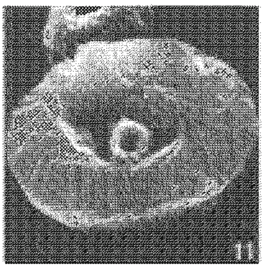
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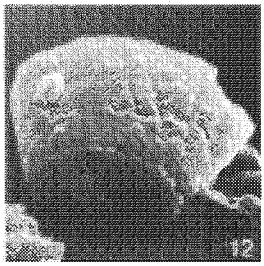
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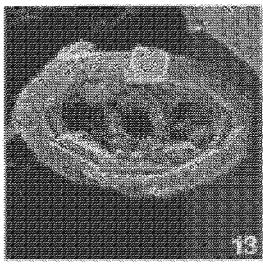
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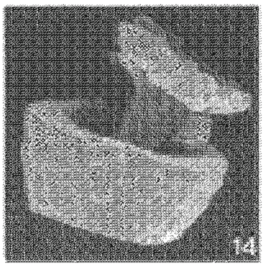
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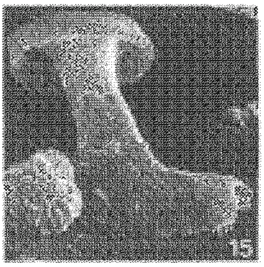
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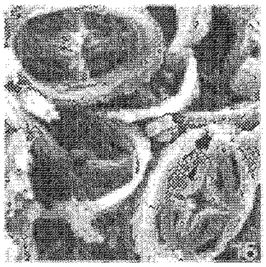
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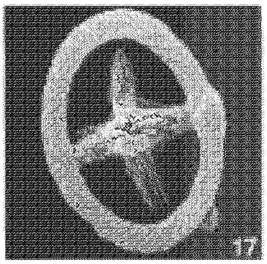
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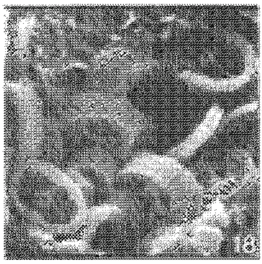
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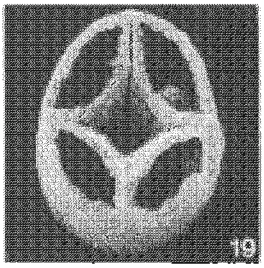
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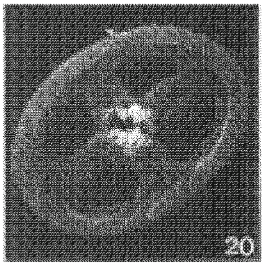
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Plate 4.2

Family CHIASTOZYGACEAE Rood *et al.*, 1973 emend. Varol and Girgis, 1994
Fig. 1. ***Zeugrhabdotus burolleti*** Goy, 1979. Distal, side and proximal views, Hambühren (Germany), L. Toarcian, UCL-3771-30, x2946. Range: L. Toarcian (?tenuicostatum) – Aalenian (opalinum).

Figs. 2–3. ***Zeugrhabdotus cooperi*** Bown, 1992b. Distal (2) and side (3) views of same specimen, DSDP Site 261 (Indian Ocean), Berriasian, UCL-2999-13/14, x3655/3933. Range: L. Tithonian – Valanginian.

Figs 4–8. ***Zeugrhabdotus erectus*** (Deflandre *in* Deflandre and Fert, 1954) Reinhardt, 1965. Distal (4, 5, 8), proximal (6) and side (7) views. 4, Mochras Borehole (UK), U. Toarcian (levesquei), UCL-1888-21, x7450; 5, Villers-sur-mer (France), L. Oxfordian (mariae), UCL-2197-25, x10250; 6, Aylesbury, U. Kimmeridgian (wheatleyensis), UCL-2634-16, x5458; 7, Dorset (UK), Bathonian (zigzag), UCL-2191-10, x5525; 8, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-1502-24, x11666. Range: L. Pliensbachian? – U. Maastrichtian.

Order STEPHANOLITHIALES Bown and Young, 1997
Family PARHABDOLITHACEAE Bown, 1987
Figs 9–11. ***Crucirhabdus primulus*** Rood *et al.*, 1973. Distal (9), side (10) and proximal (11) views, Trunch Borehole (UK), L. Pliensbachian (jamesoni), UCL-2095-8/9/12, x5150. Range: Norian – L. Toarcian (tenuicostatum).

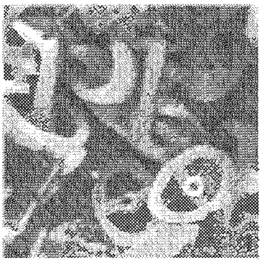
Fig. 12. ***Diductius constans*** Goy, 1979. Distal view, Brenha (Portugal), Aalenian/Bajocian, UCL-2173-6, x5120. Range: L. Toarcian (?tenuicostatum) – L. Bajocian (sauzei).

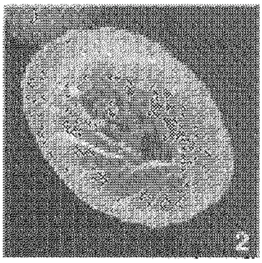
Figs 13–14. ***Mitrolithus elegans*** Deflandre *in* Deflandre and Fert, 1954. Side (13) and distal view (spine detached) (14), Trunch Borehole (UK), Lower Pliensbachian (jamesoni), UCL-2097-25/2095-25, x5650/5100. Range: L. Sinemurian (bucklandi) – U. Pliensbachian (margaritatus).

Figs 15–16. ***Mitrolithus jansae*** (Wiegand, 1984b) Bown *in* Young *et al.*, 1986. Distal (15) and side (16) views, DSDP Site 547 (Atlantic Ocean), U. Sinemurian, UCL-2190-3/2046-36, x7500. Range: L. Sinemurian (semicostatum) – L. Toarcian (falciferum).

Figs 17–18. ***Mitrolithus lenticularis*** Bown, 1987. Distal oblique (17) and distal (18) views of same specimen, Timor, L. Pliensbachian, UCL-2148-26/25, x7200. Range: U. Sinemurian (raricostatum) – ?L. Toarcian (tenuicostatum).

Figs. 19–20. ***Parhabdolithus liasicus*** Deflandre *in* Grassé, 1952 ssp. ***distinctus*** Bown, 1987. Side (19) and distal (20) views. 19, Mochras Borehole (UK), U. Sinemurian (raricostatum), UCL-1917-17, x6500; 20, DSDP Site 547 (Atlantic Ocean), U. Sinemurian, UCL-2190-14, x6150. Range: Hettangian (angulata) – L. Toarcian (?falciferum).





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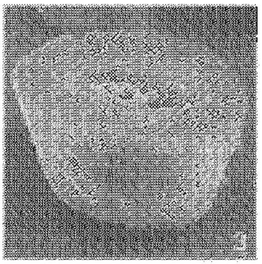

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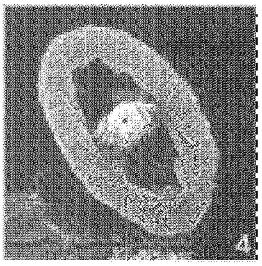

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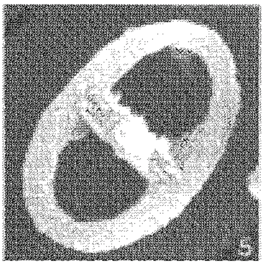

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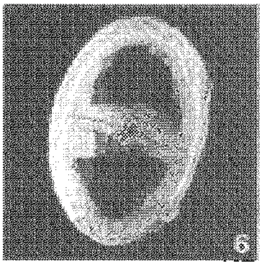

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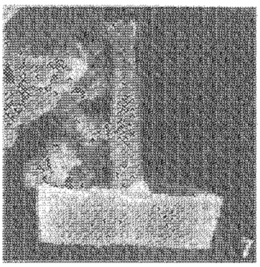

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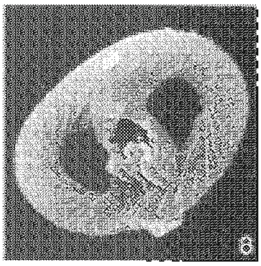

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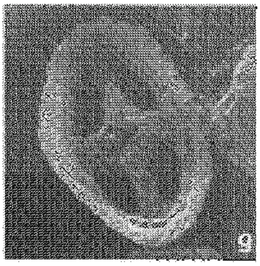

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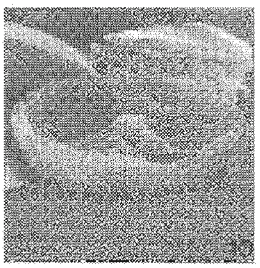

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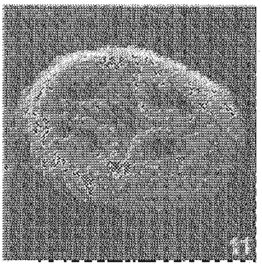

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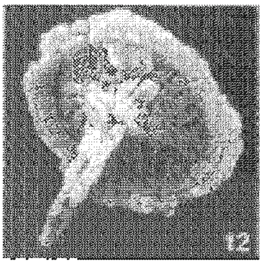

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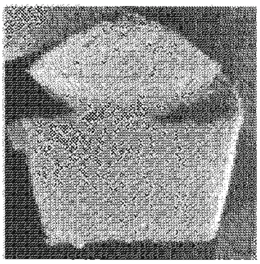

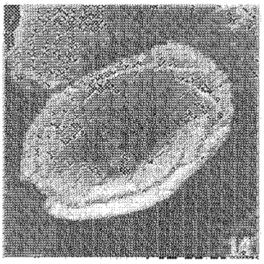

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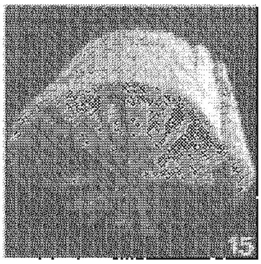

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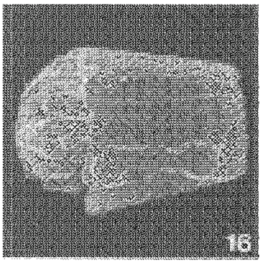

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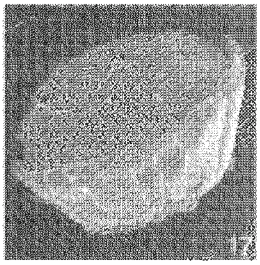

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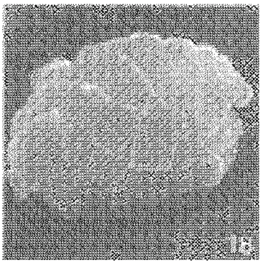

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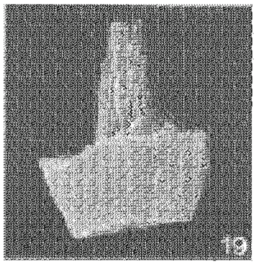

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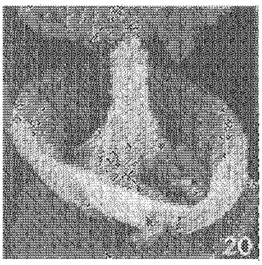

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Plate 4.3

Family PARHABDOLITHACEAE Bown, 1987
Fig. 1. ***Parhabdolithus liasicus*** Deflandre *in* Grassé, 1952 ssp. ***liasicus***. Side view, DSDP Site 547 (Atlantic Ocean), L. Pliensbachian, UCL-2028-36, x4365. Range: Hettangian (angulata) – L. Toarcian (?falciferum).

Fig. 2. ***Parhabdolithus marthae*** Deflandre *in* Deflandre and Fert, 1954. Side view, Hock Cliff (UK), L. Sinemurian (bucklandi), UCL-2268-33, x4390. Range: L. Sinemurian (bucklandi – semicostatum).

Figs 3–4. ***Parhabdolithus robustus*** Noël, 1965. Side (3) and distal (4) views of the same specimen, Timor, L. Pliensbachian, UCL-2117-27/25, x6200/6400. Range: L. Sinemurian (turneri) – L. Pliensbachian (ibex).

Figs 5–6. ***Timorella cypella*** Bown, 1987. Distal (5) and side (6) views of the same specimen, Timor, Lower Pliensbachian, UCL-2149-6/4, x4900/6490. Range: L. Pliensbachian.

Family STEPHANOLITHIACEAE Black, 1968
Fig. 7. ?***Thurmannolithion clatratum*** Grün and Zweili, 1980. Distal view, Roslyn Pit (UK), U. Kimmeridgian (?eudoxus), UCL-1411-11, x4791. Range: Callovian? – ?Kimmeridgian

Fig. 8. ***Stephanolithion atmetos*** Cooper, 1987. Distal view, Gorodische (Russia), M. Volgian (panderi), UCL-1506-21, x8685. Range: L. Volgian (klimovi) – M. Volgian (panderi).

Fig. 9–11. ***Stephanolithion bigotii*** Deflandre, 1939 ssp. ***bigotii***. Distal (9, 10) and proximal (11) views. 9, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-1513-7, x5485; 10, Villers-sur-mer (France), Oxfordian (cordatum), UCL-2039-14, x5129; 11, Villers-sur-mer (France), Oxfordian (mariae), UCL-2197-5, x6295. Range: L. Callovian (calloviense) – U. Tithonian (panderi).

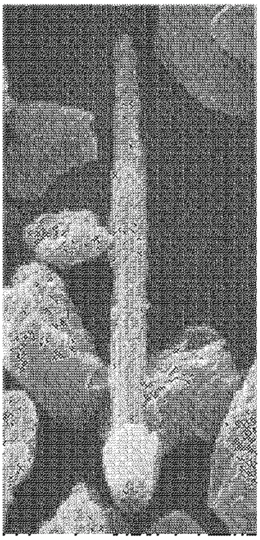
Fig. 12. ***Stephanolithion bigotii*** Deflandre, 1939 ssp. ***maximum*** Medd, 1979. Distal view, Villers-sur-mer (France), Oxfordian (mariae), UCL-2027-1, x4835. Range: U. Callovian (lamberti) – L. Oxfordian (cordatum).

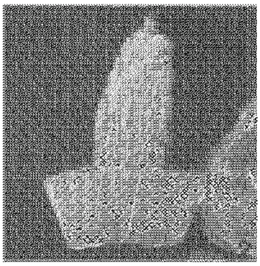
Figs 13–14. ***Stephanolithion brevispinus*** (Wind and Wise *in* Wise, 1988) Bown stat. nov.. 13, distal view, Aylesbury (UK), Bolonian (wheatleyensis), UCL-2635-27, x8222; 14, distal view, Gorodische (Russia), M. Volgian (panderi), UCL-1495-15, ?x4317. Range: U. Kimmeridgian (autissiodorensis) – M. Volgian (panderi).

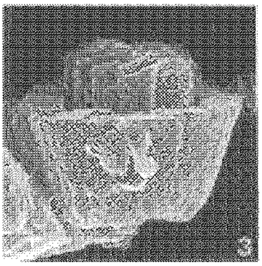
Fig. 15–16. ***Stephanolithion hexum*** Rood and Barnard, 1972. 15, distal view, Escoville (N France), U. Bathonian (discus), UCL-2075-16, x6910; 16, distal view, Dorset (UK), Bathonian, UCL-2214-6, x6128. Range: U. Bathonian (aspidoides) – U. Callovian (lamberti).

Figs 17–18. ***Stephanolithion speciosum*** Deflandre *in* Deflandre and Fert, 1954 ssp. ***speciosum***. Distal (17) and proximal (18) views, Dorset (UK), Bathonian (aspidoides/zigzag), UCL-2180-13/18, x4796/7339. Range: L. Bajocian (humphresianum) – L. Callovian (calloviense).

Fig. 19. ***Stephanolithion speciosum*** Deflandre *in* Deflandre and Fert, 1954 ssp. ***octum*** Rood and Barnard, 1972. Distal view, Escoville (France), Callovian (macrocephalus), UCL-2075-17, x5036. Range: U. Bajocian (parkinsoni) – L. Callovian (calloviense).







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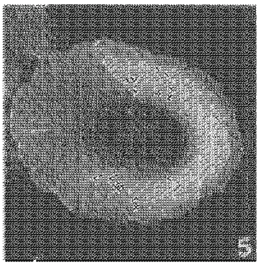

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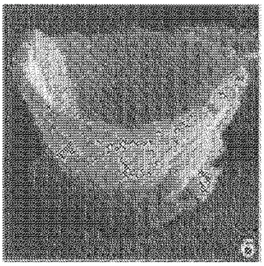

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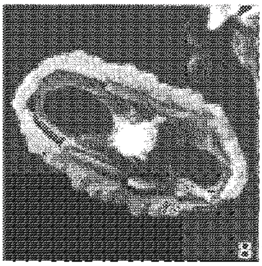

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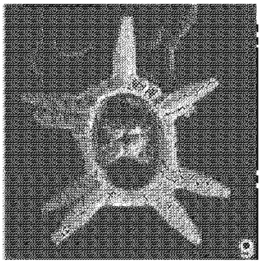

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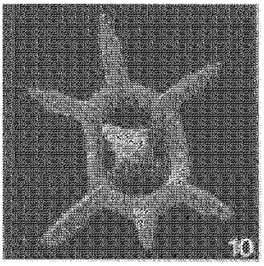

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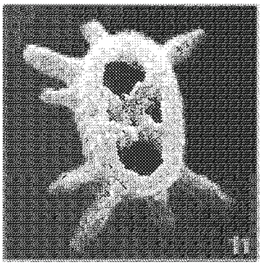

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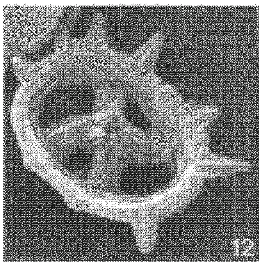

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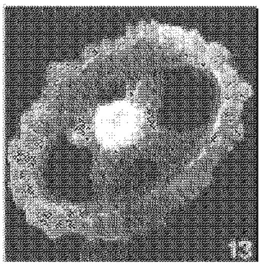

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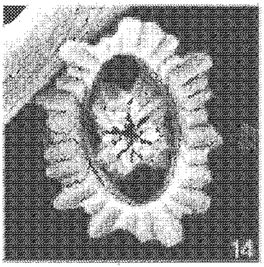

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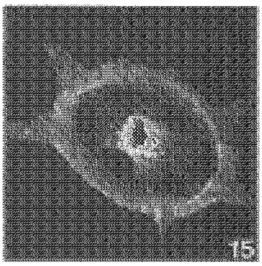

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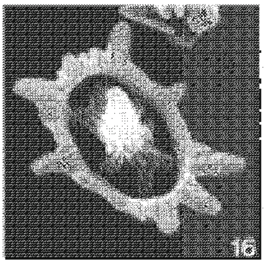

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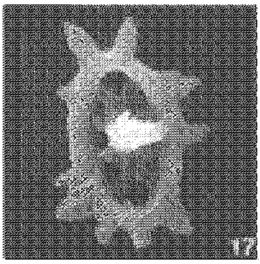

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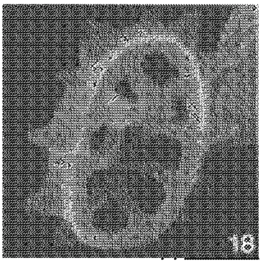

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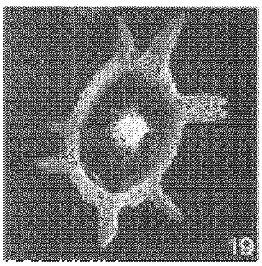

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Plate 4.4

Family STEPHANOLITHIACEAE Black, 1968
Figs 1–2. ***Stradnerlithus clatriatus*** (Rood *et al.*, 1973) Goy, 1979. Distal (1) and side (2) views, Hambühren (Germany), Lower Toarcian, UCL-3622-33/3857-6, x6861/7125. Range: L. Pliensbachian (davoei) – Aalenian (opalinum).

Fig. 3. ***Stradnerlithus comptus*** Black, 1971a. Distal view, Gorodische (Russia), M. Volgian (panderi), UCL-1525-18, x9588. Range: L. Toarcian (?tenuicostatum) – M. Volgian (panderi).

Fig. 4. ***Stradnerlithus fragilis*** (Rood and Barnard, 1972) Perch-Nielsen, 1984. Distal view, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-1499-4, x9363. Range: U. Callovian (lamberti) – M. Volgian (panderi).

Fig. 5. ***Stradnerlithus geometricus*** (Górka, 1957) Bown and Cooper, 1989a. Distal view, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-1502-21, x11333. Range: L. Oxfordian (mariae) – M. Volgian (panderi).

Fig. 6. ***Stradnerlithus* spp.** Hambühren (Germany), Upper Toarcian/Lower Aalenian, UCL-3856-29, x4531.

Fig. 7. ***Stradnerlithus asymmetricus*** (Rood *et al.*, 1971) Medd, 1979. Distal view.

Fig. 8. ***Truncatoscaphus intermedius*** Perch-Nielsen, 1986b. Distal view, Gorodische (Russia), M. Volgian/U. Kimmeridgian (panderi/eudoxus), UCL-1504-28, x11995. Range: U. Kimmeridgian (autissiodorensis) – M. Volgian (panderi).

Order PODORHABDALES Rood *et al.*, 1971 emend. Bown, 1987
Family BISCUTACEAE Black, 1971a
Fig. 9. ***Biscutum depravatum*** (Grün and Zweili, 1980) Bown 1987. Distal view, Brenha (Portugal), Aalenian/Bajocian, UCL-2173-13, x5769. Range: Aalenian? – M. Oxfordian.

Figs 10–11. ***Biscutum dorsetensis*** Varol and Girgis, 1994 Bown comb. nov.. Distal (10) and proximal (11) views, Aylesbury (UK), Bolonian (wheatleyensis), UCL-2635-12/10, x10344/10294. Range: U. Bathonian (discus) – Bolonian (pectinatus).
Basionym: *Palaeopontosphaera dorsetensis* Varol and Girgis, 1994 (*N. Jb. Geol. Paläont. Abh.*, **192**, 221–253, p.243–244, Fig. 8 (A)).

Fig. 12. ***Biscutum dubium*** (Noël, 1965) Grün in Grün *et al.*, 1974. Distal view, Warboys (UK), Oxfordian (mariae), UCL-2212-5, x8963. Range: L. Toarcian (falciferum) – ?Berriasian.

Fig. 13. ***Biscutum finchii*** Crux, 1984. Distal view, Brenha (Portugal), L. Pliensbachian (ibex), UCL-2178-37, x4715. Range: L. Pliensbachian (davoei) – L. Toarcian (falciferum).

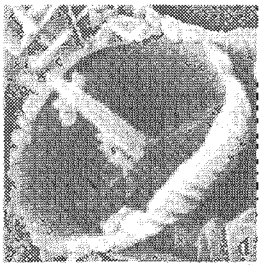
Fig. 14. ***Biscutum grande*** Bown, 1987. Distal view, Brenha (Portugal), L. Pliensbachian (ibex), UCL-2170-15, x4850. Range: U. Pliensbachian (spinatum) – L. Toarcian (falciferum).

Fig. 15. ***Biscutum intermedium*** Bown, 1987. Distal view, Brenha (Portugal), Aalenian/Bajocian, UCL-2173-20, x5800. Range: U. Toarcian (levesquei) – U. Bathonian (discus).

Figs 16–17. ***Biscutum novum*** (Goy, 1979) Bown, 1987. 16, Distal view, Trimeusel (Germany), L. Toarcian (bifrons), UCL-2049-34, x6847; 17, proximal view, Ballrechten (Germany), U. Toarcian (thoursense), UCL-2074-17, x6250. Range: U. Pliensbachian (margaritatus) – U. Bathonian (discus).

Fig. 18. ***Discorhabdus corollatus*** Noël, 1965. Distal oblique view, Villers-sur-mer (France), Oxfordian (mariae), UCL-2027-10, x6287. Range: L. Callovian – U. Tithonian (panderi).

Figs 19–20. ***Discorhabdus criotus*** Bown, 1987. Distal (19) and proximal (20) views, Brenha (Portugal), U. Toarcian, UCL-2178-3/2170-6, x8377/5353. Range: U. Toarcian (variabilis) – M. Oxfordian (densiplicatum).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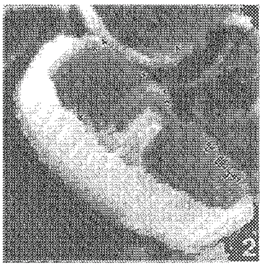
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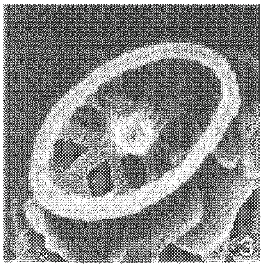
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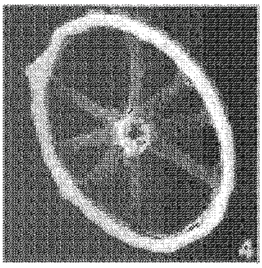
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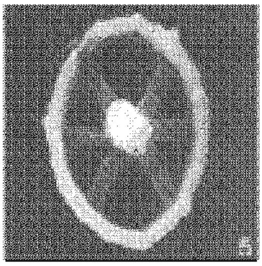
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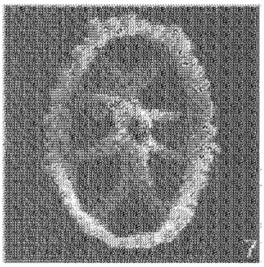
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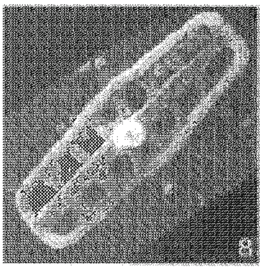
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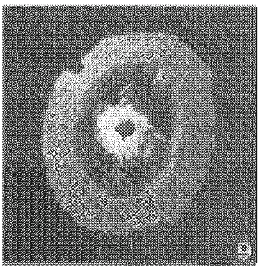
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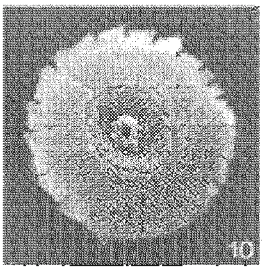
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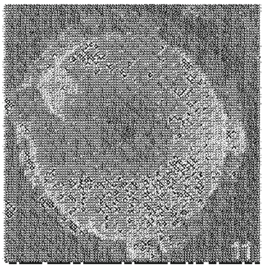
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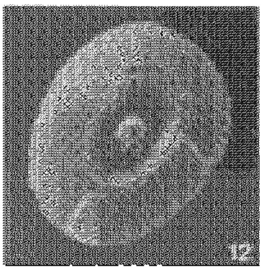
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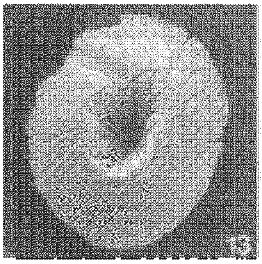
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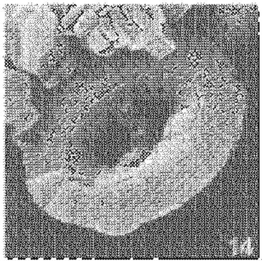
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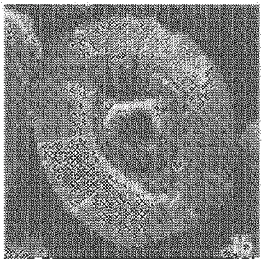
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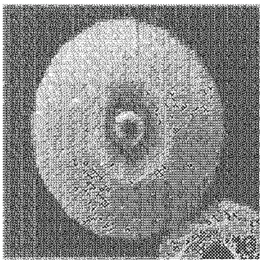
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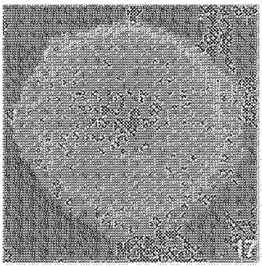
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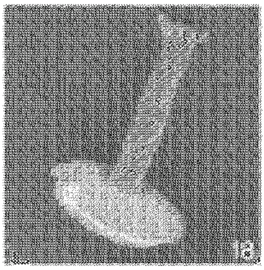
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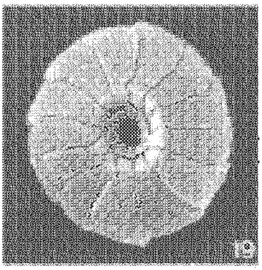
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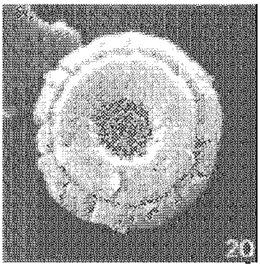
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Plate 4.5

Family BISCUTACEAE Black, 1971a
Fig. 1. ***Discorhabdus ignotus*** (Górka, 1957) Perch-Nielsen, 1968. Distal view, Warboys (UK), Oxfordian (mariae), UCL-2114-22, x8105. Range: Oxfordian? – Maastrichtian.

Fig. 2. ***Discorhabdus striatus*** Moshkovitz and Ehrlich, 1976. Distal view, Brenha (Portugal), L. Pliensbachian (davoei), UCL-2173-36, x4700. Range: L. Toarcian (falciferum) – U. Oxfordian (glosense).

Figs 3–4. ***Similiscutum cruciulus*** de Kaenel and Bergen, 1993. Distal (3) and proximal (4) views, DSDP Site 547 (Atlantic Ocean), L. Pliensbachian, UCL-2199-24/2014-2, x8741/9729. Range: L. Pliensbachian (ibex) – L. Toarcian (tenuicostatum).

Fig. 5. ***Similiscutum ?avitum*** de Kaenel and Bergen, 1993. Distal view, Mochras Borehole (UK), L. Pliensbachian (ibex), UCL-1952-19, x7625. Range: L. Pliensbachian (ibex) – L. Toarcian (tenuicostatum).

Fig. 6–7. ***Sollasites arctus*** (Noël, 1973) Bown, 1987. Distal views, Unterstürmig (Germany), L. Toarcian, UCL-2268-22/2036-7, x6375/8250. Range: ?L. Toarcian.

Fig. 8. ***Sollasites lowei*** (Bukry, 1969) Rood *et al.*, 1971. Distal view, Hambühren (Germany), Lower Toarcian, UCL-3848-17, x8000. Range: L. Pliensbachian (jamesoni)? – ?Campanian.

Family CALYCULACEAE Noël, 1973
Fig. 9. ***Calyculus* sp. indet.**. Distal view, displaying typical rim structure but lacking central area grill, Unterstürmig, (Germany), L. Toarcian, UCL-2034-23, x6150.

Fig. 10. ***Calyculus serrai*** (Goy, 1981) Crux, 1987. Side, proximal and cross-section views, Hambühren (Germany), Upper Toarcian/Lower Aalenian, UCL-3889-37, x4800. Range: L. Toarcian – Aalenian.

Fig. 11. ***Calyculus cribrum*** Noël, 1973. Distal and proximal views, Hambühren (Germany), L. Toarcian, UCL-3781-26, x6000. Range: U. Pliensbachian (spinatum)? – L. Bajocian (sauzei).

Fig. 12. ***Calyculus noeliae*** (Goy, 1979) Crux, 1987. Distal, side and cross-section views, Hambühren (Germany), L. Toarcian, UCL-3848-12, x6513. Range: ?L. Toarcian.

Figs 13–14. ***Carinolithus magharensis*** (Moshkovitz and Ehrlich, 1976) Bown, 1987. Side (13) and distal (14) views of the same specimen, Brenha (Portugal), Aalenian/Bajocian, UCL-2173-16/15, x3685/5200. Range: Aalenian? – U. Bajocian (subfurcatum).

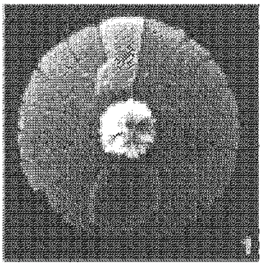
Figs 15–16. ***Carinolithus superbus*** (Deflandre *in* Deflandre and Fert, 1954) Prins *in* Grün *et al.*, 1974. Side (15) and proximal oblique (16) views of the same specimen, Ilminster (UK), Toarcian, UCL-2616-33/31, x3816/5416. Range: L. Toarcian (falciferum) – L. Bajocian (humphresianum).

Family CRETARHABDACEAE Thierstein, 1973
Fig. 17. ***Cretarhabdus conicus*** Bramlette and Martini, 1964. Distal view, Aylesbury (UK), Bolonian (wheatleyensis), UCL-2635-5, x7789. Range: U. Kimmeridgian (eudoxus) – Maastrichtian.

Fig. 18. ***Polypodorhabdus escaigii*** Noël, 1965. Distal view, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-1520-22, x5715. Range: Aalenian (opalinum) – ?Albian.

Fig. 19. ***Retecapsa incompta*** Bown, 1987. Brenha (Portugal), Aalenian/Bajocian, UCL-2622-33, x5666. Range: U. Toarcian (levesquei) – ?M. Oxfordian.

Fig. 20. ***Retecapsa* cf. *R. schizobrachiata*** (Gartner, 1968) Grün *in* Grün and Allemann, 1975 Distal view, Gorodische (Russia), U. Kimmeridgian (eudoxus), UCL-1502-5, x6900. Range: L. Callovian (macrocephalus) – Maastrichtian. Originally described from the Upper Cretaceous (Campanian – Maastrichtian); these Jurassic forms are smaller, more delicate, and may not represent the same species.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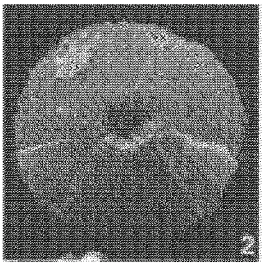
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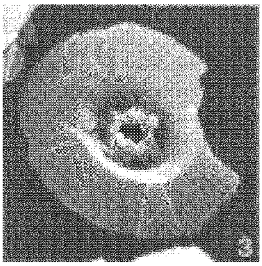
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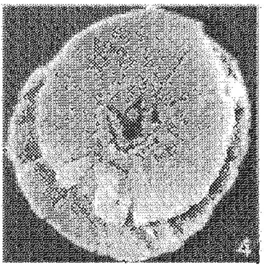
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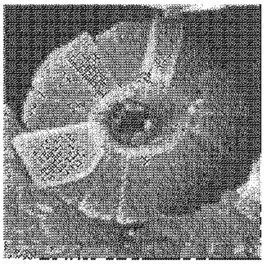

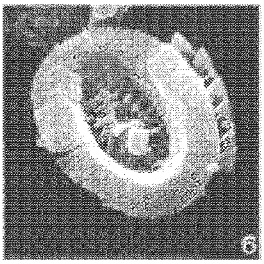
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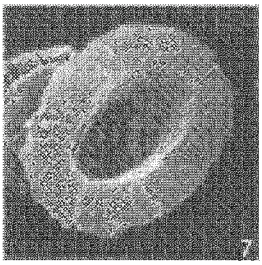
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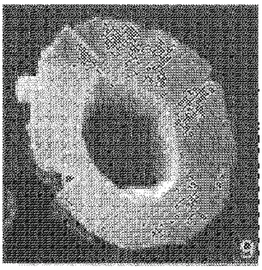
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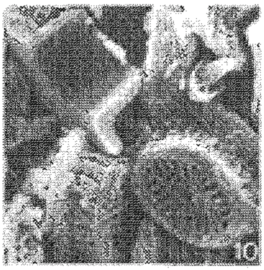
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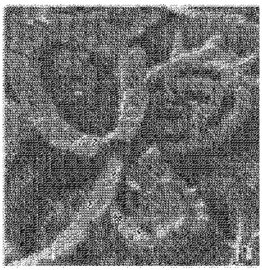
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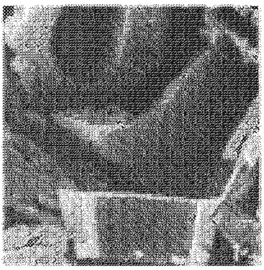
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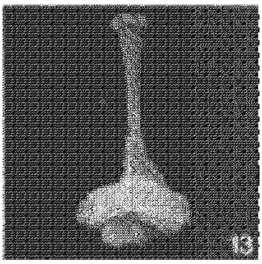
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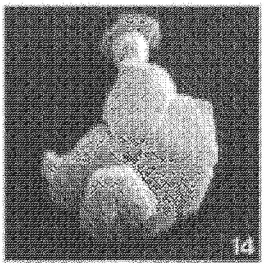
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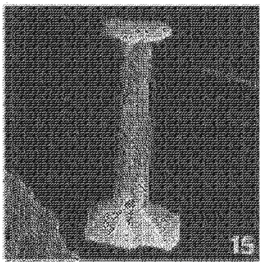
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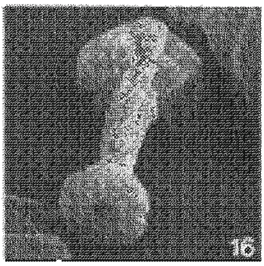
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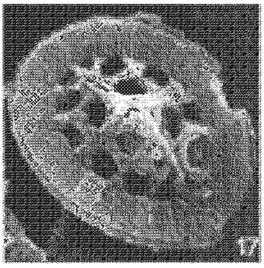
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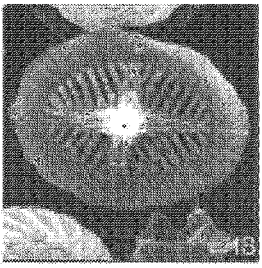
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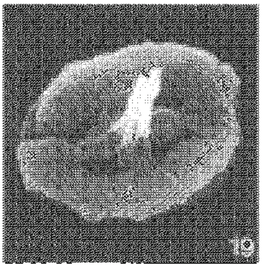
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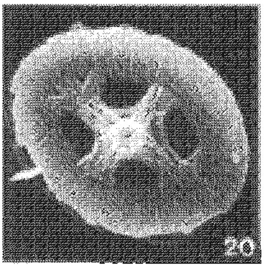
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Plate 4.6

Family MAZAGANELLACEAE Bown, 1987
Figs 1–3. ***Mazaganella protensa*** Bown, 1987. Distal (1), side (2) and proximal views (3), DSDP Site 547 (Atlantic Ocean), L. Pliensbachian, UCL-2007-33/31/22, x4900. Range: L. Pliensbachian (?jamesoni – ?spinatum).

Figs 4–5. ***Mazaganella pulla*** Bown, 1987. Distal (4) and proximal (5) views, DSDP Site 547 (Atlantic Ocean), Sinemurian, UCL-2049-36/2046-7, x7950/6200. Range: U. Sinemurian (?obtusus) – ?L. Pliensbachian (?davoei).

Figs 6–8. ***Triscutum beaminsterensis*** Dockerill, 1987. Distal (6), proximal (7) and side (8) views, Dorset (UK), Bathonian (zigzag), UCL-1894-29/1891-23/2048-5, x3350/3650/4100. Range: L. Bathonian (zigzag) – M. Oxfordian (tenuiserratum).

Figs 9–10. ***Triscutum expansus*** (Medd, 1979) Dockerill, 1987. Distal (9) and distal oblique (10) views, Warboys (UK), Oxfordian (mariae), UCL-1921-13/20, x4625/4160. Range: Aalenian? – ?Kimmeridgian.

Figs 11–12. ***Triscutum sullivanii*** de Kaenel and Bergen, 1993. Distal (11) and side (12) views of same specimen, Picun Leufu (Argentina), U. Toarcian/L. Aalenian, UCL-2065-13/12, x3750. Range: Aalenian (murchisonae) – L. Bajocian (sauzei).

Family AXOPODORHABDACEAE Bown and Young, 1997
Fig. 13. ***Axopodorhabdus atavus*** (Grün *et al.*, 1974) Bown, 1987. Distal view, Hambühren (Germany), Lower Toarcian, UCL-3889-1, x6450. Range: U. Pliensbachian (spinatum) – ?L. Tithonian (?pallasioides).

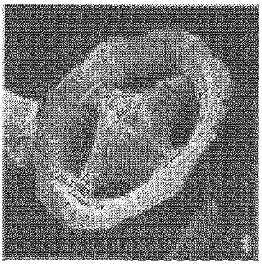
Figs 14–15. ***Axopodorhabdus cylindratus*** (Noël, 1965) Wind and Wise *in* Wise and Wind, 1977. 14, Distal view, Roslyn Pit (UK), U. Kimmeridgian (?eudoxus), UCL-1411-20, x4047; 15, Distal view, Villers-sur-mer (France), Oxfordian (densiplicatum), 2039-16, x4341. Range: U. Pliensbachian (spinatum) – ?L. Tithonian (?pallasioides).

Fig. 16. ***Axopodorhabdus rahla*** (Noël, 1965) Grün and Zweili, 1980. Side view, Warboys (UK), Oxfordian (mariae), UCL-1921-18, x4530. Range: L. Callovian (macrocephalus) – M. Oxfordian (tenuiserratum).

Fig. 17. ***Ethmorhabdus anglicus*** Rood *et al.*, 1971. Distal view, Dorset (UK), Bathonian (zigzag), UCL-2207-24, x6860. Range: L. Oxfordian (mariae) – ?U. Tithonian (?fittoni).

Fig. 18. ***Ethmorhabdus crucifer*** Noël, 1965. Distal view, Hambühren (Germany), Lower Toarcian, UCL-3620-24, x5166. Range: L. Toarcian (?tenuicostatum – falciferum).

Figs 19–20. ***Ethmorhabdus gallicus*** Noël, 1965. Distal (19) and proximal (20) views. 19, Roslyn Pit (UK), U. Kimmeridgian (?eudoxus), UCL-1411-18, x4268. 20, Aylesbury (UK), Bolonian (wheatleyensis), UCL-2634-11, x4789. Range: L. Toarcian (falciferum) – U. Tithonian (?fittoni).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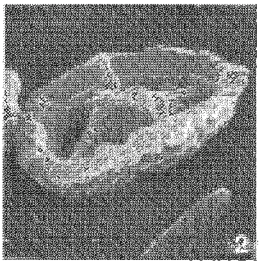
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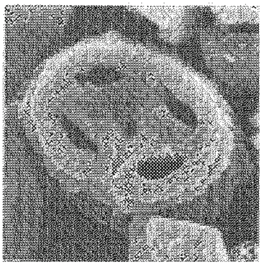
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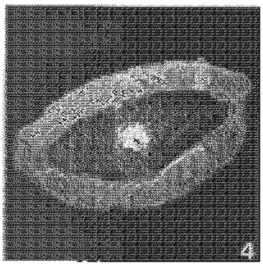
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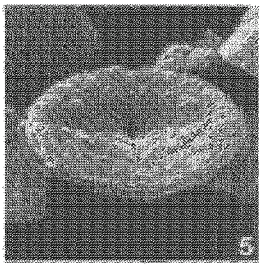
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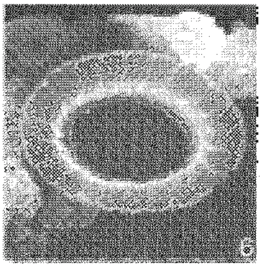
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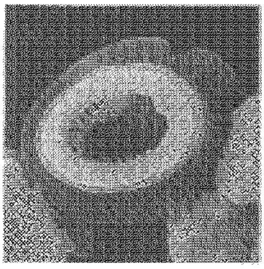

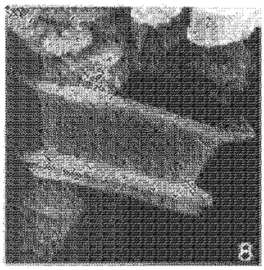
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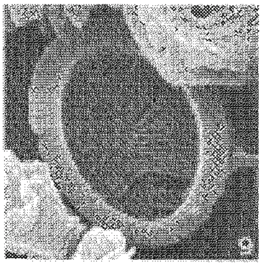
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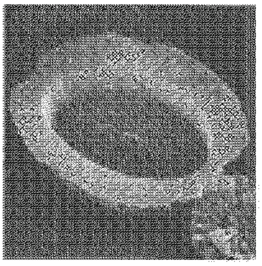

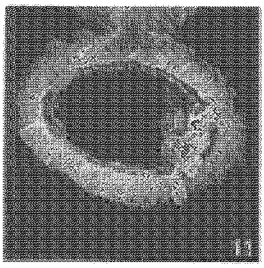
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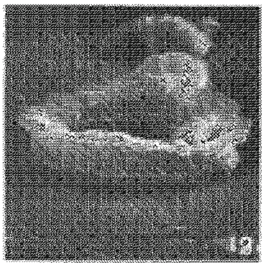
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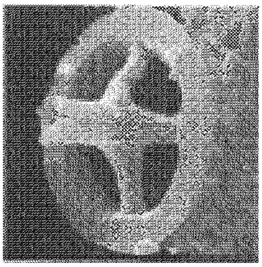

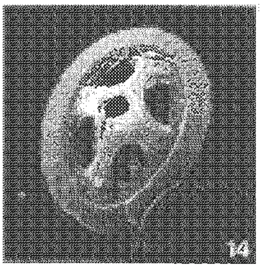
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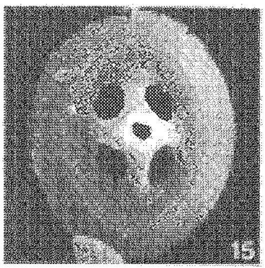
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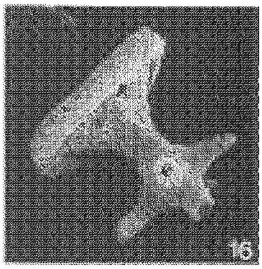
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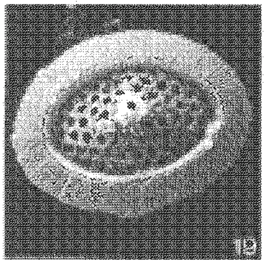
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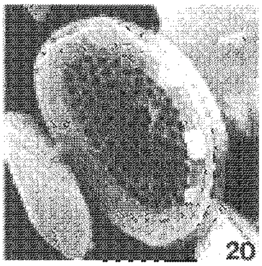
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Plate 4.7

Family AXOPODORHABDACEAE Bown and Young, 1997
Figs 1–2. ***Hexapodorhabdus cuvillieri*** Noël, 1965. Distal (1) and proximal (2) views, Villers-sur-mer (France), L. Oxfordian (cordatum/mariae), UCL-1903-2/2207-7, x7750/6450. Range: U. Bajocian (parkinsoni) – U. Kimmeridgian (autissiodorensis).

Figs 3–4. ***Octopodorhabdus decussatus*** (Manivit, 1961) Rood *et al.*, 1971. Distal (2) and proximal (3) views. 1, Warboys (UK), Oxfordian (mariae), UCL-1921-7, x5240; 2, Dorset (UK), Bathonian (zigzag), UCL-1891-13, x7120. Range: L. Bathonian (zigzag) – L. Oxfordian (cordatum).

Figs 5–7. ***Podorhabdus grassei*** Noël, 1965. Distal (5), side (6) and proximal oblique (7) views. 5, Dorset (UK), Bathonian (zigzag), UCL-1891-2, x5250; 6-7, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-1502-13/14, x4320. Range: L. Bajocian (discus) – L. Tithonian (scitulus).

Fig. 8. ***Tetrapodorhabdus shawensis*** Medd, 1979. Distal view, Dorset (UK), Bathonian (zigzag), UCL-1891-12, x7350. Range: U. Bajocian (parkinsoni) – U. Bathonian (hodsoni).

Order WATZNAUERIALES Bown, 1987
Family WATZNAUERIACEAE Rood *et al.*, 1971
Figs 9–10. ***Ansulasphaera helvetica*** Grün and Zweili, 1980. Distal (9) and proximal oblique (10) views. 9, Denver Borehole (UK), Callovian (athleta), UCL-2166-9, x9250; 10, Clapgate Farm (UK), Callovian (athleta), UCL-1912-2, x7885. Range: U. Bathonian (aspidoides) – U. Callovian (lamberti).

Figs 11–12. ***Bussonius prinsii*** (Noël, 1973) Goy, 1979. Distal (11) and distal oblique (12) views of the same specimen, Ilminster (UK), Toarcian, UCL-2615-9/10, x6483. Range: L. Pliensbachian (jamesoni) – Aalenian (murchisonae).

Fig. 13. ***Cyclagelosphaera margerelii*** Noël, 1965. Coccosphere, DSDP Site 105 (N Atlantic Ocean), Oxfordian, UCL-509-22, x2689. Range: U. Bajocian (parkinsoni) – L. Paleocene.

Fig. 14. ***Cyclagelosphaera tubulata*** (Grün and Zweili, 1980) Cooper, 1987. Distal view, Roslyn Pit (UK), U. Kimmeridgian (?eudoxus), UCL-1465-14, x6010. Range: U. Bajocian (parkinsoni) – M. Volgian (fittoni).

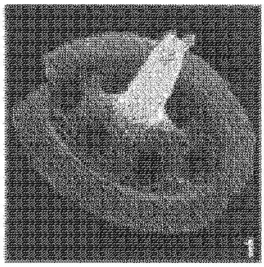
Fig. 15. ***Lotharingius barozii*** Noël, 1973. Distal views on coccosphere, Hambühren (Germany), Lower Toarcian, UCL-3848-34, x5750. Range: L. Toarcian (tenuicostatum) – ?Aalenian.

Fig. 16–17. ***Lotharingius contractus*** Bown and Cooper, 1989a. Brenha (Portugal), Aalenian/Bajocian, UCL-2645-34/2622-2, x4513/4642. Range: Aalenian (murchisonae) – L. Callovian (macrocephalus).

Fig. 18. ***Lotharingius crucicentralis*** (Medd, 1971) Grün and Zweili, 1980. Distal view, Ilminster, Dorset (UK), Toarcian, UCL-2616-11, x6956. Range: L. Toarcian (tenuicostatum) – U. Oxfordian (regulare).

Fig. 19. ***Lotharingius hauffii*** Grün and Zweili *in* Grün *et al.*, 1974. Collapsed coccosphere, Unterstürmig (Germany), L. Toarcian, UCL-2034-10, x2425. Range: U. Pliensbachian (margaritatus) – U. Bathonian (discus).

Fig. 20. ***Lotharingius sigillatus*** (Stradner, 1961) Prins *in* Grün *et al.*, 1974. Distal view, Trimeusel (Germany), Lower Toarcian (bifrons), UCL-2049-13, x5940. Range: U. Pliensbachian (spinatum) – M. Oxfordian (tenuiserratum).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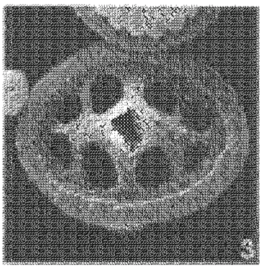
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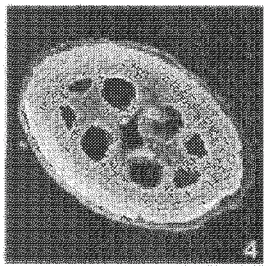
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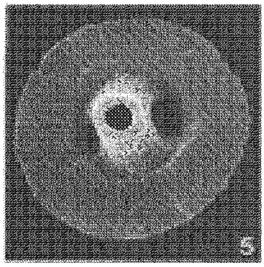
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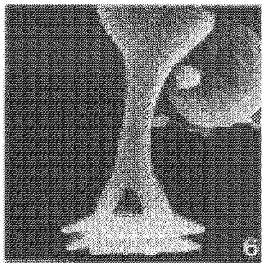
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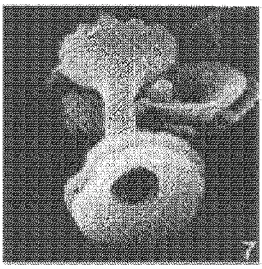
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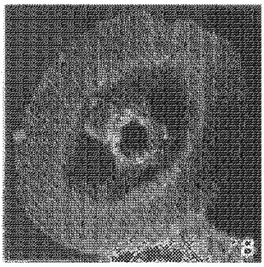
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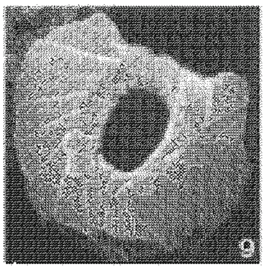
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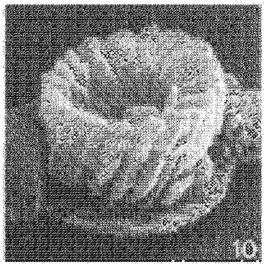
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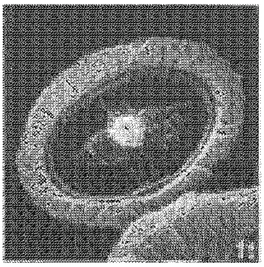
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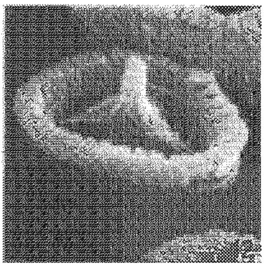
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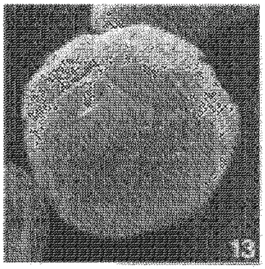
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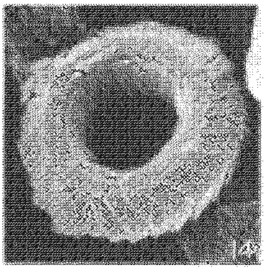
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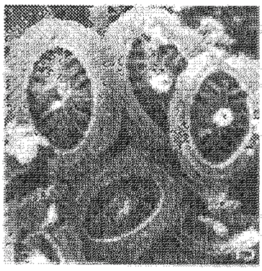
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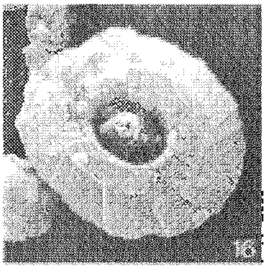
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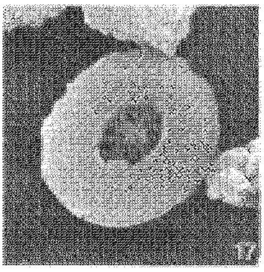
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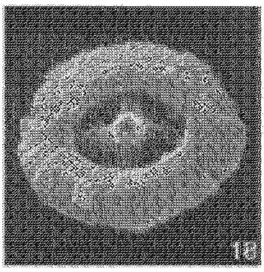
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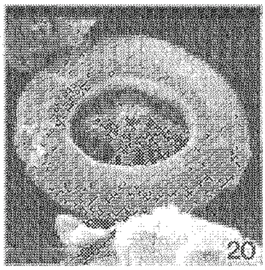
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Plate 4.8

Family WATZNAUERIACEAE Rood *et al.*, 1971
Fig. 1. ***Lotharingius velatus*** Bown and Cooper, 1989a. Distal view, St. Honorine (France), Bajocian, UCL-2689-25, x5500. Range: Aalenian (concavum) – L. Callovian (macrocephalus).

Fig. 2. ***Watznaueria barnesae*** (Black, 1959) Perch-Nielsen, 1968. Distal view, St. Honorine (France), Bajocian (humphresianum-parkinsoni), UCL-2689-7, x4080. Range: L. Bajocian (laeviuscula) – Maastrichtian.

Figs 3–6. ***Watznaueria britannica*** (Stradner, 1963) Reinhardt, 1964. 3, coccosphere, Clapgate Farm (UK), Callovian (athleta), UCL-1912-5, x3150; 4-6, distal (4), distal oblique (5) and proximal (6) views, Aylesbury (UK), Bolonian (wheatleyensis), UCL-2635-21/23/2634-5, x~5000. Range: L. Bajocian (laeviuscula) – L. Cenomanian.

Fig. 7. ***Watznaueria fossacincta*** (Black, 1971a) Bown *in* Bown and Cooper, 1989a. Coccosphere, Gorodische (Russia), M. Volgian (panderi), UCL-1513-4, x3350. Range: L. Bajocian (laeviuscula) – Maastrichtian.

Fig. 8. ***Watznaueria manivitiae*** Bukry, 1973d. Distal view, DSDP Site 261 (Indian Ocean), L. Tithonian, UCL-3000-33, x2200. Range: L. Callovian (macrocephalus) – U. Maastrichtian.

Family CALYPTROSPHAERACEAE Boudreaux and Hay, 1969
Figs 9–10. ***Anfractus harrisonii*** Medd, 1979. 9, distal view, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-1506-20, x8905; 10, proximal view, Villers-sur-mer (France), L. Oxfordian (mariae), UCL-2207-15, x8750. Range: Aalenian (?opalinum) – Kimmeridgian (autissiodorensis).

Fig. 11. ***Anfractus youngii*** Bown, 1993. Side view, Hambühren (Germany), Lower Toarcian, UCL-3889-9, x10000. Range: L. Toarcian (falciferum) – Aalenian (?opalinum).

Fig. 12. ***Pseudoconus enigma*** Bown and Cooper, 1989b. Side view, Dorset (UK), U. Bathonian (aspidoides), UCL-2512-11, x5675. Range: U. Bajocian (parkinsoni) – L. Callovian (macrocephalus).

NANNOLITHS

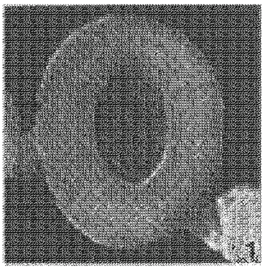
Family EOCONUSPHAERACEAE Krystan-Tollmann, 1988a
Figs 13–15. ***Conusphaera mexicana*** Trejo, 1969 ssp. ***mexicana***. Side (13), distal (14) and proximal (15) views, DSDP Site 534 (N Atlantic Ocean), Tithonian, UCL-1652-2/1976-20/19, x3677/4530/4850. Range: L. Tithonian (?u. hybonotum) – L. Aptian.

Family NANNOCONACEAE Deflandre, 1959
Fig. 16. ***Nannoconus compressus*** Bralower and Thierstein *in* Bralower *et al.*, 1989. Side view, DSDP Site 534 (N Atlantic Ocean), Tithonian, UCL-1671-1, x6000. Range: L. Tithonian – L. Berriasian.

?Family POLYCYCLOLITHACEAE Forchheimer, 1972 emend. Varol, 1992
Fig. 17. ***Hexalithus noeliae*** Loeblich and Tappan, 1966. DSDP Site 534 (N Atlantic Ocean), Tithonian, UCL-1744-17, x7000. Range: U. Tithonian – L. Berriasian.

Family SCHIZOSPHAERELLACEAE Deflandre, 1959
Fig. 18–19. ***Schizosphaerella punctulata*** Deflandre and Dangeard, 1938. Side view (18) and ultrastructure detail (19). 18, Trimeusel (Germany), U. Toarcian (levesquei), UCL-2052-12, x3064; 19, Hambühren (Germany), Lower Toarcian, UCL-3857-8, x9680. Range: L. Hettangian (?planorbis) – ?U. Bathonian (discus).

INCERTAE SEDIS NANNOLITHS
Fig. 20. ***Orthogonoides hamiltoniae*** Wiegand, 1984. DSDP Site 547 (Atlantic Ocean), L. Pliensbachian, UCL-2028-22, x4920. Range: U. Sinemurian (oxynotum) – L. Toarcian (falciferum).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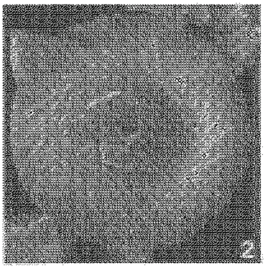
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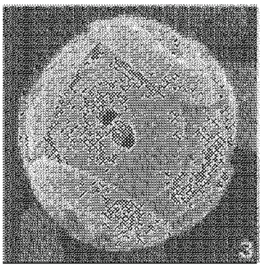
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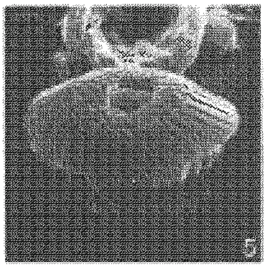
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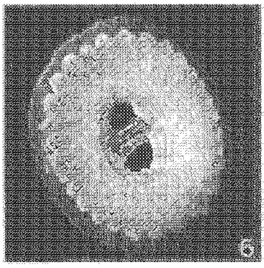
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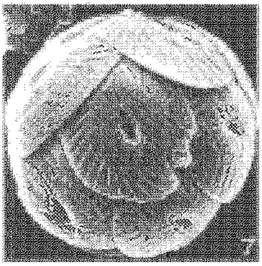
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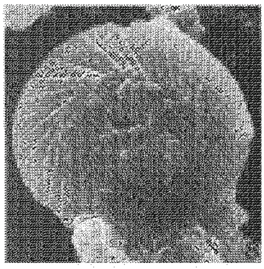
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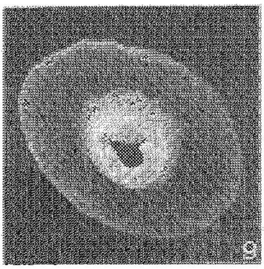
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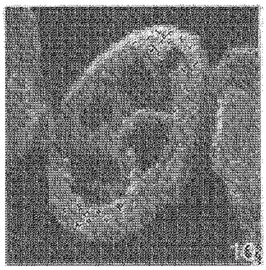
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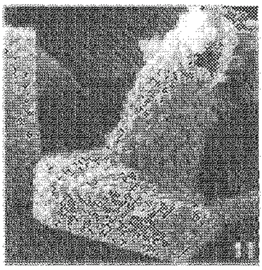
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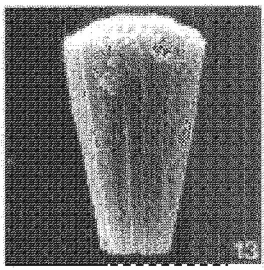
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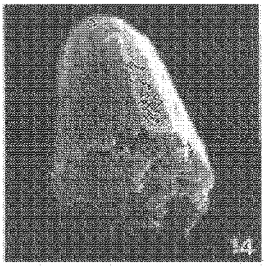
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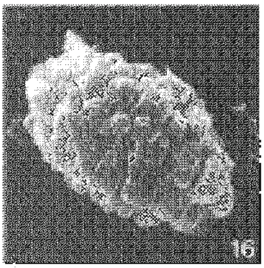
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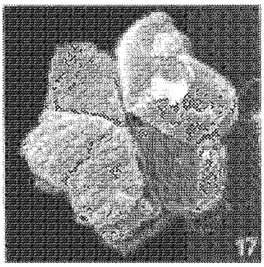
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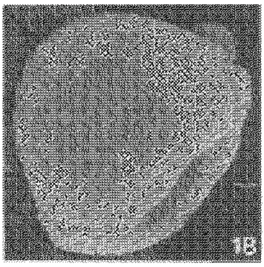
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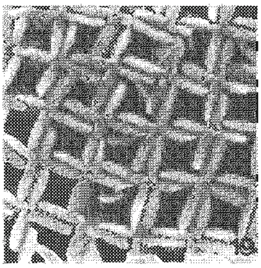
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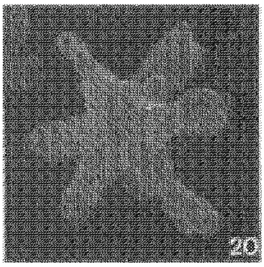
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Plate 4.9

Order EIFFELLITHALES Rood *et al.*, 1971

Family CHIASTOZYGACEAE Rood *et al.*, 1973 emend. Varol and Girgis, 1994

Figs 1–2. ***Crepidolithus crassus*** (Deflandre *in* Deflandre and Fert, 1954) Noël, 1965. XPL (1) and PC (2), Trimeusel, (Germany), L. Toarcian (bifrons), UCL-5625-9/10.

Figs 3–5. ***Crepidolithus granulatus*** Bown, 1987. XPL (2, 3) and PC (4), Brenha (Portugal), L. Plienbachian (davoei), UCL-5627-13/19/20.

Figs 6–7. ***Crepidolithus impontus*** (Grün *et al.*, 1974) Goy, 1979. XPL (6) and PC (7), Hambühren (Germany), Aalenian, UCL-5626-20/19.

Figs 8–10. ***Crepidolithus perforata*** (Medd, 1979) Grün and Zweili, 1980. XPL (8, 10) and PC (9). 8-9, BGS Denver Borehole (UK), Callovian (athleta), UCL-5563-14/13; 10, Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-19.

Figs 11–12. ***Crepidolithus pliensbachensis*** Crux, 1985. XPL (11) and PC (12), Timor, L. Pliensbachian, UCL-5625-32/31.

Figs 13–15. ***Crepidolithus timorensis*** (Krystan-Tollmann, 1988a) Bown comb. nov.. XPL (13, 15) and PC (14), 14 is side view, Timor, Sinemurian, UCL-5630-18/19/16. Basionym given in Pl. 4.1.

Figs 16–17. ***Tubirhabdus patulus*** Rood *et al.*, 1973. Small morphotype, XPL (16) and PC (17), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-13/14.

Figs 18–19. ***Tubirhabdus patulus*** Rood *et al.*, 1973. Large morphotype, XPL (18) and PC (19), Port en Bessin (N France), L. Bathonian (tenuiplicatus), UCL5628-5/6.

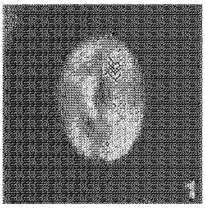
Fig. 20. ***Staurolithites leptostaurus*** (Cooper, 1987a) Bown comb. nov.. PC, Gorodische (Russia), Volgian (panderi), UCL-5628-32. Range: Kimmeridgian (eudoxus) – M. Volgian (panderi).
Basionym: *Chiastozygus leptostaurus* Cooper, 1987 (*N. Jb. Geol. Paläont. Mh.*, **1987**, H10, 606–612, p. 611, Fig. 1.1).

Figs 21–25. ***Staurolithites lumina*** Bown sp. nov.. XPL (21, 23) and PC (22, 24, 25), Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-5628-28/29/25/26, UCL-5638-33.

Fig. 26. ***Staurolithites* cf. *S. lumina*** Bown sp. nov.. XPL (unicyclic rim), Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-5631-18.

Figs 27–28. ***Staurolithites quadriarculla*** (Noël, 1965) Wilcoxon, 1972. XPL (27) and PC (28), Hambühren (Germany), Aalenian, UCL-5626-21/22.

Figs 29-30. ***Staurolithites quadriarculla*** (Noël, 1965) Wilcoxon, 1972. XPL (29) and PC (30), Gorodische (Russia), M. Volgian (panderi), UCL-5629-1/2.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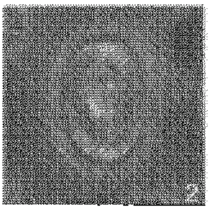
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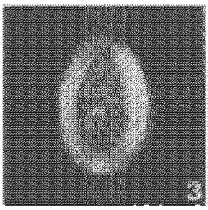
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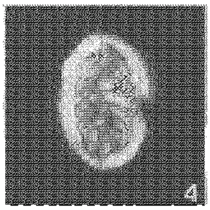
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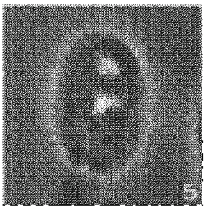
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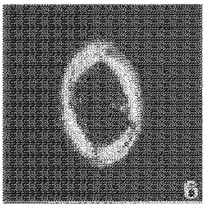
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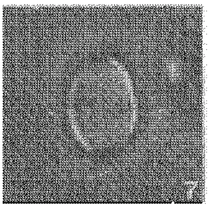
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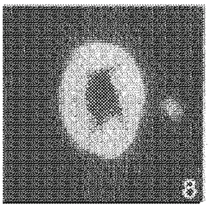
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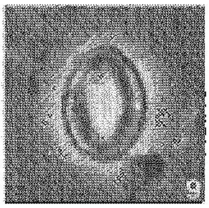
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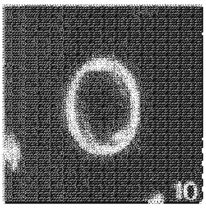
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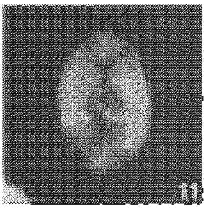
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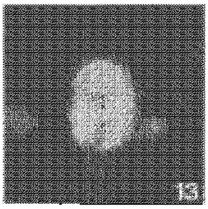
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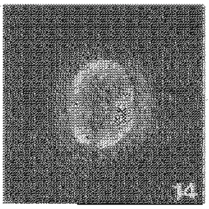
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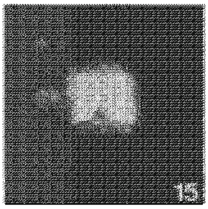
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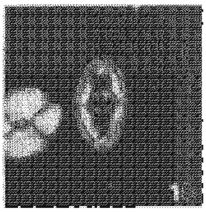
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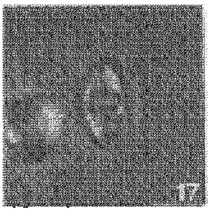
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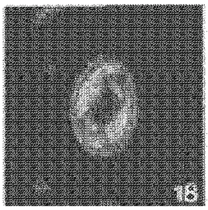
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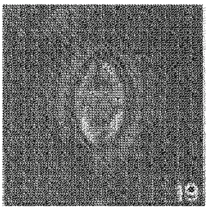
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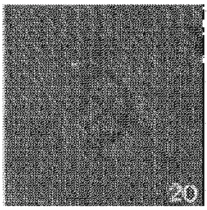
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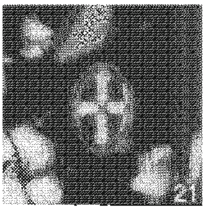
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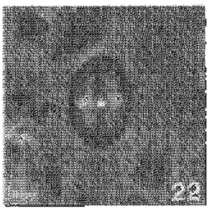
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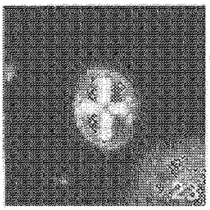
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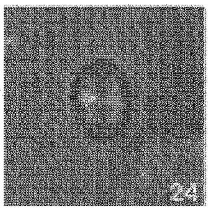
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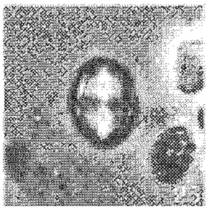
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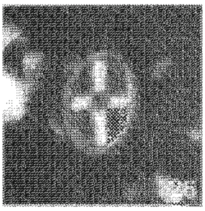
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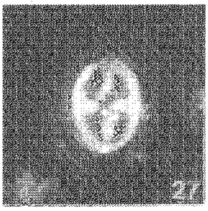
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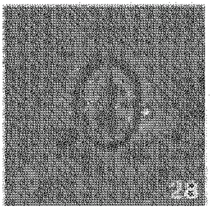
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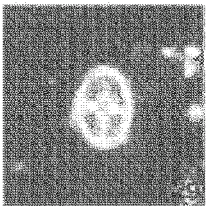
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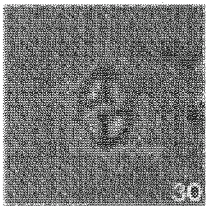
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Plate 4.10

Family CHIASTOZYGACEAE Rood *et al.*, 1973 emend. Varol and Girgis, 1994
Figs 1–3. ***Zeugrhabdotus cooperi*** Bown, 1992b. Distal (1, 2, XPL and PC different specimens) and side (3, XPL) views, DSDP Site 261 (Indian Ocean), Berriasian, UCL-5631-8/10/5630-11.

Figs 4–5. ***Zeugrhabdotus embergeri*** (Noël, 1959) Perch-Nielsen, 1984. XPL (4) and PC (5), DSDP Site 261 (Indian Ocean), Berriasian, UCL-5631-12/13.

Figs 6–10. ***Zeugrhabdotus erectus*** (Deflandre *in* Deflandre and Fert, 1954) Reinhardt, 1965. XPL (6, 9) and PC (7, 8, 10). 6-8, Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-33/34, UCL-5331-19; 9-10, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-5628-33/34.

Figs 11–12. ***Zeugrhabdotus fissus*** Grün and Zweili, 1980. XPL (11) and PC (12), Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-5560-4, UCL-5628-22. Range: M. Oxfordian – ?U. Valanginian.

Order STEPHANOLITHIALES Bown and Young, 1997
Family PARHABDOLITHACEAE Bown, 1987
Fig. 13. ***Bucanthus decussatus*** Bown, 1987. XPL, Timor, L. Pliensbachian, UCL-5652-23. Range: ?L. Pliensbachian.

Figs 14–15. ***Crucirhabdus primulus*** Rood *et al.*, 1973. XPL (14) and PC (15), Timor, L. Pliensbachian, UCL-5626-6/5.

Figs 16–17. ***Diductius constans*** Goy, 1979. XPL (16) and PC (17), Brenha (Portugal), Aalenian/Bajocian, UCL-5626-25/26.

Figs 18–20. ***Mitrolithus elegans*** Deflandre *in* Deflandre and Fert, 1954. XPL side view with spine (18); XPL plan view without spine (19) and isolated spine in XPL plan view (20), Timor, L. Pliensbachian, UCL-5626-1/5625-35/5652-18.

Figs 21–23. ***Mitrolithus jansae*** (Wiegand, 1984b) Bown *in* Young *et al.*, 1986. XPL (21) and PC (22) of tall morphotype; XPL (23) of short morhotype, DSDP Site 547 (Atlantic Ocean), U. Sinemurian, UCL-5627-23/24/25.

Figs 24–25. ***Mitrolithus lenticularis*** Bown, 1987. XPL (24) and PC (25), Timor, L. Pliensbachian, UCL-5626-3/4.

Figs 26–29. ***Parhabdolithus liasicus*** Deflandre *in* Grassé, 1952 ssp. ***distinctus*** Bown, 1987. Plan view XPL (26) and PC (27); side view XPL (28) and PC (29), Timor, L. Pliensbachian, UCL-5652-16/17/5625-21/22.

Figs 30–31. ***Parhabdolithus liasicus*** Deflandre *in* Grassé, 1952 ssp. ***liasicus***. Side view XPL (30) and PC (31), Timor, L. Pliensbachian, UCL-5625-27/28.

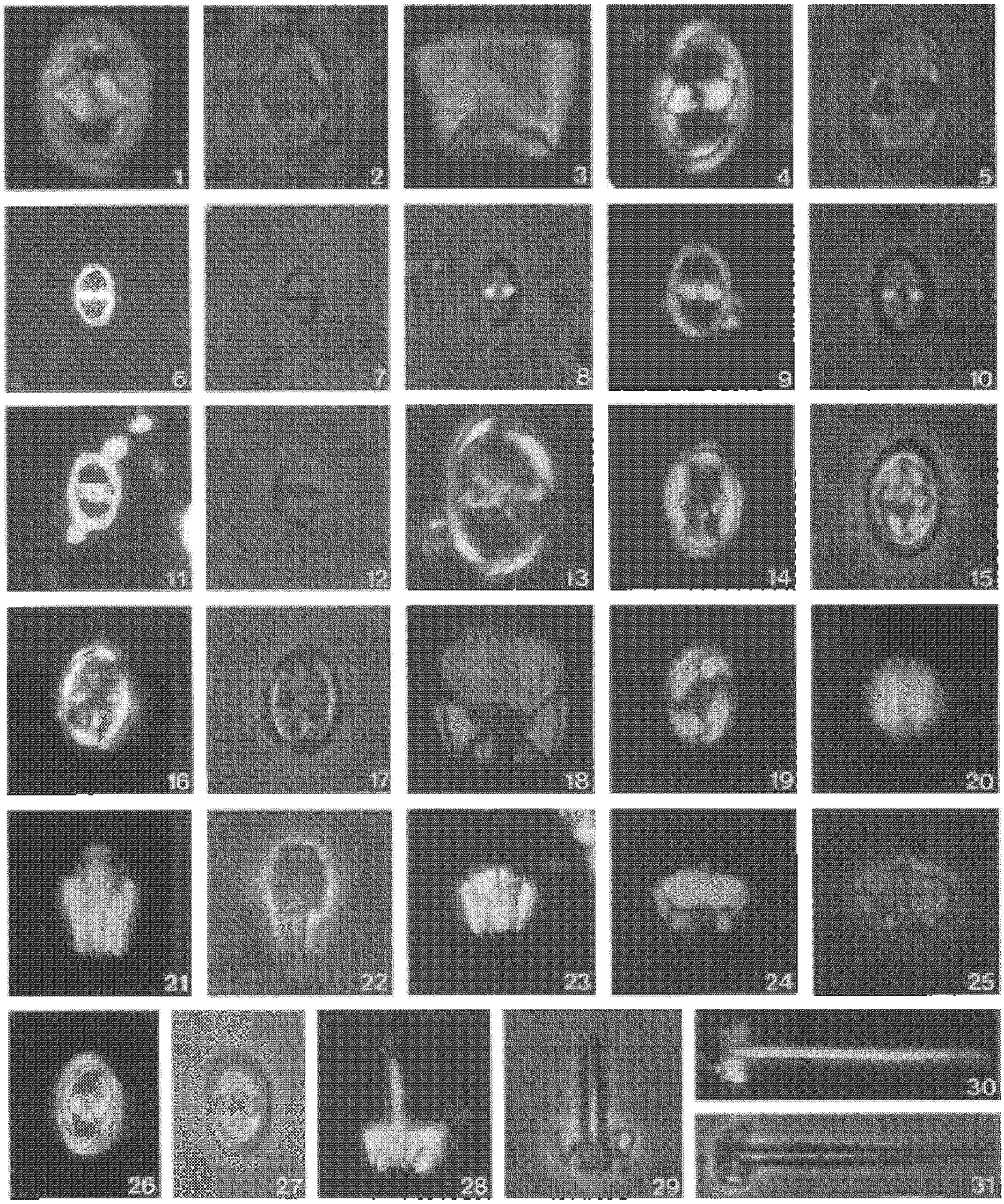
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Plate 4.11

Family PARHABDOLITHACEAE Bown, 1987
Figs 1–2. ***Parhabdolithus marthae*** Deflandre *in* Deflandre and Fert, 1954. Side view XPL (1) and PC (2, different specimen), Hock Cliff (UK), L. Sinemurian (bucklandi), UCL-5627-30/5545-7.

Fig. 3. ***Parhabdolithus robustus*** Noël, 1965. Side view XPL, Timor, L. Pliensbachian, UCL-5626-33.

Figs 4–5. ***Timorella cypella*** Bown, 1987. Side view XPL (4) and PC (5), Timor, L. Pliensbachian, UCL-5626-7/8.

Figs 6–7. ***Umbria granulosa*** Bralower and Thierstein *in* Bralower *et al.*, 1989. XPL (6) and PC (7, different specimen), DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5630-6/5564-28. Range: U. Tithonian – U. Berriasian.

Family STEPHANOLITHIACEAE Black, 1968
Figs 8–10. ***Stephanolithion atmetos*** Cooper, 1987a. XPL (8) and PC (9, 10, latter different specimen), Gorodische (Russia), M. Volgian (panderi), UCL-5628-35/36/5560-25.

Figs 11–13. ***Stephanolithion bigotii*** Deflandre, 1939 ssp. ***bigotii***. XPL (11) and PC (12, 13, latter different specimen), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-27/28/5331-29.

Figs 14–15. ***Stephanolithion bigotii*** Deflandre, 1939 ssp. ***maximum*** Medd, 1979. XPL (14) and PC (15, different specimen), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-24/5331-28.

Figs 16–17. ***Stephanolithion brevispinus*** (Wind and Wise *in* Wise, 1988) Bown stat. nov.. Large morphotype, XPL (16) and PC (17), Gorodische (Russia), L. Volgian (klimovi), UCL-5629-13/12.

Figs 18–19. ***Stephanolithion brevispinus*** (Wind and Wise *in* Wise, 1988) Bown stat. nov.. Large, narrow morphotype (approaching *S. atmetos* outline), XPL (18) and PC (19), Gorodische (Russia), L. Volgian (klimovi), UCL-5629-10/11.

Fig. 20. ***Stephanolithion brevispinus*** (Wind and Wise *in* Wise, 1988) Bown stat. nov. Small morphotype, PC, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-5560-6.

Figs 21–22. ***Stephanolithion hexum*** Rood and Barnard, 1972. XPL (21) and PC (22), Escoville (N France), Callovian (macrocephalus), UCL-5628-15/14.

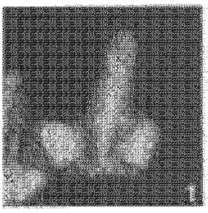
Figs 23–24. ***Stephanolithion speciosum*** Deflandre *in* Deflandre and Fert, 1954 ssp. ***octum*** Rood and Barnard, 1972. XPL (23) and PC (24), Port en Bessin (N France), L. Bathonian (tenuiplicatus), UCL-5628-7/8.

Fig. 25. ***Stephanolithion speciosum*** Deflandre *in* Deflandre and Fert, 1954 ssp. ***speciosum***. PC, Watton Cliff (S England), U. Bathonian (aspidoides), UCL-5628-4.

Figs 26–27. ***Stradnerlithus clatriatus*** (Rood *et al.*, 1973) Goy, 1979. XPL (26, the bright image is an artefact of the photograph; this species is inconspicuous in XPL but does exhibit a distinctive flaring rim image and occasionally the major cross-bars are visible), Hambühren (Germany), Aalenian, UCL-5545-27/5626-17.

Fig. 28. ***Stradnerlithus comptus*** Black, 1971a. PC, Gorodische (Russia), M. Volgian (panderi), UCL-5631-16.

Figs 29–30. ***Stradnerlithus fragilis*** (Rood and Barnard, 1972) Perch-Nielsen, 1984. PC, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-5628-27/5560-16.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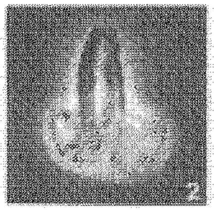
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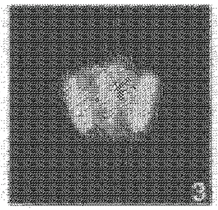
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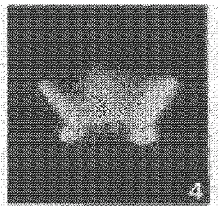
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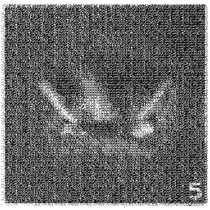
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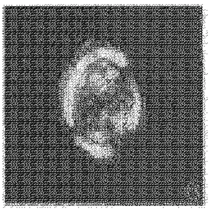
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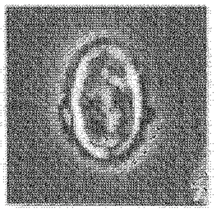
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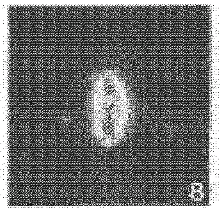
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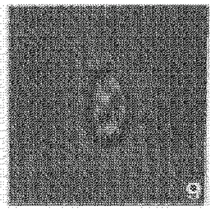
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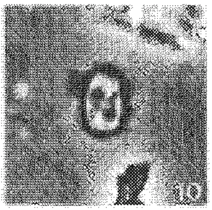
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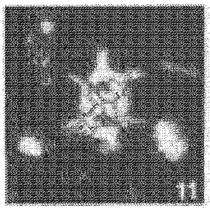
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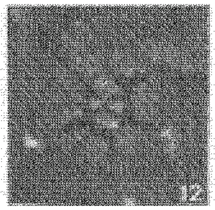
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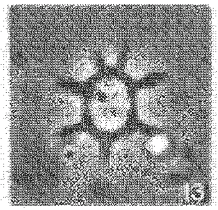
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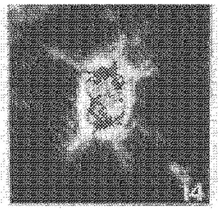
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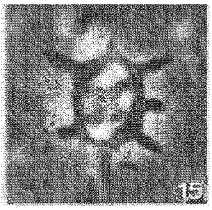
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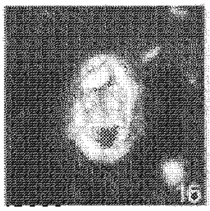
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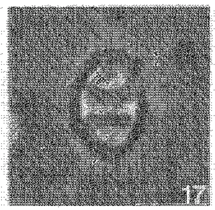
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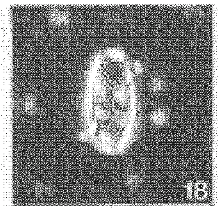
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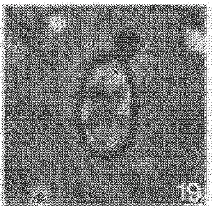
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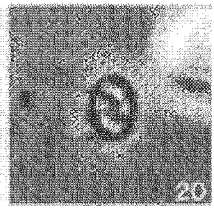
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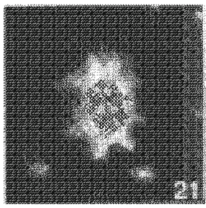
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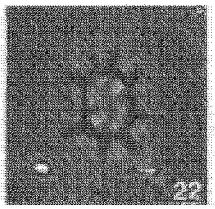
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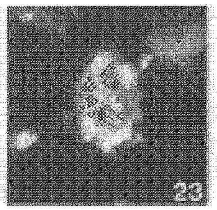
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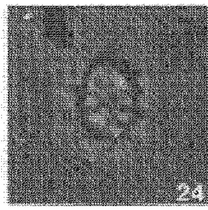
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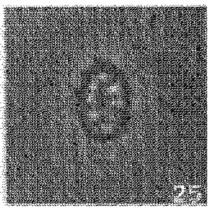
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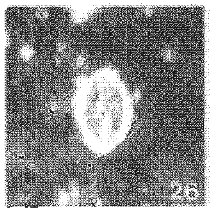
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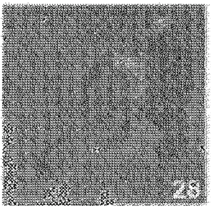
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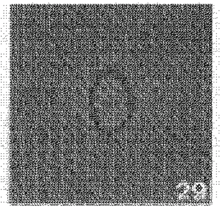
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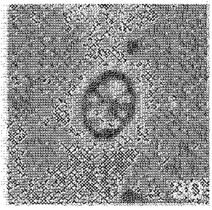
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Plate 4.12

Family STEPHANOLITHIACEAE Black, 1968
Fig. 1. ***Stradnerlithus geometricus*** (Górka, 1957) Bown and Cooper, 1989a. PC, Gorodische (Russia), M. Volgian (panderi), UCL-5629-5. Range: L. Oxfordian (mariae) – M. Volgian (panderi).

Fig. 2. ***Stradnerlithus primitus*** (Rood *et al.*, 1973) Bown comb. nov.. XPL, Hambühren (Germany), Aalenian, UCL-5631-36. Range: U. Sinemurian (raricostatum)? – ?Aalenian (opalinum).
Basionym: *Chiastozygus primitus* Rood *et al.*, 1973 (*Eclogae Geologicae Helvetiae*, **66**, 365–382, p. 370, Pl. 1, fig. 8).

Figs 3–4. ***Truncatoscaphus intermedius*** Perch-Nielsen, 1986b. XPL (3, the high colours are an artefact of the photograph; this species is small and inconspicuous in XPL but exhibits high relief in PC), and PC (4), Gorodische (Russia), M. Volgian/U. Kimmeridgian (panderi/eudoxus), UCL-1504-28/22.

Fig. 5. ***Truncatoscaphus pauciramus*** (Black, 1973) Perch-Nielsen, 1984 (?= *Stradnerlithus tortuosus* Noël, 1973). PC, Watton Cliff (UK), U. Bathonian (aspidoides), UCL-5628-3.

Order PODORHABDALES Rood *et al.*, 1971 emend. Bown, 1987
Family BISCUTACEAE Black, 1971a
Fig. 6. ***Biscutum depravatum*** (Grün and Zweili, 1980) Bown 1987. PC, Brenha (Portugal), Aalenian, UCL-5632-8.

Figs 7–8. ***Biscutum dorsetensis*** Varol and Girgis, 1994 Bown comb. nov. XPL (7) and PC (8), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5331-17/16. Basionym given in Pl. 4.4.

Figs 9–10. ***Biscutum dubium*** (Noël, 1965) Grün in Grün *et al.*, 1974. XPL (9) and PC (10), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-6/5.

Figs 11–12. ***Biscutum finchii*** Crux, 1984. Small morphotype with transverse bar (*Similiscutum gephyrion* of de Kaenel and Bergen, 1993), XPL (11) and PC (12), Brenha (Portugal), L. Pliensbachian (davoei), UCL-5627-9/10.

Figs 13–14. ***Biscutum finchii*** Crux, 1984. Large morphotype, XPL (13) and PC (14), Picun Leufu (Argentina), U. Pliensbachian/L. Toarcian, UCL-5630-12/13.

Figs 15–16. ***Biscutum grande*** Bown, 1987. XPL (15) and PC (16), Brenha (Portugal), L. Pliensbachian (davoei), UCL-5627-17/18.

Figs 17–18. ***Biscutum intermedium*** Bown, 1987. XPL (17) and PC (18), Brenha (Portugal), Aalenian/Bajocian, UCL-5626-31/32.

Figs 19–21. ***Biscutum novum*** (Goy, 1979) Bown, 1987. XPL (19, 21) and PC (20). 19-20, Unterstürmig (Germany), L. Toarcian, UCL-5652-9-10; 21, Brenha (Portugal), Aalenian/Bajocian.

Fig. 22. ***Discorhabdus corollatus*** Noël, 1965. PC, Warboys (UK), Oxfordian (mariae), UCL-5631-27.

Figs 23–25. ***Discorhabdus criotus*** Bown, 1987. 23-24, XPL (23) and PC (24), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-29/30. 25, PC, Brenha (Portugal), Aalenian/Bajocian, UCL-5562-20.

Figs 26–27. ***Discorhabdus striatus*** Moshkovitz and Ehrlich, 1976. XPL (26) and PC (27), Brenha (Portugal), Aalenian/Bajocian, UCL-5626-27/28.

Figs 28–30. ***Similiscutum cruciulus*** de Kaenel and Bergen, 1993. XPL (28) and PC (29, 30, latter is a different specimen), Brenha (Portugal), L. Pliensbachian (davoei), UCL-5627-11/12/16.


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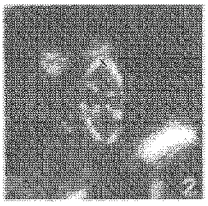
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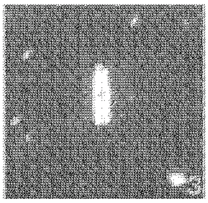
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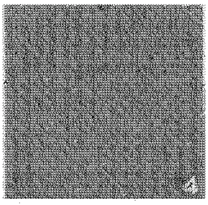
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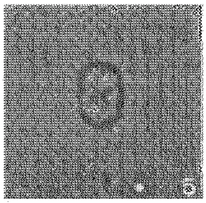
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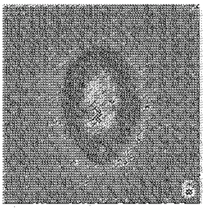
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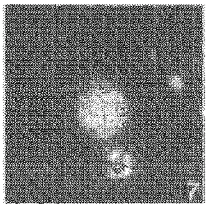
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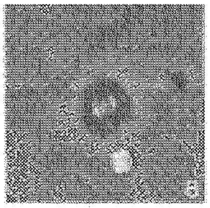
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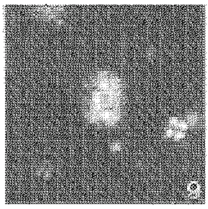
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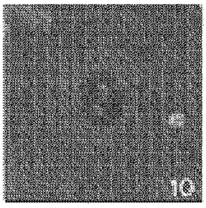
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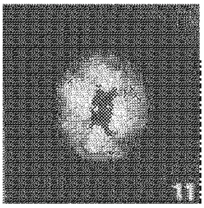
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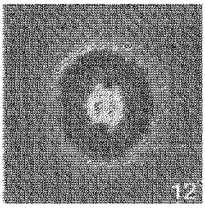
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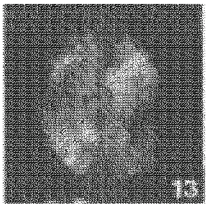
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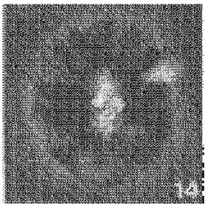
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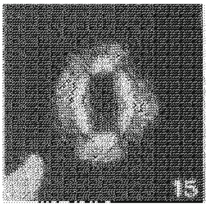
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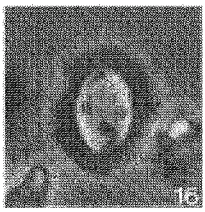
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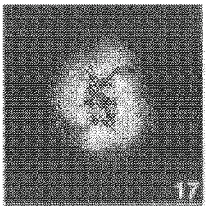
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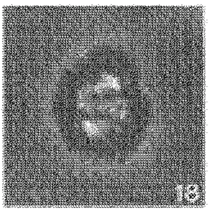
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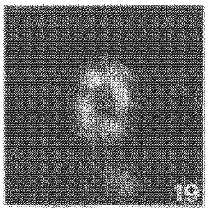
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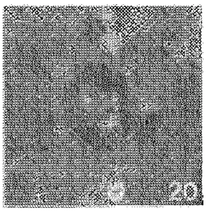
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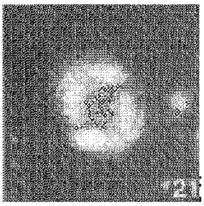
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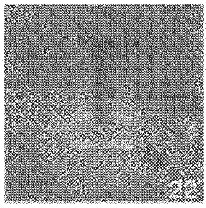
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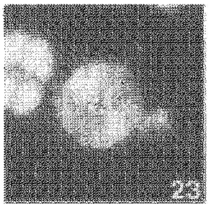
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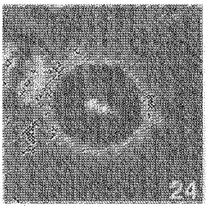
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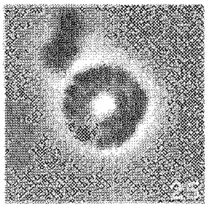
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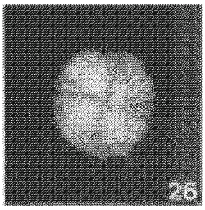
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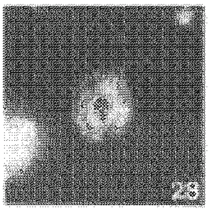
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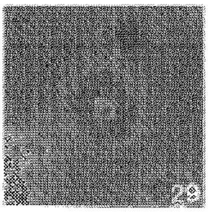
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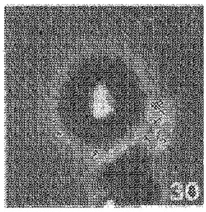
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Plate 4.13

Family BISCUTACEAE Black, 1971a
Fig. 1. ***Sollasites arctus*** (Noël, 1973) Bown, 1987. PC, Unterstürmig (Germany), L. Toarcian, UCL-5545-14.

Family CALYCULACEAE Noël, 1973
Figs 2–5. ***Calyculus* spp. indet.**. 2-3, plan XPL (2) and PC (3), Ballrechten (Germany), L. Toarcian (bifrons), UCL-5562-14/15; 4-5, plan XPL (4) and side XPL (5), Hambühren (Germany), Aalenian, UCL-5631-34/32.

Figs 6–9. ***Carinolithus magharensis*** (Moshkovitz and Ehrlich, 1976) Bown, 1987. Side view, XPL (6, 8) and plan view of distal 'shield' termination, XPL (7) and PC (9), Brenha (Portugal), Aalenian/Bajocian, UCL-5562-33/5627-1/3/5562-30.

Figs 10–11. ***Carinolithus superbus*** (Deflandre *in* Deflandre and Fert, 1954) Prins *in* Grün *et al.*, 1974. Side views, XPL, Ilminster (UK), Toarcian, UCL-2616-33/31.

Family CRETARHABDACEAE Thierstein, 1973
Figs 12–13. ***Cretarhabdus conicus*** Bramlette and Martini, 1964. XPL (12) and PC (13), Gorodische (Russia), L. Volgian (klimovi), UCL-5629-8/9.

Figs 14–15. ***Helenea chiastia*** Worsley, 1971. XPL (14) and PC (15, different specimen), DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5630-3/5564-21. Range: U.Tithonian – L. Turonian (devonense).

Fig. 16. ***Helenea staurolithina*** Worsley, 1971 (= *Microstaurus quadrata* Black, 1971a). XPL, specimen is close to the morphometric *chiastia/staurolithina* boundary, DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5630-1. Range: Tithonian – Hauterivian.

Fig. 17. ***Miravetesina favula*** Grün *in* Grün and Allemann, 1975. XPL, DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5629-36. Range: Kimmeridgian? – ?Valanginian.

Figs 18–20. ***Polypodorhabdus escaigii*** Noël, 1965. XPL (18) and PC (19), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-1/2/5331-13.

Figs 21–22. ***Retecapsa incompta*** Bown, 1987. XPL (21) and PC (22), Brenha (Portugal), Aalenian/Bajocian, UCL-5626-30/29.

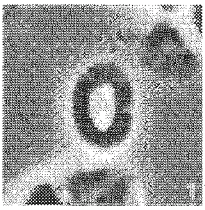
Fig. 23. ***Retecapsa octofenestrata*** (Bralower *in* Bralower *et al.*, 1989) Bown comb. nov.. XPL, DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5564-2/3. Range: L. Callovian (macrocephalus) – ?Maastrichtian.
Basionym: *Cretarhabdus octofenestratus* Bralower *in* Bralower *et al.*, 1989 (*Marine Micropaleontology*, **14**, 153–234, p.212–213, pl. 3, figs 1–3).

Fig. 24. ***Retecapsa* cf. *R. schizobrachiata*** (Gartner, 1968) Grün *in* Grün and Allemann, 1975. XPL, Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-5631-17.

Family MAZAGANELLACEAE Bown, 1987
Figs 25–26. ***Mazaganella protensa*** Bown, 1987. XPL (25) and PC (26), DSDP Site 547 (Atlantic Ocean), L. Pliensbachian, UCL-5652-5/6.

Figs 27–28. ***Mazaganella pulla*** Bown, 1987. XPL (27) and PC (28), Timor, L. Pliensbachian, UCL-5625-24/23.

Fig. 29. ***Triscutum ?beaminsterensis*** Dockerill, 1987. XPL, Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-25.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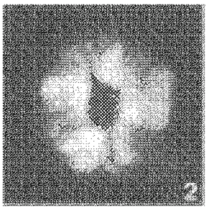
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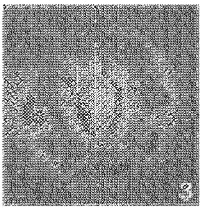
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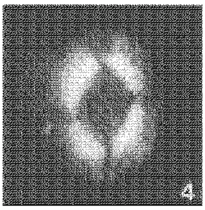
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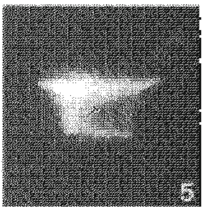
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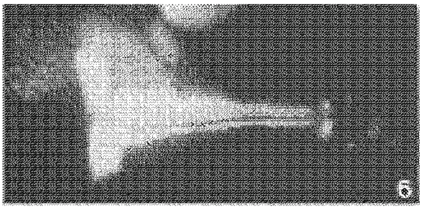
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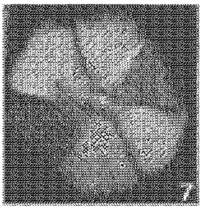
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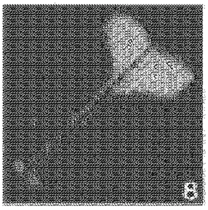
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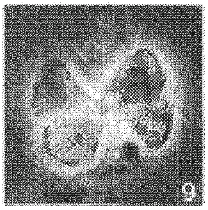
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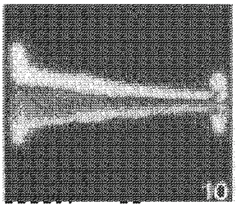
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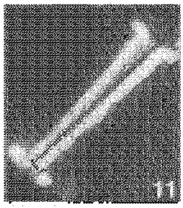
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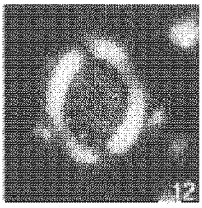
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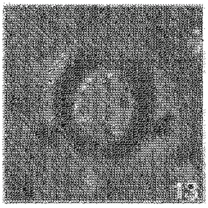
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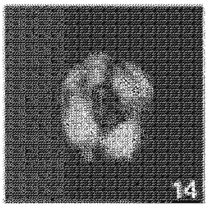
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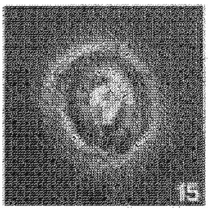
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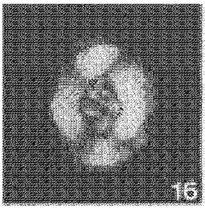
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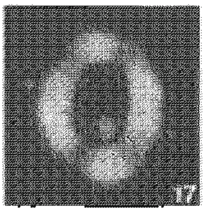
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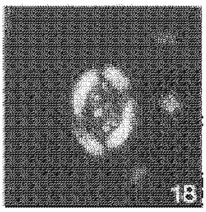
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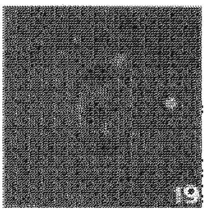
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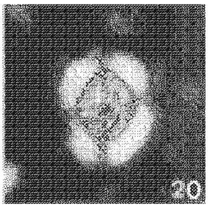
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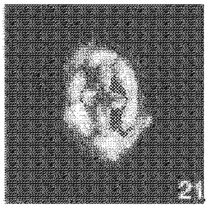
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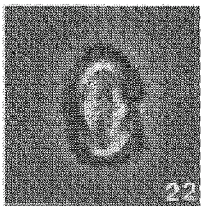
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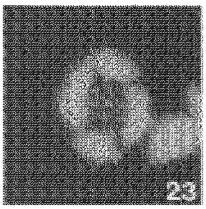
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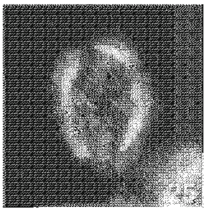
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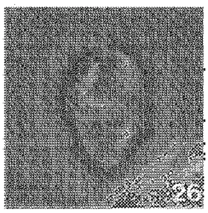
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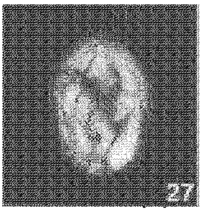
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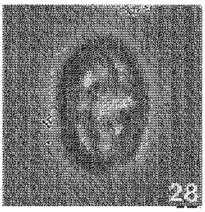
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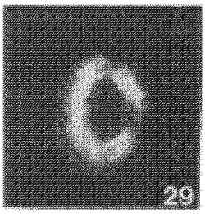
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Plate 4.14

Family MAZAGANELLACEAE Bown, 1987
Figs 1–2. ***Triscutum ?expansus*** (Medd, 1979) Dockerill, 1987. XPL (1) and PC (2), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5331-33/34.

Figs 3–4. ***Triscutum ?expansus*** (Medd, 1979) Dockerill, 1987. XPL (3) and PC (4), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5625-1/2.

Figs 5–6. ***Triscutum sullivanii*** de Kaenel and Bergen, 1993. XPL (5) and PC (6), Hambühren (Germany), Aalenian, UCL-5626-13/14.

Figs 7–8. ***Triscutum sullivanii*** de Kaenel and Bergen, 1993. XPL (7) and PC (8), Brenha (Portugal), Aalenian/Bajocian, UCL-5626-35/36.

Figs 9–10. ***Triscutum tiziense*** de Kaenel and Bergen, 1993. XPL (different specimens), Brenha (Portugal), Aalenian/Bajocian, UCL-5562-34/5627-7. Range: Aalenian (opalinum) – L. Bajocian (discites).

Family AXOPODORHABDACEAE Bown and Young, 1997
Figs 11–12. ***Axopodorhabdus atavus*** (Grün *et al.*, 1974) Bown, 1987. XPL (11) and PC (12), Hambühren (Germany), Aalenian, UCL-5626-9/10.

Figs 13–14. ***Axopodorhabdus cylindratus*** (Noël, 1965) Wind and Wise *in* Wise and Wind, 1977. XPL (13) and PC (14), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-31/32.

Fig. 15. ***Axopodorhabdus rahla*** (Noël, 1965) Grün and Zweili, 1980. Side view PC, Warboys (UK), Oxfordian (mariae), UCL-5631-26.

Figs 16–17. ***Ethmorhabdus gallicus*** Noël, 1965. XPL (16) and PC (17), Gorodische (Russia), U. Kimmeridgian (autissiodorensis), UCL-5628-31/30.

Fig. 18. ***Hexapodorhabdus cuvillieri*** Noël, 1965. PC, Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-15.

Figs 19. ***Octopodorhabdus decussatus*** (Manivit, 1961) Rood *et al.*, 1971. PC, Warboys (UK), Oxfordian (mariae), UCL-5631-24.

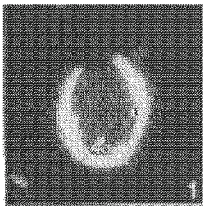
Figs 20–23. ***Podorhabdus grassei*** Noël, 1965. Side XPL (20) and plan XPL (21) and PC (22, 23) views, Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-11/17/18.

Figs 24–25. ***Tetrapodorhabdus shawensis*** Medd, 1979. XPL (24) and PC (25), Port en Bessin (N France), L. Bathonian (tenuiplicatus), UCL5628-12/13.

Order WATZNAUERIALES Bown, 1987

Family WATZNAUERIACEAE Rood *et al.*, 1971
Figs 26–28. ***Ansulasphaera helvetica*** Grün and Zweili, 1980. Side XPL (26) and PC (27) and plan XPL (28) views, Denver Borehole (UK), Callovian (athleta), UCL-5627/35/5563-16/5627-31.

Figs 29–30. ***Bibreviconus atlanticus*** Rahman and Roth, 1991. Side XPL (29) and plan XPL (30) views, DSDP Site 534 (N Atlantic Ocean), L. Tithonian, UCL-5629-32/30. Range: L. Tithonian (?hybonotum).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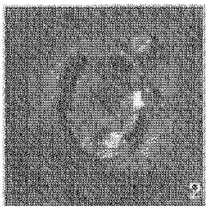
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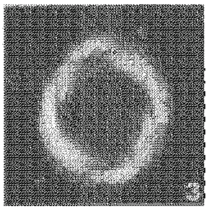
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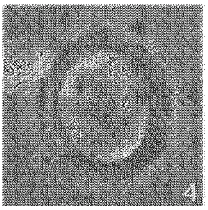
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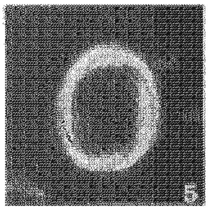
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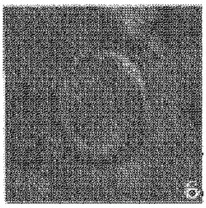
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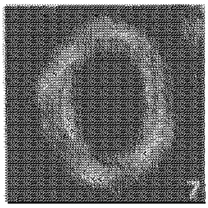
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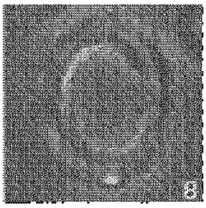
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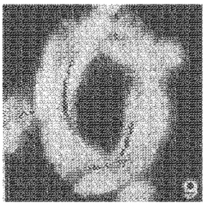
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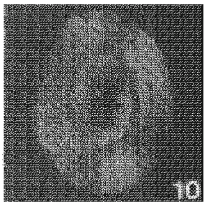
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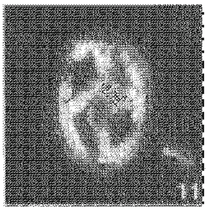
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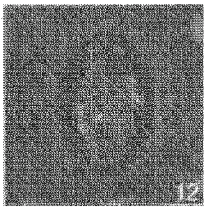
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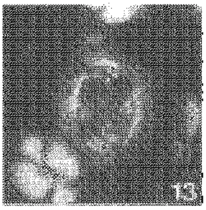
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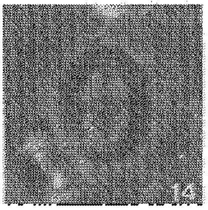
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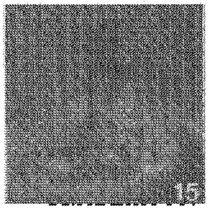
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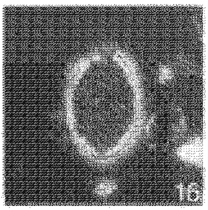
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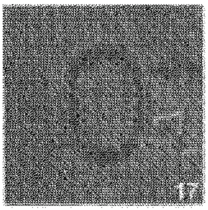
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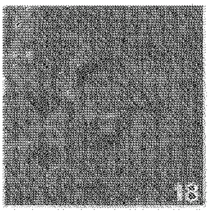
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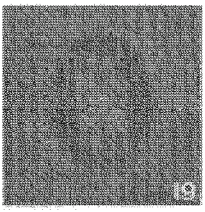
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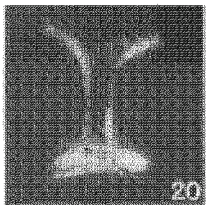
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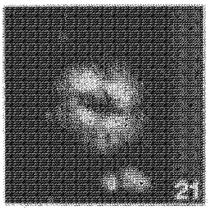
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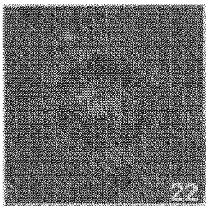
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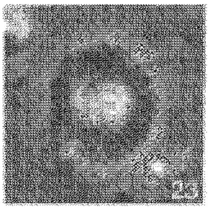
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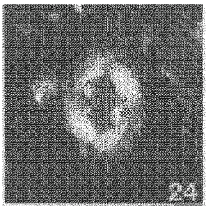
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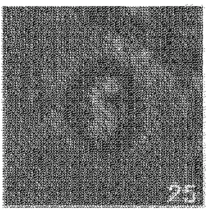
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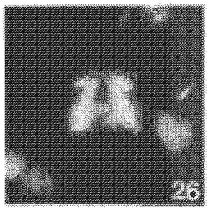
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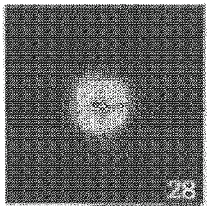
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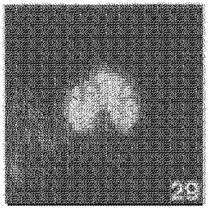
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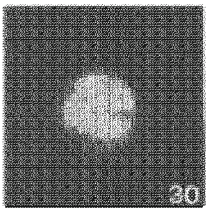
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Plate 4.15

Family WATZNAUERIACEAE Rood *et al.*, 1971
Figs 1–2. ***Bussonius prinsii*** (Noël, 1973) Goy, 1979. XPL (1) and PC (2, different specimen), Trimeusel, (Germany), L. Toarcian (bifrons); Hambühren (Germany), Aalenian, UCL-5625-5/5545-36.

Fig. 3. ***Cyclagelosphaera argoensis*** Bown, 1992b. XPL, DSDP Site 261 (Indian Ocean), Tithonian, UCL-5631-6. Range: Tithonian – Maastrichtian.

Figs 4–5. ***Cyclagelosphaera deflandrei*** (Manivit, 1966) Roth, 1973. XPL (4) and PC (5), DSDP Site 534 (N Atlantic Ocean), L. Tithonian, UCL-5564-10/11.

Fig. 6. ***Cyclagelosphaera margerelii*** Noël, 1965. XPL, Denver Borehole (UK), Callovian (athleta), UCL-5627/33.

Figs 7–8. ***Cyclagelosphaera tubulata*** (Grün and Zweili, 1980) Cooper, 1987. XPL (7) and PC (8), Gorodische (Russia), M. Volgian (panderi), UCL-5631-14/15.

Figs 9–10. ***Diazomatolithus lehmanii*** Noël, 1965. XPL (9) and PC (10), DSDP Site 534 (Atlantic Ocean), U. Tithonian, UCL-5564-18/19. Range: Tithonian? – ?M./U. Albian.

Fig. 11. ***Lotharingius barozii*** Noël, 1973. Collapsed coccosphere XPL, Hambühren (Germany), Aalenian, UCL-5626-23.

Figs 12–15. ***Lotharingius contractus*** Bown and Cooper, 1989a. XPL (12-14) and PC (15), Brenha (Portugal), Aalenian/Bajocian, UCL-5562-23/5627-5/5626-33/34.

Figs 16–18. ***Lotharingius crucicentralis*** (Medd, 1971) Grün and Zweili, 1980. XPL (16, 17) and PC (18), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5625-3/5368-23/24.

Figs 19–20. ***Lotharingius hauffii*** Grün and Zweili *in* Grün *et al.*, 1974. XPL (19) and PC (20), Unterstürmig (Germany), L. Toarcian, UCL-5625-20/19.

Figs 21–22. ***Lotharingius sigillatus*** (Stradner, 1961) Prins *in* Grün *et al.*, 1974. XPL (21) and PC (22), Trimeusel, (Germany), L. Toarcian (bifrons), UCL-5625-8/7.

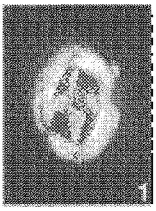
Figs 23–24. ***Watznaueria barnesae*** (Black *in* Black and Barnes, 1959) Perch-Nielsen, 1968. XPL (23) and PC (24), Gorodische (Russia), M. Volgian (panderi), UCL-5629-3/4.

Figs 25–26. ***Watznaueria britannica*** (Stradner, 1963) Reinhardt, 1964. XPL, Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-21/5331-24.

Fig. 27. ***Watznaueria fossacincta*** (Black, 1971a) Bown *in* Bown and Cooper, 1989a. XPL, Gorodische (Russia), L. Volgian (klimovi), UCL-5629-6.

Fig. 28. ***Watznaueria manivitiae*** Bukry, 1973d. XPL, Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5331-7.

Family CALYPTROSPHAERACEAE Boudreaux and Hay, 1969
Figs 29–30. ***Anfractus harrisonii*** Medd, 1979. XPL (29) and PC (30, different specimen), Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-3/5331-32.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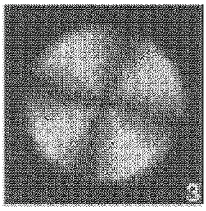
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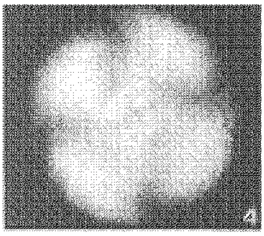
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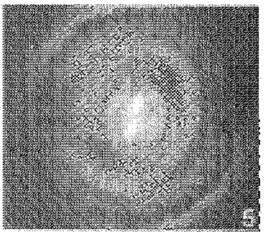
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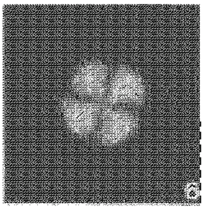
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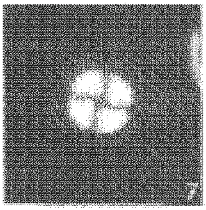
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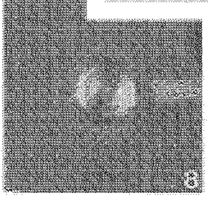
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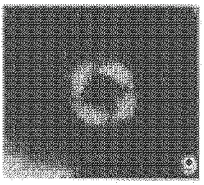
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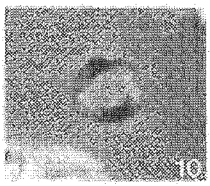
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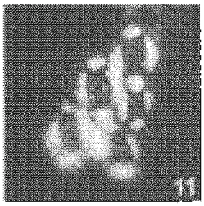
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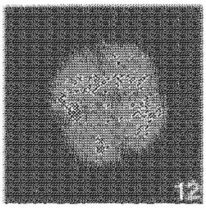
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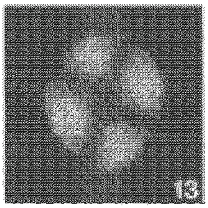
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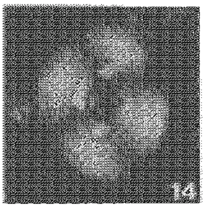
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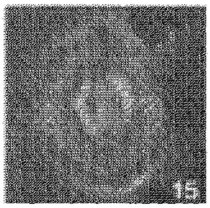
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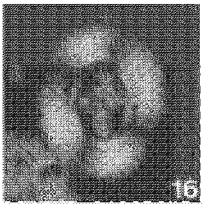
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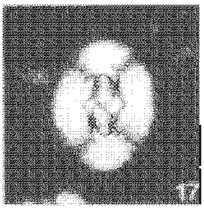
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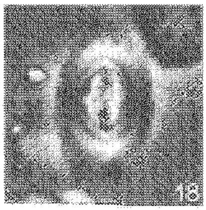
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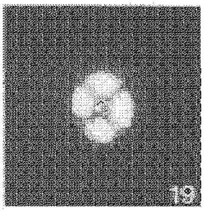
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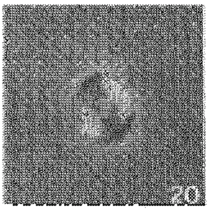
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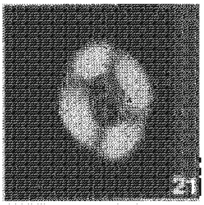
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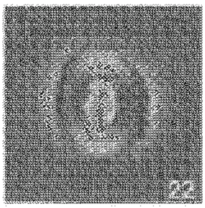
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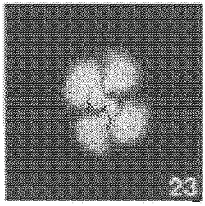
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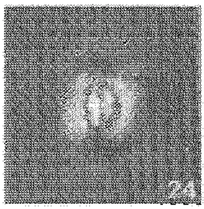
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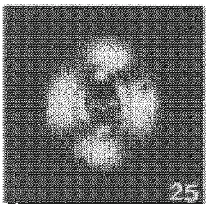
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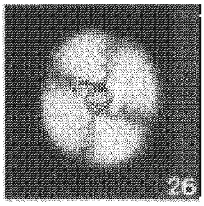
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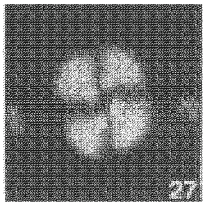
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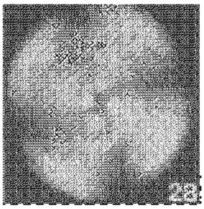
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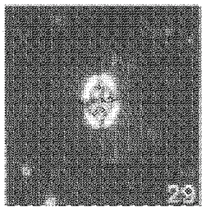
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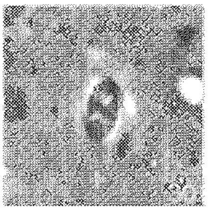
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Plate 4.16

Family CALYPTROSPHAERACEAE Boudreaux and Hay, 1969
Figs 1–2. ***Pseudoconus enigma*** Bown and Cooper, 1989b. XPL (1) and PC (2), Port en Bessin (N France), L. Bathonian (tenuiplicatus), UCL5628-11/10.

NANNOLITHS

Family EOCONUSPHAERACEAE Krystan-Tollmann, 1988a
Figs 3–4. ***Conusphaera mexicana*** Trejo, 1969 ssp. ***mexicana***. XPL (3) and PC (4), DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5563-23/24.

Figs 5–6. ***Conusphaera mexicana*** Trejo, 1969 ssp. ***minor*** Bown and Cooper, 1989b. XPL (5) and PC (6), DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5629-20/21. Range: L. Tithonian (?m. hybonotum) – U. Tithonian.

Family NANNOCONACEAE Deflandre, 1959
Figs 7–10. ***Faviconus multicolumnatus*** Bralower *in* Bralower *et al.*, 1989. XPL (7, 9) and PC (8, 10), DSDP Site 534 (N Atlantic Ocean), L. Tithonian, UCL-5564-4/5/5629-34/35. Range: Oxfordian? – L. Berriasian.

Figs 11–12. ***Nannoconus compressus*** Bralower and Thierstein *in* Bralower *et al.*, 1989. XPL (11) and PC (12), DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5629-16/17.

Fig. 13. ***Nannoconus kamptneri*** Brönnimann, 1955 ssp. ***minor*** Bralower *in* Bralower *et al.*, 1989. XPL, DSDP Site 534 (N Atlantic Ocean), L. Berriasian, UCL-5564-31. Range: ?Berriasian.

Fig. 14. ***Nannoconus steinmannii*** Kamptner, 1931 ssp. ***minor*** Deres and Achéritéguy, 1980. XPL (14) and PC (15, different specimen), Middle East, L. Berriasian, UCL-5652-29/36. Range: Berriasian – ?Valanginian.

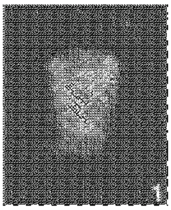
Family POLYCYCLOLITHACEAE Forchheimer, 1972 emend. Varol, 1992
Figs 16–17. ***Hexalithus noeliae*** Loeblich and Tappan, 1966. XPL (16) and PC (17), DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5629-22/23. Range: U. Tithonian – L. Berriasian.

Figs 18–19. ***Polycostella beckmanii*** Thierstein, 1971. XPL (18) and PC (19, different specimen), DSDP Site 534 (N Atlantic Ocean), U. Tithonian, UCL-5629-25/5564-26. Range: Tithonian.

Fig. 20. ***Polycostella senaria*** Thierstein, 1971. XPL, Middle East, L. Berriasian. Range: U. Tithonian – L. Berriasian.

Family SCHIZOSPHAERELLACEAE Deflandre, 1959
Figs 21–22. ***Schizosphaerella punctulata*** Deflandre and Dangeard, 1938. XPL (21) and PC (22) of single disarticulated valve, Cleveland Farm Pit, Wiltshire (UK), L. Oxfordian (mariae), UCL-5624-35/36.

INCERTAE SEDIS NANNOLITHS
Figs 23–24. ***Orthogonoides hamiltoniae*** Wiegand, 1984b. XPL (23) and PC (24, different specimen), Unterstürmig (Germany), L. Toarcian, UCL-5625-15/5545-18.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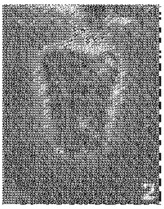
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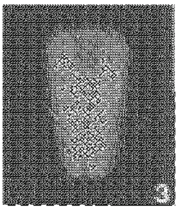
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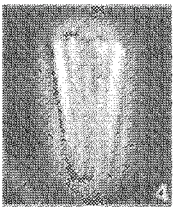
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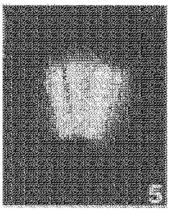
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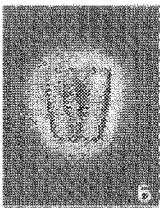
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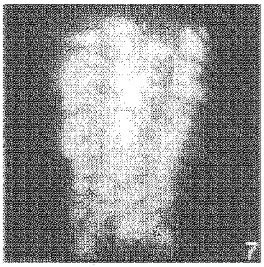
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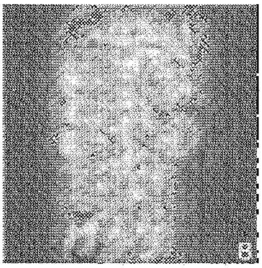
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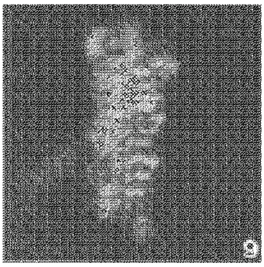
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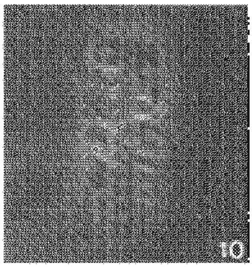
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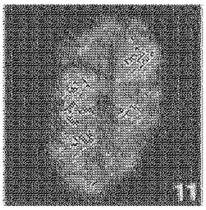
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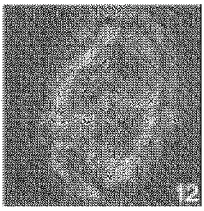
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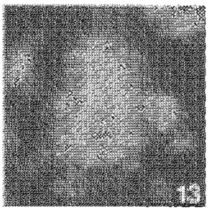
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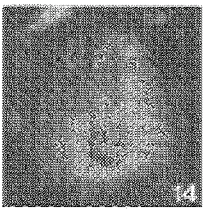
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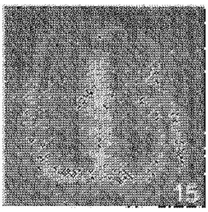
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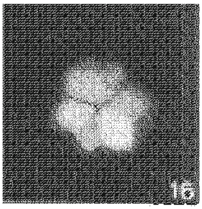
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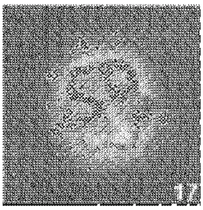
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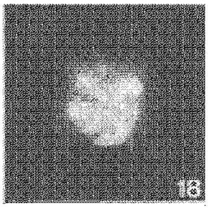
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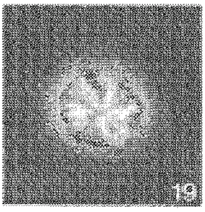
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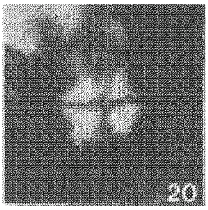
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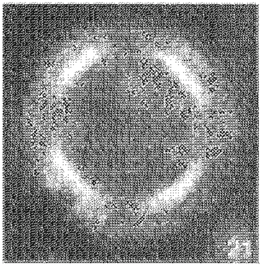
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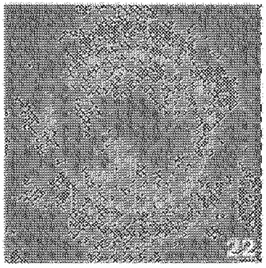
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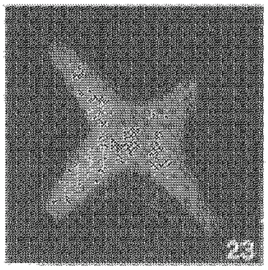
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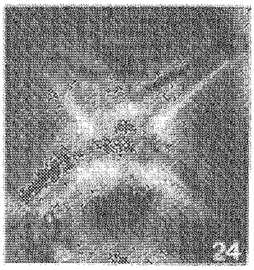
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5

Lower Cretaceous

P.R. Bown, D.C. Rutledge, J.A. Crux and L.T. Gallagher

5.1 INTRODUCTION

Lower Cretaceous nannofossil biostratigraphy has a research history spanning the last 40 years, from Brönnimann (1955), whose nannoconid biostratigraphy of Cuba was one of the first applied nannofossil studies, through to the last ten years which has seen an immense amount of research, much of which has been directed at sections and industrial applications in the North Sea Basin and adjacent areas.

The first refined biostratigraphic zonation was developed by Thierstein (1971, 1973) based on low-latitude sample material, primarily the stage-stratotype and parastratotype sections of SE France. The marker-species utilized in this, and the subsequent but comparable zonations of Sissingh (1977) and Roth (1978), were predominantly large and distinctive tethyan taxa, essentially limiting biostratigraphic application to low latitudes or more strictly, western Tethys and the proto-Atlantic Ocean regions.

Perch-Nielsen (1979a) recognized the geographic limitations of these zonations, and using data from Speeton (NE England) and the North Sea Basin, inserted a number of important boreal events into the tethyan-based schemes. Since then, a progression of boreal Lower Cretaceous studies, both industry- and university-based, have described many new boreal nannofossil taxa and developed successively refined zonations, largely based upon Speeton, North Sea borehole data, and sections in northern Germany. Much of the impetus for this research has come from hydrocarbon exploration and development, with an unprecedented amount of data having been provided for this area.

Other valuable contributions have come from DSDP and ODP research from all of the world's oceans, providing new information concerning palaeobiogeography and global correlation. There has also been some re-evaluation of southern European tethyan sections, which have provided calibration to the geomagnetic polarity time-scale.

Nannofossil biostratigraphy in the Lower Cretaceous now provides a resolution which is closely comparable to that of cephalopods, but more significant is the potential value of the group for global correlation in both epeiric and oceanic sediments. In addition, great advances are also being made in the fields of palaeobiogeography and palaeoceanography, which for the first time have used nannofossils as indicators of Cretaceous ocean environments.

5.2 IMPORTANT REFERENCES

Early biostratigraphic studies include Thierstein (1971, 1973), Sissingh (1977, 1978) and Roth (1978). The CC zones of Sissingh (1977) and NC zones of Roth (1978) have subsequently been widely applied although they have been substantially subdivided in recent years by Perch-Nielsen (1979a, 1985a), Bralower (1987), Applegate and Bergen (1988) and Bralower *et al.* (1989, 1993).

Lower Cretaceous calcareous nannofossils are now known from a wide geographic area including North America (Hill, 1976; Bralower, 1990), the N Atlantic Ocean (Wind and Cepek, 1979; Roth, 1983; Covington and Wise, 1987; Applegate and Bergen, 1988; Bralower *et al.*, 1989), S Atlantic Ocean (Wise and Wind, 1977), Indian Ocean (Mutterlose, 1992a; Bown, 1992b; Bralower, 1992), Pacific Ocean (Cepek, 1981; Roth, 1981; Erba and Covington, 1992) and Southern Ocean (Mutterlose and Wise, 1990) and recently from previously unstudied continental areas, including Papua New Guinea (Howe, 1995) and South America (Bown and Ellison, 1995; Mostajo *et al.,* 1995).

Over 40 published studies address the NW European area, the most important sources of stratigraphic information being Black (1971a, 1972, 1973, 1975), Taylor (1978, 1982), Perch-Nielsen (1979a), Köthe (1981), Jakubowski (1987), Thomsen (1987), Crux (1989, 1991b), Mutterlose (1991), Bralower (1991), Jeremiah (1996) and Rutledge and Bown (in prep.).

Important re-evaluations of southern European tethyan sections are provided by Bralower *et al.* (1989), Bralower (1987), Bergen (1994) and Cecca *et al.* (1994).

Palaeoceanographic studies have provided many new ideas on the palaeoecology and palaeobiogeography of Early Cretaceous nannoplankton, including observations on bipolar and tropical/subtropical distributions (Roth and Bowdler, 1981; Roth and Krumbach, 1986; Mutterlose, 1992a, b, 1996), indices of high surface-water fertility (Erba *et al.,* 1992; Erba, 1992), and even the dynamics of subannual nannoplankton blooms (Thomsen, 1989a, b).

5.3 LOWER CRETACEOUS NANNOFOSSIL SUCCESSION

The earliest Cretaceous nannofossil succession was a continuation of the Tithonian evolutionary radiation, which introduced several new nannolith and coccolith families as well as new taxa within established Jurassic families. Provincialism became less pronounced as the new groups became more widely distributed, but remained significant throughout the Early Cretaceous. The general trend through the interval was one of steady diversity increase.

The Tithonian radiation was characterized by the appearance of the new nannolith groups, *Conusphaera*, Nannoconaceae (*Nannoconus*), Microrhabdulaceae (*Lithraphidites*), Polycyclolithaceae (*Polycostella*) and Braarudosphaeraceae (*Micrantholithus*), all of which appeared cryptogenically. The timing of these appearances was originally thought to have been in the earliest Cretaceous, but recent studies of complete and well-preserved N Atlantic DSDP sites have shown that most were in the latest Tithonian (Bralower *et al.*, 1989).

Many of the Jurassic families which had undergone high species-level extinctions in the Late Jurassic were also re-established during this radiation, although the timings of these events are still uncertain. The Cretarhabdaceae, in particular, diversified rapidly, having been rare and poorly-represented through most of the Jurassic.

The genus *Watznaueria* continued to dominate assemblages but the prevailing Jurassic species, *W. britannica*, was superseded by *W. fossacincta* and *W. barnesae.*

Following the Tithonian radiation, Neocomian assemblages were relatively stable, the commonest components including *Watznaueria barnesae, W. fossacincta, Micrantholithus obtusus/hoschulzii, Rhagodiscus asper, Diazomatolithus lehmanii,* and the simple murolith genera *Zeugrhabdotus* and *Staurolithites*. Low-latitude assemblages are characterized by abundant *Nannoconus*, although restricted acmes of this genus have also been recorded in higher latitudes (Mutterlose, 1989, 1992b). A low-magnitude and temporally-extended taxonomic turnover occurred at the Barremian/Aptian boundary, during which a number of new groups became established, including *Eprolithus*, *Flabellites* and *Hayesites*, whilst nannoconids declined, with the extinction of boreal species and a pronounced global nannoconid reduction in the Early Aptian ('nannoconid crisis' of Erba, 1994). By Late Aptian–Albian times, assemblages were significantly different to those of the Neocomian: *Micrantholithus* was replaced by rarer but closely-related *Braarudosphaera*; *Rhagodiscus asper* became rarer but was joined by new species of the same genus, particularly *R. achlyostaurion*; and a number of important new groups had appeared including *Prediscosphaera* and early representatives of the Arkhangelskiales (*Acaenolithus, Broinsonia, Crucicribrum, Gartnerago*), both of which went on to become characteristic components of Late Cretaceous nannofloras.

5.4 BIOSTRATIGRAPHY

The most refined biostratigraphic zonation schemes for the Lower Cretaceous have resulted from intense study of the NW European area, and therefore much of the following section will be concerned with data from this area. The most recent boreal zonations will provide the biostratigraphic framework and will be described in some detail. Later parts of the chapter will discuss the potential for worldwide correlation of these schemes, and correlation charts incorporate data from southern Europe and the ocean basins.

Research from the North Sea Basin and adjacent areas has produced a large amount of stratigraphic data including critical, macrofossil-dated outcrop material. Nannofossil biostratigraphic resolution down to ammonite-zone level is now achievable through much of the Lower Cretaceous, without recourse to any specific nannofossil zonation. While such a 'bioevent' approach is flexible, it is also desirable to have the framework zonation scheme against which other events may be calibrated. Additionally, it has become apparent that in certain intervals, e.g. the Upper Hauterivian and Lower Barremian, the sequence of nannofossil events is more rigorously defined than the cephalopod zones recognized onshore. Thus, while separate ammonite zonal terminologies are applied in Germany and England (e.g. discofalcatus AZ = marginatus and variabilis AZs), these strata are more easily and precisely correlated using nannofossils.

The boreal zonation presented below and in the biostratigraphic charts (Figs 5.1 and 5.2) is primarily drawn from Rutledge and Bown (in prep.) which represents the latest reappraisal of the Ryazanian–Aptian boreal nannofossil biostratigraphy based largely on Speeton and North Sea sections. However, this essentially represents a refinement of previous zonations, particularly those of Jakubowski (1987) and Crux (1989). The Albian zones are largely based upon well-established events but also include data from Crux (1991b) and Jeremiah (1996). Although these zonal schemes were developed in the North Sea Basin area, many of the events are much more widely applicable, and allow correlation with low latitude (~tethyan) and southern high-latitude zonations, as shown in Figs 5.1 and 5.2. The stratigraphic ranges of selected Lower Cretaceous nannofossil taxa are shown in Fig. 5.4. Marker species and principal assemblage components are illustrated in Plates 5.1 to 5.15.

Abundance terminology used in this chapter is as follows:

	#/300+	% of assemb.	~#/FOV
Rare	0	<1%	–
Frequent/Few	1–5	c.1%	<1
Common	6–60	2-20%	>1
Abundant	>60	>20%	>10

Rare is used where one or several specimens, respectively, were recorded outside the standard 300 specimen count. The term *acme* is used for intervals of exceptional abundance (common/abundant) of a consistently present species.

BC1 Retecapsa angustiforata Zone

Author. Jakubowski (1987, NLK19B).
Definition. FO of *Retecapsa angustiforata* to the FO of *Sollasites arcuatus*.
Range. Ryazanian.
Remarks. The FO of *R. angustiforata* recorded in the Lower Berriasian of Tethys (Bergen, 1994) provides a convenient datum for the definition of a lower boundary. This zone is rarely encountered in the North Sea area, due to non-calcareous facies, and a regional unconformity between the Valhall Formation/Speeton Clay Formation and the underlying Kimmeridge Clay Formation.

BC2 Sollasites arcuatus Zone

Author. Jakubowski (1987, NLK19A).
Definition. Total range of *Sollasites arcuatus*.
Range. Upper Ryazanian (albidum AZ *pars*).
Remarks. *S. arcuatus* may be rare within this zone, which is otherwise characterized by frequent/common *Sollasites* spp. and *Crucibiscutum salebrosum*.

BC3 Crucibiscutum salebrosum Zone

Author. Crux (1989, Unnamed Zone).
Definition. LO of *Sollasites arcuatus* to the FO of *Micrantholithus speetonensis*.
Range. Uppermost Ryazanian (albidum AZ) to Lower Valanginian (Paratollia spp. AZ).
Remarks. Dominated by *C. salebrosum*, with conspicuous *Kokia* spp. and, in the upper part, *Triquetrorhabdulus shetlandensis*. *Micrantholithus*

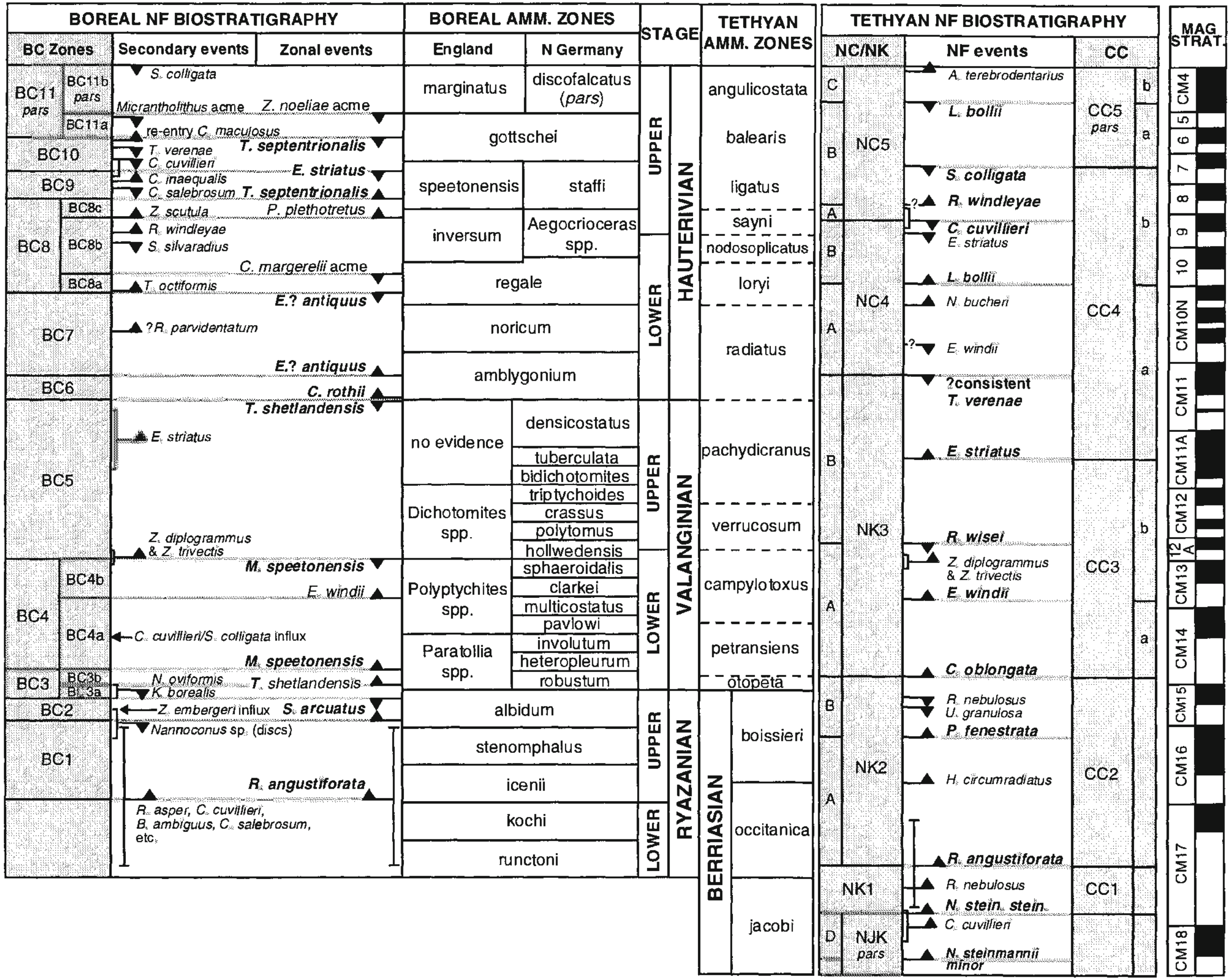


Fig. 5.1 Neocomian nannofossil biostratigraphy. Boreal BC zones after Rutledge and Bown (in prep.); all events are calibrated to the boreal cephalopod zonation scheme. Tethyan NC zones after Roth (1978, 1983) with subdivisions after Bralower (1987) and Bralower *et al.* (1993). NK zones after Bralower *et al.* (1989). CC zones after Sissingh (1977, 1978) with modifications by Perch-Nielsen (1979a, 1985a) and Applegate and Bergen (1988). Most events are calibrated against ammonite zones (predominantly using Bergen, 1984). Correlation between the boreal and tethyan biostratigraphies is made via ammonite zone correlations, based largely on Rawson (1995). The magnetostratigraphic scale is not well calibrated with the cephalopod stratigraphy and is included as a guide only, based on Bralower (1987), Bralower *et al.* (1989) and Cecca *et al.* (1994).

brevis, the precursor of *M. speetonensis*, is a rare element of this and the underlying zone, and it is important that the definitions of these species are strictly applied.

BC3a Subzone

Author. Rutledge and Bown (in prep.).
Definition. LO of *Sollasites arcuatus* to the FO of *Triquetrorhabdulus shetlandensis*.
Range. Uppermost Ryazanian and ?lowermost Valanginian (upper albidum AZ and possibly lower Paratollia spp. AZ).
Remarks. *C. salebrosum* is the dominant taxon. *Kokia curvata*, *Kokia borealis* and *Nannoconus oviformis* are conspicuous elements, while *Sollasites* spp. are rare. *K. borealis* and *N. oviformis* have their LOs in this subzone (Perch-Nielsen, 1988).

BC3b Subzone

Author. Rutledge and Bown (in prep.).
Definition. FO of *Triquetrorhabdulus shetlandensis* to the FO of *Micrantholithus speetonensis*.
Range. Lower Valanginian (Paratollia spp. AZ).
Remarks. Dominated by *C. salebrosum*, with conspicuous *T. shetlandensis* and *K. curvata*. The latter species has only been recorded in the northern North Sea and Barents Sea, and may not have ranged into the southern North Sea.

BC4 Micrantholithus speetonensis Zone

Author. (Taylor, 1982) Crux (1989, M. speetonensis Zone).
Definition. The total range of *Micrantholithus speetonensis*.
Range. Lower Valanginian (Paratollia spp. to Polyptychites spp. AZs).
Remarks. This zone is subdivided using the FO of *Eiffellithus windii*, an important, interregionally correlatable event which is, however, difficult to precisely identify in the boreal area due to condensed Valanginian sections.

BC4a Subzone

Author. Rutledge and Bown (in prep.).
Definition. FO of *Micrantholithus speetonensis* to the FO of *Eiffellithus windii*.
Range. Lower Valanginian (upper Paratollia spp. to lower Polyptychites spp. AZs).
Remarks. Assemblages are dominated by *C. salebrosum*, with conspicuous *M. speetonensis*, *T. shetlandensis* and *Cyclagelosphaera brezae*. *Cruciellipsis cuvillieri* and *Speetonia colligata* are first recorded in boreal sections within this interval (the latter species commonly).

BC4b Subzone

Author. Rutledge and Bown (in prep.).
Definition. FO of *Eiffellithus windii* to the LO of *Micrantholithus speetonensis*.
Range. Lower Valanginian (upper Polyptychites spp. AZ) to lowermost Upper Valanginian (?basal Dichotomites spp. AZ).
Remarks. Due to regional unconformities and barren intervals, this interval has not yet been confidently identified in the boreal area.

BC5 Triquetrorhabdulus shetlandensis Zone

Author. Rutledge and Bown (in prep.).
Definition. LO of *Micrantholithus speetonensis* to the LO of *Triquetrorhabdulus shetlandensis*.
Range. Upper Valanginian ?and lowermost Hauterivian (Dichotomites spp. to ?lowermost amblygonium AZs).
Remarks. Frequent/common *C. salebrosum* and *Cyclagelosphaera margerelii*, with frequent *E. windii* and rare but conspicuous *T. shetlandensis*. Subdivision of this relatively long interval is difficult due to the limited amount of boreal Upper Valanginian material available. *E. windii* is the dominant form of *Eiffellithus* in the middle-upper Valanginian, and is largely superseded by *Eiffellithus striatus* (= '*Tegumentum tripes*' in Mutterlose, 1991) in the uppermost Valanginian, but exact placement of the FO of *E. striatus* is presently problematical.

M. speetonensis has been recorded from the hollwedensis AZ (lower Upper Valanginian) of Central Poland (Mutterlose, 1993), slightly later than most boreal records.

BC6 Conusphaera rothii Zone

Author. (Mutterlose, 1991) Rutledge and Bown (in prep.).
Definition. LO of *Triquetrorhabdulus shetlandensis* to the FO of *Eprolithus*? *antiquus*.
Range. Lower Hauterivian (amblygonium AZ) (but possibly ranges lower, i.e. uppermost Valanginian).
Remarks. The base of this zone is also marked by the FO of *Conusphaera rothii*, although this

probably represents a first consistent occurrence in the boreal area, having been recorded sporadically from the Ryazanian (Crux, pers. obs.). Also characterized by common *C. margerelii*, frequent *E. striatus* and less frequent *E. windii*. *C. brezae* and *Stradnerlithus silvaradius* may be conspicuous.

BC7 Eprolithus? antiquus Zone

Author. (Crux, 1989) Mutterlose (1991).
Definition. Total range of *Eprolithus*? *antiquus*.
Range. Lower Hauterivian (upper amblygonium to lower regale AZs).
Remarks. Abundant to common *C. margerelii*, with frequent/common *C. salebrosum*, frequent *E. striatus* and subordinate *E. windii*. *E.*? *antiquus* is rare to common. This zone is characterized by tethyan influences in the boreal area. *C. cuvillieri* and *Calcicalathina oblongata*, in particular, may be frequent.

BC8 Cyclagelosphaera margerelii Zone

Author. (Mutterlose, 1991) Rutledge and Bown (in prep.).
Definition. LO of *Eprolithus*? *antiquus* to the FO of *Tegulalithus septentrionalis*.
Range. Lower to lower Upper Hauterivian (regale to speetonensis AZs).
Remarks. *E. striatus* is a frequent and conspicuous element throughout, while *C. salebrosum* is frequent/common. *C. margerelii* is common in the lower part, and the top of this long-term acme is a useful subzonal event. *Perissocyclus plethotretus*, *Perissocyclus tayloriae*, *Rucinolithus windleyae* and *Zeugrhabdotus scutula* first appear towards the top of the zone. There appear to be no extinctions during this interval, other than the premature, regional (boreal) disappearances of *Helenea quadrata*, *C. oblongata* and *S. silvaradius*.

Jakubowski (1987) and Crux (1989) both subdivided this interval using the LO of *S. silvaradius*, however, this species is extremely rare in all but the basal Hauterivian of Germany (Crux, 1989; Mutterlose, 1991). In any case, Bergen (1994) recorded this species into the Upper Hauterivian of France and DSDP Site 534, and it was originally described from the Aptian of the Falkland Plateau (Wise and Wind, 1977). This interval is therefore subdivided using alternative bioevents; the top of a *C. margerelii* acme, and a number of approximately synchronous FOs.

BC8a Subzone

Author. Rutledge and Bown (in prep.).
Definition. LO of *Eprolithus*? *antiquus* to the last consistent occurrence of common (~10%) *Cyclagelosphaera margerelii*.
Range. Lower Hauterivian (regale AZ *pars*).
Remarks. Common *C. margerelii*, with frequent *E. striatus*, rare *E. windii* and variable abundances of *C. salebrosum*. *C. cuvillieri* is relatively frequent.

C. margerelii is common throughout the Upper Valanginian (Mutterlose, 1991) and much of the Lower Hauterivian, and the top of this acme is utilized here. However, additional acmes of *C. margerelii* are recorded in the Upper Hauterivian and 'middle' Barremian, but it is relatively rare in the intervening strata. These acme events seem to be correlatable on a basin-wide scale (certainly between England and Germany, and within the North Sea).

BC8b Subzone

Author. Rutledge and Bown (in prep.).
Definition. Last consistent occurrence of common *Cyclagelosphaera margerelii* to the FO of *Perissocyclus plethotretus* (and/or *Perissocyclus tayloriae* and/or *Zeugrhabdotus scutula*).
Range. Lower to lower Upper Hauterivian (upper regale to uppermost inversum AZs).
Remarks. *E. striatus* is a frequent and conspicuous element, along with *C. salebrosum*. *C. margerelii* is much reduced in abundance compared to the underlying subzone (<3%). *R. windleyae* first appears towards the top of this interval. The three FOs given to mark the top of this zone cannot yet be satisfactorily sequenced, but are sufficiently close to be complimentary. The FO of *P. plethotretus* is given precedence, since this species seems the most widely-distributed within the boreal area. A strict species concept must be applied: *P. plethotretus* is used herein for large, birefringent-strutted forms only.

BC8c Subzone

Author. Rutledge and Bown (in prep.).
Definition. FO of *Perissocyclus plethotretus* (and/or *P. tayloriae* and/or *Z. scutula*) to the FO of *Tegulalithus septentrionalis*.
Range. Lower Upper Hauterivian (uppermost inversum to lower speetonensis/staffi AZs).
Remarks. Frequent/common *C. salebrosum*, fre-

quent *E. striatus*, with rare to frequent (but conspicuous) *P. plethotretus*, *P. tayloriae* and *Z. scutula*. *Assipetra infracretacea* is frequent/common throughout.

BC9 Eiffellithus striatus Zone

Author. Rutledge and Bown (in prep.).
Definition. FO of *Tegulalithus septentrionalis* to the LO of *Eiffellithus striatus*.
Range. Upper Hauterivian (speetonensis/staffi AZ *pars*).
Remarks. *T. septentrionalis* is frequent/common throughout, and its sudden *en masse* appearance is an excellent datum. There is a dramatic reduction in the abundance of *C. salebrosum* within the lower part which may represent the extinction of this species; later, rare records are probably reworked or belong to another, similar species (*Crucibiscutum ?pinnatus* or *Crucibiscutum hayi*). The LO of *C. cuvillieri* was recorded within this interval, but this species is extremely rare in its upper range and may extend into BC10 (Bralower, 1991). *E. striatus* is frequent throughout its range and its LO provides a reliable datum that is correlatable worldwide. *C. margerelii* has a brief acme around the extinction level of *E. striatus*.

BC10 Tegulalithus septentrionalis Zone

Author. Rutledge and Bown (in prep.).
Definition. LO of *Eiffellithus striatus* to the LO of *Tegulalithus septentrionalis*.
Range. Upper Hauterivian (upper speetonensis/staffi to lower gottschei AZs).
Remarks. *Micrantholithus* spp. become common towards the top. *Clepsilithus maculosus* reappears just below the LO of *T. septentrionalis*, after a long absence from the boreal area. The highest occurrence of *Tubodiscus verenae* was recorded in this zone; this species is rare at boreal latitudes, and of no real biostratigraphic potential, but these late occurrences are significant because the species' LO has previously been used to mark the top of the Valanginian.

T. septentrionalis is frequent/common throughout its range and its LO is abrupt. Previous records of *T. septentrionalis* in the Lower Barremian (Jakubowski, 1987; Crux, 1989; Mutterlose, 1991) are interpreted here as reworking. Records of 'middle' Barremian *T. septentrionalis* (Mutterlose and Harding, 1987; Crux, 1989) are thought to represent observations of the light-microscopically similar *Nannoconus pseudoseptentrionalis*.

BC11 Clepsilithus maculosus Zone

Author. (Crux, 1989, S. comptus Zone) Rutledge and Bown (in prep.).
Definition. LO of *Tegulalithus septentrionalis* to the LO of *Clepsilithus maculosus*.
Range. Upper Hauterivian to lowermost Barremian (upper gottschei to basal variabilis AZs).
Remarks. *C. maculosus* is entirely absent from North Sea 'middle' Hauterivian sections but occurs consistently, and often frequently, throughout this zone. *P. plethotretus* and *Z. scutula* are conspicuous throughout. *Micrantholithus* is abundant towards the base of the interval. The diminutive *Zeugrhabdotus noeliae* is abundant throughout the lower half of this zone; this long-term acme appears to be correlatable basin-wide, and is used to subdivide the interval.

BC11a Subzone

Author. Rutledge and Bown (in prep.).
Definition. LO of *Tegulalithus septentrionalis* to the last consistent occurrence of abundant (>20%) *Zeugrhabdotus noeliae*, within the range of *Clepsilithus maculosus*.
Range. Upper Hauterivian (upper gottschei AZ).
Remarks. *Z. noeliae* is dominant, constituting 20–50% (generally 30–40%) of assemblages, with >15 individuals in an average FOV. *C. maculosus* is a conspicuous component but never common.

Z. noeliae declines suddenly at the top of this zone; it is still frequent/common throughout the remainder of the range of *C. maculosus*, but does not dominate assemblages (constituting <15%, generally much less). This acme event may not be easily recognizable in ditch-cutting material, since *Z. noeliae* is occasionally abundant in the overlying zone; the *Micrantholithus* spp. acme (also noted by Jakubowski, 1987) may be a more easily utilized event.

BC11b Subzone

Author. Rutledge and Bown (in prep.).
Definition. Last consistent occurrence of abundant (>20%) *Zeugrhabdotus noeliae* to the LO of *Clepsilithus maculosus*.
Range. Upper Upper Hauterivian (marginatus AZ) to lowermost Barremian (basal variabilis AZ).

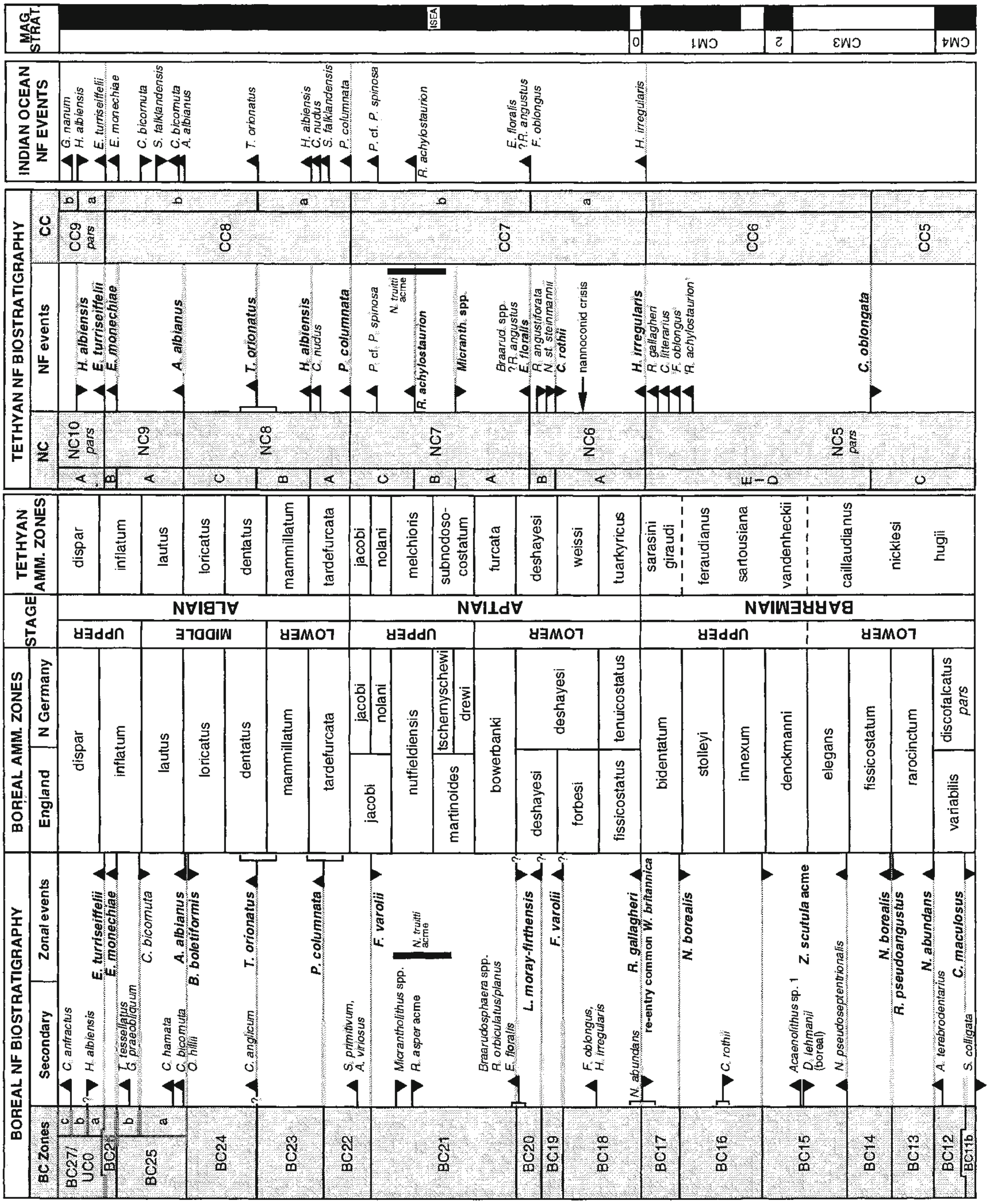


Fig. 5.2 Barremian-Albian nannofossil biostratigraphy. Boreal BC zones after Rutledge and Bown (in prep.). Albian events also based on Crux (1991), Burnett *in* Gale *et al.* (1996) and Jeremiah (1996). Most events are calibrated to the boreal cephalopod zones. See also Fig. 5.1 caption.

Remarks. As for BC11a, but *Z. noeliae* and *Micrantholithus* spp. are much depleted, although both may be frequent/common. *Rhagodiscus asper* and *Watznaueria* spp. are the dominant taxa. *Rhagodiscus pseudoangustus* is occasionally frequent.

BC12 Cretarhabdus inaequalis Zone

Author. (Crux, 1989) Rutledge and Bown (in prep.).

Definition. LO of *Clepsilithus maculosus* to the FO of *Nannoconus abundans.*

Range. Lower Barremian (variabilis AZ *pars*).

Remarks. Dominated by *Watznaueria* spp., *R. asper* and *Biscutum constans. C. inaequalis*, *R. pseudoangustus* and *Tegumentum stradneri* (small variety) are often frequent and characteristic of this interval. *P. plethotretus* and *Z. scutula* occur throughout. *Rhabdophidites parallelus* is unusually common. Tethyan species of *Nannoconus* (*N. globulus*, *N. kamptneri*, *N. steinmannii*) are frequent within the paler horizons of boreal, rhythmically-bedded sediments. *Nannoconus inornatus* becomes common in the upper part, just prior to the inception of *N. abundans* (these events are synchronous at Speeton due to condensation). *Assipetra terebrodentarius* appears towards the top, providing a reliable secondary datum.

BC13 Nannoconus abundans Zone

Author. (Crux, 1989) Rutledge and Bown (in prep.).

Definition. FO of *Nannoconus abundans* to the FO of *Nannoconus borealis* (or the LO of *Rhagodiscus pseudoangustus*).

Range. Lower Barremian (rarocinctum AZ).

Remarks. *N. inornatus* is common, and the dominant nannoconid, but fully-developed *N. abundans* is also conspicuous. *R. pseudoangustus* is a frequent and conspicuous element, and its LO is close to the top of the zone. Small forms of *Crucibiscutum* are last recorded here, but are rare and inconspicuous. *A. infracretacea* and *A. terebrodentarius* are frequent/common; the latter species is especially characteristic. As in BC12, *R. parallelus* is unusually common. *C. margerelii* becomes common in the upper part, marking the base of another major ('middle' Barremian) acme.

Several previous authors (Taylor, 1982; Thomsen, 1987) have included short, flangeless nannoconids (here assigned to *N. inornatus*) in *N. abundans*, thus giving this species an anomalously early FO.

BC14 Nannoconus borealis Zone

Author. (Crux, 1989, C. conicus Zone) Rutledge and Bown (in prep.).

Definition. FO of *Nannoconus borealis* (or the LO of *Rhagodiscus pseudoangustus*) to the first consistent occurrence of frequent/common *Zeugrhabdotus scutula.*

Range. Lower Barremian (fissicostatum AZ to basal elegans AZ/Aulacoteuthis spp. Bel. Zone).

Remarks. Boreal assemblages are often of low diversity and dominated by a few conspicuous elements, e.g. *R. asper*, *C. margerelii*, *Micrantholithus* spp. and *Nannoconus* spp.. Both *N. inornatus* and *N. abundans* are frequent/common throughout; the latter is generally dominant. *N. borealis* is more sporadic in its occurrence but very conspicuous and occasionally common.

BC15 Zeugrhabdotus scutula Zone

Author. Rutledge and Bown (in prep.).

Definition. Interval during which *Zeugrhabdotus scutula* is consistently frequent/common (2–15%), in the presence of other characteristic Barremian forms (notably *N. abundans* and *N. borealis*).

Range. Upper Lower to lower Upper Barremian (elegans to ?innexum AZs).

Remarks. The FO of *N. pseudoseptentrionalis* also approximates the base of this zone. *Acaenolithus*? sp.1 (= ?*Vagalapilla matalosa*) first appears in the middle of this interval. The regional (boreal) LO of *Diazomatolithus lehmanii* is also recorded here.

This and the following four zones have been further subdivided by Gallagher (pers. obs. and herein) based on high-resolution stratigraphic studies of the Valhall and Sola formations from the Britannia Field (Moray Firth Basin). The subdivision is based upon discrete LOs together with acme/influx abundance events. The ability to correlate some of these events away from this subbasin of the North Sea is uncertain at present and the subzones are therefore presented informally (Fig. 5.3).

BC16 Acaenolithus? sp. Zone

Author. Rutledge and Bown (in prep.).

Definition. Last consistent occurrence of frequent/common (2–15% of assemblage) *Zeugrhabdotus scutula* to the LO of *Nannoconus borealis.*

Range. Upper Barremian (?innexum to ?bidenta-

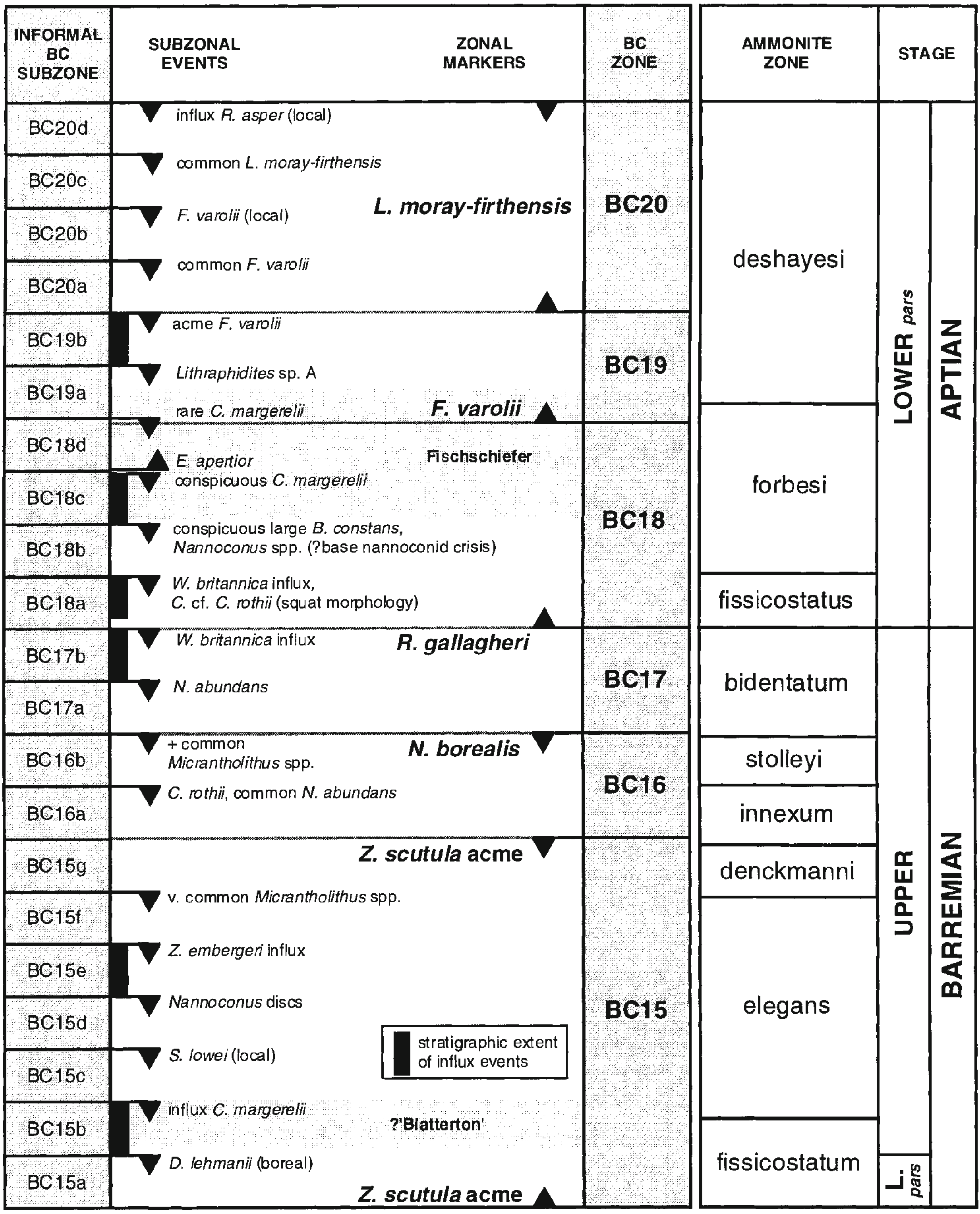


Fig. 5.3 High-resolution subdivision of BC zones 15-20 (Barremian-Aptian), based on analysis of the Valhall Formation, Britannia Field (Moray Firth Basin). Subzonal status is informal. Ammonite zones are inferred.

tum AZs).
Remarks. Evidence for the existence of this zone is scant due to non-exposure of this interval at Speeton, and to the rarity of ammonites in the German sections. The LO of *C. rothii* occurs within this zone, but the event may be difficult to apply due to its discontinuous occurrence. *N. borealis* also has a discontinuous range, but would seem to be consistently present in the Upper Barremian.

BC17 Biscutum constans Zone

Author. Rutledge and Bown (in prep.).
Definition. LO of *Nannoconus borealis* to the FO of *Rhagodiscus gallagheri* and/or the re-entry of frequent *Watznaueria britannica.*
Range. Upper Barremian (bidentatum AZ).

BC18 Watznaueria britannica Zone

Author. Rutledge and Bown (in prep.).
Definition. FO of *Rhagodiscus gallagheri* (or the re-entry of frequent *Watznaueria britannica*) to the FO of *Farhania varolii.*
Range. Lower Aptian (fissicostatus to forbesi AZs).
Remarks. *R. gallagheri* has previously been included within the species concept of *R. angustus* (Thomsen, 1987; Mutterlose, 1991). It has been recorded from the Lower Aptian of the North Sea and adjacent areas (e.g. Skegness Clay and basal Atherfield Clay) by Rutledge and Bown (in prep.). The FO of *R. gallagheri* coincides approximately with an influx of *W. britannica* (a predominantly Jurassic species that is very rare in the Neocomian). Gallagher (pers. obs. and Fig. 5.3) has observed two closely-spaced but discrete *W. britannica* influx events at this level.

R. gallagheri increases in abundance through the zone becoming frequent/common. Small forms of *Acaenolithus*? (3–4µm) are often frequent. *Flabellites oblongus* and *Hayesites irregularis* are first recorded here in boreal sections but may have earlier FOs in tethyan sections.

The LO of *N. abundans* was recorded within this zone by Rutledge and Bown (in prep.) although this species has been used as a uppermost Barremian datum by others (Taylor, 1982; Jakubowski, 1987; Mutterlose, 1991) and is used to subdivide BC17 by Gallagher (herein Fig. 5.3).

BC19 Farhania varolii Zone

Author. Rutledge and Bown (in prep.).
Definition. FO of *Farhania varolii* to the FO of *Lithraphidites moray-firthensis.*
Range. Lower Aptian (upper forbesi to ?lower deshayesi AZs).
Remarks. Abundant *B. constans*, with frequent *R. gallagheri*, *F. varolii*, and *F. oblongus. W. britannica* declines in abundance to its normal, background level (rare) early in this zone. Influxes of *Repagulum parvidentatum* and *Zeugrhabdotus xenotus* have also been recorded in boreal sections (Rutledge and Bown, in prep.). *Lithraphidites* cf. *L. pseudoquadratus*, the likely precursor of *L. moray-firthensis*, may be fairly frequent.

F. varolii is a distinctive and dissolution-resistant species, with a wide geographic distribution. Previous records of '*Lithastrinus septentrionalis*' from low-latitude Aptian sections (Thierstein, 1973; Roth, 1983) almost certainly belong to this species.

BC20 Lithraphidites moray-firthensis Zone

Author. Rutledge and Bown (in prep.).
Definition. Total range of *Lithraphidites moray-firthensis.*
Range. Lower Aptian (?deshayesi AZ).
Remarks. Frequent *L. moray-firthensis*, with *F. varolii* and *R. parvidentatum.* Jakubowski (1987) recorded *L. moray-firthensis* rarely in the Upper Aptian, and hence used the last common occurrence of the species as a datum. However, this species has never been described from Upper Aptian outcrop material, and is probably restricted to the Lower Aptian (?deshayesi AZ).

BC21 Rhagodiscus asper Zone

Author. (Jakubowski, 1987) Rutledge and Bown (in prep.).
Definition. Last consistent occurrence of *Lithraphidites moray-firthensis* to the LO of *Farhania varolii.*
Range. Upper Lower Aptian to Upper Aptian (?bowerbanki to jacobi AZs).
Remarks. *R. asper* is abundant (~20–50%) throughout, but declines in abundance towards the top of the zone. *R. parvidentatum* is frequent/common, particularly towards the top. *Nannoconus* spp. (especially *N. truitti* and *N. quadriangulus*) may be frequent. *Braarudosphaera* spp.

(especially *B. africana*), *Radiolithus orbiculatus/planus* and *Eprolithus floralis* are also characteristic; these species have their FOs near the base (possibly in the underlying zone). *Crucibiscutum* cf. *C. salebrosum* may be frequent towards the top of the zone. *Micrantholithus* spp. become rare, and may disappear entirely towards the top of this interval. *F. varolii* is rare but consistently present.

Jakubowski (1987) subdivided this interval using the LO of 'common' *R. asper* but utilized the LO of 'frequent/common' *R. asper*, above the LO of *F. varolii*, to define another zonal boundary. Jeremiah (1996) utilizes the last consistent occurrence of a 'high relative abundance' of *R. asper* to define an ?uppermost Aptian or Lower Albian zonal boundary. However the placement of this abundance-decline event relative to the LO of *F. varolii* remains uncertain. The presently available onshore data suggests that a major decline in the abundance of *R. asper* (from >20% to ~5%) occurs within the nutfieldiensis AZ, prior to the LO of *F. varolii* (jacobi AZ) .

BC22 Repagulum parvidentatum Zone

Author. (Jakubowski, 1987) Rutledge and Bown (in prep.).
Definition. LO of *Farhania varolii* to the FO of *Prediscosphaera columnata*.
Range. Uppermost Aptian (jacobi AZ) to Lower Albian (precise level uncertain).
Remarks. *R. asper* is much reduced in abundance relative to BC21. *R. parvidentatum* is frequent/common. *Acaenolithus viriosus* and *Seribiscutum primitivum* first appear here; the former species is almost restricted to this interval (having its LO shortly above the FO of *P. columnata*), while the latter is particularly common, upon its appearance. The first consistent occurrence of *Rhagodiscus splendens* lies within this interval; earlier, generally rare, records of this species may be aberrant specimens of *R. asper* or *R. fenestratus*.

BC23 Prediscosphaera columnata Zone

Author. Equivalent to the CC8a Subzone of Perch-Nielsen (1979a).
Definition. FO of *Prediscosphaera columnata* to the FO of *Tranolithus orionatus*.
Range. ?Aptian/Albian boundary interval to Middle Albian (?dentatus AZ).
Remarks. A small, elliptical species of *Prediscosphaera, P.* cf. *P. spinosa*, precedes the FO of *P. columnata* but the precise timing of these events has yet to be satisfactorily established in boundary stratotype sections. The differentiation of these two distinct species must be recognized in order to preserve the integrity of this zonal datum.

BC24 Tranolithus orionatus Zone

Author. Equivalent to the NC8C Subzone of Bralower *et al.* (1993).
Definition. FO of *Tranolithus orionatus* to the FO of *Axopodorhabdus albianus*.
Range. Middle Albian (?dentatus to loricatus AZs).
Remarks. The upper boundary of this zone is also approximated by the LO of *Braloweria boletiformis*.

BC25 Axopodorhabdus albianus Zone

Author. Equivalent to the NC9A Subzone of Bralower *et al.* (1993).
Definition. FO of *Axopodorhabdus albianus* to the FO of *Eiffellithus monechiae*.
Range. Middle to Upper Albian (lautus to inflatum AZs).

BC25a Subzone

Author. Defined herein.
Definition. FO of *Axopodorhabdus albianus* to the LO of *Ceratolithina bicornuta*.
Range. Upper Middle Albian (lautus AZ) to lowermost Upper Albian (lower inflatum AZ).
Remarks. *C. bicornuta* is a distinctive nannolith which has been recorded from S England (Perch-Nielsen, 1988) and the Indian Ocean (Burnett, 1997a). In both areas it appears to have a restricted stratigraphic range, which in S England corresponds to the lautus-inflatum AZs. The subzone includes, and is approximately equivalent to, the total range of *C. bicornuta*.

BC25b Subzone

Author. Defined herein.
Definition. LO of *Ceratolithina bicornuta* to the FO of *Eiffellithus monechiae*.
Range. Upper Albian (inflatum AZ).

BC26 Eiffellithus monechiae Zone

Author. Equivalent to the NC9B Subzone of Bralower *et al.* (1993).
Definition. FO of *Eiffellithus monechiae* to the FO of *Eiffellithus turriseiffelii*.

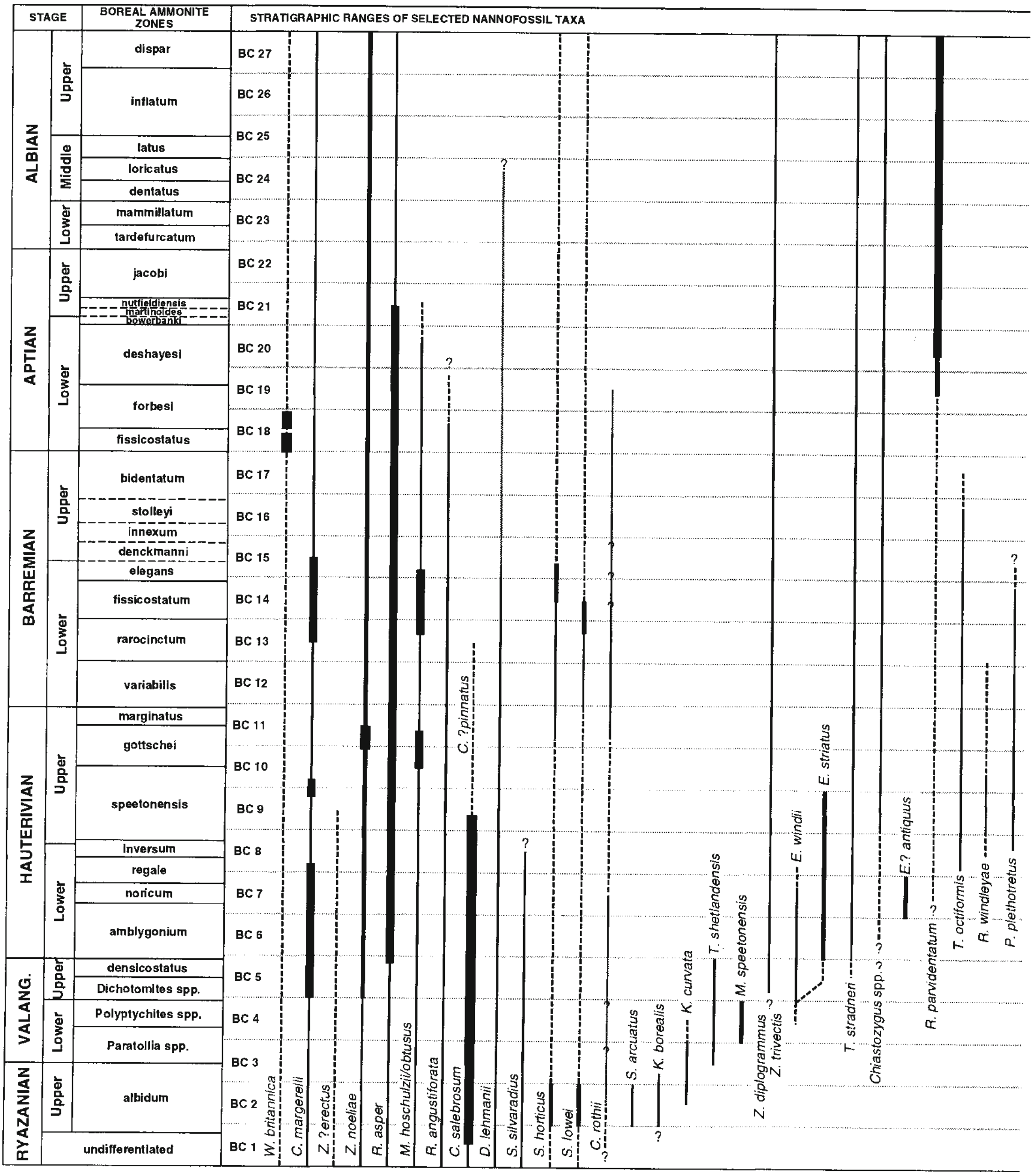
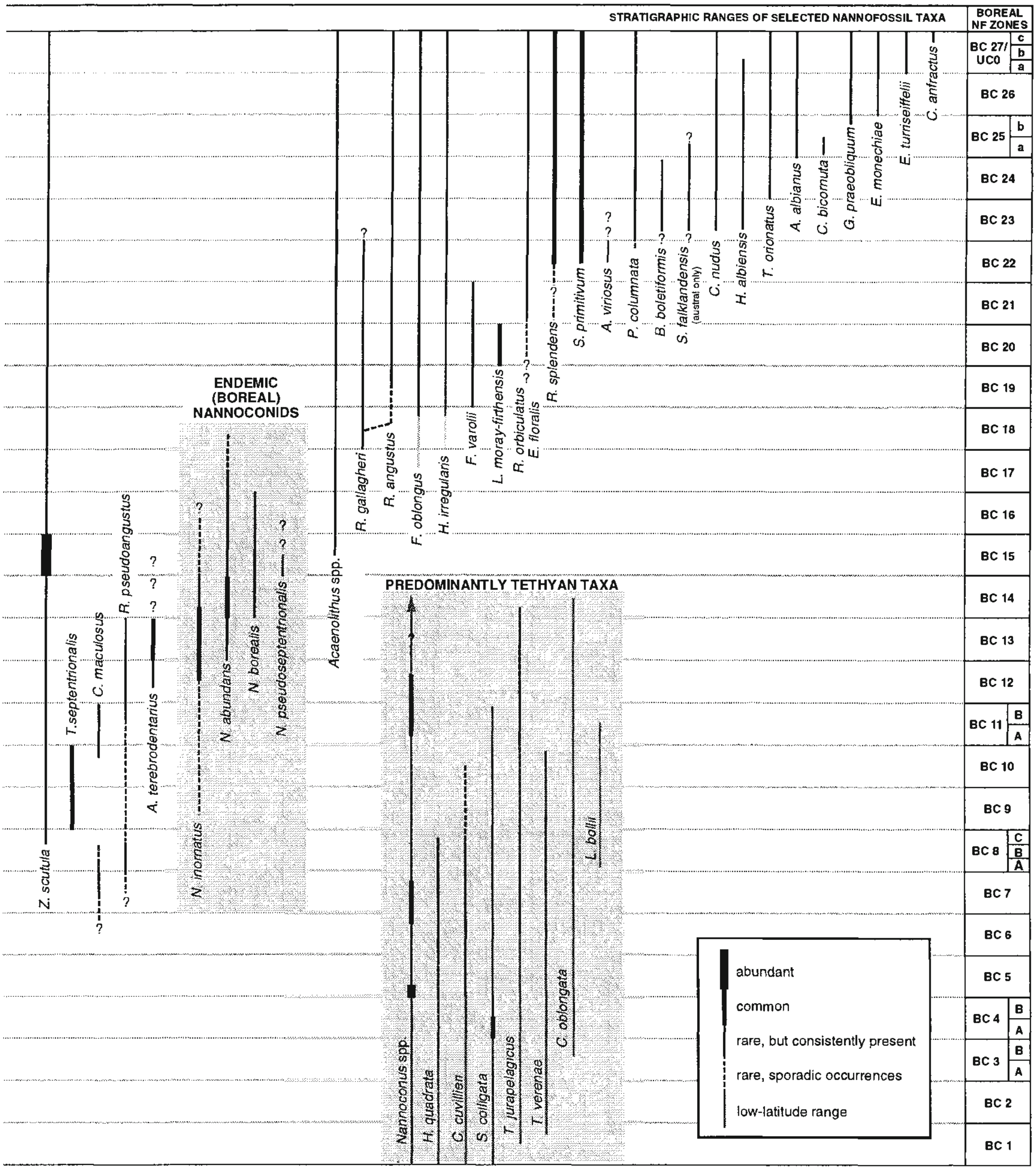


Fig. 5.4 Stratigraphic ranges of selected Lower Cretaceous taxa.


STRATIGRAPHIC RANGES OF SELECTED NANNOFOSSIL TAXA
BOREAL NF ZONES
BC 27/ UC0
c
b
a
BC 26
BC 25
b
a
BC 24
BC 23
BC 22
BC 21
BC 20
BC 19
BC 18
BC 17
BC 16
BC 15
BC 14
BC 13
BC 12
BC 11
B
A
BC 10
BC 9
BC 8
C
B
A
BC 7
BC 6
BC 5
BC 4
B
A
BC 3
B
A
BC 2
BC 1
Z. scutula
T. septentrionalis
C. maculosus
R. pseudoangustus
A. terebrodentarius
ENDEMIC (BOREAL) NANNOCONIDS
N. inornatus
N. abundans
N. borealis
N. pseudoseptentrionalis
Acaenolithus spp.
R. gallagheri
R. angustus
F. oblongus
H. irregularis
F. varolii
L. moray-firthensis
R. orbiculatus
E. floralis
R. splendens
S. primitivum
A. viriosus
P. columnata
B. boletiformis
S. falklandensis (austral only)
C. nudus
H. albiensis
T. orionatus
A. albianus
C. bicornuta
G. praeobliquum
E. monechiae
E. turriseiffelii
C. anfractus
PREDOMINANTLY TETHYAN TAXA
Nannoconus spp.
H. quadrata
C. cuvillieri
S. colligata
T. jurapelagicus
T. verenae
C. oblongata
L. bollii
abundant
common
rare, but consistently present
rare, sporadic occurrences
low-latitude range
?

Range. Upper Albian (upper inflatum AZ).

BC27 Eiffellithus turriseiffelii Zone
Author. Equivalent to the NC10A Subzone of Bralower *et al.* (1993).
Definition. FO of *Eiffellithus turriseiffelii* to the FO of *Corollithion kennedyi.*
Range. Upper Albian (upper inflatum AZ) to Lower Cenomanian.

Subzones BC27a–c/UC0a–c
See Chapter 6, p. 139 and Fig. 5.2.

5.5 GLOBAL CORRELATION

The standard Lower Cretaceous stages are defined in SE France by means of ammonite biostratigraphy, and correlation of the Neocomian stages with more northerly, boreal areas has always been problematical due to faunal provincialism. Mixing of ammonite faunas through certain intervals, e.g. Valanginian and Hauterivian, has allowed limited calibration of the regional zonations, however, the correlation of stage and substage boundaries remains difficult.

Nannofossil zonation schemes applied to the Neocomian of boreal and tethyan areas have seemed virtually irreconcilable, utilizing entirely different suites of marker-species. While it is clear that some of the most easily-utilized markers in each realm have restricted geographic distributions, improved documentation of sections in the tethyan area (Applegate and Bergen, 1988; Bergen, 1994) and the boreal area (Rutledge and Bown, in prep.) has revealed the potential for direct interregional correlation. Following Thierstein (1971, 1973), tethyan zonations have relied heavily on two species, *C. oblongata* and *Lithraphidites bollii*, to subdivide the Neocomian. These highly restricted (?stenothermal) species only rarely reached boreal latitudes, if at all, and are also relatively long-ranging, so brief influxes into boreal areas are of little use in correlation. Fortunately, some of the most useful boreal markers are very short-ranging (e.g. *M. speetonensis*, *E.*? *antiquus*, *T. septentrionalis*), and even limited occurrences in tethyan sections are potentially useful for correlation. Bergen (1994) has recently documented two such 'boreal' species, *M. speetonensis* and *E.*? *antiquus*, in tethyan sections and several others are also known to be present there, e.g. *T. shetlandensis* has been observed frequently with *M. speetonensis* in a Lower Valanginian sample from Angles, SE France (Rutledge, pers. obs.); and *T. septentrionalis* is known to occur in the western N Atlantic (Roth, 1983), California (Bralower, 1990), Indonesia (Varol, 1991), and SE France (S. Gardin, pers. comm. 1994). This latter species is an extremely useful marker, with a total range of comparable duration to an ammonite zone.

Taxonomic improvements, with the application of more-restricted species concepts, have shown that many other species are common to both realms. Thus, *E. windii*, *E. striatus*, *Zeugrhabdotus diplogrammus*, *Z. trivectis*, *Z. scutula* and *A. terebrodentarius* have been previously overlooked or masked by broad species concepts, yet they are potentially useful interregional markers. In addition, improved documentation of the ranges of *C. cuvillieri* and *S. colligata*, which have previously been used as markers in both boreal and tethyan areas, has provided further interregional datums.

The Aptian is problematical, not because of a lack of potential datums, but due to a lack of complete, nannofossiliferous sections in which to calibrate the many FOs within this interval. *H. irregularis*, which is widely used as a basal Aptian marker at low-latitudes (e.g. Bergen, 1994) is rare and sporadic in boreal sections, and its FO is probably not a reliable datum. It is interesting that the markers which Jakubowski (1987) used to zone the Aptian of the North Sea (*L. morayfirthensis*, *F. varolii*) have not been recorded from the tethyan stratotypes, even though *F. varolii* is now known to be widely distributed (Varol, 1992). These species have probably been overlooked, or grouped with similar forms, in the less well-preserved tethyan material.

The Albian stage is known from many of the ocean basins, and all the zonal marker-species are cosmopolitan. Therefore, global correlation using nannofossils is readily achievable at a relatively high stratigraphic resolution, and is well demonstrated by Bralower (1992) and Bralower *et al.* (1993), who presented around 20 widely recognizable bioevents through this interval.

Thus, although further work is required, particularly the confirmation of stratigraphic ranges of newly described species and the testing of the geographic range of acme events, there is great potential for interregional correlation using nannofossils.

5.6 MAGNETOBIOCHRONOLOGY

Calibration of nannofossil bioevents with the geomagnetic polarity time-scale has been undertaken almost exclusively on sections from the tethyan region and the Atlantic Ocean, e.g. Bralower (1987), Channell *et al.* (1987), Ogg and Steiner (1988), Bralower *et al.* (1989), Channell and Erba (1992) and Cecca *et al.* (1994). As yet, magnetostratigraphic studies on boreal sections have failed to provide satisfactory results.

5.7 BIOGEOGRAPHY

One of the most significant advances in Cretaceous nannopalaeontology in recent years has been the recognition of considerable palaeobiogeographic differentiation throughout this time interval. This has come about largely as a result of industrial biostratigraphy in the North Sea Basin together with DSDP/ODP research, particularly the drilling of sections in the southern hemisphere (Indian and Southern Oceans).

Early Cretaceous nannoplankton provincialism is generally recognized by limited endemism at species and, rarely, generic level, together with considerable abundance variations of cosmopolitan assemblage components. The number of endemic taxa varies somewhat through the Cretaceous but a consistent feature is the presence of species which apparently display bipolar distribution. This feature may actually represent high abundances at high latitudes and very rare occurrences in lower latitudes. By analogy with modern nannoplankton, these distributions are most likely primarily controlled by the nutrient and temperature characteristics of surface-waters, and comprise broadly parallel latitudinal regions.

Lower Cretaceous nannoplankton distributions broadly define three major provinces: northern high-latitude (Boreal), subtropical-tropical (Tethyan) and southern high-latitude (Austral), although these may be further subdivided, and transitional zones are recognized. Particularly well-defined provincialism is observed in the Tithonian-Berriasian time-interval but long-ranging species, such as *C. salebrosum, S. primitivum* and *R. parvidentatum,* consistently display bipolar distributions for most of the time-interval under discussion.

North Sea Basin research has produced a large number of new nannofossil species, many of which have been interpreted as endemic 'boreal' taxa, although this may simply reflect the intensity of research, with many of these taxa having been overlooked or undifferentiated in earlier, low-latitude studies. A number of recent studies in low latitudes have, in fact, begun to extend the ranges of some of these taxa, although they may be rare and stratigraphically restricted in these areas. Similarly, Southern Ocean DSDP/ODP sites have yielded a number of new taxa and these have been interpreted as 'austral' taxa, although more precise constraints on the palaeobiogeographies of these taxa await further research. However, despite some doubt about the precise distributions of some of these new taxa, it is almost certain that some are truly high-latitude-endemic, or at least only found commonly at these latitudes. These studies have also recognized the paucity or sporadic occurrence of other taxa which have been consistently utilized in low-latitude biostratigraphies, and these have been labelled low-latitude or 'tethyan' taxa. Again there have been problems with a number of these species, in that many appear to have much wider geographic distributions than first thought but only through restricted stratigraphic intervals. However, a number of these 'tethyan' taxa are clearly virtually cosmopolitan, e.g. *C. cuvillieri* and *S. colligata.*

5.8 ATLAS OF SPECIES

Most Lower Cretaceous calcareous nannofossils are illustrated in Plates 5.1–5.15. Taxa are listed according to the classification of Bown and Young (1997). EMs are not uniformly enlarged but magnifications are given in plate captions. LMs are uniformly enlarged at x2300. Stratigraphic information is given as stages (L=Lower, U=Upper) and ammonite zones (in brackets), where possible; question marks indicate a degree of uncertainty. Photographs are identified by a UCL number (film and frame). The majority of photographs come from the research of Drs Paul Bown, Jason Crux, Dave Rutledge and Rosanna Taylor.

Plate 5.1

Order EIFFELLITHALES Rood *et al.*, 1971

FAMILY CHIASTOZYGACEAE Rood *et al.*, 1973 emend. Varol and Girgis, 1994

Fig. 1. ***Braloweria boletiformis*** (Black, 1972) Crux, 1991b. Side view, Munday's Hill (UK), M. Albian (loricatus), JC-103-13, x5250. Range: L.? – M. Albian (loricatus).

Fig. 2. ***Bukrylithus ambiguus*** Black, 1971a. Distal view, Speeton (UK), L. Barremian, JC-99-17, x7384. Range: Berriasian – ?Campanian.

Fig. 3. ***Chiastozygus litterarius*** (Górka, 1957) Manivit, 1971. Distal view, Copt Point (UK), U. Albian (inflatum), UCL-1029-4, x4312. Range: U. Barremian – Maastrichtian.

Fig. 4. ***Chiastozygus ?tenuis*** Black, 1971a. Distal view, Speeton (UK), U. Hauterivian (marginatus), UCL-525-3, x4719.

Figs 5–6. ***Clepsilithus maculosus*** Rutledge and Bown, 1996. Distal (5) and proximal (6) views. 5, BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-4061-11, x8657; 6, Speeton (UK), U. Hauterivian (marginatus), UCL-518-11, x6688. Range: L. Hauterivian – L. Barremian (variabilis).

Fig. 7. ***Diadorhombus rectus*** Worsley, 1971. Distal view, DSDP Site 534 (N Atlantic Ocean), Hauterivian, UCL-1744-6, x6970. Range: U. Berriasian (boissieri) – ?Aptian.

Fig. 8. ***Loxolithus armilla*** (Black *in* Black and Barnes, 1959) Noël, 1965. Distal view, BGS Borehole 81/43 (North Sea), L. Barremian, UCL-4079-13, x3700. Range: L. Hauterivian – Maastrichtian.

Figs 9–10. ***Rhabdophidites parallelus*** (Wind and Cepek, 1979) Lambert, 1987. 9, side view, DSDP Site 534 (Atlantic Ocean), Hauterivian, UCL-1729-19, x2213; 10, view of coccolith group (?collapsed coccosphere), North Jens-1 (North Sea), Barremian, UCL-2953-2, x1700. Range: L. Valanginian (campylotoxus) – Albian.

Fig. 11. ***Staurolithites crux*** (Deflandre and Fert, 1954) Caratini, 1963. Distal view, Speeton (UK), U. Hauterivian (marginatus), UCL-525-13, x5600.

Figs 12–13. ***Staurolithites mutterlosei*** Crux, 1989. Distal and side views, BGS Borehole 81/43 (North Sea), L. Barremian (variabilis), UCL-4068-35/36, x5971/5843. Range: L. Valanginian? – ?L. Cenomanian.

Fig. 14. ***Zeugrhabdotus embergeri*** (Noël, 1959) Perch-Nielsen, 1984. Distal view, BGS Borehole 81/43 (North Sea), U. Hauterivian (gottschei), UCL-4076-25, x3333. Range: L. Tithonian? – Maastrichtian.

Fig. 15. ***Zeugrhabdotus noeliae*** Rood *et al.*, 1971. Distal view, Gr. Lafferde (N Germany), Barremian, UCL-468-9, x9710. Range: Jurassic – Santonian.

Fig. 16. ***Zeugrhabdotus scutula*** (Bergen, 1994) Rutledge and Bown, 1996. Distal view, BGS Borehole 81/43 (North Sea), L. Barremian, UCL-4069-4, x3828. Range: U. Hauterivian (inversum/sayni) – Santonian.

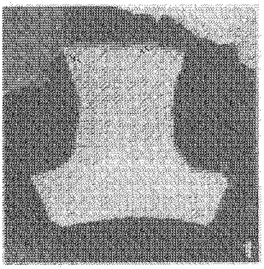
Family EIFFELLITHACEAE Reinhardt, 1965

Fig. 17. ***Diloma galiciense*** Bergen, 1994. Distal view, BGS Borehole 81/43 (North Sea), L. Barremian, UCL-4074-24, x4289. Range: L. Hauterivian (radiatus) – L. Barremian.

Fig. 18. ***Diloma primitiva*** (Worsley, 1971) Wind and Cepek, 1979. Distal view, DSDP Site 534 (Atlantic Ocean), Hauterivian, UCL-1722-7, x4384. Range: Valanginian – L. Barremian.

Fig. 19. ***Eiffellithus striatus*** (Black, 1971a) Applegate and Bergen, 1988. Distal view, DSDP Site 547B (Atlantic Ocean), U. Valanginian/Hauterivian, UCL-1744-19, x4639. Range: U. Valanginian – U. Hauterivian (speetonensis–gottschei/sayni).

Fig. 20. ***Eiffellithus windii*** Applegate and Bergen, 1988. Distal view, BGS Borehole 81/43 (North Sea), U. Valanginian (Dichotomites spp.), UCL-4073-13, x5957. Range: L. Valanginian (campylotoxus) – ?L. Hauterivian (radiatus).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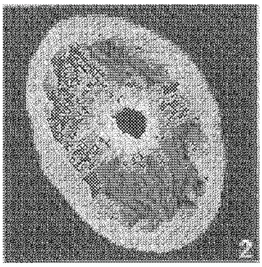
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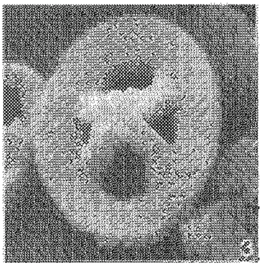
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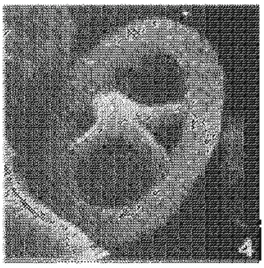
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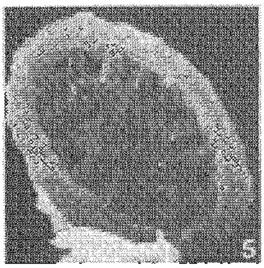
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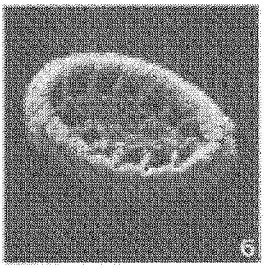
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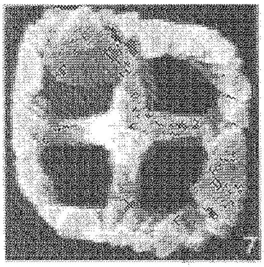
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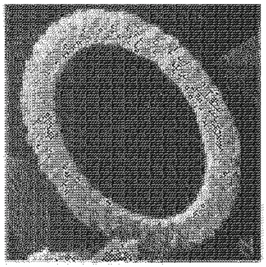
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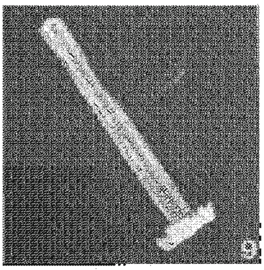
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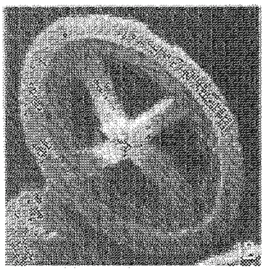
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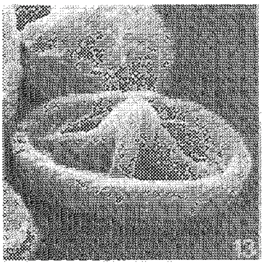
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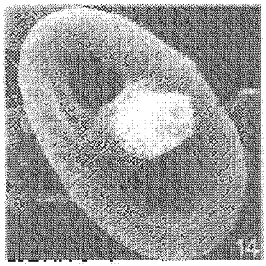
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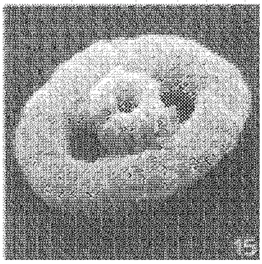
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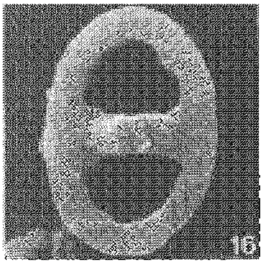
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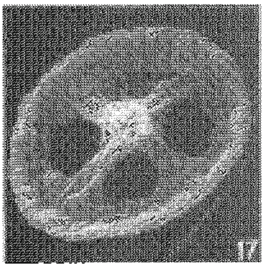
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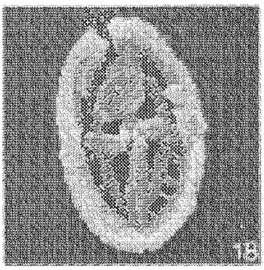
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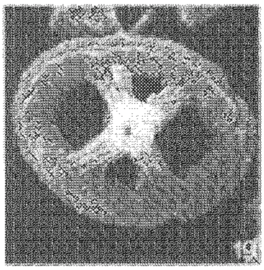
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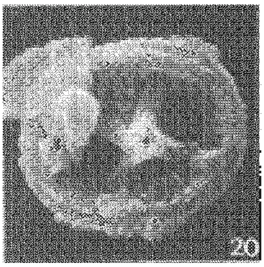
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Plate 5.2

Family EIFFELLITHACEAE Reinhardt, 1965
Fig. 1. ***Tegumentum octiformis*** (Köthe, 1981) Crux, 1989. Proximal view, Speeton (UK), U. Hauterivian (marginatus), UCL-525-9, x5000. Range: L. Hauterivian? – U. Barremian.

Fig. 2. ***Tegumentum stradneri*** Thierstein *in* Roth and Thierstein, 1972. Distal view, BGS Borehole 81/43 (North Sea), U. Hauterivian (gottschei), UCL-4067-16, x5156. Range: Valanginian – Maastrichtian.

Family RHAGODISCACEAE Hay, 1977
Figs 3–4. ***Calcicalathina oblongata*** (Worsley, 1971) Thierstein, 1971. Distal (3) and side (4) views, DSDP Site 547B (Atlantic Ocean), U. Valanginian/Hauterivian, UCL-1488-16/1744-22, x3126/3290. Range: L. Valanginian (otopeta) – L. Barremian (?nicklesi).

Fig. 5. ***Percivalia fenestrata*** (Worsley, 1971) Wise, 1983. Distal view, BGS Borehole 81/43 (North Sea), U. Hauterivian (gottschei), UCL-4067-30, x4500. Range: U. Berriasian (boissieri) – Campanian.

Fig. 6. ***Rhagodiscus achlyostaurion*** (Hill, 1976) Doeven, 1983. Distal view, Skegness Borehole, U. Aptian, UCL-1091-14, x5077. Range: U. Aptian? – Coniacian.

Fig. 7. ***Rhagodiscus angustus*** (Stradner, 1963) Reinhardt, 1971. Distal view, Munday's Hill (UK), U. Albian (inflatum), JC-102-10, ~x5800. Range: L. Aptian? – Maastrichtian.

Figs 8–9. ***Rhagodiscus asper*** (Stradner, 1963) Reinhardt, 1967. 8, distal view, BGS Borehole 81/43 (North Sea), L. Barremian, UCL-4068-24, x4307; 9, proximal view, Speeton (UK), U. Hauterivian (marginatus), UCL-525-30/4, ?x4252. Range: U. Tithonian? – U. Cenomanian.

Fig. 10. ***Rhagodiscus cepekii*** (Crux, 1987b) Rutledge and Bown comb. nov.. Distal view, BGS Borehole 81/43 (North Sea), L. Barremian (variabilis), UCL-4068-32, x7437. Range: ?L. Barremian (variabilis).
Basionym: *Chiastozygus cepekii* Crux, 1987b (*INA Newsletter*, **9** (1), p. 30, pl. 1, figs 1–3, 6, 18-20, holotype fig. 1)

Figs 11–12. ***Rhagodiscus infinitus*** (Worsley, 1971) Applegate *et al.* *in* Covington and Wise, 1987. Distal views, BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-4081-25, x3193 and DSDP Site 534 (Atlantic Ocean), Hauterivian, UCL-1729-14, x4287. Range: Valanginian? – ?Maastrichtian.

Figs 13–14. ***Rhagodiscus pseudoangustus*** Crux, 1987b. Distal (13) and side (14) views, BGS Borehole 81/43 (North Sea), L. Barremian (variabilis), UCL-4068-15/4069-6, x6181/6912. Range: Hauterivian – L. Barremian (rarocinctum).

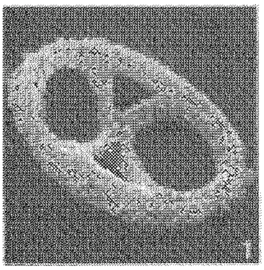
Order STEPHANOLITHIALES Bown and Young, 1997
?Family PARHABDOLITHACEAE Bown, 1987
Fig. 15. **'*Parhabdolithus*' *stubbingsii*** Black, 1971a. Proximal oblique view, BGS Borehole 81/43 (North Sea), U. Hauterivian (gottschei), UCL-4076-12, x4687. Range: L. Hauterivian – L. Barremian.

Family STEPHANOLITHIACEAE Black, 1968
Figs 16–17. ***Rotelapillus laffittei*** (Noël, 1957) Noël, 1973. Distal (16) and proximal (17) views. Fig. 16, DSDP Site 547B (Atlantic Ocean), U. Valanginian/Hauterivian, UCL-1729-12, x6000. Fig. 17, Otto Gott (N Germany), Barremian, UCL-540-18, x6534. Range: U. Tithonian – Maastrichtian.

Fig. 18. ***Stradnerlithus geometricus*** (Górka, 1957) Bown and Cooper, 1989a. Distal view, Speeton (UK), U. Hauterivian, JC-101-24, x10000.

Fig. 19. ***Stradnerlithus silvaradius*** (Filewicz *et al.* *in* Wind and Wise, 1977) Rahman and Roth, 1991. Distal view, DSDP Site 534 (Atlantic Ocean), Hauterivian, UCL-1744-29, x6537. Range: U. Berriasian – Hauterivian (inversum/sayni).

Fig. 20. ***Scapholithus fossilis*** Deflandre *in* Deflandre and Fert, 1954. Distal view, Hoheneggelsen (N Germany), U. Barremian, UCL-439-9, x8120. Range: L. Hauterivian – ?present day.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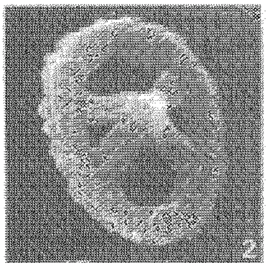
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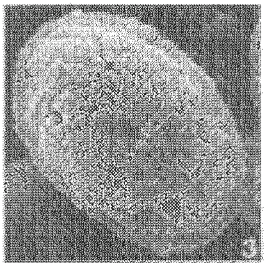
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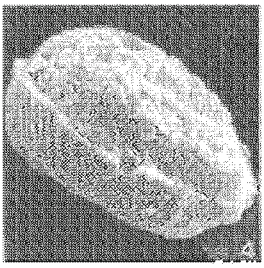
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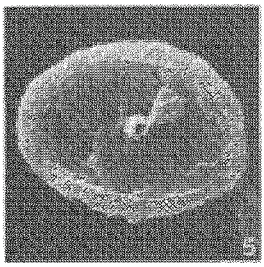
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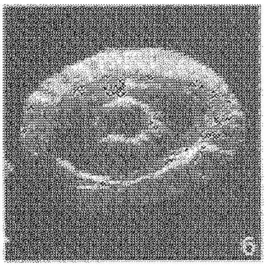
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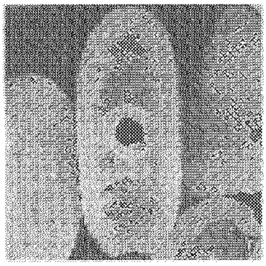
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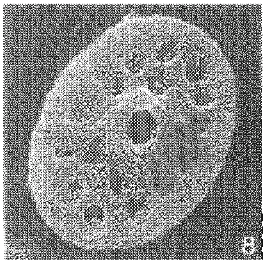
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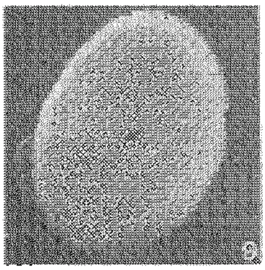
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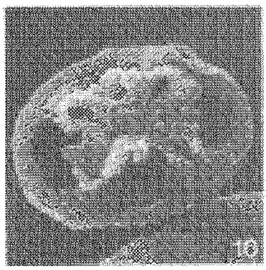
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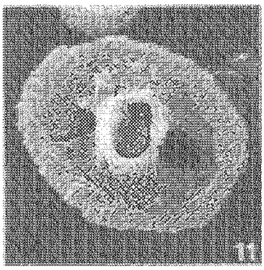
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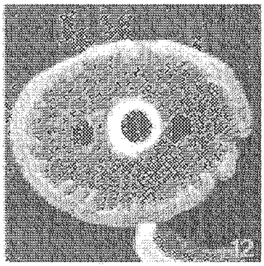
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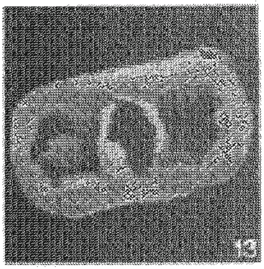
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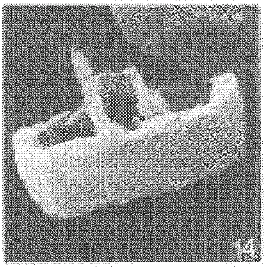
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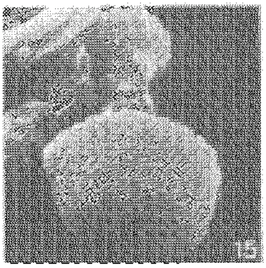
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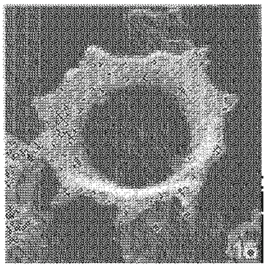
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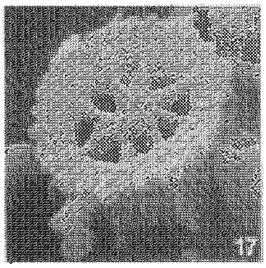
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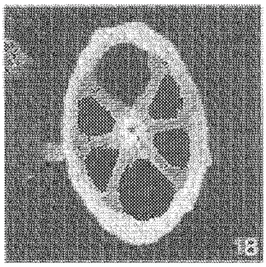
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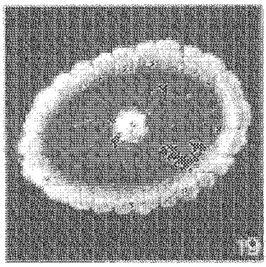
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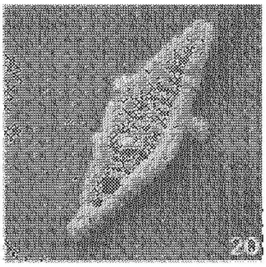
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Plate 5.3

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

Family AXOPODORHABDACEAE Bown and Young, 1997

Fig. 1. ***Axopodorhabdus albianus*** (Black, 1967) Wind and Wise *in* Wise and Wind, 1977. Distal view, English Channel Borehole R330 (UK), Albian, UCL-585-5, x3100. Range: M. Albian (lautus) – U. Cenomanian.

Fig. 2. ***Axopodorhabdus dietzmannii*** (Reinhardt, 1965) Wind and Wise, 1983. Distal view, Speeton (UK), L. Hauterivian (amblygonium), UCL-653-33, x4115. Range: Berriasian? – Cenomanian.

Fig. 3. ***Hemipodorhabdus gorkae*** (Reinhardt, 1969) Grün *in* Grün and Allemann, 1975. Distal view, Speeton (UK), U. Hauterivian (marginatus), UCL-17-20, x5800. Range: Berriasian? – ?Turonian.

Fig. 4. ***Perissocyclus noeliae*** Black, 1971a. Distal view, Speeton (UK), L. Barremian, UCL-3699-7, x5275.

Fig. 5. ***Perissocyclus plethotretus*** (Wind and Cepek, 1979) Crux, 1989. Distal view, Borehole 81/43 (North Sea), L. Barremian, UCL-4069-3, x4250. Range: U. Hauterivian (inversum) – ?Aptian.

Figs 6–7. ***Perissocyclus tayloriae*** Crux, 1989. Distal (6) and side (7) views. 6, Otto Gott (N Germany, Aptian, JC-90-15, x6700; 7, Speeton (UK), L. Barremian, JC-100-14, x5870.

Fig. 8. ***Tetrapodorhabdus coptensis*** Black, 1971a. Distal view, Speeton (UK), L. Barremian (variabilis), UCL-521-6, x6000. Range: Berriasian? – Maastrichtian.

Family BISCUTACEAE Black, 1971a

Figs 9–10. ***Biscutum constans*** (Górka, 1957) Black *in* Black and Barnes, 1959. Distal view (9) and coccosphere (10). 9, Gorodische (Russia), M.Volgian (panderi), UCL-1499-17, x6392; 10, DSDP Site 398D (Atlantic Ocean), Hauterivian, UCL-723-17. Range: U. Bathonian – Maastrichtian.

Fig. 11. ***Crucibiscutum hayi*** (Black, 1973) Jakubowski, 1986. Distal view, BGS Borehole 81/43 (North Sea), L. Barremian (variabilis), UCL-4068-23, x7109. Range: Albian – Cenomanian.

Fig. 12. ***Crucibiscutum pinnatus*** (Black, 1971a) Rutledge and Bown comb. nov.. Distal view, Otto Gott (N Germany), U. Hauterivian, JC-96-12, x9230. Range: Hauterivian – L. Barremian. Basionym: *Cruciplacolithus pinnatus* Black, 1971a (*Proceedings of the Yorkshire Geological Society*, **38** (3), 381–424, p. 397, Pl. 30, fig. 5).

Fig. 13. ***Crucibiscutum salebrosum*** (Black, 1971a) Jakubowski, 1986. Distal view, Speeton (UK), L. Hauterivian (amblygonium), UCL-676-28, x8400. Range: Ryazanian – ?U. Hauterivian.

Fig. 14. ***Discorhabdus ignotus*** (Górka, 1957) Perch-Nielsen, 1968. Coccosphere, Speeton (UK), L. Barremian (rarocinctum), UCL-21-31, x3160. Range: Oxfordian – Maastrichtian.

Fig. 15. ***Seribiscutum primitivum*** (Thierstein, 1974) Filewicz *et al. in* Wise and Wind, 1977. Distal view, English Channel Borehole R330 (UK), Cenomanian, UCL-581-22, x4393. Range: L. Albian – Campanian.

Fig. 16. ***Sollasites arcuatus*** Black, 1971a. Distal view, Speeton (UK), Ryazanian (albidum), JC-97-5, x6439. Range: U. Ryazanian (albidum).

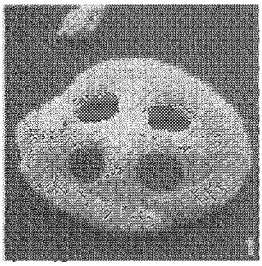
Fig. 17. ***Sollasites horticus*** (Stradner *et al. in* Stradner and Adamiker, 1966) Cepek and Hay, 1969. Distal view, Speeton (UK), Ryazanian (albidum), JC-99-27, x9075. Range: L. Oxfordian? – Maastrichtian.

Family CRETARHABDACEAE Thierstein, 1973

Fig. 18. ***Cretarhabdus conicus*** Bramlette and Martini, 1964. Distal view, BGS Borehole 81/43 (North Sea), L. Barremian (variabilis), UCL-4069-15, x4120. Range: Kimmeridgian (eudoxus) – Maastrichtian.

Fig. 19. ***Cretarhabdus inaequalis*** Crux, 1987b. Distal view, Otto Gott (N Germany), U. Hauterivian (discofalcatus), JC-97-22, x5715. Range: U. Hauterivian (speetonensis) – ?Albian.

Fig. 20. ***Cretarhabdus striatus*** (Stradner, 1963) Black, 1973. Distal view, Copt Point (UK), U. Albian (inflatum), UCL-1029-9, x4650. Range: U. Aptian? – U. Cenomanian.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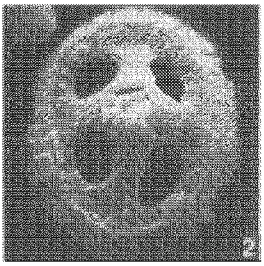
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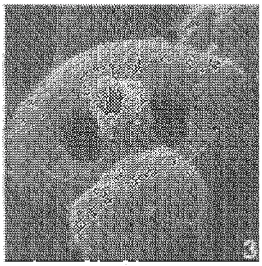
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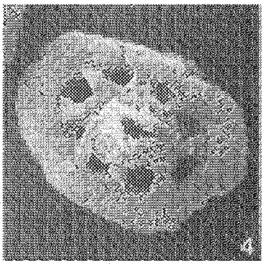
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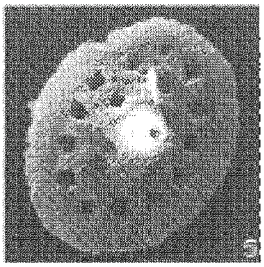
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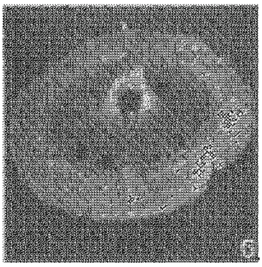
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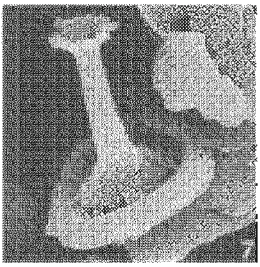
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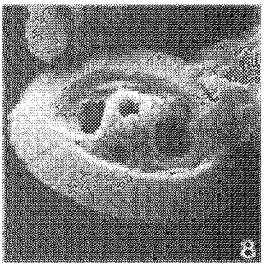
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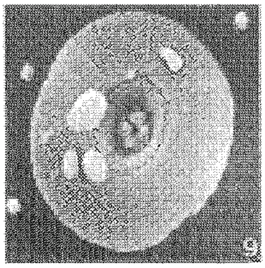
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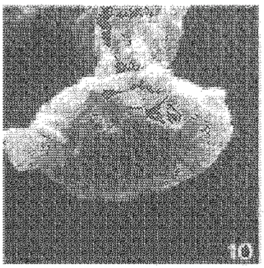
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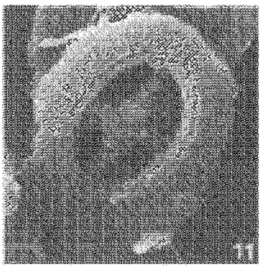
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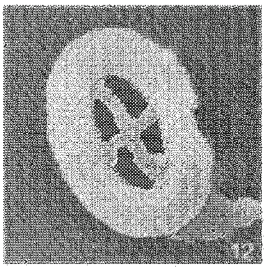
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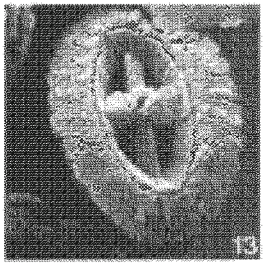
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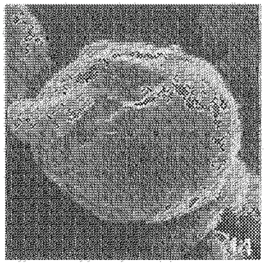
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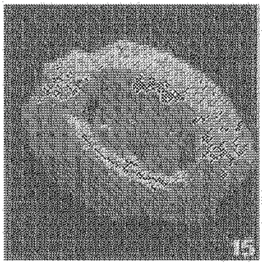
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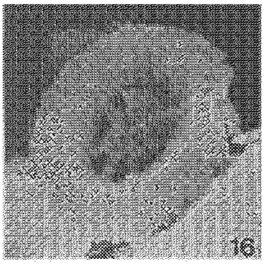
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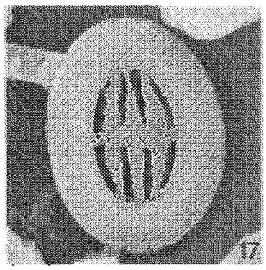
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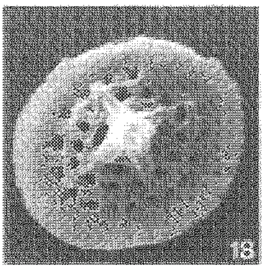
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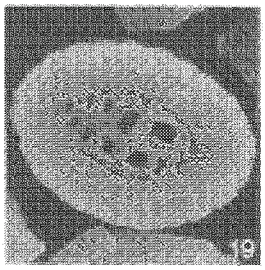
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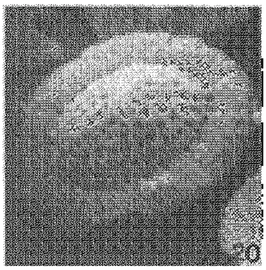
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Plate 5.4

Family CRETARHABDACEAE Thierstein, 1973
Fig. 1. ***Cruciellipsis cuvillieri*** (Manivit, 1966) Thierstein, 1971. Distal view, DSDP Site 547B (Atlantic Ocean), U. Valanginian/Hauterivian, UCL-1520-5, x3426. Range: L. Berriasian (?grandis) – U. Hauterivian (?gottschei/sayni).

Fig. 2. ***Grantarhabdus meddii*** Black, 1971a. Distal view, BGS Borehole 81/43 (North Sea), L. Barremian (variabilis), UCL-4079-5, x4768. Range: U. Tithonian – ?Albian.

Fig. 3. ***Helenea chiastia*** Worsley, 1971. Distal view, Speeton (UK), U. Hauterivian (marginatus), UCL-525-5, x5127. Range: Tithonian – L. Turonian (devonense).

Fig. 4. ***Helenea conus*** (Worsley, 1971) Rutledge and Bown comb. nov.. Distal view, DSDP Site 534 (Atlantic Ocean), Hauterivian, UCL-1729-15, x5544. Range: U. Berriasian? – ?L. Barremian.
Basionym: *Staurolithites*? *conus* Worsley, 1971 (*Proceedings of the Second Planktonic Conference Roma 1970,* (ed. A. Farinacci), Edizioni Tecnoscienza, Rome, **2**, p. 1313, pl. 2, figs 17–19, holotype fig. 19).

Fig. 5. ***Helenea quadrata*** (Worsley, 1971) Rutledge and Bown comb. nov.. Distal view, DSDP Site 547B (Atlantic Ocean), U. Valanginian/Hauterivian, UCL-1488-13, x4644. Range: L. Berriasian (grandis) – U. Hauterivian (inversum/ligatus).
Basionym: *Watznaueria quadrata* Worsley, 1971 (*Proceedings of the Second Planktonic Conference Roma 1970,* (ed. A. Farinacci), Edizioni Tecnoscienza, Rome, **2**, p. 1315, pl. 2, figs 20–22, holotype fig. 22)

Fig. 6. ***Pickelhaube furtiva*** (Roth, 1983) Applegate *et al. in* Covington and Wise, 1987. Distal view, DSDP Site 547B (Atlantic Ocean), U. Valanginian/Hauterivian, UCL-1700-8, x3039. Range: Tithonian? – ?Aptian.

Fig. 7. ***Polypodorhabdus madingleyensis*** Black, 1971a. Distal view, Speeton (UK), L. Hauterivian (amblygonium), UCL-653-35, ?x3579. Range: Valanginian? – ?Barremian.

Figs 8–10. ***Retecapsa angustiforata*** Black, 1971a. Distal (8), side (9) and proximal (10) views, DSDP Site 547B (Atlantic Ocean), U. Valanginian, UCL-1488-26/25/27, x3260. Range: L. Berriasian (jacobi) – U. Maastrichtian.

Fig. 11. ***Retecapsa crenulata*** (Bramlette and Martini, 1964) Grün *in* Grün and Allemann, 1975. Distal view, BGS Borehole 81/43 (North Sea), U. Hauterivian (gottschei), UCL-4061-18, x5303. Range: Berriasian? – Maastrichtian.

Fig. 12. ***Retecapsa surirella*** (Deflandre and Fert, 1954) Grün *in* Grün and Allemann, 1975. Distal view, DSDP Site 547B (Atlantic Ocean), U. Valanginian, UCL-1488-17. x4135. Range: Berriasian? – Maastrichtian.

Fig. 13. ***Speetonia colligata*** Black, 1971a. Distal view, DSDP Site 534 (Atlantic Ocean), Berriasian, UCL-1752-1, x4308. Range: L. Berriasian (?grandis) – U. Hauterivian (marginatus/ligatus).

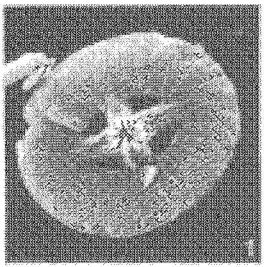
Family PREDISCOSPHAERACEAE Rood *et al.*, 1971
Figs 14–15. ***Prediscosphaera columnata*** (Stover, 1966) Perch-Nielsen, 1984. Distal view, Copt Point (UK), U. Albian (inflatum), UCL-1029-13/1090-13, x6800/4605. Range: L. Albian – Turonian.

Fig. 16. ***Prediscosphaera spinosa*** (Bramlette and Martini, 1964) Gartner, 1968. Distal view, Munday's Hill (UK), U. Albian, JC-102-14, ~x8000. Range: U. Aptian – Maastrichtian.

Family TUBODISCACEAE Bown and Rutledge *in* Bown and Young, 1997
Figs 17–18. ***Manivitella pemmatoidea*** (Deflandre *in* Manivit, 1965) Thierstein, 1971. Distal (17) and proximal (18) views, BGS Borehole 81/43 (North Sea), U. Hauterivian (gottschei), UCL-4060-32/4081-23, x2578/3409. Range: uppermost Tithonian (CM19n) – Maastrichtian.

Fig. 19. ***Tubodiscus jurapelagicus*** (Worsley, 1971) Roth, 1973. Proximal view, Otto Gott (N Germany), Barremian, UCL-507-3, x3906. Range: U. Berriasian – L. Barremian.

Fig. 20. ***Tubodiscus verenae*** Thierstein, 1973 emend. Grün *in* Grün and Allemann, 1975. Side view, DSDP Site 547B (Atlantic Ocean), U. Valanginian/Hauterivian, UCL-1744-24, x4000. Range: U. Berriasian – U. Hauterivian (?sayni).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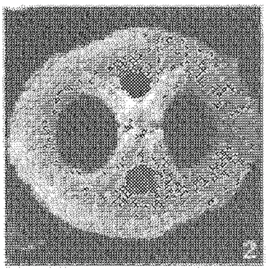
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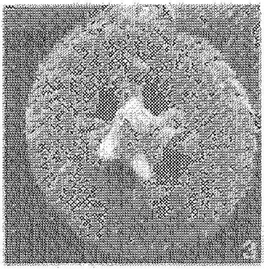
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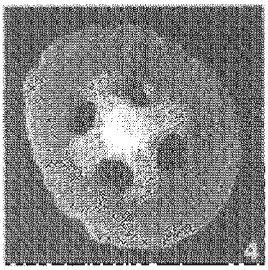
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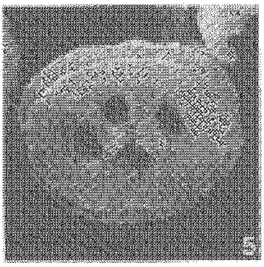
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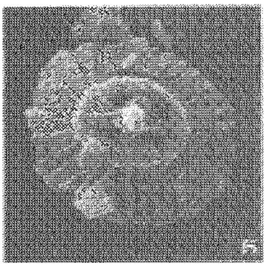
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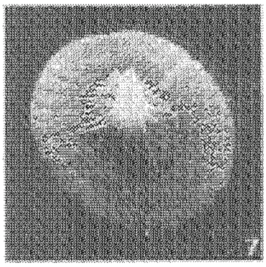
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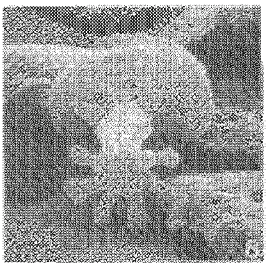
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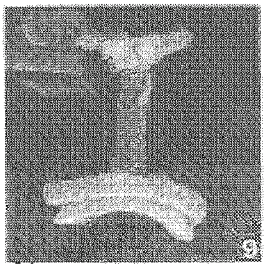
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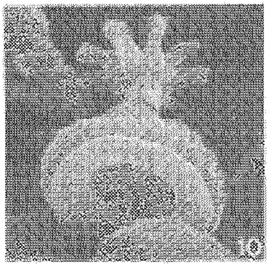
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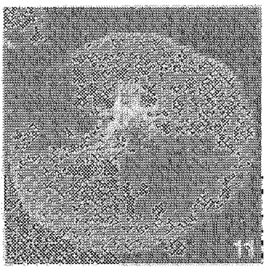
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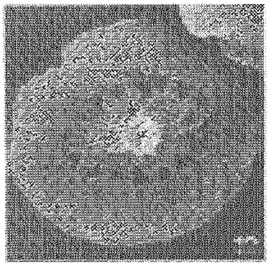
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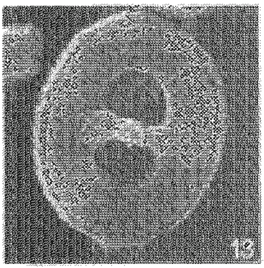
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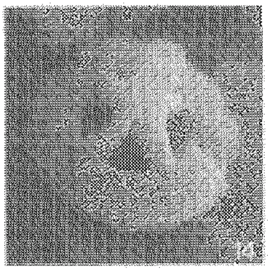
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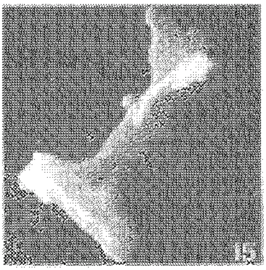
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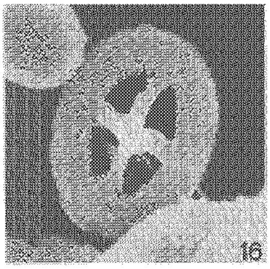
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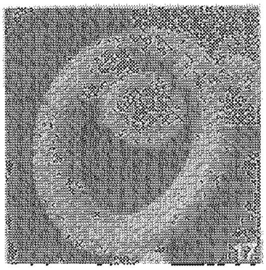
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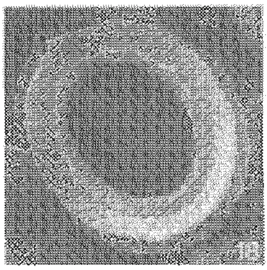
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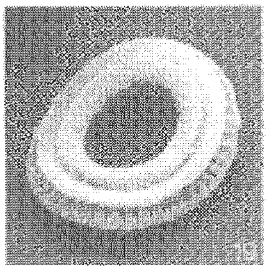
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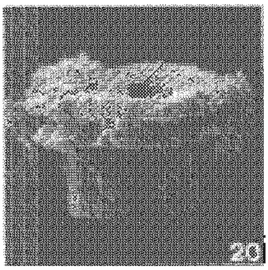
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Plate 5.5

Order WATZNAUERIALES Bown, 1987

Family WATZNAUERIACEAE Rood *et al.*, 1971

Fig. 1. ***Cyclagelosphaera argoensis*** Bown, 1992b. Distal view, DSDP Site 261 (Indian Ocean), U. Tithonian, UCL-2999-33, x3536. Range: Tithonian – Maastrichtian.

Fig. 2. ***Cyclagelosphaera margerelii*** Noël, 1965. Coccosphere, BGS Borehole 81/43 (North Sea), U. Valanginian (Dichotomites spp.), UCL-4073-20, x3650. Range: U. Bajocian (parkinsoni) – L. Paleocene.

Figs 3–4. ***Diazomatolithus lehmanii*** Noël, 1965. Distal (3) and side (4) views, BGS Borehole 81/43 (North Sea), L. Barremian/U. Valanginian, UCL-4073-9/4068-26, x5711/6400. Range: U. Jurassic – ?M./U. Albian.

Fig. 5. ***Watznaueria barnesae*** (Black *in* Black and Barnes, 1959) Perch-Nielsen, 1968. Coccosphere, Speeton (UK), U. Hauterivian (marginatus), UCL-525-8, x3009. Range: L. Bajocian (laeviuscula) – Maastrichtian.

Fig. 6. ***Watznaueria biporta*** Bukry, 1969. Distal view, DSDP Site 547B (Atlantic Ocean), U. Valanginian/ Hauterivian, UCL-1686-12, x3089. Range: Albian? – Maastrichtian.

Fig. 7. ***Watznaueria fasciata*** Wind and Cepek, 1979. Distal view, Otto Gott (N Germany), U. Hauterivian, JC-96-14, x10888. Range: U. Ryazanian? – ?Aptian.

Fig. 8. ***Watznaueria rawsonii*** Crux, 1987b. Distal view, Otto Gott, U. Hauterivian, JC-97-12, x8181. Range: Valanginian? – L. Barremian.

Order ARKHANGELSKIALES Bown and Hampton *in* Bown and Young, 1987

Family KAMPTNERIACEAE Bown and Hampton *in* Bown and Young, 1987

Fig. 9. ***Crucicribrum anglicum*** Black, 1973. Distal view, Folkestone (UK), U. Albian (inflatum), UCL-1029-2, x4800. Range: M. Albian (dentatus) – Cenomanian.

Fig. 10. ***Gartnerago praeobliquum*** Jakubowski, 1986 (?junior synonym of *Cribricatillus robustus* Black, 1973). Distal view, Folkestone (UK), U. Albian (dispar), UCL-5289-17, x4203. Range: U. Albian (inflatum) – L. Cenomanian (mantelli).

UNCERTAIN HETEROCOCCOLITHS

Figs 11–12. ***Haqius circumradiatus*** (Stover, 1966) Roth, 1978. Distal (11) and proximal (12) views, Speeton (UK), L./M. Hauterivian (regale/marginatus), UCL-452-20/525-20, x3400/3337. Range: U. Berriasian (?boissieri) – Campanian.

Fig. 13. ***Haqius ellipticus*** (Grün *in* Grün and Allemann, 1975) Bown, 1992b. Distal view, BGS Borehole 81/43 (North Sea), U. Hauterivian (gottschei), UCL-4081-22, x3241. Range: U. Tithonian? – L. Barremian (rarocinctum/hugii).

Figs 14–15. ***Repagulum parvidentatum*** (Deflandre and Fert, 1954) Forchheimer, 1972. Distal (14) and proximal (15) views, Otto Gott (N Germany), U. Barremian, UCL-529-8/540-24, x7800/7840. Range: (Valanginian, Indian Ocean) L. Hauterivian – Maastrichtian.

HOLOCOCCOLITHS – Family CALYPTROSPHAERACEAE Boudreaux and Hay, 1969

Fig. 16. ***Isocrystallithus compactus*** Verbeek, 1976b (= *Owenia hillii* Crux, 1991b). Distal view, Munday's Hill (UK), U. Albian (inflatum), x8975. Range: M. Albian (lautus) – U. Cenomanian (guerangeri).

NANNOLITHS

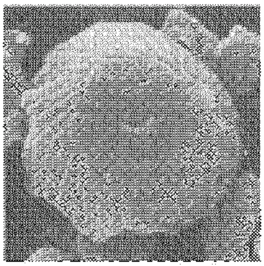
Family BRAARUDOSPHAERACEAE Deflandre, 1947a

Fig. 17. ***Braarudosphaera africana*** Stradner, 1961. Copt Point (UK), M. Albian (lautus), UCL-3949-3, x5862. Range: Albian? – Cenomanian.

Fig. 18. ***Micrantholithus hoschulzii*** (Reinhardt, 1966) Thierstein, 1971. BGS Borehole 81/43 (North Sea), L. Barremian (variabilis), UCL-4079-19, x3187. Range: Berriasian – U. Aptian.

Fig. 19. ***Micrantholithus obtusus*** Stradner, 1963. DSDP Site 398D (Atlantic Ocean), Barremian, UCL-718-18, x2761. Range: Berriasian – U. Aptian.

Fig. 20. ***Micrantholithus* sp.** Djebel Oust (Tunisia), Barremian, UCL-482-25, x4541.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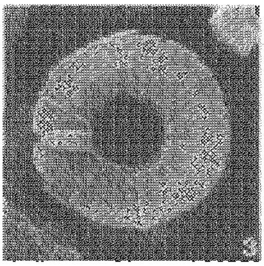
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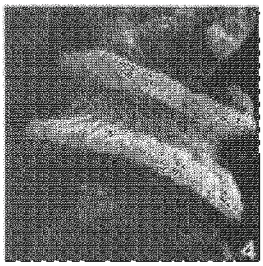
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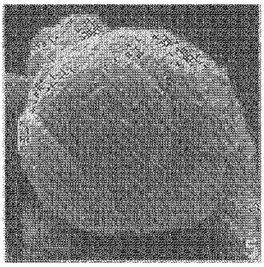
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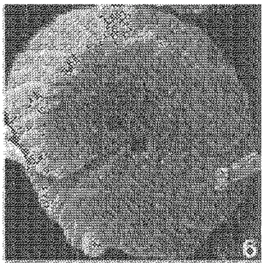
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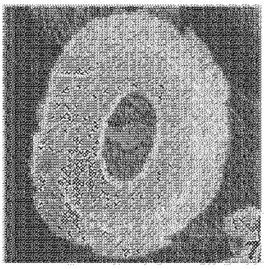
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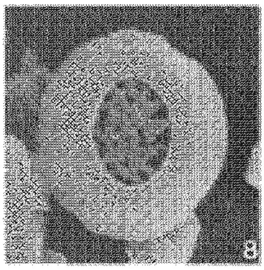
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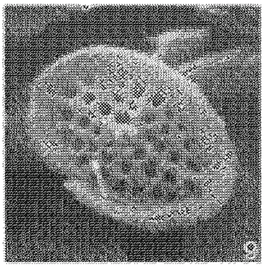
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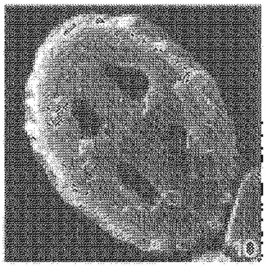
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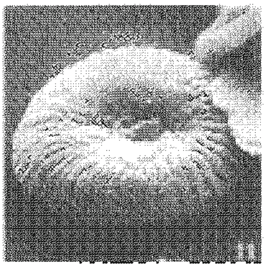
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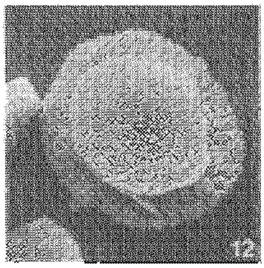
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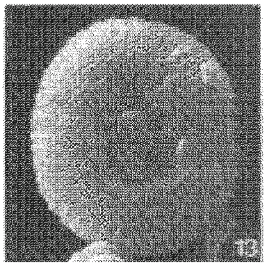
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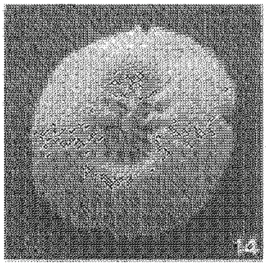
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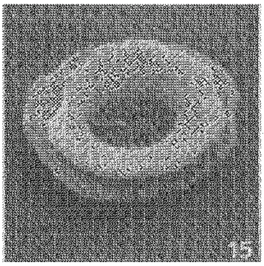
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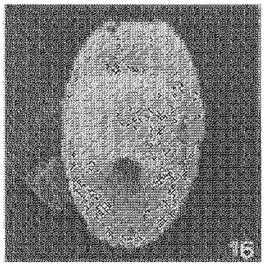
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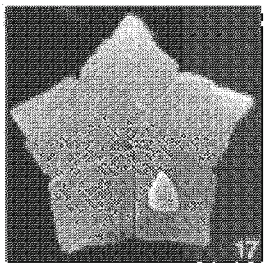
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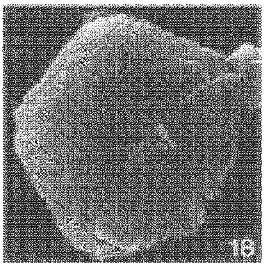
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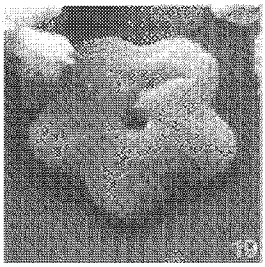
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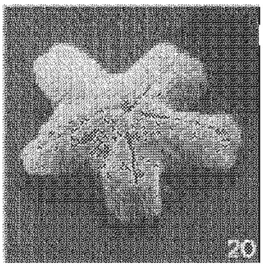
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Plate 5.6

Family NANNOCONACEAE Deflandre, 1959
Fig. 1. ***Nannoconus abundans*** Stradner and Grün, 1973. Side view, UCL-4069-29, x3808. Range: Barremian (rarocintum – bidentatum)/?L. Aptian.

Figs 2–3. ***Nannoconus borealis*** Perch-Nielsen, 1979. Side views, Speeton (UK), L. Barremian (fissicostatum), UCL-4069-21/26, x2200. Range: Barremian (fissicostatum – stolleyi).

Fig. 4. ***Nannoconus circularis*** Deres and Achéritéguy, 1980. DSDP Site 398D (Atlantic Ocean), Barremian, UCL-714-19, x3127. Range: Barremian – U. Aptian.

Fig. 5. ***Nannoconus inornatus*** Rutledge and Bown, 1996. Oblique view, BGS Borehole 81/43 (North Sea), L. Barremian (variabilis), UCL-4079-17, x4266. Range: U. Hauterivian – Barremian.

Fig. 6. ***Nannoconus* sp. (discs)** *sensu* Crux, 1989.

Fig. 7. ***Nannoconus pseudoseptentrionalis*** Rutledge and Bown, 1996. Plan view, Otto Gott (N Germany), L. Barremian (Aulacoteuthis spp.), JC-101-19, x7000. Range: L. Barremian (?elegans).

Fig. 8. ***Nannoconus steinmannii*** Kamptner, 1931 ssp. ***steinmannii***. Side view, DSDP Site 398D (Atlantic Ocean), Barremian, UCL-715-35, x3283. Range: L. Berriasian (jacobi) – ?L. Aptian.

Family POLYCYCLOLITHACEAE Forchheimer, 1972 emend. Varol, 1992
Fig. 9. ***Eprolithus apertior*** Black, 1973. Plan view, Copt Point (UK), U. Albian (inflatum), UCL-1029-16, x5310. Range: L. Aptian – Turonian.

Fig. 10. ***Farhania varolii*** (Jakubowski, 1986) Varol, 1992. BGS Heslerton Borehole (UK), L. Aptian, UCL-4067-3, x4533. Range: Aptian (?forbesi – jacobi).

Fig. 11. ***Eprolithus? antiquus*** Perch-Nielsen, 1979a. Plan view, BGS Borehole 81/43 (North Sea), L. Hauterivian, UCL-4062-30, x4400. Range: L. Hauterivian (amblygonium – regale).

Uncertain polycycloliths
Fig. 12. ***Assipetra infracretacea*** (Thierstein, 1973) Roth, 1973. BGS Borehole 81/43 (North Sea), L. Hauterivian, UCL-4868-2, x7411. Range: L. Berriasian (jacobi) – ?U. Cretaceous.

Fig. 13. ***Assipetra terebrodentarius*** (Applegate *et al. in* Covington and Wise, 1987) Rutledge and Bergen *in* Bergen, 1994. BGS Borehole 81/43 (North Sea), L. Barremian (variabilis), UCL-4074-23, x5333. Range: U. Hauterivian (angulicostata) – ?U. Cretaceous.

Fig. 14. ***Rucinolithus windleyae*** Rutledge and Bown, 1996. BGS Borehole 81/43 (North Sea), U. Hauterivian (gottschei), UCL-4063-31, x3187. Range: U. Hauterivian (inversum) – L. Barremian.

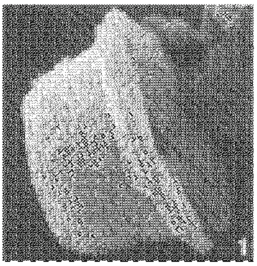
Figs 15–16. ***Tegulalithus septentrionalis*** (Stradner, 1963) Crux, 1986. BGS Borehole 81/43 (North Sea) and Moorberg (N Germany), U. Hauterivian (gottschei), UCL-4060-23/398-12, x3517/3559. Range: U. Hauterivian (speetonensis – gottschei).

Family LAPIDEACASSACEAE Bown and Young, 1997
Fig. 17. ***Lapideacassis glans*** Black, 1971b. Copt Point (UK), M. Albian (lautus), UCL-3949-25. Range: Albian – Coniacian/Santonian.

Family MICRORHABDULACEAE Deflandre, 1963
Fig. 18. ***Lithraphidites carniolensis*** Deflandre, 1963. DSDP Site 547B (Atlantic Ocean), Valanginian, UCL-1700-1, x1700. Range: L. Berrisian (?jacobi) – Maastrichtian.

INCERTAE SEDIS NANNOLITHS
Fig. 19. ***Ceratolithina hamata*** Martini, 1967. Copt Point (UK), Albian, UCL-3839-36, x4570. Range: M. Albian (lautus) – ?lowermost Turonian.

Fig. 20. ***Kokia borealis*** Perch-Nielsen, 1988. North Jens-1 (North Sea), ?Ryazanian, UCL-2830-4, x3645. Range: Ryazanian – L. Valanginian.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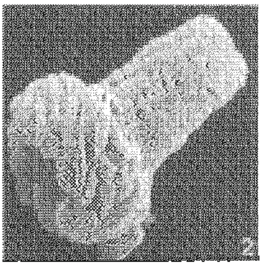
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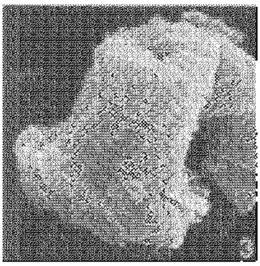
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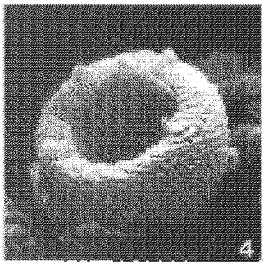
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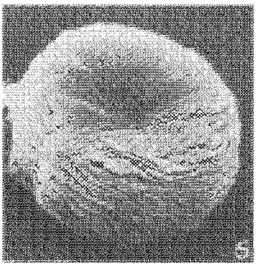
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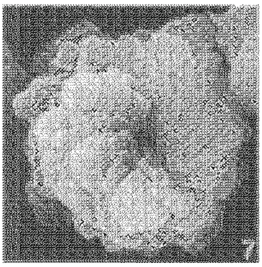
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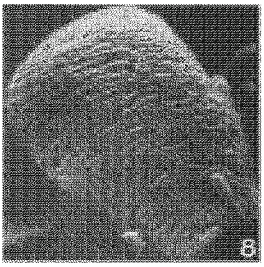
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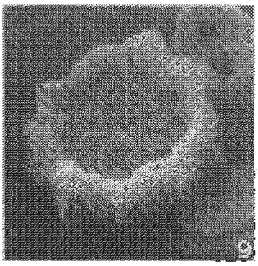
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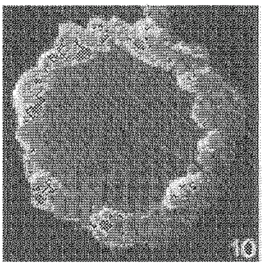
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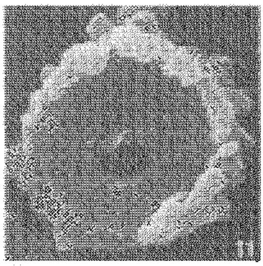
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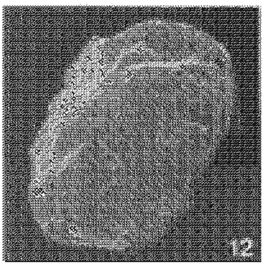
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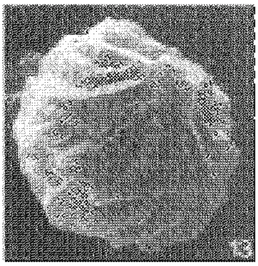
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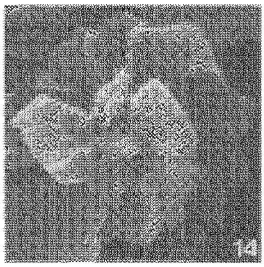
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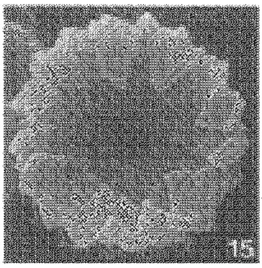
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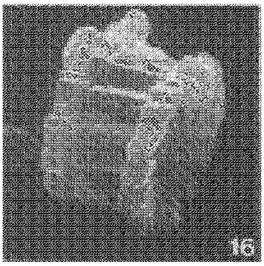
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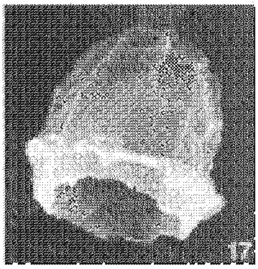
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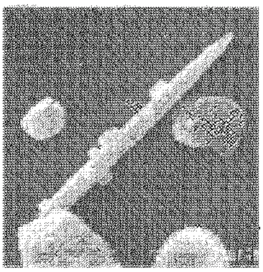

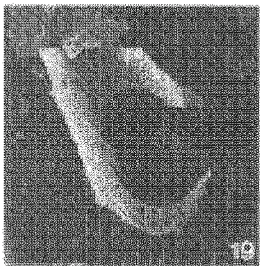
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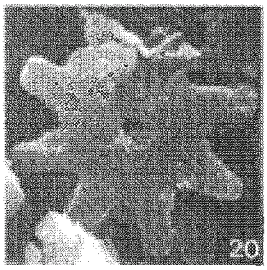
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Plate 5.7

Order EIFFELLITHALES Rood *et al.*, 1971
Family CHIASTOZYGACEAE Rood *et al.*, 1973 emend. Varol and Girgis, 1994

Fig. 1. ***Braloweria boletiformis*** (Black, 1972) Crux, 1991b. Side view XPL, Munday's Hill (UK), M. Albian (loricatus), JC-119-6.

Fig. 2. ***Bukrylithus ambiguus*** Black, 1971a. XPL (large specimen), Folkestone (UK), U. Albian (dispar), UCL-5671-21.

Fig. 3. ***Chiastozygus litterarius*** (Górka, 1957) Manivit, 1971. XPL, Folkestone (UK), M. Albian (lautus), UCL-5688-27.

Figs 4–5. ***Chiastozygus ?platyrethus*** Hill, 1976. XPL (4) and PC (5), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-10/11. Range: Aptian? – Coniacian.

Figs 6–7. ***Chiastozygus* sp. 1**. XPL (6) and PC (7), BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5690-30/31.

Figs 8–9. ***Clepsilithus maculosus*** Rutledge and Bown, 1996. XPL (8) and PC (9), BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5690-16/17.

Fig. 10. ***Diadorhombus rectus*** Worsley, 1971. XPL, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-29.

Fig. 11. ***Loxolithus armilla*** (Black *in* Black and Barnes, 1959) Noël, 1965. XPL, BGS Borehole 81/43 (North Sea), L. Barremian, UCL-5691-7.

Fig. 12. ***Rhabdophidites parallelus*** (Wind and Cepek, 1979) Lambert, 1987. XPL, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5568-32.

Fig. 13. ***Staurolithites crux*** (Deflandre and Fert, 1954) Caratini, 1963. XPL, BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5690-15.

Figs 14–15. ***Staurolithites* cf. *S. crux*** (Deflandre and Fert, 1954) Caratini, 1963. XPL (14) and PC (15), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-3/4.

Fig. 16. ***Staurolithites mitcheneri*** (Applegate and Bergen, 1988) Rutledge and Bown comb. nov.. XPL, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5701-21. Range: L. Valanginian? – ?L. Aptian.
Basionym: *Vekshinella mitcheneri* Applegate and Bergen, 1988 (*Proceedings of the ODP, Scientific Results*, **103**, p. 317, pl. 23, figs 7–9).

Figs 17–18. ***Staurolithites mutterlosei*** Crux, 1989. 17, XPL, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-11; 18, XPL, BGS Borehole 81/43 (North Sea), L. Barremian, UCL-5691-26.

Figs 19–20. ***Staurolithites glabra*** (Jeremiah, 1996) Burnett, 1998. XPL (19) and PC (20), Folkestone (UK), U. Albian (dispar), UCL-5671-16/17. Range: L. Aptian – L. Cenomanian (mantelli).

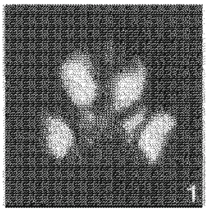
Figs 21–22. ***Staurolithites* sp. 1**. XPL (21) and PC (22) (specimen displays a bicyclic XPL image but two cycles are not visible in the PC image), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-26/27.

Figs 23–24. ***Staurolithites* sp. 2**. XPL (23) and PC (24), Folkestone (UK), M. Albian (lautus), UCL-5688-25/24.

Fig. 25. ***Tranolithus gabalus*** Stover, 1966. PC, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-9. Range: L. Valanginian (Paratollia)? – Maastrichtian.

Figs 26–27. ***Tranolithus orionatus*** Reinhardt, 1966. XPL (26) and PC (27), Folkestone (UK), U. Albian (dispar), UCL-5670-20/21. Range: Albian – Maastrichtian.

Figs 28–30. ***Zeugrhabdotus diplogrammus*** (Deflandre *in* Deflandre and Fert, 1954) Burnett *in* Gale *et al.* 1996. XPL (28, 30) and PC (29). 28-29, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-35/36; 30, Folkestone (UK), U. Albian (dispar), UCL-5671-18. Range: L. Valanginian (campylotoxus) – Campanian.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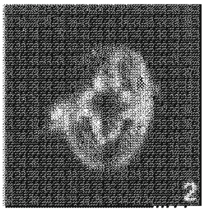
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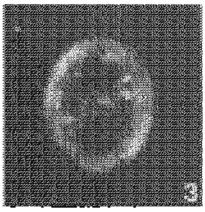
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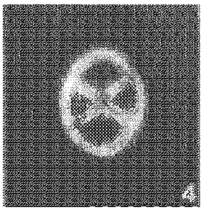
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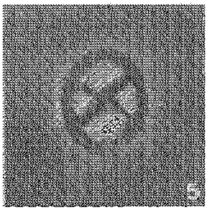
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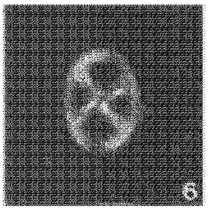
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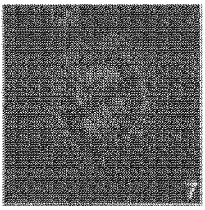
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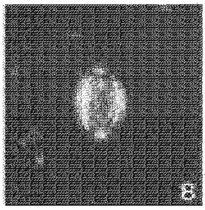
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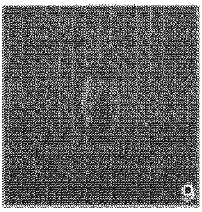
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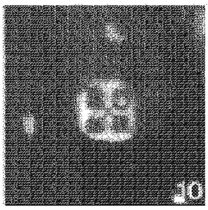
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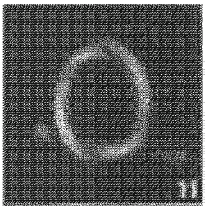
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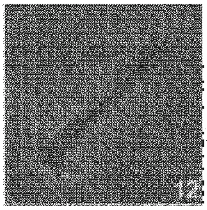
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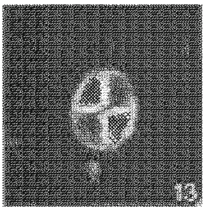
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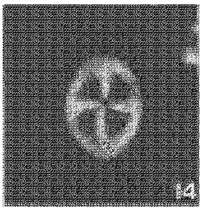
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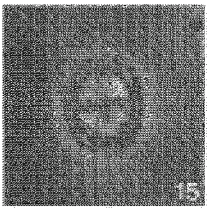
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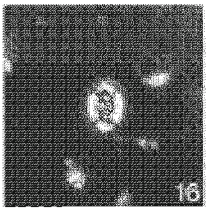
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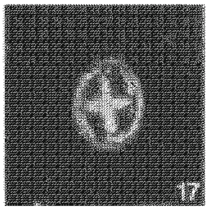
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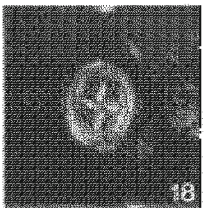
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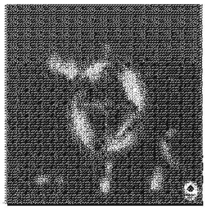
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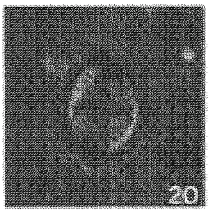
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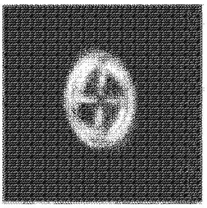
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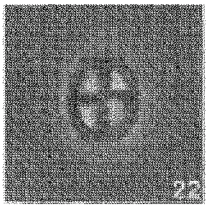
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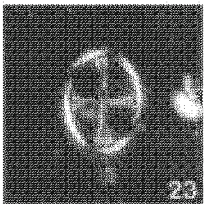
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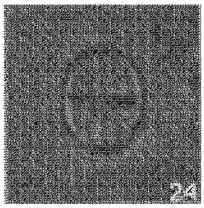
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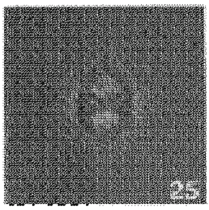
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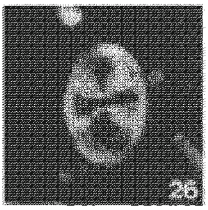
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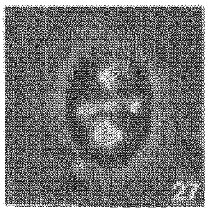
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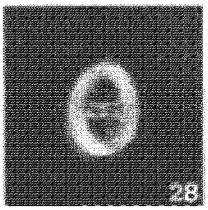
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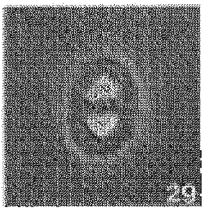
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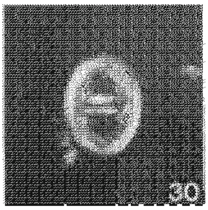
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Plate 5.8

Family CHIASTOZYGACEAE Rood *et al*., 1973 emend. Varol and Girgis, 1994
Figs 1–4. ***Zeugrhabdotus* 'elegans'** (Gartner, 1968) Burnett *in* Gale *et al.* 1996. XPL (1, 3) and PC (2, 4). 1-2, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-24/25; 3-4, Folkestone (UK), U. Albian (dispar), UCL-5670-8/9. Range: L. Barremian? – ?Campanian.

Fig. 5. ***Zeugrhabdotus embergeri*** (Noël, 1959) Perch-Nielsen, 1984. XPL, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-33.

Fig. 6. ***Zeugrhabdotus scutula*** (Bergen, 1994) Rutledge and Bown, 1996. XPL (long axis at 45°), Speeton (UK), L. Barremian (elegans), UCL-5689-11. Range: U. Hauterivian (inversum/sayni) – Santonian.

Figs 7. ***Zeugrhabdotus trivectis*** Bergen, 1994. XPL, BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5690-18. Range: L. Valanginian (campylotoxus) – Maastrichtian.

Figs 8–10. ***Zeugrhabdotus xenotus*** (Stover, 1966) Burnett *in* Gale *et al.* 1996. XPL (8 at 45°, 9 at 0°) and PC (10), Folkestone (UK), M. Albian (lautus), UCL-5688-22/21/23. Range: L. Valanginian (campylotoxus) – Cenomanian.

Family EIFFELLITHACEAE Reinhardt, 1965
Fig. 11. ***Diloma galiciense*** Bergen, 1994. XPL, BGS Borehole 81/43 (North Sea), L. Barremian, UCL-4065-7.

Figs 12–13. ***Diloma primitiva*** (Worsley, 1971) Wind and Cepek, 1979. XPL (12) and PC (13), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-20/21.

Fig. 14. ***Eiffellithus monechiae*** Crux, 1991b. XPL, Folkestone (UK), U. Albian (dispar), UCL-5671-29. Range: U. Albian (inflatum) – L. Cenomanian (mantelli).

Fig. 16. ***Eiffellithus (Rothia) striatus*** (Black, 1971a) Applegate and Bergen, 1988. XPL, Speeton (UK), L. Hauterivian (amblygonium–noricum), UCL-5689-31.

Fig. 15 and 17. ***Eiffellithus turriseiffelii*** (Deflandre *in* Deflandre and Fert, 1954) Reinhardt, 1965. PC (15) and XPL (17), Folkestone (UK), U. Albian (dispar), UCL-5671-1/2. Range: U. Albian (inflatum) – U. Maastrictian.

Fig. 18. ***Eiffellithus (Rothia)windii*** Applegate and Bergen, 1988. XPL, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-1.

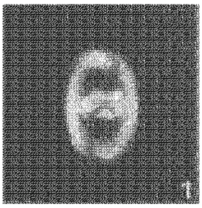
Figs 19–20. ***Helicolithus trabeculatus*** (Górka, 1957) Verbeek, 1977. XPL (19) and PC (20), Folkestone (UK), U. Albian (dispar), UCL-5671-24/25. Range: Albian – Maastrichtian.

Figs 21–22. ***Helicolithus* cf. *H. compactus*** (Bukry, 1969) Varol and Girgis, 1994. XPL (21) and PC (22), Folkestone (UK), U. Albian (dispar), UCL-5670-34/35.

Figs 23–25. ***Tegumentum octiformis*** (Köthe, 1981) Crux, 1989. XPL (23 at 0° and 24 at 45°) and PC (25), BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5690-28/27/29. Range: L. Hauterivian – U. Barremian.

Figs 26–27. ***Tegumentum stradneri*** Thierstein *in* Roth and Thierstein, 1972. XPL (26) and PC (27), Folkestone (UK), U. Albian (dispar), UCL-5670-14/15.

Family RHAGODISCACEAE Hay, 1977
Figs 28–29. ***Calcicalathina oblongata*** (Worsley, 1971) Thierstein, 1971. XPL distal (28) and side (29) views, Bulgaria, Hauterivian, UCL-5691-15 and DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-17.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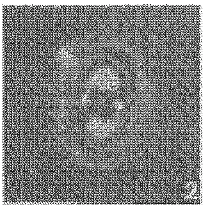
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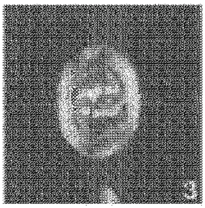
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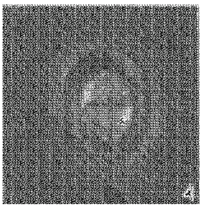
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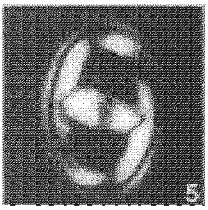
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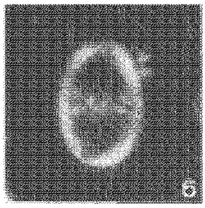
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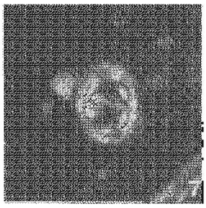
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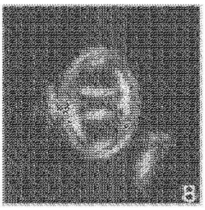
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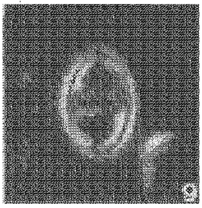
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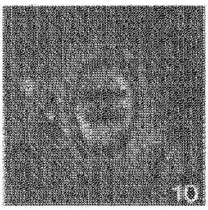
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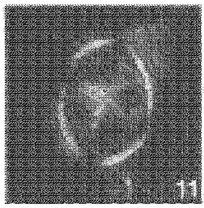
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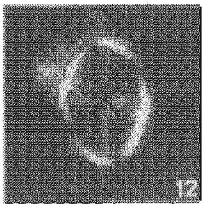
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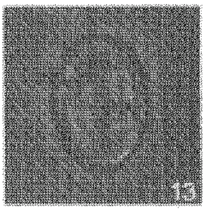
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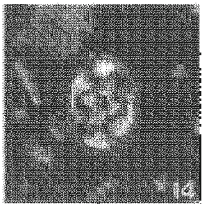
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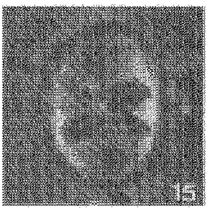
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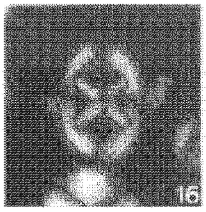
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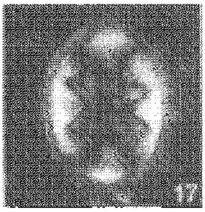
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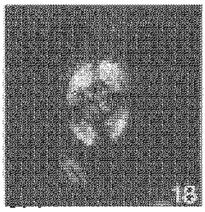
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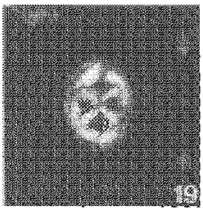
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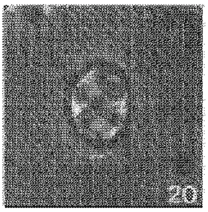
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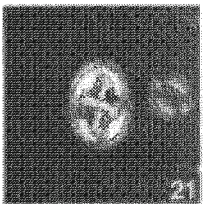
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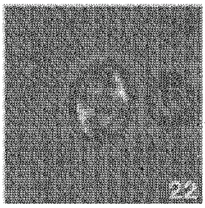
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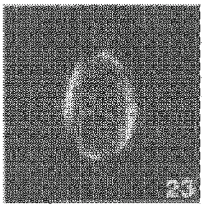
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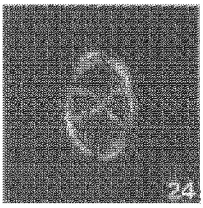
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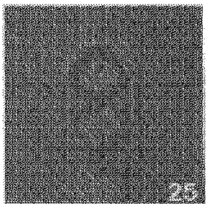
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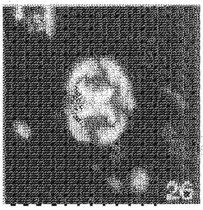
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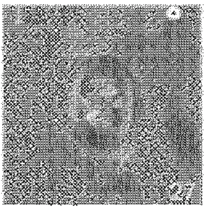
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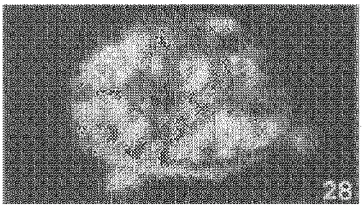
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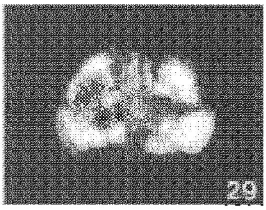
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Plate 5.9

Family RHAGODISCACEAE Hay, 1977
Figs 1–2. ***Percivalia fenestrata*** (Worsley, 1971) Wise, 1983. XPL (4) and PC (5), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5568-4/5.

Figs 3–5. ***Rhagodiscus achlyostaurion*** (Hill, 1976) Doeven, 1983. XPL (3, 5) and PC (4), Folkestone (UK), U. Albian (inflatum), UCL-5671-12/13/5688-1.

Figs 6–7. ***Rhagodiscus angustus*** (Stradner, 1963) Reinhardt, 1971. XPL (6) and PC (7), Folkestone (UK), U. Albian (dispar), UCL-5670-10/11.

Figs 8–9. ***Rhagodiscus asper*** (Stradner, 1963) Reinhardt, 1967. XPL (8) and PC (9), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5568-14/15.

Figs 10–11. ***Rhagodiscus dekaenelii*** Bergen, 1994. XPL (10 – high focus; 11 – low focus), DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5701-29/28. Range: L. Valanginian – L. Hauterivian.

Figs 12–13. ***Rhagodiscus gallagheri*** Rutledge and Bown, 1996. XPL (12) and PC (13), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5568-20/21. Range: U. Barremian?/L. Aptian – Cenomanian.

Figs 14–15. ***Rhagodiscus infinitus*** (Worsley, 1971) Applegate *et al.* *in* Covington and Wise, 1987. XPL (14) and PC (15), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5568-26/27.

Figs 16–20. ***Rhagodiscus pseudoangustus*** Crux, 1987b. 16, XPL, BGS Borehole 81/43 (North Sea), L. Barremian, Beauvoir (Tunisia), L. Hauterivian, UCL-5700-24; 17, 18 (XPL and PC) and 19, 20 (side view XPL and PC), BGS Borehole 81/43 (North Sea), L. Barremian, UCL-5700-8/4/5/7. Range: Hauterivian – L. Barremian (rarocinctum).

Fig. 21. ***Rhagodiscus splendens*** (Deflandre, 1953) Verbeek, 1977. XPL, Folkestone (UK), U. Albian (dispar), UCL-5671-9. Range: Aptian – Maastrichtian.

Order STEPHANOLITHIALES Bown and Young, 1997
?Family PARHABDOLITHACEAE Bown, 1987
Fig. 22. ***'Parhabdolithus' stubbingsii*** Black, 1971a. XPL side view, BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5691-28.

Family STEPHANOLITHIACEAE Black, 1968
Figs 23–24. ***Rotelapillus laffittei*** (Noël, 1957) Noël, 1973. XPL (23) and PC (24), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-1/2.

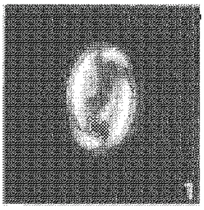
Fig. 25. ***Stoverius achylosus*** (Stover, 1966) Perch-Nielsen, 1986. XPL, Folkestone (UK), M. Albian (lautus), UCL-5688-35. Range: Aptian? – Turonian.

Fig. 26. ***Stradnerlithus geometricus*** (Górka, 1957) Bown and Cooper, 1989a. PC, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-26.

Fig. 27. ***Stradnerlithus rhombicus*** (Stradner and Adamiker, 1966) Bukry, 1969. PC, Folkestone (UK), U. Albian (dispar), UCL-5671-31. Range: ?Jurassic – U. Maastrichtian.

Figs 28–29. ***Stradnerlithus silvaradius*** (Filewicz *et al.* *in* Wind and Wise, 1977) Rahman and Roth, 1991. XPL (28) and PC (29), DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-9/10. Range: U. Berriasian – Hauterivian (inversum/sayni) (Falkland Plateau, Aptian).

Fig. 30. ***Scapholithus fossilis*** Deflandre *in* Deflandre and Fert, 1954. XPL and PC (right inset), DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-18; Folkestone (UK), U. Albian (dispar), UCL-5670-4.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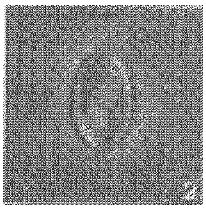
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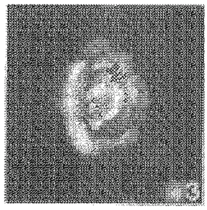
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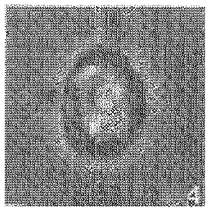
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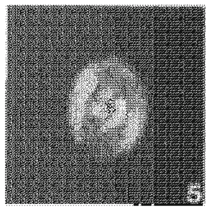
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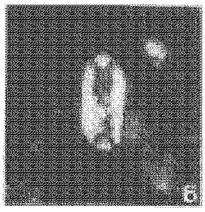
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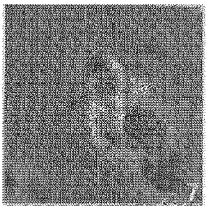
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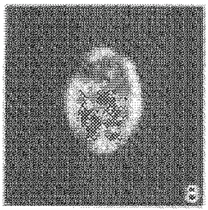
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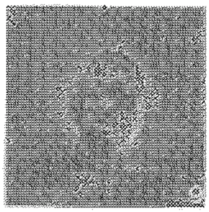
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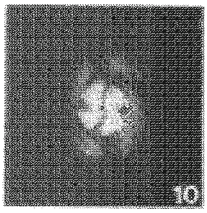
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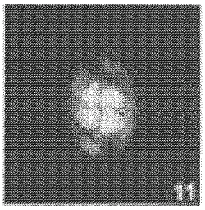
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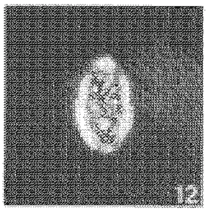
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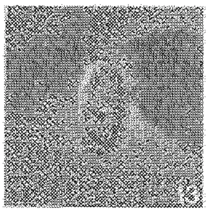
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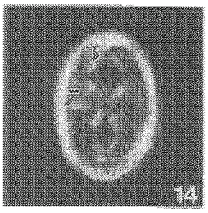
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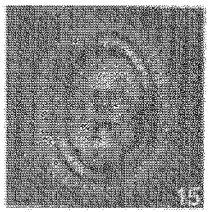
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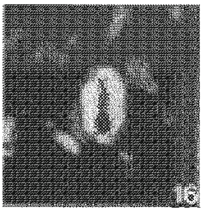
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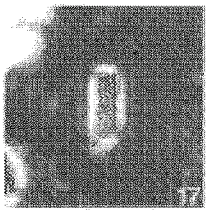
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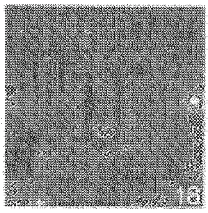
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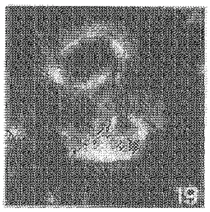
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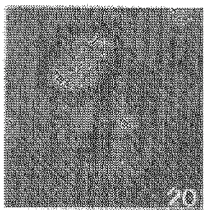
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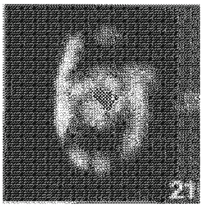
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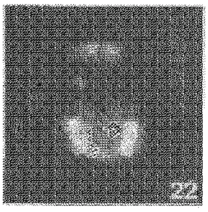
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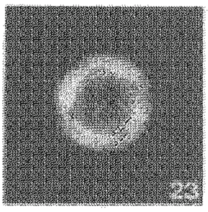
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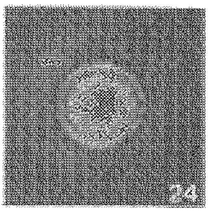
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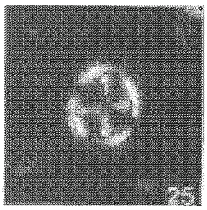
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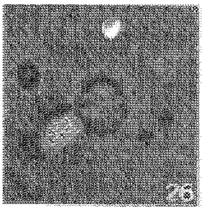
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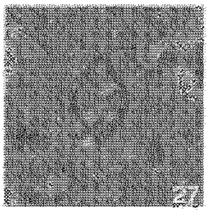
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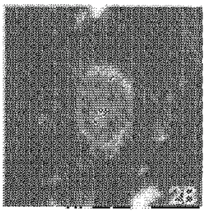
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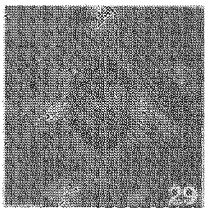
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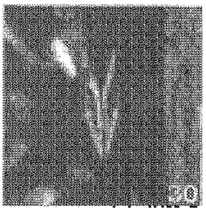
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Plate 5.10

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

Family AXOPODORHABDACEAE Bown and Young, 1997

Figs 1–4. ***Axopodorhabdus albianus*** (Black, 1967) Wind and Wise *in* Wise and Wind, 1977. XPL (1 at 0°, 2 at ~20° and 3 at ~45°) and PC (4), Folkestone (UK), U. Albian (dispar), UCL-5670-24-27.

Figs 5–6. ***Axopodorhabdus dietzmannii*** (Reinhardt, 1965) Wind and Wise *in* Wise, 1983. XPL (5) and PC (6), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5568-10/11.

Figs 7–8. ***Cribrosphaerella ehrenbergii*** (Arkhangelsky, 1912) Deflandre, 1952. XPL (7) and PC (8), Folkestone (UK), U. Albian (dispar), UCL-5670-28/29. Range: U. Albian (inflatum) – U. Maastrichtian.

Figs 9–10. ***Ethmorhabdus hauterivianus*** Black, 1971a. XPL (9) and PC (10), BGS Borehole 81/43 (North Sea), U. Hauterivian and Speeton (UK), L. Hauterivian (regale), UCL-5691-32/3723-25. Range: Berriasian – Barremian.

Figs 11–12. ***Hemipodorhabdus gorkae*** (Reinhardt, 1969) Grün *in* Grün and Allemann, 1975. XPL (11) and PC (12, different specimen), BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5690-22/21.

Figs 13–14. ***Octocyclus magnus*** Black, 1972. XPL (13) and PC (14, different specimen), Folkestone (UK), M./U. Albian (lautus/inflatum), UCL-5689-6/5688-10. Range: Albian – Maastrichtian.

Figs 15–17. ***Perissocyclus plethotretus*** (Wind and Cepek, 1979) Crux, 1989. PC (15, 17) and XPL (16), Speeton (UK), L. Barremian (fissicostatus), UCL-5689-13/22/23.

Figs 18–19. ***Perissocyclus tayloriae*** Crux, 1989. XPL (18) and PC (19), BGS Borehole 81/43 (North Sea), L. Barremian, UCL-5691-6/5.

Fig. 20. ***Tetrapodorhabdus coptensis*** Black, 1971a. PC, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-12/13.

Family BISCUTACEAE Black, 1971a

Figs 21–22. ***Biscutum constans*** (Górka, 1957) Black *in* Black and Barnes, 1959. XPL (21) and PC (22), Folkestone (UK), U. Albian (dispar), UCL-5670-5/6.

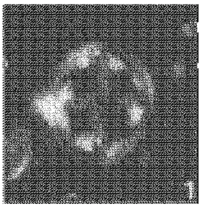
Figs 23–24. ***Crucibiscutum hayi*** (Black, 1973) Jakubowski, 1986. XPL (23) and PC (24), Folkestone (UK), U. Albian (dispar), UCL-5670-14/15.

Fig. 25. ***Crucibiscutum salebrosum*** (Black, 1971a) Jakubowski, 1986. XPL, North Sea Borehole, Ryazanian, UCL-5690-6.

Figs 26–27. ***Discorhabdus ignotus*** (Górka, 1957) Perch-Nielsen, 1968. XPL (26) and PC (27), Folkestone (UK), U. Albian (dispar), UCL-5670-33/32.

Figs 28–29. ***Gaarderella granulifera*** Black,1973. XPL, Folkestone (UK), M./U. Albian (lautus/dispar), UCL-5688-20/5671-32. Range: Albian – Maastrichtian.

Fig. 30. ***Seribiscutum primitivum*** (Thierstein, 1974) Filewicz *et al.* *in* Wise and Wind, 1977. XPL, Folkestone (UK), U. Albian (dispar), UCL-5670-30.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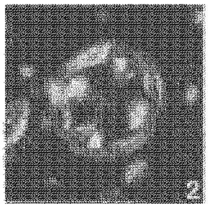
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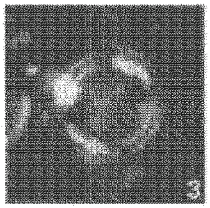
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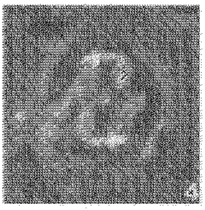
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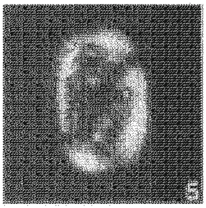
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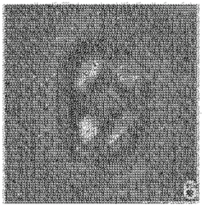
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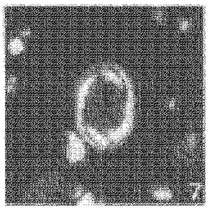
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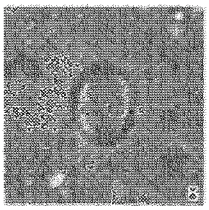
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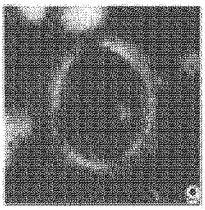
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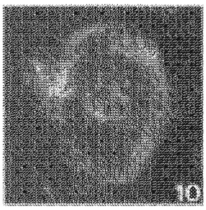
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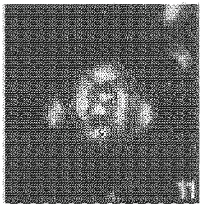
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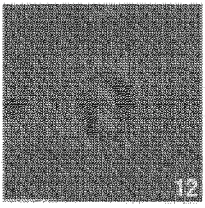
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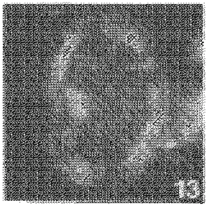
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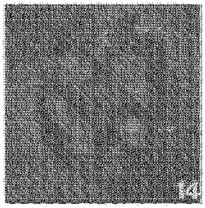
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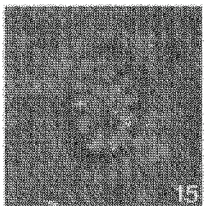
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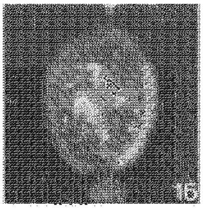
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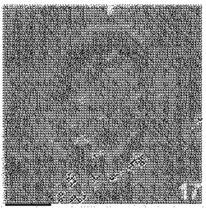
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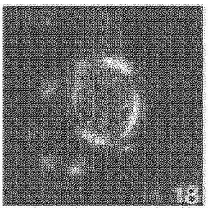
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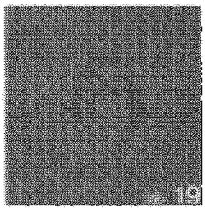
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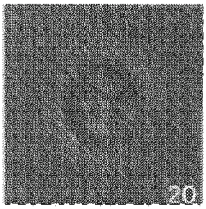
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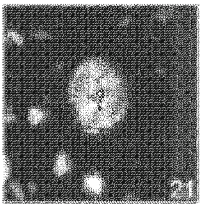
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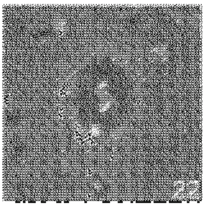
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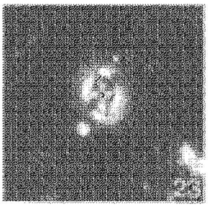
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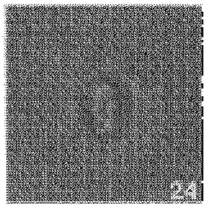
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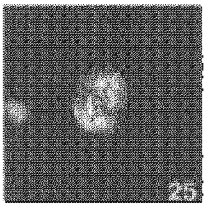
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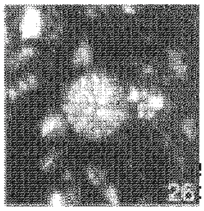
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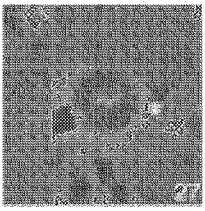
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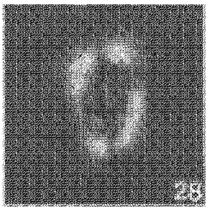
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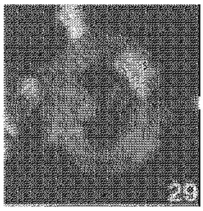
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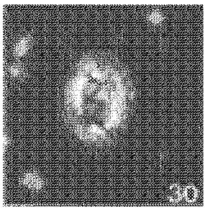
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Plate 5.11

Family BISCUTACEAE Black, 1971a
Figs 1–2. ***Sollasites arcuatus*** Black, 1971a. XPL (1) and PC (2), North Sea Borehole, Ryazanian, UCL-5690-8/9.

Fig. 3. ***Sollasites falklandensis*** Filewicz *et al.* *in* Wind and Wise, 1977. XPL (small specimen), DSDP Site 257 (E Indian Ocean), L.–M. Albian, UCL-3696-32. Range: L. – M. Albian.

Figs 4–5. ***Sollasites horticus*** (Stradner *et al.* *in* Stradner and Adamiker, 1966) Cepek and Hay, 1969. 4, XPL, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-25; 5, North Sea Borehole, Ryazanian, UCL-5690-4.

Family CRETARHABDACEAE Thierstein, 1973
Fig. 6. ***Cretarhabdus conicus*** Bramlette and Martini, 1964. XPL, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5568-8.

Fig. 7. ***Cretarhabdus inaequalis*** Crux, 1987b. XPL, BGS Borehole 81/43 (North Sea), L. Barremian, UCL-5691-37.

Figs 8–9. ***Cretarhabdus striatus*** (Stradner, 1963) Black, 1973. XPL, Folkestone (UK), M. Albian (lautus), UCL-5689-1/2.

Fig. 10. ***Cruciellipsis cuvillieri*** (Manivit, 1966) Thierstein, 1971. XPL, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5701-24.

Figs 11–12. ***Flabellites oblongus*** (Bukry, 1969) Crux, 1982. XPL (4) and PC (5, different specimen), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5668-12/5569-15. Range: U. Barremian – Santonian.

Fig. 13. ***Grantarhabdus coronadventis*** (Reinhardt, 1966) Grün *in* Grün and Allemann, 1975. XPL, Folkestone (UK), U. Albian (inflatum), UCL-5688-7. Range: Aptian? – Campanian.

Figs 14–15. ***Grantarhabdus meddii*** Black, 1971a. XPL (14) and PC (15), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5669-18/19.

Figs 16–18. ***Helenea chiastia*** Worsley, 1971. XPL at 0° low focus (16), XPL at ~45° high focus (17) and PC (18), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5669-18/19.

Figs 19–22. ***Pickelhaube furtiva*** (Roth, 1983) Applegate *et al.* *in* Covington and Wise, 1987. XPL (19), PC at low focus (20), PC at high focus (21), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5669-28/29/30; 22, XPL side view, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5701-34.

Fig. 23. ***Pickelhaube* cf. *P. furtiva*** (Roth, 1983) Applegate *et al.* *in* Covington and Wise, 1987. XPL, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5669-5.

Figs 24–25. ***Polypodorhabdus madingleyensis*** Black, 1971a. XPL (24), BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5691-3; PC (25), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5669-32.

Figs 26–27. ***Retecapsa angustiforata*** Black, 1971a. XPL (26) and PC (27), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5668-16/17.

Fig. 28. ***Retecapsa surirella*** (Deflandre and Fert, 1954) Grün *in* Grün and Allemann, 1975. DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5668-18.

Figs 29–30. ***Speetonia colligata*** Black, 1971a. XPL at 0° (29) and ~45° (30), Speeton (UK), L. Hauterivian (amblygonium–noricum), UCL-5689-33/34.

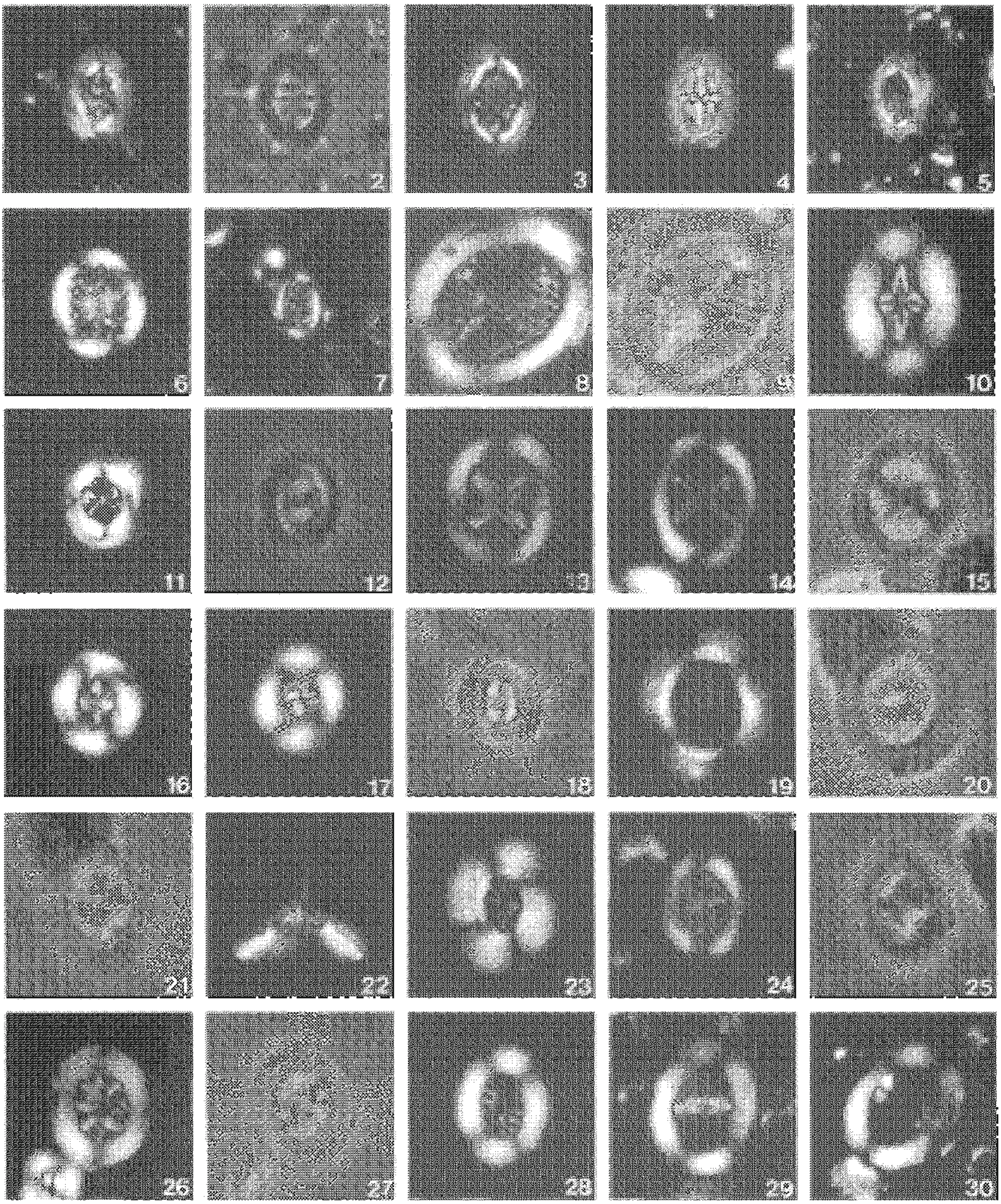
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Plate 5.12

Family PREDISCOSPHAERACEAE Rood *et al.*, 1971
Figs 1–2. ***Prediscosphaera columnata*** (Stover, 1966) Perch-Nielsen, 1984. XPL distal (1) and side (2) views, Folkestone (UK), M./U. Albian (dispar/lautus), UCL-5671-20/5688-26.

Fig. 3. ***Prediscosphaera spinosa*** (Bramlette and Martini, 1964) Gartner, 1968. XPL (small 'middle' Cretaceous variety), Mont Risou (SE France), U. Albian (dispar), UCL-5183-5. Range: U. Aptian – U. Maastrichtian.

Family TUBODISCACEAE Bown and Rutledge, 1997
Fig. 4. ***Manivitella pemmatoidea*** (Deflandre *in* Manivit, 1965) Thierstein, 1971. PC, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-6.

Figs 5–6. ***Tubodiscus jurapelagicus*** (Worsley, 1971) Roth, 1973. XPL (5) and PC (6), Speeton (UK), L. Barremian (variabilis), UCL-5015-12/15.

Figs 7–8. ***Tubodiscus verenae*** Thierstein, 1973 emend. Grün *in* Grün and Allemann, 1975. 7, distal view (XPL), DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5701-31; 8, side view (PC), DSDP Site 261 (E Indian Ocean), U. Valanginian/L. Hauterivian, UCL-5701-14.

Figs 9–10. ***Tubodiscus* sp. 1**. XPL (9) and PC (10), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5569-16/17. Range: Valanginian – Albian.

Order WATZNAUERIALES Bown, 1987
Family WATZNAUERIACEAE Rood *et al.*, 1971
Figs 11–12. ***Cylindralithus nudus*** Bukry, 1969. Distal (11, XPL) and side (12, XPL and PC) views, DSDP Site 258 (E Indian Ocean), L. Cenomanian, UCL-3675-26/24/25. Range: Albian – Maastrichtian.

Fig. 13. ***Diazomatolithus lehmanii*** Noël, 1965. XPL, Bulgaria, Hauterivian, UCL-5691-12.

Figs 14–15. ***Diazomatolithus* cf. *D. lehmanii*** Noël, 1965. XPL (14) and PC (15), narrow rimmed, wide central area morphotype, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-15/16.

Fig. 16. ***Watznaueria biporta*** Bukry, 1969. XPL, Folkestone (UK), U. Albian (inflatum), UCL-5688-8.

Order ARKHANGELSKIALES Bown and Hampton *in* Bown and Young, 1997
Family ARKHANGELSKIELLACEAE Bukry, 1969 emend. Bown and Hampton, 1997 *in* Bown and Young, 1997
Figs 17–20. ***Broinsonia* (*Acaenolithus*) *matalosa*** (Stover, 1966) Burnett *in* Gale *et al.*, 1996. XPL (17, 19) and PC (18, 20), ODP Site 765 (E Indian Ocean), Hauterivian, UCL-5701-10-13. Range: (Valanginian, E Indian Ocean –) U. Barremian – ?Campanian.

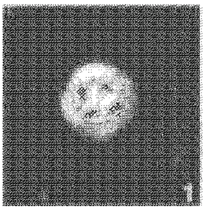
Figs 21–22. ***Broinsonia signata*** (Noël, 1969) Noël, 1970 (?*Acaenolithus galloisii*). XPL (21) and PC (22), Folkestone (UK), U. Albian (dispar), UCL-5670-16/17. Range: Aptian? – U. Maastrichtian.

Figs 23–25. ***Broinsonia* sp. 1**. XPL (23 at 0°, 24 at ~45°), Folkestone (UK), M. Albian (lautus), UCL-5688-30/31/32.

Family KAMPTNERIACEAE Bown and Hampton *in* Bown and Young, 1997
Fig. 26. ***Crucicribrum anglicum*** Black, 1973. XPL, Folkestone (UK), M. Albian (lautus), UCL-5688-28.

Figs 27–28. ***Gartnerago praeobliquum*** Jakubowski, 1986 (?junior synonym of *Cribricatillus robustus* Black, 1973). XPL (27) and PC (28), Folkestone (UK), U. Albian (dispar), UCL-5670-22/23.

UNCERTAIN HETEROCOCCOLITHS
Figs 29–30. ***Haqius circumradiatus*** (Stover, 1966) Roth, 1978. XPL (29) and PC (30), DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5668-2/3.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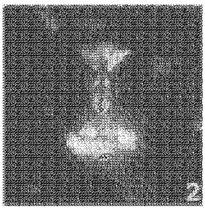
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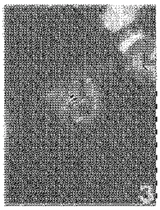
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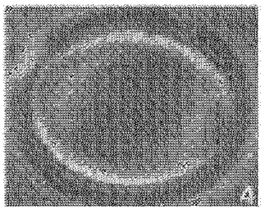
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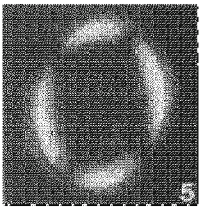
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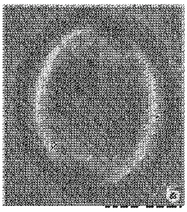
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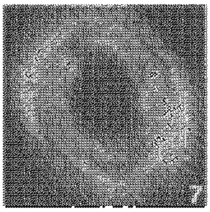
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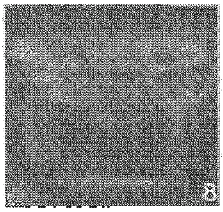
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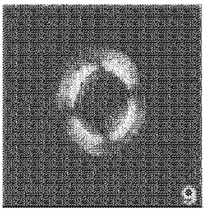
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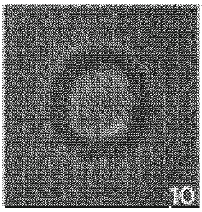
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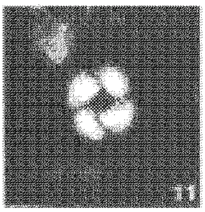
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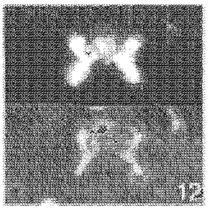
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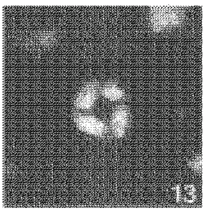
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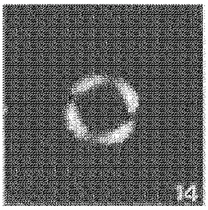
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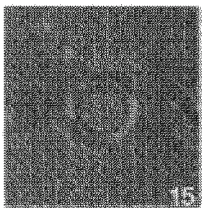
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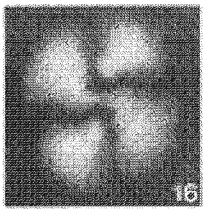
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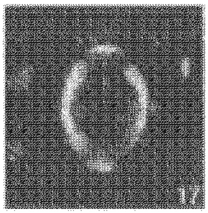
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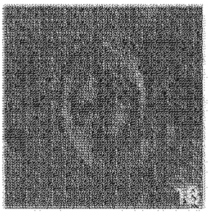
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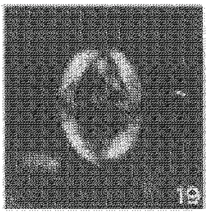
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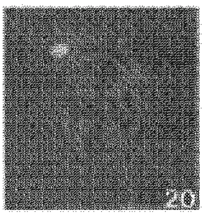
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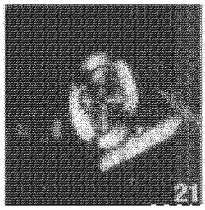
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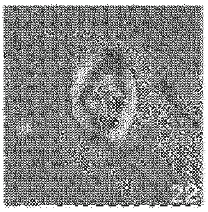
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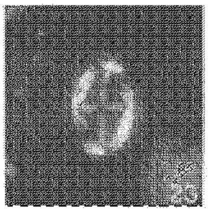
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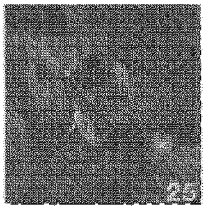
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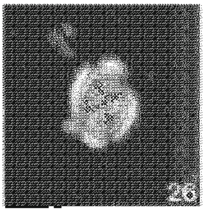
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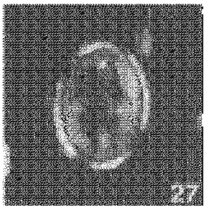
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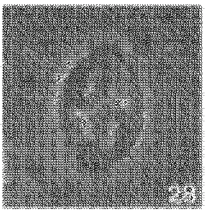
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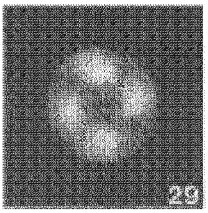
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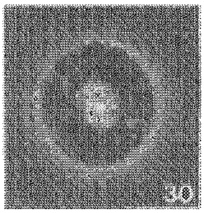
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Plate 5.13

UNCERTAIN HETEROCOCCOLITHS

Figs 1–2. ***Haqius ellipticus*** (Grün *in* Grün and Allemann, 1975) Bown, 1992b. XPL (1) and PC (2), DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-19/20.

Fig. 3. ***Laguncula dorotheae*** Black, 1971b. XPL, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5701-27. Range: Valanginian? – ?Cenomanian.

Figs 4–5. ***Laguncula montrisouensis*** Burnett, 1998. XPL, side view, low focus (4) and high focus (5), DSDP Site 259 (E Indian Ocean), L.?M. Albian (CC8a), UCL-3737-8/12.

Figs 6–7. ?***Markalius inversus*** (Deflandre *in* Deflandre and Fert, 1954) Bramlette and Martini, 1964. XPL (6) and PC (7), BGS Borehole 81/43 (North Sea), L. Barremian, UCL-5700-9/10. Range: recorded range Campanian – Palaeogene.

Figs 8–10. ***Repagulum parvidentatum*** (Deflandre and Fert, 1954) Forchheimer, 1972. XPL (8, 10 – birefringence is exaggerated in photograph, this species has an inconspicuous LM image which is nevertheless distinctive once recognized) and PC (9), Folkestone (UK), U. Albian (dispar), UCL-5670-18/5671-8/7.

HOLOCOCCOLITHS

Family CALYPTROSPHAERACEAE Boudreaux and Hay, 1969

Figs 11–12. ***Anfractus harrisonii*** Medd, 1979. XPL distal (11) and side (12) views, DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5701-22/5702-30. Range: Pliensbachian? – ?Albian.

Fig. 13. ***Calculites anfractus*** (Jakubowski, 1986) Varol and Jakubowski, 1989. XPL, Mont Risou (SE France), L. Cenomanian (mantelli), UCL-2329-18. Range: uppermost Albian (dispar) – L. Cenomanian (mantelli).

Figs 14–15. ***Isocrystallithus compactus*** Verbeek, 1976b (=*Owenia hillii* Crux, 1991b). 14, XPL distal view, Munday's Hill (UK), U. Albian (inflatum), JC-119-34; 15, side view, Mont Risou (SE France), L. Cenomanian (mantelli), UCL-5184-25.

Figs 16–17. **'*Lucianorhabdus*' *phlaskus*** Wind and Cepek, 1979. Side view, XPL (16) and PC (17), DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-35/36. Range: ?U. Valanginian.

Fig. 18. ***Metadoga mecurius*** Wind and Cepek, 1979. Side view, XPL, Site DSDP 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-23. Range: ?U. Valanginian (verrucosum).

Figs 19–20. ***Zebrashapka vanhintei*** Covington and Wise, 1987. XPL (19) and PC (20), Bulgaria, U. Hauterivian/L. Barremian, UCL-5700-31/32. Range: ?U. Hauterivian – L. Aptian.

Fig. 21. ***Orastrum partitum*** Varol *in* Al-Rifaiy *et al.*, 1990. XPL, Bulgaria, U. Hauterivian/L. Barremian, UCL-5700-30. Range: U. Hauterivian? – ?M. Albian.

Fig. 22–25. ***Calculites*? sp. 1**. XPL (22 at 0°, 23/25 at ~45°) and PC (24). 22-24, Beauvoir (Tunisia), L. Hauterivian, UCL-5700-25/26/27; 25, Bulgaria, U. Hauterivian/L. Barremian, UCL-5700-33. Range: L. Hauterivian? – ?L. Barremian.

Fig. 26–28 ***Calculites*? sp. 2**. XPL (26, 27) and PC (28, same specimen as 27), BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-4071-31/24/25. Range: ?Hauterivian.

Fig. 29–30. **Holococcolith indet.**. XPL (29) and PC (30), DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5702-14/13.

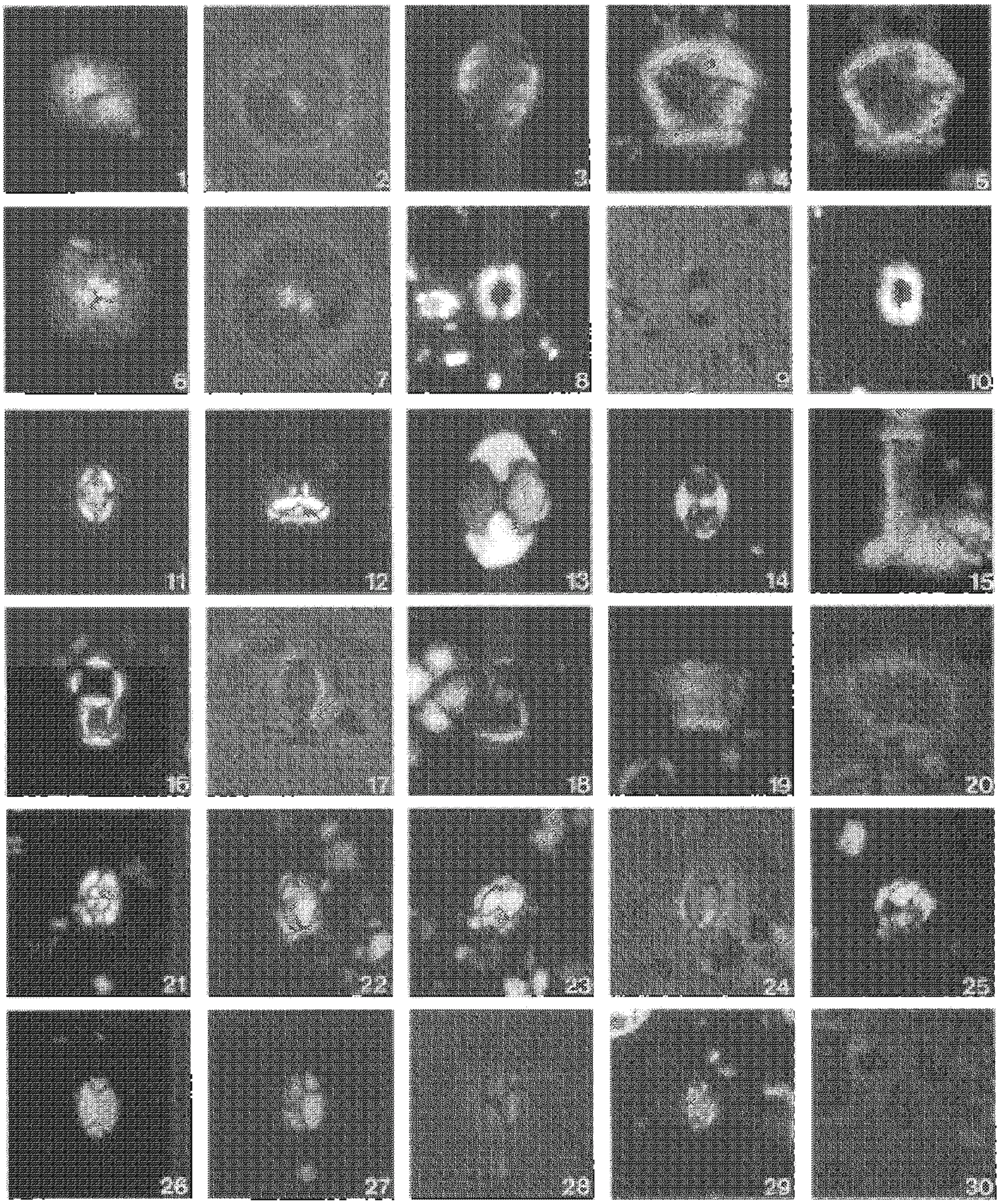
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Plate 5.14

NANNOLITHS

Family BRAARUDOSPHAERACEAE Deflandre, 1947a
Fig. 1. ***Braarudosphaera africana*** Stradner, 1961. XPL, Tunisia, U. Aptian, UCL-5701-8.

Figs 2–3. ***Braarudosphaera stenorhetha*** Hill, 1976. XPL (2) and PC (3), Folkestone (UK), U. Albian (inflatum), UCL-5688-12/13.

Fig. 4. ***Micrantholithus hoschulzii*** (Reinhardt, 1966) Thierstein, 1971. XPL, BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5690-24.

Figs 5–6. ***Micrantholithus obtusus*** Stradner, 1963. XPL (5) and PC (6), Speeton (UK), L. Barremian (fissicostatum), UCL-5689-27/28.

Fig. 7. ***Micrantholithus speetonensis*** Perch-Nielsen, 1979. XPL, Speeton (UK), L. Valanginian (Polyptychites), UCL-5005-1. Range: Valanginian (Paratollia – hollwedensis).

Fig. 9. ***Trapezopentus sarmatus*** Wind and Cepek, 1979. PC (8) and XPL (9), DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5701-18/20. Range: ?U. Valanginian.

Family EOCONUSPHAERACEAE Krystan-Tollmann, 1988a
Fig. 10. ***Conusphaera rothii*** (Thierstein, 1971) Jakubowski, 1986. XPL, Bulgaria, U. Hauterivian/L. Barremian, UCL-5700-34. Range: Ryazanian – L. Aptian.

Family NANNOCONACEAE Deflandre, 1959
Figs 11–12. ***Nannoconus abundans*** Stradner and Grün, 1973. XPL (11) and PC (12), Speeton (UK), L. Barremian (fissicostatum), UCL-5689-25/26.

Figs 13–14. ***Nannoconus borealis*** Perch-Nielsen, 1979. XPL (13) and PC (14, not same specimen), Speeton (UK), L. Barremian (fissicostatum), UCL-5689-18/21.

Fig. 15. ***Nannoconus circularis*** Deres and Achéritéguy, 1980. Top view, XPL, Beauvoir (Tunisia), L. Barremian, UCL-5701-3.

Figs 16–18. ***Nannoconus inornatus*** Rutledge and Bown, 1996. Side (16 XPL, 17 PC) and top (18 XPL) views, BGS Borehole 81/43 (North Sea), L. Barremian, UCL-5691-19/20/21.

Fig. 19. ***Nannoconus oviformis*** Perch-Nielsen, 1988. IKU Core 7B (N North Sea/offshore mid Norway), L. Valanginian, UCL-3724-8. Range: Berriasian? – L. ?Valanginian.

Fig. 20. ***Nannoconus pseudoseptentrionalis*** Rutledge and Bown, 1996. Top view, Speeton (UK), L. Barremian (elegans), UCL-5689-8.

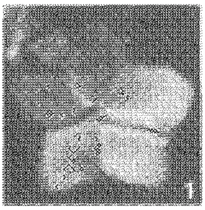
Figs 21–22. ***Nannoconus steinmannii*** Kamptner, 1931 ssp. ***steinmannii***. XPL (21) and PC (22), DSDP Site 397 (E Atlantic Ocean), U. Valanginian, UCL-5701-15/16.

Family POLYCYCLOLITHACEAE Forchheimer, 1972 emend. Varol, 1992
Fig. 23. ***Eprolithus? antiquus*** Perch-Nielsen, 1979a. XPL, Speeton (UK), L. Hauterivian (amblygonium–noricum), UCL-5689-29.

Fig. 24. ***Eprolithus floralis*** (Stradner, 1962) Stover, 1966. XPL, Folkestone (UK), U. Albian (inflatum), UCL-5688-6. Range: L. Aptian – ?L. Campanian.

Figs 25–27. ***Farhania varolii*** (Jakubowski, 1986) Varol, 1992. XPL (25), PC (26) and side view (XPL, 27), BGS Heslerton Borehole (UK), L. Aptian, UCL-5700-12/11/17.

Figs 28–29. ***Radiolithus hollandicus*** Varol, 1992. XPL (28) and PC (29), Folkestone (UK), U. Albian (inflatum), UCL-5688-14/15. Range: Aptian? – Cenomanian.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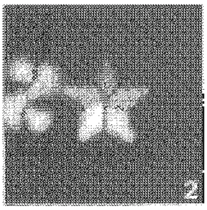
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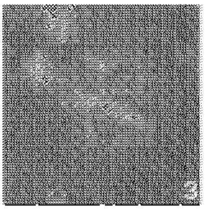
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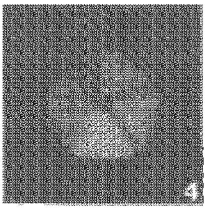
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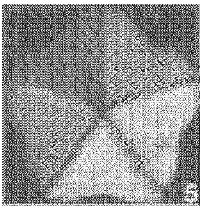
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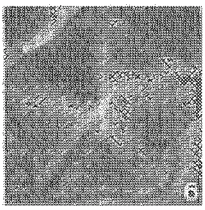
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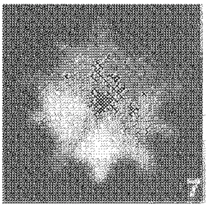
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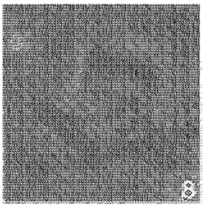
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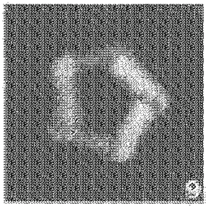
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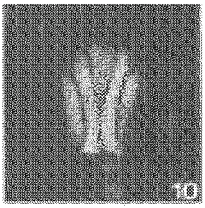
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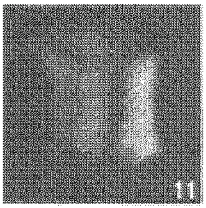
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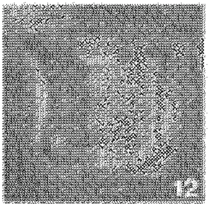
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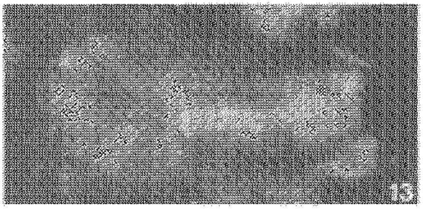
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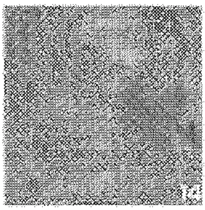
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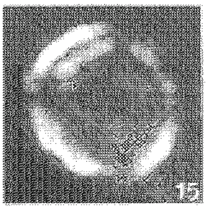
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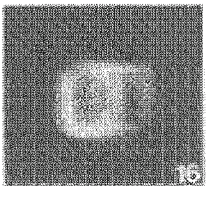
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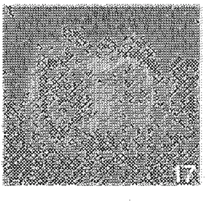
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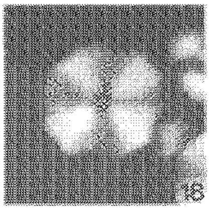
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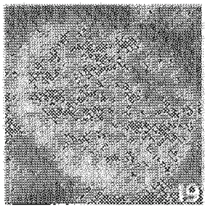
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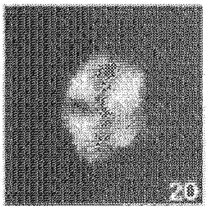
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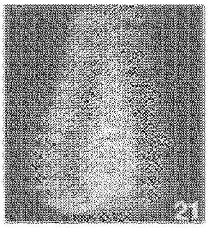
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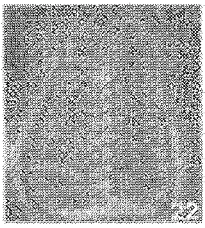
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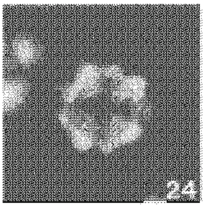
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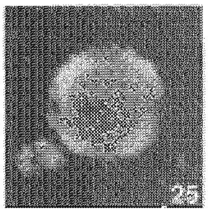
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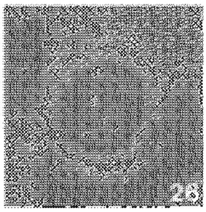
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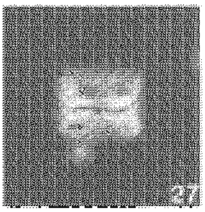
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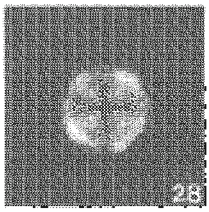
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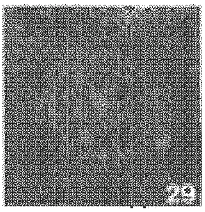
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Plate 5.15

Uncertain polycycloliths
Fig. 1. ***Assipetra infracretacea*** (Thierstein, 1973) Roth, 1973. Upper specimen (lower specimen is *Watznaueria barnesae*) XPL, BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5691-35.

Figs 2–3. ***Assipetra terebrodentarius*** (Applegate *et al.* *in* Covington and Wise, 1987) Rutledge and Bergen *in* Bergen, 1994. XPL, Beauvoir (Tunisia), L. Barremian, UCL-5701-5 and BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5691-36.

Figs 4–5. ***Hayesites albiensis*** Manivit, 1971. XPL (4) and PC (5), Folkestone (UK), M. Albian (lautus), UCL-5688-16/17. Range: Albian (tardefurcata – dispar).

Figs 6–7. ***Hayesites irregularis*** (Thierstein *in* Roth and Thierstein, 1972) Applegate *et al.* *in* Covington and Wise, 1987. XPL (6) and PC (7), Tunisia, U. Aptian, UCL-5701-6/7. Range: uppermost Barremian – ?Albian.

Figs 8–9. ***Rucinolithus windleyae*** Rutledge and Bown, 1996. XPL, BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5691-30/34.

Figs 10–11. ***Tegulalithus septentrionalis*** (Stradner, 1963) Crux, 1986. Side (10, 11) and plan (10 upper right) views, XPL, BGS Borehole 81/43 (North Sea), U. Hauterivian, UCL-5691-2/5690-34.

Family LAPIDEACASSACEAE Bown and Young, 1997
Fig. 12. ***Lapideacassis tricornus*** Wind and Wise *in* Wise and Wind, 1977. XPL, Folkestone (UK), M. Albian (lautus), UCL-5689-4. Range: Albian – Maastrichtian.

Figs 13–14. ***Lapideacassis mariae*** Black, 1971b. XPL (13) and PC (14), Folkestone (UK), U. Albian (dispar), UCL-5671-5/4. Range: Albian – Maastrichtian.

Family MICRORHABDULACEAE Deflandre, 1963
Figs 15, 16, 19. ***Lithraphidites bollii*** (Thierstein, 1971) Thierstein, 1973. XPL (15, 16) and PC (19, same specimen as 16 – appears to possess a basal structure/?coccolith). 15, Bulgaria, Hauterivian, UCL-5691-17; 16 and 19, Beauvoir (Tunisia), L. Hauterivian, UCL-5700-22/23. Range: Hauterivian (loryi – angulicostata).

Figs 17–18. ***Lithraphidites carniolensis*** Deflandre, 1963. XPL (17) and PC (18), large specimen, DSDP Site 603B (N Atlantic Ocean), Aptian, UCL-5568-22/23.

Figs 20–21. ***Lithraphidites moray-firthensis*** Jakubowski, 1986. XPL (20) and PC (21), BGS Heslerton Borehole (UK), L. Aptian, UCL-5700-13/14. Range: L. Aptian (?deshayesi).

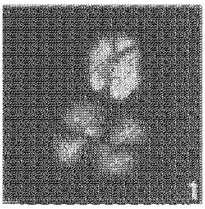
INCERTAE SEDIS NANNOLITHS
Fig. 24. ***Ceratolithina bicornuta*** Perch-Nielsen, 1988. XPL, Folkestone (UK), M. Albian (lautus), UCL-5689-5. Range: M. Albian (lautus) – U. Albian (inflatum).

Figs 25–26. ***Ceratolithina hamata*** Martini, 1967. XPL (25) and PC (26), Folkestone (UK), U. Albian (inflatum), UCL-5688-4/5.

Fig. 27. ***Kokia borealis*** Perch-Nielsen, 1988. IKU Core 7B (N North Sea/offshore mid-Norway), L. Valanginian, UCL-3724-10.

Fig. 22. ***Kokia curvata*** Perch-Nielsen, 1988. IKU Core 7B (N North Sea/offshore mid Norway), L. Valanginian, UCL-3724-16. Range: Ryazanian – L. Valanginian.

Fig. 23. ***Triquetrorhabdulus shetlandensis*** Perch-Nielsen, 1988. XPL, Speeton (UK), L. Valanginian (Polyptychites), UCL-4019-15. Range: Valanginian (Paratollia – ?densicostatus).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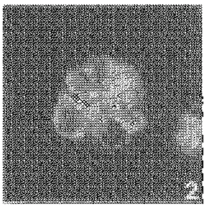
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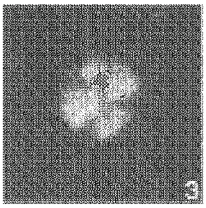
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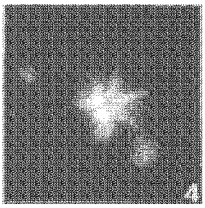
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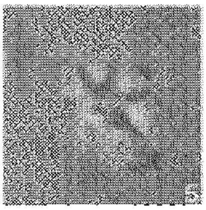
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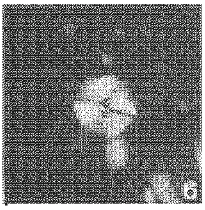
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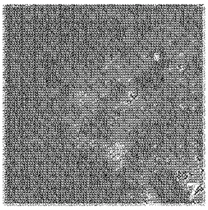
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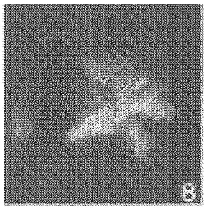
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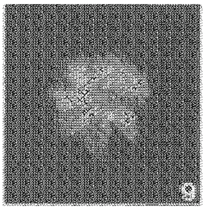
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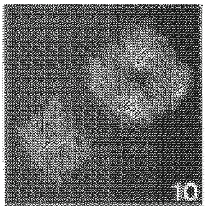
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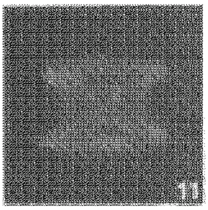
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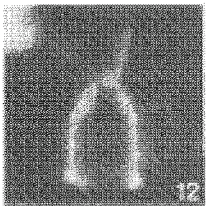
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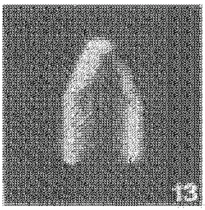
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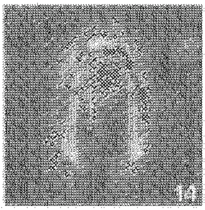
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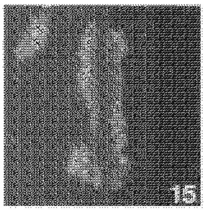
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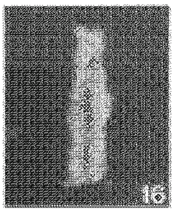
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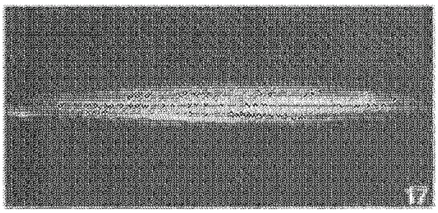
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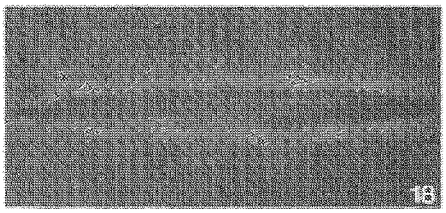
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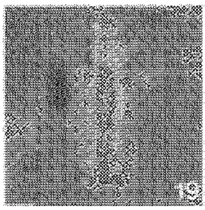
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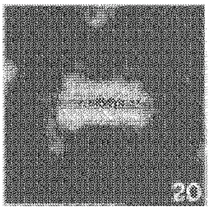
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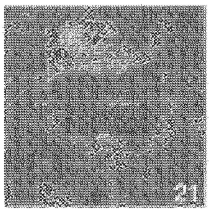
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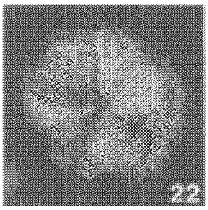
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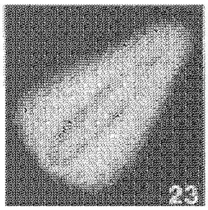
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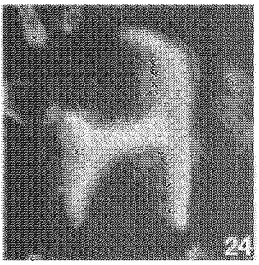
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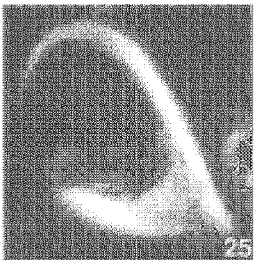
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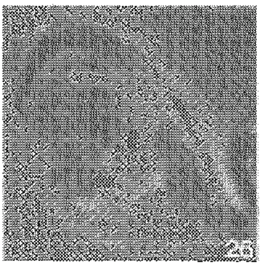
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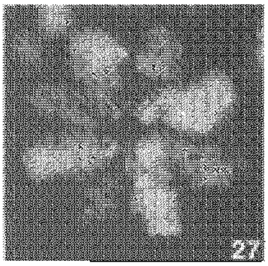
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6

Upper Cretaceous

J.A. Burnett
(with contributions from L.T. Gallagher
and M.J. Hampton)

6.1 INTRODUCTION

Upper Cretaceous lithologies, particularly the highly nannofossiliferous chalks and marls which are characteristic of the interval, are the most geographically widespread, and most completely preserved, of the Mesozoic. High sea-levels and low relief gave rise to geographically-extensive epeiric and shelf seas, and most of the Present Day ocean pathways were accessible, so that global dispersal of the majority of taxa was unhindered. High atmospheric CO_2 concentrations promoted a warm global climate, the consequently shallow global temperature gradient supporting broad biogeographic provinces. This Late Cretaceous world saw an acme of nannofossil diversity for the Mesozoic.

Due to the porous nature of chalk it is an important reservoir for oil in many parts of the world, e.g. the North Sea, USA, CIS and E Caspian Sea, and this industry has been partly responsible for promoting research into the biostratigraphic utility of Upper Cretaceous nannofossils. The continuing drive behind refining and improving the correlation potential of Upper Cretaceous nannofossil biostratigraphy however stems also from the reliance of numerous geologic disciplines on a time-frame which can be used globally. Early zones tended to be broad, parochial and only tenuously assigned to stages. The first attempt at a biozonation scheme and its application was by Stradner (1963), who identified four Upper Cretaceous nannofossil 'associations' based on *Eiffellithus turriseiffelii* (Cenomanian), *Quadrum gartneri* (Turonian), *Uniplanarius trifidus* (Campanian) and *Arkhangelskiella cymbiformis* (Maastrichtian). A steady succession of nannofossil biozonations, based variously on assemblage characteristics and FO, LO or acme events, followed through the remaining 1960s and early 1970s. Although these early biozonations are obsolete, a number of the nannofossil events on which they were based have been retained in the proliferation of more-recent schemes. Additionally, in the last decade, a combination of onshore and ODP studies have begun to clarify the characteristics of provincialism, and the complications associated with biozonations are thus becoming better understood.

Whilst the biostratigraphic potential of Upper Cretaceous nannofossils has mainly been exploited by the oil industry, e.g. through studies of the Norwegian chalk reservoirs, a number of disciplines have also realized this potential. Most notably, nannofossils have provided time-frames for magnetostratigraphy (e.g. Stradner and Steinmetz, 1984; Monechi and Thierstein, 1985; Montgomery *et al.*, 1998) and Sr-isotope chemostratigraphy (McArthur *et al.*, 1993; Sugarman *et al.*, 1995). Following the publication of Haq *et al.*'s (1987) sea-level curves, Upper Cretaceous nannofossil biostratigraphy has also become much used as a fundamental sequence stratigraphic tool.

6.2 IMPORTANT REFERENCES

Thierstein (1976), using a geographically widespread dataset, including many DSDP sites, produced the first attempt at a global Cretaceous biozonation. However, this scheme lacked the resolution provided by slightly later global schemes, and it was almost immediately superseded. In the late 1970s, formal biozonations for the Upper Cretaceous were published which were tied in to the stage-stratotypes. Manivit *et al.* (1977) proposed a biozonation for the 'Middle' Cretaceous. Verbeek (1976a, b, 1977) investigated the nannofloras of Tunisia, southern Spain and France, including the stratotype sections, to produce his biozonation for the 'Middle' and Upper Cretaceous. He was one of the first to illustrate the evolutionary quiescence of the Campanian of mid-western Europe and (with Wonders in 1977) to attempt to integrate nannofossil and planktonic foraminiferal bioevents. Sissingh (1977) based his scheme on a mixture of onshore stage-stratotype (western European) and other (French, Tunisian) sections, and also on industrial well spot-samples primarily from the North Sea region but also from Oman and Turkey. In 1978, using planktonic foraminifera datums as his basis for recalibration, Sissingh reinterpreted the stratigraphic positions of two of his bioevents. He also noted the incomplete nature of the stratotype sections.

Roth (1978) compiled his comparable biozonation from a number of previously described zones based on DSDP material, using similar bioevents to those used by Sissingh, and thereby proving the correlation potential of nannofossil biostratigraphy from onshore to oceanic sequences. Roth's zonation incorporated an arbitrary link with the 'classical European' stages, whilst he erected oceanic stages based on nannofossil bioevents. Both of these latter schemes have been used extensively, their popularity partly lying in the fact that they substituted alphanumeric zones (CC and NC, respectively) for the unwieldy, and overly redefined, taxonomic zonal names used by others.

Crux's (1980, 1982) work was based primarily on sections in SE England, which represent one of the most complete Cenomanian to Campanian sequences in the world. He tied in his nannofossil events with macrofossil zones and stages, providing an additional, more-refined line of correlation. His work also emphasized the dearth of nannofossil events in the Campanian of this part of Europe, as originally documented by Verbeek (1977). All of these schemes provided the robust framework from which all later local and global schemes have evolved.

The first attempts at incorporating 'boreal' and 'tethyan' nannofossil events into one scheme, using Sissingh's framework, were those of Perch-Nielsen (1979a, 1983, 1985a). She used her own and Ben Prins's data, reflecting a broad geographic experience of nannofossil biostratigraphy, with the result that the events she used for the Upper Cretaceous are the most robust to date. However, it became clear that low- and high-latitude nannofossil successions were significantly different during certain periods of the Upper Cretaceous, most conspicuously in the Campanian, and that the Sissingh/Perch-Nielsen scheme is now known to be generally inapplicable outside low palaeolatitudes through this interval. Burnett (1990) provided a 'boreal' biozonation for the Campanian. Later research, on Southern Ocean material, has shown that Burnett's scheme is not applicable to southern high-latitudes. Watkins *et al.* (1996) attempted to consolidate Upper Cretaceous nannofossil biostratigraphy for the Southern Ocean based on information generated in recent years by DSDP/ODP drilling in southern high-latitudes (particularly Wind, 1975; Wind and Wise, 1983; Wise and Wind, 1977, 1985; Wise, 1988; Pospichal and Wise, 1990; Crux, 1991a; Watkins, 1992). They did not attempt to relate their scheme to that of Sissingh and Perch-Nielsen, although Watkins (1992) recorded little endemism below the Lower Campanian. Their zonation is not applicable to northern high-latitudes. Although correlating between latitudes for the Campanian to Maastrichtian interval has proved difficult, the problem is not insurmountable and certain regions which contain mixed high- and low-latitude assemblages are currently under investigation (e.g. the Czech Republic: Svábenická, 1995; Stráník *et al.*, 1996).

Published Upper Cretaceous biozonations of major oil-producing basins have been scarce: Mortimer (1987) produced a biozonation for the Upper Cretaceous of the North Sea which has been subsequently supplemented by Varol (1989a, 1991).

In the two decades since Sissingh's and Roth's seminal works, which many workers have adopted, 'new' biohorizons/-zones/-zonations have continued to be published, although these are all basically derived from those described above. However, taxonomic/bioevent works, such as

Varol (1991, 1992) and Burnett (1997, 1998a) have continued to supply potentially, biostratigraphically-useful datums. It is clear, therefore, that: (1) in the majority of new biozonations, most of the nannofossil events used, and their relative stratigraphic positions, are similar to those used previously, the major differences being in the redefining and renaming of biostratigraphic zones to fit in with missing or additional bioevents, although there are cases of reversed bioevents; (2) the geographically widespread nature of these numerous biozonations have served to highlight stratigraphic intervals and geographic regions of heightened provincialism and the consequent reduction of global correlation potential; and (3) further biostratigraphic refinement is still possible.

Nannofossil studies of the Cretaceous stage-stratotypes and equivalent sections have highlighted the fact that the majority of the stratotypes are incomplete. The search for stage-boundary stratotypes was inaugurated by the *Symposium on Cretaceous Stage Boundaries* held in Copenhagen in 1983 (Birkelund *et al.*, 1983, 1984). At this time, although Perch-Nielsen's extensive work was presented (1979a, 1983), nannofossils failed to be considered as sufficiently useful in this respect. However, the conference prompted a spate of research on potential boundary-stratotypes, a refinement and integration of stratigraphic events around such boundaries, and added impetus to 'boreal-tethyan' correlation exercises. In 1995, at the follow-up conference, nannofossil biostratigraphy was much more evident (see Rawson *et al.*, 1996). Burnett (1996) summarized the current state of knowledge of nannofossils at Upper Cretaceous stage-boundaries based on the recommendations of the working groups at this conference.

Integrated bioevents and biozonation schemes have been attempted over many years, integration implying a first-order correlation between the bioevents of different groups of fossils. Although the works of, e.g., Verbeek and Wonders (1977), Robaszynski and Amédro *et al.* (1979), Robaszynski *et al.* (1982, 1985, 1990, 1994), Marks (1984), Lamolda and Proto Decima (1986), Burnett, Hancock *et al.* (1992), Burnett *et al.* (1992), Hancock, Peake *et al.* (1993), Gale *et al.* (1995, 1996) and Schönfeld and Schulz *et al.* (1996) have provided detailed integrated data (nannofossils with a variety of planktonic and benthic foraminifera, ammonites, belemnites, isotopes) over short sedimentary sequences, Bralower *et al.* (1995) have produced a combined scheme (nannofossils with planktonic foraminifera) for the entire Upper Cretaceous.

Virtually every DSDP/ODP volume contains information on oceanic Upper Cretaceous nannofossils, and these cover all regions of the oceans. Numerous extraneous studies have also been published using this material. In addition, a plethora of onshore Upper Cretaceous nannofossil biostratigraphic studies have been published with virtual worldwide geographic coverage. However, some regions have received far more attention than others, and the number of studies published on European material is far greater than for the rest of the world. Regions such as Asia, northern North America, South America and southern and western Africa have not produced many broadly-publicised works. With a multitude of publications to choose from, it is difficult to pick out those which provide the most useful representation of the nannofossil biostratigraphy of a region; however, the following are useful as starting points, although some are primarily taxonomic works: northern Africa (Perch-Nielsen *et al.*, 1978; Gartner *in* Robaszynski *et al.*, 1990, 1994), North America (Gartner, 1968; Bukry, 1969, 1993, 1994; Hattner and Wise, 1980; Smith, 1981, 1995; Doeven, 1983; Dowsett, 1989a; Watkins *et al.*, 1993; Haggart *et al.*, 1994; Self-Trail and Bybell, 1995), Antarctica (Concheyro *et al.*, 1991), Asia (Xu and Mao, 1992; Zhong, 1992; Wan *et al.*, 1993), Australia (Shafik, 1990), eastern Europe (Shumenko, 1976; Gazdzicka, 1978; Sinnyovsky, 1988, 1992; Cech and Svábenická, 1992; Svábenická and Bubík, 1992; Mertiniené, 1993; Svábenická, 1995; Stráník *et al.*, 1996), western Europe (Manivit, 1971, 1981, *in* Robaszynski and Amédro *et al.*, 1979, *in* Robaszynski *et al.*, 1982, 1985; Monechi, 1977, 1981; Verbeek, 1977; Perch-Nielsen, 1979a; Crux, 1982; Wagreich, 1992; Wagreich and Krenmayr, 1993; Aguado, 1994; Jagt *et al.*, 1995a, b; Gale *et al.*, 1996; Schönfeld and Schulz *et al.*, 1996; Burnett, in prep. a; Burnett and Whitham, 1999), Japan (Toshimitsu *et al.*, 1995a, b), India (Saxena and Misra, 1995), Israel (Moshkovitz, 1984; Reiss *et al.*, 1985; Gvirtzman *et al.*, 1989; Eshet and Moshkovitz, 1995) and Madagascar (Herngreen *et al.*, 1982).

The palaeobiogeographic aspects of Late Cretaceous nannofloras are still relatively under-researched. Some workers have produced lists of apparently endemic taxa (e.g. Perch-Nielsen, 1979a; Wise, 1988; Crux, 1991a, b). Thierstein (1976) also provided a broad perspective on the palaeoecologic distributions of certain taxa. Others have attempted interpretations of latitudinally-related distribution patterns in terms of palaeoclimate and palaeoclimate change (e.g. Holmes and Watkins, 1992; Huber and Watkins, 1992; Burnett, in prep. b) and palaeoceanography (e.g. Roth and Bowdler, 1981; Roth and Krumbach, 1986; Fisher *et al.*, 1994; Hay, 1995). The plethora of southern high-latitude species described by Wind and Wise (*in* Wise and Wind, 1977) initiated a line of research on the Southern Ocean and other austral locations. Whilst it is common knowledge that 'boreal', 'tethyan' and 'austral' nannofossil palaeobiogeographic provinces existed in the Late Cretaceous, the precise delimitation of these has been generally overlooked, although Burnett (in prep. b, and work in train) has begun to address this.

Palaeoecologic and palaeoceanographic studies concerned with nutrient-driven nannofossil distribution patterns in the Upper Cretaceous have been produced by, particularly, Mayers and Worsley (1973), Roth (1978, 1979, 1981, 1989), Roth and Bowdler (1981), Roth and Krumbach (1986), Watkins (1986, 1989), Erba (1992), Windley (1995), Windley *et al.* (1995) and Eshet and Almogi-Labin (1996), a number of which illustrate that certain nannofossil taxa provide an excellent record of surface-water fertility, and can be seen to express Milankovitch cyclicity.

Bukry (1974) started a trend of 'correlating' nannofossil zones with absolute ages, followed by van Hinte (1976b) and Martini (1976). Thierstein (1976) correlated his bioevents with the absolute ages of Obradovich and Cobban (1975) which were derived from bentonite layers within fossiliferous sequences. Roth (1976) provided radiometric ages for certain events. How this link was made is unclear, although he 'screened' the ages he used and admitted that this was a temporary correlation. More recently, Bralower *et al.* (1995) have attempted a similar exercise. Such age calibrations should be used with caution as the Mesozoic time-scale is presently based on few radiometric tie-points.

6.3 UPPER CRETACEOUS NANNOFOSSIL SUCCESSION

High-diversity Late Albian nannofloras continued into the Early Cenomanian, with representatives of the Arkhangelskiales (*Broinsonia, Gartnerago*) and Prediscosphaeraceae becoming more diverse and abundant. These families more or less characterize Late Cretaceous assemblages. Dominant components of nannofloras for each stage are illustrated in Fig. 6.1. There was a fairly high and rapid turnover rate during this time, particularly approaching the Cenomanian/Turonian boundary event of widespread oceanic anoxia. The anoxic event is discussed by Bralower (1988), Jarvis *et al.* (1988) and Lamolda *et al.* (1994). Although some endemism existed during the Cenomanian, the biogeographic provinces appear to have been broad enough not to affected correlation to any great extent.

The Turonian is characterized by a proliferation of Polycyclolithaceae (increased diversity and abundance in *Eprolithus*, inception of *Quadrum* and *Lithastrinus*). The turnover rate was high. The cryptogenic genera, *Liliasterites* and *Marthasterites*, evolved during the stage. In 'austral' locations, *Thiersteinia ecclesiastica* and *Zeugrhabdotus kerguelenensis* were the first obviously endemic taxa of the Late Cretaceous. Despite these occurrences, provincialism does not interfere with correlation.

The Cenomanian–Turonian nannofloral régime was replaced in the Coniacian. This stage is short (approximately 3myr) and is consequently generally perceived as having a low turnover rate. The Coniacian saw the evolution of *Micula*, which eventually displaced the previously-ubiquitous and abundant *Watznaueria*, which had dominated assemblages throughout most of the Mesozoic. Other inceptions include ?*Arkhangelskiella*, and the proliferation of *Lucianorhabdus*, both of which went on to dominate younger assemblages. A number of previously dominant genera were in decline by this time, e.g. *Zeugrhabdotus, Rhagodiscus*. Biogeography does not particularly impair correlation through this stage.

Low diversity and low turnover persisted into the Santonian. The Polycyclolithaceae diversified again at this time, with Late Cretaceous forms of *Rucinolithus* and *Hexalithus* making their debuts. *Calculites* became a significant assemblage comp-

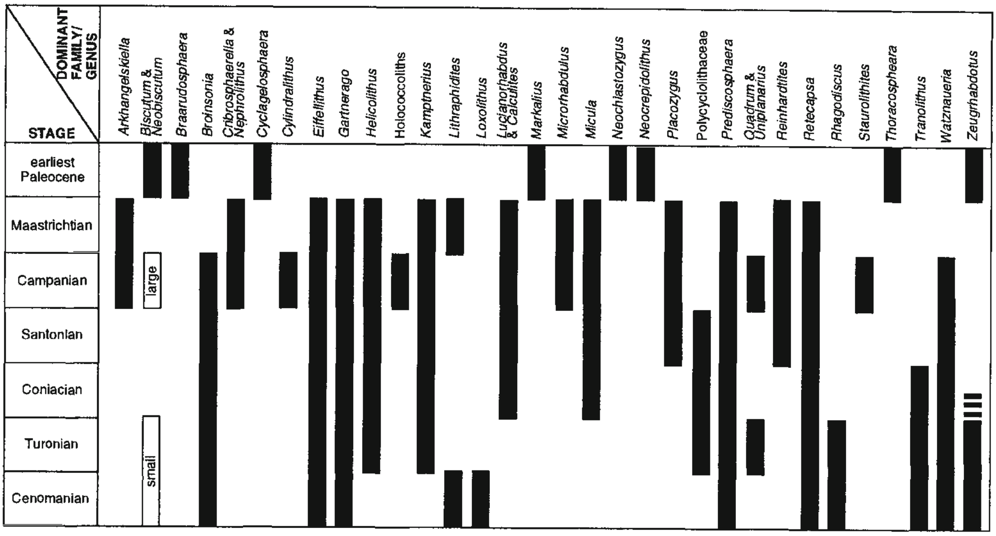


Fig. 6.1 Dominance of genera/families in Late Cretaceous and earliest Tertiary nannofloras.

onent. Endemism reached an acme. Turnover was fairly low in the Campanian, with many inceptions but relatively few extinctions. In certain parts of the world, where preservation is exceptional, holococcoliths are abundant. Inceptions during this time include those of *Bukryaster, Ceratolithoides, Heteromarginatus, Markalius, Misceomarginatus, Monomarginatus* and *Nephrolithus. Petrarhabdus* and *Neocrepidolithus* became less sporadic in occurrence. *Eprolithus, Lithastrinus* and *Nannoconus* became extinct.

The obvious distinction between polar and low-latitude nannofloras continued on into the Maastrichtian. However, turnover increased and there were a number of biostratigraphically useful extinctions in this interval, including *Reinhardtites* and the large *Biscutum*s. There is a general diminution of diversity through this interval which appears to have been related to a global cooling trend and falling sea-levels.

The extinctions at the Cretaceous/Tertiary boundary, first recognized by Bramlette and Martini in 1964, represent the most dramatic and global event in the group's history, with estimates of a 92% decrease in diversity (Bown *et al.*, 1991) and a 99% abundance reduction (Pospichal, 1994) illustrating the severity of the event. Survivor taxa, which were present in low numbers prior to the boundary event, went on to dominate immediately-post-boundary assemblages. These taxa either died out shortly after the boundary, or gave rise to Tertiary lineages. Many publications have addressed the palaeoceanographic and palaeoclimatologic ramifications of this event. Thierstein (1981), Perch-Nielsen (1986a), Pospichal (1994, 1996) and MacLeod *et al.* (1997) provide useful discussions and bibliographies, whilst Romein *et al.* (1996) and Herngreen *et al.* (1998) have raised some interesting questions concerning the biostratigraphy of the interval in the Maastrichtian type-region.

6.4 BIOSTRATIGRAPHY

6.4.1 Introduction

Although Sissingh's (1977, 1978) and Perch-Nielsen's (1979a, 1983, 1985a) combined attempt at a global scheme for this interval was imperfect (it derives too much from low-latitude bioevents at critical intervals), their 'CC' zones/subzones have proved to be robust and widely used. However, the last decade has seen improvements in our knowledge of high- and intermediate-latitude regions, and many of the bioevents used to define the 'CC' zones are now known to be inappropriate in a global context. Since the point of biozonation is to effect correlation, and since accurate time-frames are fundamental to many geological disciplines, it has become necessary to replace this scheme with one which accommodates recent advances in biogeographic and evolutionary understanding and allows a re-evaluation of the relative positions of Sissingh's and Perch-Nielsen's original events in a global context.

The newly-devised scheme presented here is an amalgamation of both old and new bioevent data, from a range of palaeolatitudes and biogeographic provinces, and from both oceanic and shelf palaeoenvironments. The zonation is alphanumeric for ease of use. The majority of the nannofossil events have been directly correlated with macrofossil events onshore. Furthermore, for the first time, they have been precisely correlated with the stage-boundary events, the importance of which has been grossly underestimated in the past. The zone-defining taxa are those which were judged to have the most reliable and widely correlatable bioevents, so that it should be possible to assign the zones to most geographic situations. As far as the author's experience allows, these bioevents are not generally affected by palaeobiogeographic constraints.

The Cenomanian to Santonian subzones are defined on taxa which have proved to be reliable over wide (if not global) geographic areas but which are subject to palaeoenvironmental constraints: it can be seen from Figs 6.2–6.4 that shelf sediments tend to record more bioevents than oceanic settings and, thus, it may not be possible to assign the subzones in every palaeoceanographic situation. Palaeobiogeographic separation of nannofloras became increasingly apparent through the Campanian and into the Maastrichtian, and global correlation of this interval has the lowest resolution in the Upper Cretaceous. This has required the erection of three different sets of subzones for disparate regions: a 'boreal' province (broadly, northern high-palaeolatitudes), an intermediate-'tethyan' province (broadly, moderate- to low-palaeolatitudes), and an 'austral' province (southern high-palaeolatitudes) (see Figs 6.5 and 6.6). Whilst the biozones remain virtually globally correlatable, the subzones cannot be widely correlated through this interval. However, work is in train to eventually effect such a refined correlation. Further, secondary age-indicative bioevents are shown within these subzones. The stratigraphic position of these events appears to vary between regions, or has been observed to be reversed with respect to another bioevent, and so they are not ascribed subzonal status.

Figures 6.2–6.6 provide correlations between the new data and biozones, and the relevant macrofossil biostratigraphy and stages. They also illustrate these data alongside the global Upper Cretaceous schemes currently available, the only southern high-palaeolatitude biozonation, and the only published North Sea scheme. The repetitive use of similar bioevents can be clearly observed from these charts, lending a high degree of confidence to these events.

6.4.2 Correlation

A precise correlation between stages and nannofossil zones is of paramount importance in global correlation. The new scheme provides a much-needed precision in this respect. Whilst laudably producing much-needed data from the open oceans, ocean drilling has actually caused a problem concerning stage-boundary definition which has become compounded in the literature. Originally, nannofossil bioevents in the oceans were not equated with those of the classical onshore stages, even though the events were demonstrably similar. Stages have been historically defined onshore using macrofossils. In the absence of macrofossil data from oceanic cores, stage boundaries started to be 'defined' using microfossil events. Indeed, Roth (1978) created a new set of stages for the oceans. The current situation, wherein stages deduced from nannofossil data from ODP appears not to match up precisely with those from outcrop material, should be unacceptable since bioevents which define most of the stage-boundaries for the Upper Cretaceous have recently been proposed and the nannofossil context clarified (Rawson *et al.*, 1996; Burnett, 1996, herein). Nannofossils do not define the bases of any Upper Cretaceous stages.

6.4.3 Abundance estimates

The estimated-abundance categories applied here reflect the generally high ratio of nannofossils to background sediment in most rocks of this age, and is rapid and easy to use. Thus, most taxa represented in a geographic region fall into the 'few' and 'common' categories, and thereby represent an average contribution to the assemblage. Taxa falling into the 'rare' and 'abundant' categories stand out as an unusual constituent of the assemblage. These categories are more likely to contain the taxa which are most affected by provincialism. The categories are:

A = Abundant = >10 specimens/FOV
C = Common = 1–10 specimens/FOV
F = Few = 1 specimen/2–50 FOV
R = Rare = 1 specimen/>50 FOV (or 1 traverse).

6.4.4 Biozonation

It was not considered necessary to provide the formally-described alphanumeric biozones described here with taxonomic epithets because: (1) In the past, continual reuse of particular taxonomic epithets has resulted in such zones becoming virtually meaningless due to the plethora of definitions for the boundaries. Shafik (1990, p.4–5 and his Tables 3 and 4) discussed this in detail and compiled a comprehensive chart illustrating the different definitions for published zones and providing correlations between them. This redefinition of zones has often been a response to anomalous occurrences of marker species (reflecting biogeography), and thus the practice has hindered biogeographic understanding and not enhanced global correlation. (2) The names and stratigraphic positions of alphanumeric zones are easier to remember!

It is hoped that this new scheme will be used as a framework for future improvement. It is presented in such a way as to encourage workers away from creating more zonal schemes based on the same old events, and move towards consolidating the use of particular events and discovering or confirming new ones to close the gaps, whilst focusing on the global utility of the group.

The new biozones are summarized in Fig. 6.7, where they are correlated with the 'CC' and 'NC' zones and the stages. Radiometric (absolute) ages for the stage-boundaries have been added to the zonation but, since definitions for some of these boundaries have recently changed (Rawson *et al.*, 1996), these ages may not be directly relevant. These dates should be used with caution and are reproduced here to give some idea of the relative lengths of the stages rather than to lend another dimension to, or increase the credence of, the nannofossil biostratigraphy.

The prefix 'UC' stands for 'Upper Cretaceous'. Subzones, particularly for the Campanian and Maastrichtian, have the suffix 'BP' ('boreal' province), 'AP' ('austral' province) or 'TP' ('intermediate-tethyan' province) after the subzone letter, referring to broad, palaeolatitudinally-linked palaeobiogeographic distinctions. The terms 'austral', 'boreal' and 'tethyan' are referred to in a loose sense because no formal definitions exist and different authors have used them in variable contexts. Approximate definitions for the biogeographic terms used are shown in Table 6.1.

Table 6.1 Approximate definitions for Late Cretaceous palaeobiogeographic nannofloral provinces, as used herein.

Province/Latitude	*Countries included*
Boreal = >50°N	Scandinavia, N CIS, Denmark, Germany, N UK, North Sea, N USA
Intermediate = 50–45°N	N France, S England, The Netherlands, Bulgaria, Czech Republic, S CIS, mid-USA
Tethyan = 45°N–10°S	Caribbean, northern S America, S USA, S Europe, N Africa, Arabia, Indonesia
Intermediate = 10–35°S	mid-S America, mid-Africa, Madagaskar, C and N Australia, India, Pakistan
Austral = >35°S, but generally >40°S	southernmost S America, S Africa and Australia; New Zealand; Kerguelen and Falkland Plateaus; Antarctica

MFZ and MFsZ stands for 'macrofossil zone' and 'subzone'.

UC0 Nannofossil Zone
Author. Equivalent to subzone NC10A of Bralower *et al.* (1993).
Definition. FO of *Eiffellithus turriseiffelii* to the FO of *Corollithion kennedyi*.
Range. Upper Albian (inflatum MFZ) to Lower

Cenomanian (mantelli MFZ, carcitanense MFsZ).
Remarks. This zone is also equivalent to zone BC27 at the top of the Lower Cretaceous, as described by Bown *et al.* (Chapter 5). Because the zone straddles the Lower/Upper Cretaceous boundary, and is thus shared by two discrete biozonations, it was decided to start the Upper Cretaceous scheme at UC0 to denote a 'special', overlapping zone. The interval is discussed in detail by Burnett (*in* Gale *et al.*, 1996). Some discrepancy between the bioevents found in the expanded Mont Risou sequence (*op. cit.*) and elsewhere, where at least part of the interval is commonly represented by a hiatus, is to be expected. However, differences in events which were determined between N France and S England which are due to provincialism include the LO of *Watznaueria britannica* (the event being older in S England) and the LO of common *Repagulum parvidentatum*. This taxon occurs in high abundances only at relatively high palaeolatitudes, and the event thus has not been identified in S France.

UC0a/BC27a Nannofossil Subzone

Author. Manivit *et al.* (1977).
Definition. FO of *Eiffellithus turriseiffelii* to the LO of *Hayesites albiensis*.
Range. Upper Albian (inflatum MFZ to dispar MFZ, perinflatum MFsZ).

UC0b/BC27b Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Hayesites albiensis* to the FO of *Calculites anfractus*.
Range. Upper Albian (dispar MFZ, perinflatum MFsZ to briacensis MFsZ).
Remarks. *C. anfractus* occurs quite rarely in the 'boreal'/North Sea region and is even more rare at lower palaeolatitudes. *Arkhangelskiella antecessor* has its FO and LO in this subzone in S France.

UC0c/BC27c Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Calculites anfractus* to the FO of *Corollithion kennedyi*.
Range. Upper Albian (dispar MFZ, briacensis MFsZ) to Lower Cenomanian (mantelli MFZ, carcitanense MFsZ).
Remarks. Both *Gartnerago theta* and *Prediscosphaera cretacea* have FOs in this subzone in S France but in S England these events seem to occur slightly higher (in subzones UC1b and UC1d, respectively). The *Gartnerago* lineage is discussed in detail in Hampton *et al.* (in prep.). The FO of *G. theta* can also be located in the 'austral' province.

UC1 Nannofossil Zone

Author. Burnett, herein.
Definition. FO of *Corollithion kennedyi* to the FO of *Gartnerago segmentatum* (= *G. obliquum* of many authors).
Range. Lower Cenomanian (mantelli MFZ, carcitanense MFsZ to basal dixoni MFZ).
Remarks. The top of the zone could not be determined in the 'austral' province.

UC1a Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Corollithion kennedyi* to the LO of *Watznaueria britannica*.
Range. Lower Cenomanian (mantelli MFZ, carcitanense MFsZ).
Remarks. Perch-Nielsen (1985a) indicated the close proximity of these events but could not separate them. The LO of *W. britannica* occurs stratigraphically higher in S France than in S England, where the event co-occurs with the LO of common *R. parvidentatum*. However, *W. britannica* has been observed to LO in the Lower Coniacian in Poland. The FOs of *Gartnerago nanum* and *C. kennedyi* are in close proximity.

UC1b Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Watznaueria britannica* to the LO of *Gartnerago chiasta*.
Range. Lower Cenomanian (mantelli MFZ, carcitanense MFsZ).
Remarks. *G. chiasta* may occur only rarely but the event has been identified in the 'austral' province and is thus useful. *G. theta* first occurs in this subzone in S England.

UC1c Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Gartnerago chiasta* to the FO of rare and sporadic *Kamptnerius magnificus* or the FO of *Helicolithus anceps*.
Range. Lower Cenomanian (mantelli MFZ, carcitanense MFsZ).

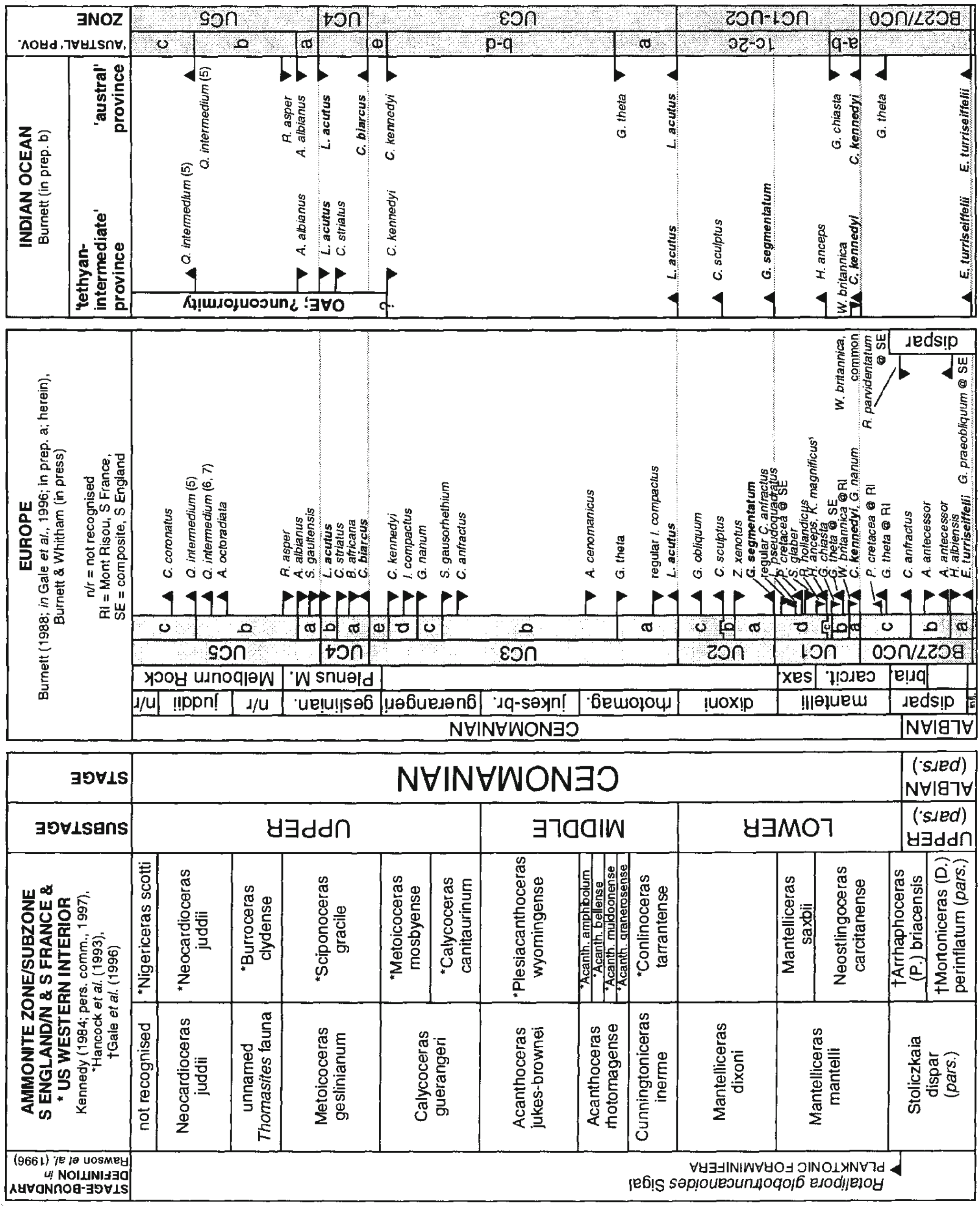


Fig. 6.2 Comparison of uppermost Albian to Upper Cenomanian biozonations with new data which has been correlated with macrofossil zones. Stages appear in quotation marks because no precise correlation of nannofossil data with the stages was attempted by the original authors.

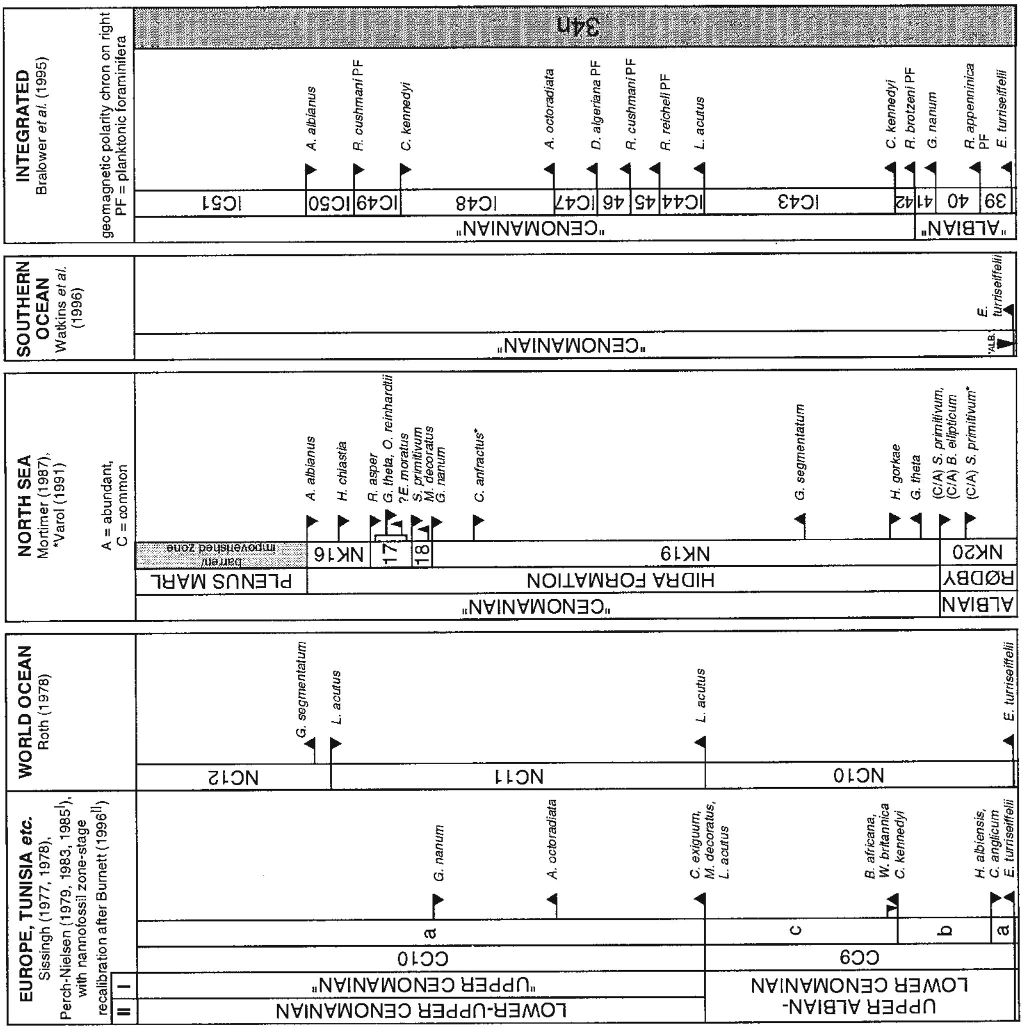


Fig. 6.2 (continued)

Remarks. *K. magnificus* makes a rare, sporadic FO at this level in S England which may be overlooked in many other, particularly oceanic, locations. This taxon does not become firmly established until the Turonian, however. The FO of *H. anceps* may occur higher (Turonian) in 'austral' locations.

UC1d Nannofossil Subzone
Author. Burnett, herein.
Definition. FO of rare and sporadic *Kamptnerius magnificus* or the FO of *Helicolithus anceps* to the FO of *Gartnerago segmentatum*.
Range. Lower Cenomanian (mantelli MFZ, carcitanense MFsZ to basal dixoni MFZ).
Remarks. *G. segmentatum* appears just above the base of the dixoni Zone. This subzone contains the LOs of *Radiolithus hollandicus*, *Staurolithites glaber* and regularly-occurring *C. anfractus*, and the FOs of *P. cretacea* (in S England) and *Lithraphidites pseudoquadratus*. *K. magnificus* is rare above this level, becoming more frequent in the Turonian. The base of this subzone was not determined in the 'austral' province.

UC2 Nannofossil Zone
Author. Burnett, herein.
Definition. FO of *Gartnerago segmentatum* (= *G. obliquum* of many authors) to the FO of *Lithraphidites acutus*.
Range. Lower (basal dixoni MFZ) to basal Middle Cenomanian (basal rhotomagense MFZ).
Remarks. This zone could not be recognized at 'austral' locations.

UC2a Nannofossil Subzone
Author. Burnett, herein.
Definition. FO of *Gartnerago segmentatum* to the LO of *Zeugrhabdotus xenotus*.
Range. Lower Cenomanian (dixoni MFZ).
Remarks. *Z. xenotus* appears to have been a shelf-preferring form, and thus this subzone might not be determinable in oceanic sequences. *G. segmentatum* is rare at this level, becoming more frequent in the later Cenomanian.

UC2b Nannofossil Subzone
Author. Burnett, herein.
Definition. LO of *Zeugrhabdotus xenotus* to the FO of *Cylindralithus sculptus*.
Range. Lower Cenomanian (dixoni MFZ).
Remarks. *C. sculptus* has not been found at 'austral' locations.

UC2c Nannofossil Subzone
Author. Burnett, herein.
Definition. FO of *Cylindralithus sculptus* to the FO of *Lithraphidites acutus*.
Range. Lower (dixoni MFZ) to basal Middle Cenomanian (basal rhotomagense MFZ).
Remarks. *Gartnerago obliquum* first occurs here in S England but predates the FO of *G. segmentatum* in the Indian Ocean. It is lumped with *G. segmentatum* in many studies and thus its FO may be overlooked. See also plate caption 6.9.

UC3 Nannofossil Zone
Author. Burnett, herein.
Definition. FO of *Lithraphidites acutus* to the FO of *Cylindralithus biarcus*.
Range. Basal Middle (basal rhotomagense MFZ) to Upper Cenomanian (geslinianum MFZ, Plenus Marl Formation).

UC3a Nannofossil Subzone
Author. Burnett, herein.
Definition. FO of *Lithraphidites acutus* to the LO of *Gartnerago theta*.
Range. Lower Middle Cenomanian (rhotomagense MFZ).
Remarks. Contains the LO of regularly-occurring *Isocrystallithus compactus* (= *Owenia hillii* of some authors). It is possible that *I. compactus* is easily susceptible to dissolution, and is thus not recorded from many locations.

UC3b Nannofossil Subzone
Author. Burnett, herein.
Definition. LO of *Gartnerago theta* to the LO of *Staurolithites gausorhethium*.
Range. Middle (rhotomagense MFZ) to Upper Cenomanian (guerangeri MFZ).
Remarks. *S. gausorhethium* appears to have been a shelf-preferring form. This subzone contains the LOs of *Acaenolithus cenomanicus* and *C. anfractus*, the latter occurring only very rarely and sporadically towards its extinction datum.

UC3c Nannofossil Subzone
Author. Burnett, herein.
Definition. LO of *Staurolithites gausorhethium* to the LO of *Gartnerago nanum*.

Range. Upper Cenomanian (guerangeri MFZ).
Remarks. The LO of *G. nanum* could not be identified in oceanic or 'austral' settings.

UC3d Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Gartnerago nanum* to the LO of *Corollithion kennedyi*.
Range. Upper Cenomanian (guerangeri MFZ).
Remarks. Contains the LO of *I. compactus*.

UC3e Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Corollithion kennedyi* to the FO of *Cylindralithus biarcus*.
Range. Upper Cenomanian (guerangeri MFZ to geslinianum MFZ/Plenus Marl Formation).

UC4 Nannofossil Zone

Author. Burnett, herein.
Definition. FO of *Cylindralithus biarcus* to the LO of *Lithraphidites acutus*.
Range. Upper Cenomanian (geslinianum MFZ/ Plenus Marl Formation).
Remarks. The Plenus Marl Formation, and equivalents (e.g. the Black Band of N England), has formed the basis of, or been remarked upon in, a number of nannofossil studies (*e.g.* Bralower, 1988; Cooper *in* Jarvis *et al.*, 1988; Lamolda *et al.*, 1994, 1997; Hradecká and Svábenická, 1995; Burnett and Whitham, 1999; Burnett, in prep. a). However, the relative positions of the main bioevents through the interval varies between these works because the sequence constitutes a local expression of oceanic anoxia which was experienced globally, and contains hiati and condensed sequences, probably with associated reworking, and has also been associated with a barren interval in the North Sea (Mortimer, 1987). Consequently, the sequence of events proposed here may disagree with previously published works and the interval remains slightly enigmatic. A number of useful LOs occur, although it is uncertain whether these extinctions were directly related to the anoxic event. The base of this zone cannot be applied at lower palaeolatitudes.

UC4a Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Cylindralithus biarcus* to the LO of *Cretarhabdus striatus* (= *Cretarhabdus loriei* of some authors).
Range. Upper Cenomanian (geslinianum MFZ/ Plenus Marl Formation).
Remarks. The LO of *C. striatus* may occur earlier at 'austral' locations. The LO of *Braarudosphaera africana* was found in this subzone.

UC4b Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Cretarhabdus striatus* (= *Cretarhabdus loriei* of some authors) to the LO of *Lithraphidites acutus*.
Range. Upper Cenomanian (geslinianum MFZ/ Plenus Marl Formation).

UC5 Nannofossil Zone

Author. Burnett, herein.
Definition. LO of *Lithraphidites acutus* to the LO of *Helenea chiastia* (= *Microstaurus chiastius* of many authors).
Range. Upper Cenomanian (geslinianum MFZ/Plenus Marl Formation) to Lower Turonian (devonense MFZ).
Remarks. The LO of *H. chiastia* corresponds to the LO of *Ceratolithina* spp. at 'austral' locations. Certain oceanic sequences appear to have a barren interval and hiatus around this level, which corresponds to the Oceanic Anoxic Event.

UC5a Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Lithraphidites acutus* to the LO of *Axopodorhabdus albianus*.
Range. Upper Cenomanian (geslinianum MFZ/ Plenus Marl Formation).
Remarks. *Seribiscutum gaultensis* last occurs here.

UC5b Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Axopodorhabdus albianus* to the FO of *Quadrum intermedium* with 5 elements in each cycle.
Range. Upper Cenomanian (geslinianum MFZ/ Plenus Marl Formation to juddii MFZ).
Remarks. The LO of *Rhagodiscus asper*, and the FO of forms of *Q. intermedium* with 6 and 7 elements in each cycle, occur in this subzone. The FO of *Ahmuellerella octoradiata* is tentatively placed here, although similar forms with more-delicate and complete central crosses (perhaps *Stauro-*

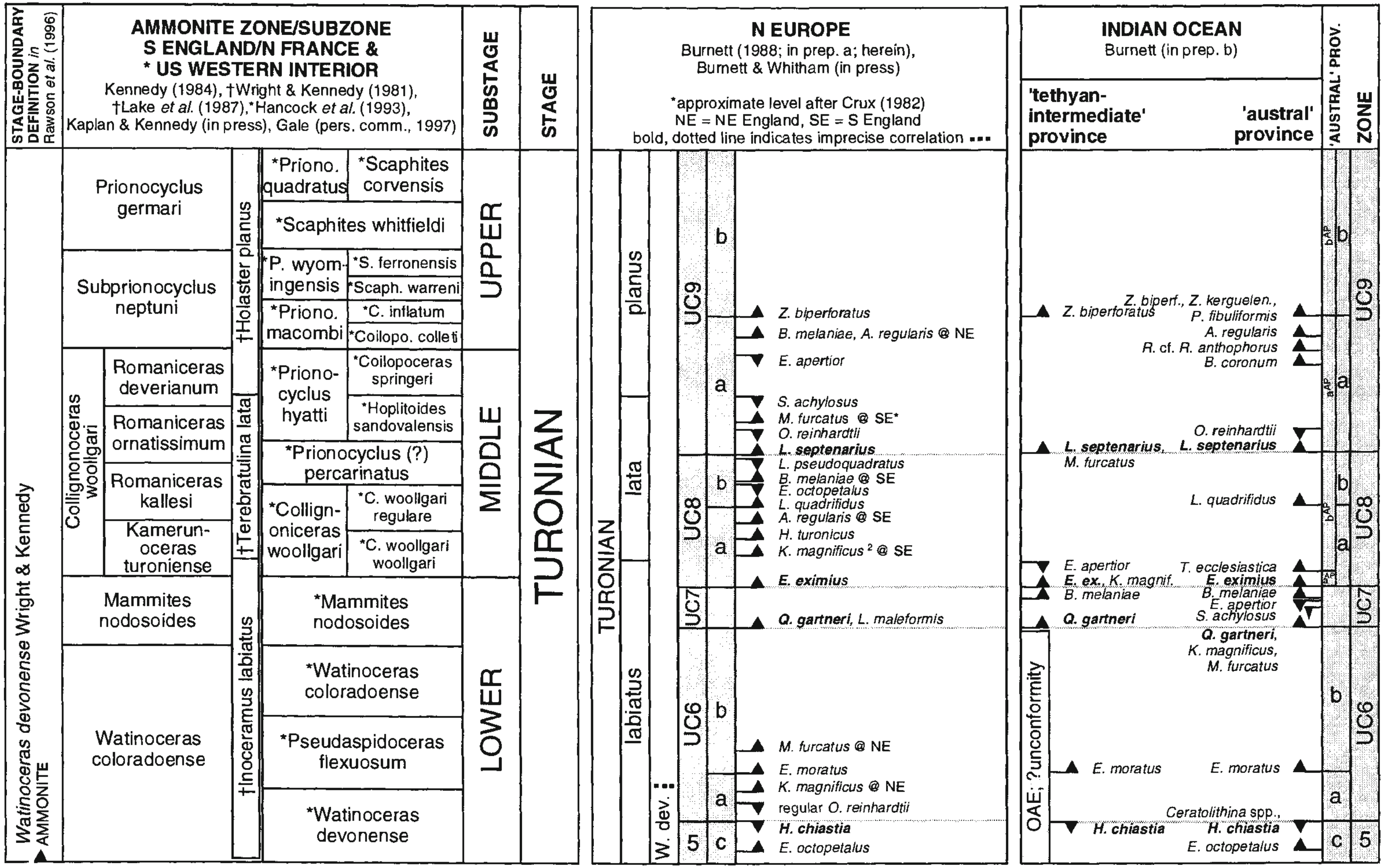


Fig. 6.3 Comparison of Turonian biozonations with new data which has been correlated with macrofossil zones. Stages appear in quotation marks because no precise correlation of nannofossil data with the stages was attempted by the original authors.

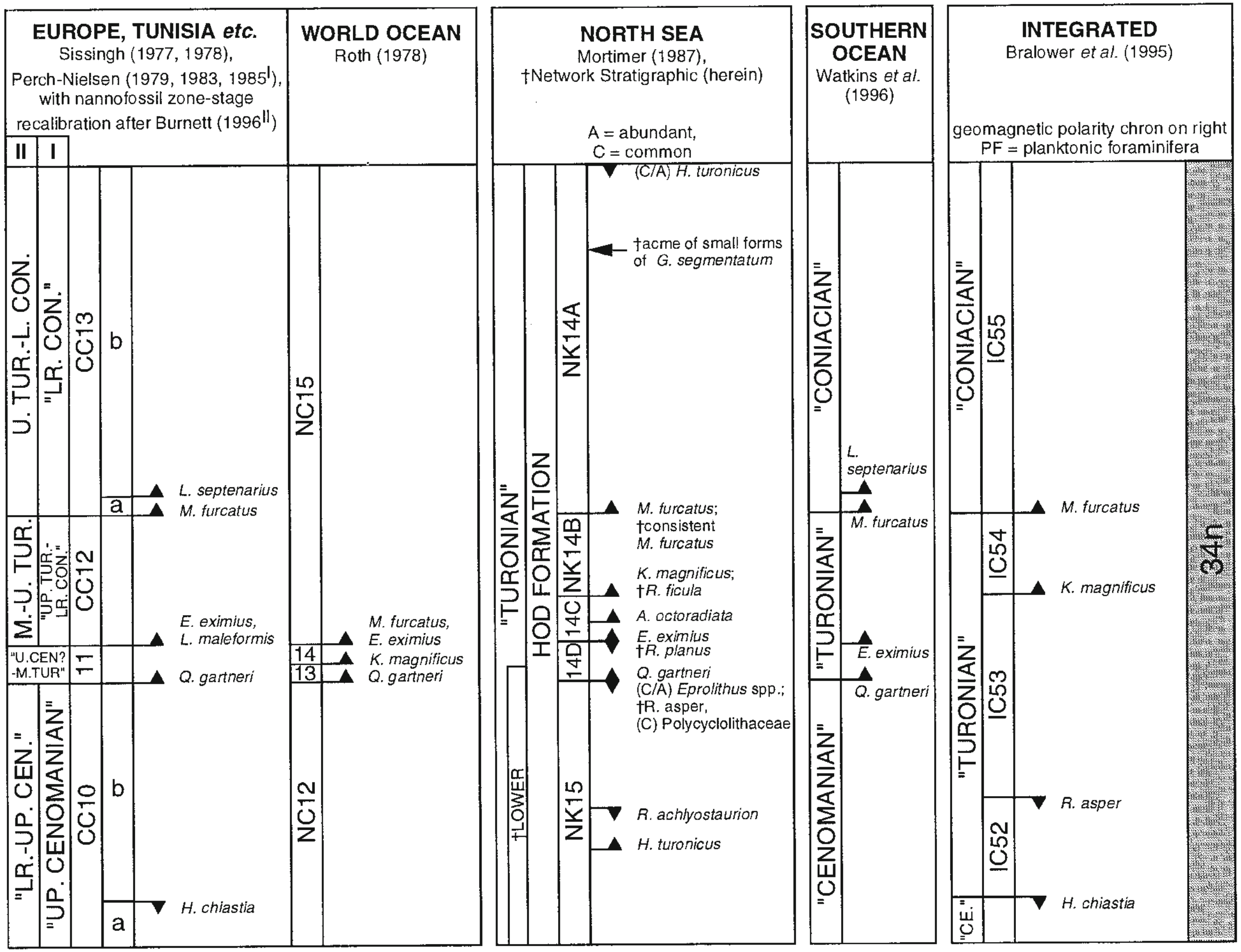


Fig. 6.3 (continued)

lithites) are seen below this. Other workers have placed *A. octoradiata* stratigraphically lower in the Cenomanian.

UC5c Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Quadrum intermedium* with 5 elements in each cycle to the LO of *Helenea chiastia*.
Range. Upper Cenomanian (juddii MFZ) to Lower Turonian (devonense MFZ).
Remarks. *Cylindralithus coronatus* and *Eprolithus octopetalus* have their FOs in this subzone.

UC6 Nannofossil Zone

Author. Equivalent to subzone CC10b of Perch-Nielsen (1985a).
Definition. LO of *Helenea chiastia* (= *Microstaurus chiastius* of many authors) to the FO of *Quadrum gartneri*.
Range. Lower Turonian (devonense and labiatus MFZs).
Remarks. This zone may be condensed or occur in association with a barren interval, particularly in oceanic sequences.

UC6a Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Helenea chiastia* to the FO of *Eprolithus moratus* (= *E. eptapetalus* of Varol, 1992).
Range. Lower Turonian (devonense to ?labiatus MFZs).
Remarks. The base of this subzone corresponds to the extinction level of *Ceratolithina* spp., a particularly distinctive event in the 'austral' province. Regularly-occurring *Octocyclus reinhardtii* last occurs here in shelf settings. *K. magnificus* first occurs here in N England.

UC6b Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Eprolithus moratus* to the FO of *Quadrum gartneri*.
Range. Lower Turonian (labiatus MFZ).
Remarks. *Marthasterites furcatus* first occurs here at higher palaeolatitudes. At 'austral' locations, *K. magnificus* seems to FO here. In S England, the FO of *Lucianorhabdus maleformis* is in close proximity to the FO of *Q. gartneri*.

UC7 Nannofossil Zone

Author. Equivalent to zone CC11 *sensu* Perch-Nielsen (1979a).
Definition. FO of *Quadrum gartneri* to the FO of *Eiffellithus eximius*.
Range. Lower Turonian (labiatus MFZ).
Remarks. The FO of consistently-occurring *K. magnificus* lies around the FO of *E. eximius*. It appears that *K. magnificus* first occurs consistently below the FO of *E. eximius* predominantly in 'austral' and low-palaeolatitude environments and above in 'boreal' locations. *Biscutum melaniae* first occurs below the top of the zone in oceanic locations. The LOs of *Stoverius achylosus* and *Eprolithus apertior* occur here at 'austral' locations.

UC8 Nannofossil Zone

Author. Burnett, herein.
Definition. FO of *Eiffellithus eximius* to the FO of *Lithastrinus septenarius* (= *L. moratus* of Varol, 1992).
Range. Lower (labiatus MFZ) to Middle Turonian (lata MFZ).
Remarks. Many authors have used the FO of *M. furcatus* to subdivide this interval. Personal observations have shown that this event is unreliable, the FO lying stratigraphically much lower at higher latitudes. The zone can be subdivided into both AP and global subzones.

UC8a Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Eiffellithus eximius* to the FO *Lucianorhabdus quadrifidus*.
Range. Lower (labiatus MFZ) to Middle Turonian (lata MFZ).
Remarks. The FO of *L. quadrifidus* may be difficult to use in lower-palaeolatitude or oceanic sequences, possibly due to preservational difficulties. Onshore, this subzone contains the FOs of *Helicolithus turonicus*, *Ahmuellerella regularis* and the apparently higher second 'inception' of *K. magnificus*. *E. apertior* last occurs here at lower palaeolatitudes. *Thiersteinia ecclesiastica* FOs here in 'austral' locations.

UC8b Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Lucianorhabdus quadrifidus* to the FO of *Lithastrinus septenarius*.
Range. Middle Turonian (lata MFZ).

Remarks. *E. octopetalus* and *L. pseudoquadratus* last occur here. *B. melaniae* first occurs here in S England, later than at other palaeolatitudes. The FO of *L. septenarius* coincides with the FO of *M. furcatus* at lower palaeolatitudes.

UC8a^{AP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Eiffellithus eximius to* the FO of *Thiersteinia ecclesiastica*.
Extrapolated range. Lower to Middle Turonian (labiatus to lata MFZs. Not identified in an MF-dated sequence).
Remarks. Although subzones UC8a and UC8b can be recognized at 'austral' locations, the more-obvious and abundant *T. ecclesiastica* can be used as an additional subdivision of UC8 here.

UC8b^{AP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Thiersteinia ecclesiastica* to the FO of *Lithastrinus septenarius*.
Extrapolated range. Lower to Middle Turonian (labiatus to lata MFZs. Not identified in an MF-dated sequence).
Remarks. *Lucianorhabdus quadrifidus* FOs here.

UC9 Nannofossil Zone

Author. Equivalent to subzone CC13b of Perch-Nielsen (1985a).
Definition. FO of *Lithastrinus septenarius* (= *L. moratus* of Varol, 1992) to the FO of *Micula staurophora*.
Range. Middle Turonian (lata MFZ) to Lower or Middle Coniacian (cortestudinarium MFZ).
Remarks. It is important to be aware that forms closely resembling *M. staurophora* (i.e. *M. adumbrata*) occur just below its true FO in more-complete sequences. Although global subzones have been erected for this zone, the 'austral'-endemic FO of *Zeugrhabdotus kerguelenensis* allows the erection of AP subzones as well. Svábenická (pers. comm., 1996) confirmed that the FO of *M. furcatus* is diachronous, first occurring in this zone in the Bohemian Cretaceous Basin.

UC9a Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Lithastrinus septenarius* to the FO of *Zeugrhabdotus biperforatus*.
Range. Middle to Upper Turonian (lata MFZ to planus MFZ).
Remarks. The apparent LO of *O. reinhardtii* occurs here at intermediate palaeolatitudes or in shelf settings but has been observed much higher (~Maastrichtian) at higher palaeolatitudes. Crux (1982) found the FO of *M. furcatus* here in S England. The LOs of *E. apertior* and *S. achylosus* occur here in S England stratigraphically higher then elsewhere. The FO of *B. melaniae* is also here, in N England, stratigraphically higher than elsewhere. *A. regularis* first occurs here at higher palaeolatitudes.

UC9b Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Zeugrhabdotus biperforatus* to the FO of *Broinsonia parca expansa* (= ?*B. lacunosa* and *Aspidolithus parcus expansus* of some authors).
Range. Upper Turonian (planus MFZ) to Lower Coniacian (cortestudinarium MFZ).

UC9c Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Broinsonia parca expansa* (= ?*B. lacunosa* and *Aspidolithus parcus expansus* of some authors) to the FO of *Micula staurophora*.
Range. Lower to ?Middle Coniacian (cortestudinarium MFZ).
Remarks. The LO of *H. turonicus* is here. In expanded sequences, *M. adumbrata* first occurs here.

UC9a^{AP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Lithastrinus septenarius* to the FO of *Zeugrhabdotus kerguelenensis*.
Extrapolated range. Middle Turonian (lata MFZ) to Lower or Middle Coniacian (cortestudinarium MFZ. Not identified in an MF-dated sequence).
Remarks. *Z. kerguelenensis* appears to be endemic to southern high-latitudes. Its FO is approximately equivalent to the FO of *Z. biperforatus* (and *Placozygus fibuliformis*), and can be used in addition to this datum at 'austral' locations. The subzone also contains the FOs of *Biscutum coronum*, *Reinhardtites* cf. *R. anthophorus* and *A. regularis*, and the apparent LO of *O. reinhardtii*.

UC9b^{AP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Zeugrhabdotus kerguelenensis*

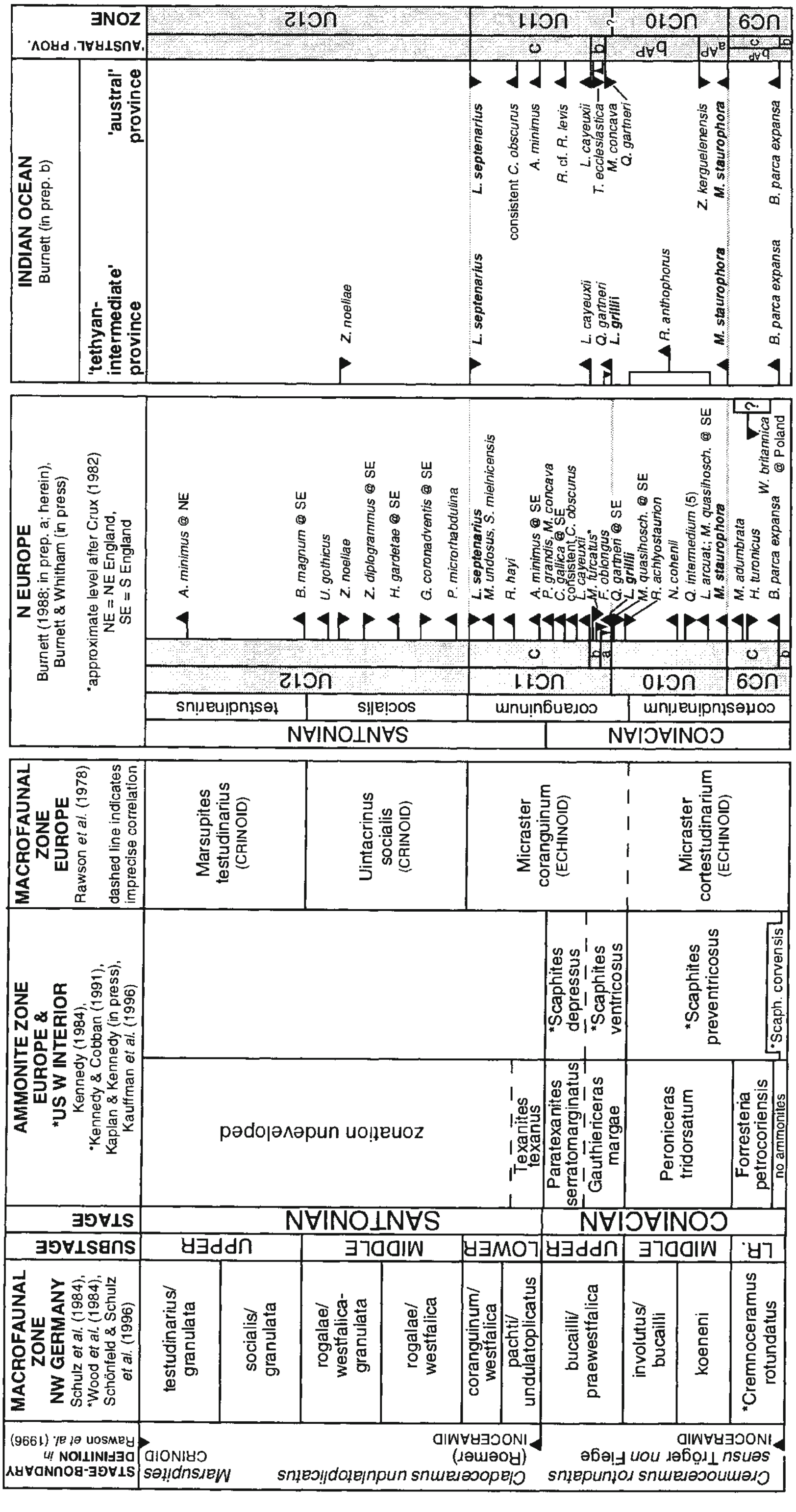


Fig. 6.4 Comparison of Coniacian to Santonian biozonations with new data which has been correlated with macrofossil zones. Stages appear in quotation marks because no precise correlation of nannofossil data with the stages was attempted by the original authors.

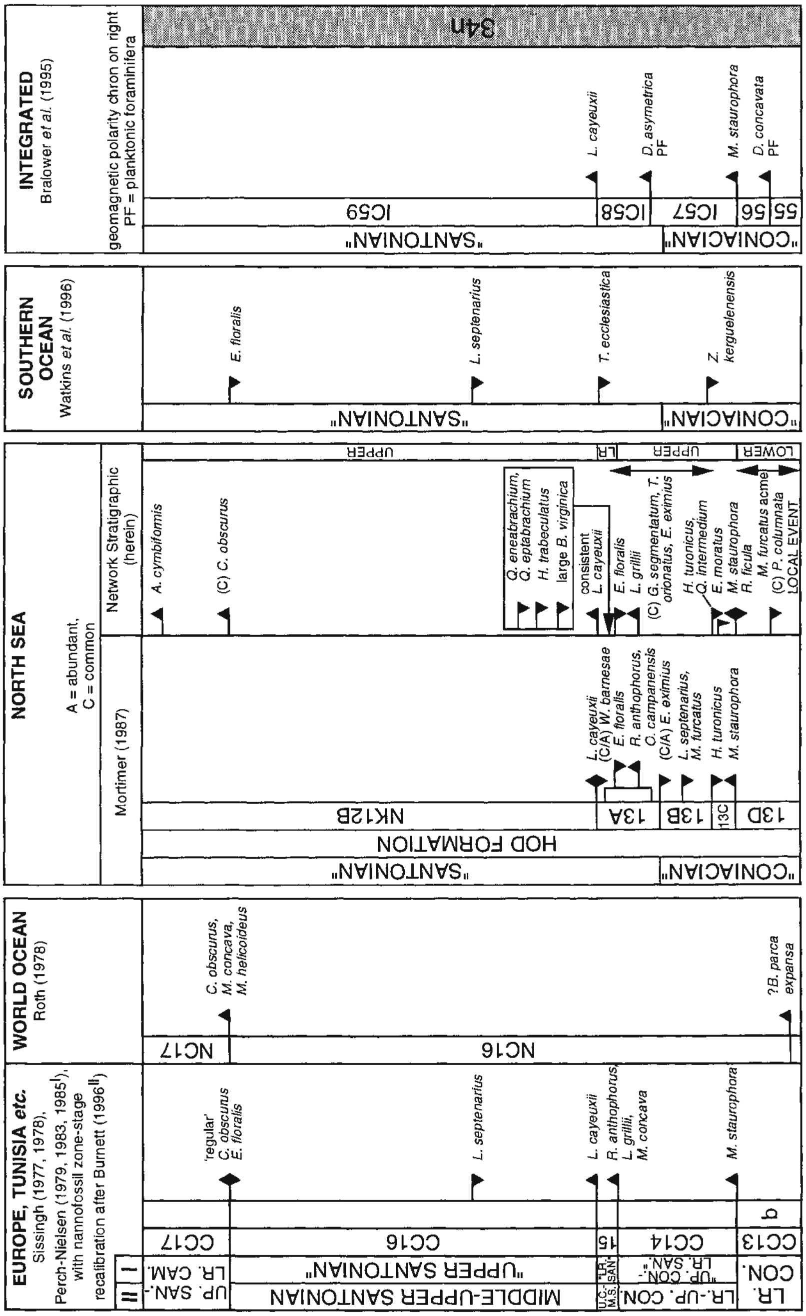


Fig. 6.4 (continued)

to the FO of *Micula staurophora*.
Extrapolated range. Upper Turonian (planus MFZ) to Lower or Middle Coniacian (cortestudinarium MFZ. Not identified in an MF-dated sequence).

UC10 Nannofossil Zone

Author. Approximately equivalent to zone CC14 *sensu* Perch-Nielsen (1985a).
Definition. FO of *Micula staurophora* to the FO of *Lithastrinus grillii*.
Range. Middle? to Upper Coniacian (cortestudinarium MFZ to coranguinum MFZ).
Remarks. The top of this zone cannot be distinguished in 'austral' locations. No global subzones, but two 'austral' subzones, have been erected. The FO of *Reinhardtites anthophorus* is an unreliable datum. Its inception, which is widely believed to be in the Coniacian, is somewhat obscure particularly in less than pristinely-preserved material. Forming part of an evolutionary trend from *Zeugrhabdotus scutula* through to *Reinhardtites levis* by a gradual closing of the two central-area perforations, documentation of its FO has been subject to problems associated with diagenetic overgrowth, which produces a preservational effect similar to the evolutionary modification, and differences in taxonomic interpretation. It has also become apparent that this taxon probably evolved much earlier than the Coniacian (probably in the Turonian) at higher palaeolatitudes (e.g. Burnett, in prep. b). Svábenická (pers. comm., 1996) noted that the FO of *M. staurophora* lies below the koeneni Inoceramid Zone, i.e. in the Lower Coniacian, in Bohemia.

UC10a^{AP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Micula staurophora* to the LO of *Zeugrhabdotus kerguelenensis*.
Extrapolated range. Middle? to Upper Coniacian (cortestudinarium MFZ to coranguinum MFZ. Not identified in an MF-dated sequence).

UC10b^{AP} Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Zeugrhabdotus kerguelenensis* to the LO of *Quadrum gartneri*.
Extrapolated range. Middle? to Upper Coniacian (cortestudinarium MFZ to coranguinum MFZ).
Remarks. The FO of *L. grillii* is approximated in many settings by the LO of *Q. gartneri*, which LOs immediately above the FO of *L. grillii*, although *Q. gartneri* has been observed rarely above this level at some locations. Thus, although the top of UC10 cannot be strictly identified in southern high-latitudes due to the absence of *L. grillii*, it can be approximated using the higher datum, thus UC10b^{AP} is equivalent to the upper portion of UC10 plus UC11a.

UC11 Nannofossil Zone

Author. Approximately equivalent to zone CC15 *sensu* Perch-Nielsen (1985a).
Definition. FO of *Lithastrinus grillii* to the LO of *Lithastrinus septenarius* (= *L. moratus* of Varol, 1992).
Range. Upper Coniacian (coranguinum MFZ) to Lower? Santonian (coranguinum MFZ).
Remarks. The Coniacian/Santonian boundary is not a particularly well-documented one in nannofossil terms, and there is some confusion in the literature as to precisely where the events in this interval fall. *Placozygus* becomes a significant assemblage component in the Santonian, as does *Reinhardtites*.

UC11a Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Lithastrinus grillii* to the LO of *Quadrum gartneri*.
Range. Upper Coniacian (coranguinum MFZ).

UC11b Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Quadrum gartneri* to the FO of *Lucianorhabdus cayeuxii*.
Range. Upper Coniacian (coranguinum MFZ).
Remarks. *L. cayeuxii* is believed to have preferred a shelf environment and its FO may thus be compromised in oceanic settings. Its FO as described here seems to be anomalously low. The LOs of *Flabellites oblongus* and *M. furcatus* (the latter according to Crux (1982)) are here but were not found in oceanic settings. *T. ecclesiastica* last occurs and *Micula concava* first occurs in this subzone at 'austral' locations.

UC11c Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Lucianorhabdus cayeuxii* to the LO of *Lithastrinus septenarius*.

Range. Upper Coniacian to Lower Santonian (coranguinum MFZ).

Remarks. The consistent occurrence of rare to frequent *Calculites obscurus* has been recorded in this zone but cannot be relied on as a datum since the form has been observed to occur well below this level, albeit sporadically and very rarely (as has *Calculites ovalis*). Additionally, it has been argued that *Calculites* represents the basal plate of *Lucianorhabdus*. Farhan *et al.* (1994) refuted this, and illustrated the apparent differences between the two genera in exceptionally well-preserved material. However, it is likely that earlier specimens of *Calculites* may indeed represent the detached basal plates of the early *Lucianorhabdus* species (*L. maleformis, L. quadrifidus*). Thus, it is also possible that the increased abundance of *Calculites* observed in the Coniacian/Santonian, particularly in shelf sediments, is partly attributable to this. The increase in abundance of *Calculites* does appear to coincide with an increase in abundance of *Lucianorhabdus* species in this interval, but not with the FO of *L. cayeuxii*. No problems with latitudinal endemism are observed in this interval, although it appears that *Lucianorhabdus* (and *Calculites*) preferred relatively shallow-water conditions which makes correlation between epeiric and oceanic settings difficult.

This subzone also contains the FOs of *Cribrocorona gallica* (in S England), *Prediscosphaera grandis*, *M. concava*, *Amphizygus minimus* (in S England and the 'austral' province), *Rucinolithus hayi*, *Microrhabdulus undosus* and *Staurolithites mielnicensis*. These events were not consistently identified in oceanic locations. *Reinhardtites* cf. *R. levis* first occurs here in 'austral' locations.

UC12 Nannofossil Zone

Author. Burnett, herein.

Definition. LO of *Lithastrinus septenarius* (= *L. moratus* of Varol, 1992) to the FO of *Arkhangelskiella cymbiformis sensu* Burnett, 1998b.

Range. Lower Santonian (uppermost coranguinum MFZ) to lower Lower Campanian (granulataquadrata or pilula MFZ).

Remarks. Global correlation begins to break down from this zone upwards and the lack of reliable bioevents resulted in no subdivision of this zone. In many settings, the top of the Santonian/base of the Campanian is missing (e.g. Burnett, in prep. b). This roughly corresponds to the start of a global transgressive episode which obviously greatly affected the prevailing oceanic régime. The Campanian witnessed the highest nannofossil diversity in the Mesozoic, and also the peak in latitudinal endemism which corresponds to a breakdown in global biostratigraphic correlation potential, and which is partly related to a global fall in sea-level in the later Campanian. This stage is approximately 12myr long and thus this biostratigraphic problem is a serious one.

In shelf sequences, the FOs of *Prediscosphaera microrhabdulina, Hexalithus gardetae* (in S England), *Uniplanarius gothicus, Biscutum magnum* (in S England and lower palaeolatitudes), *Biscutum dissimilis* (at low palaeolatitudes) and *A. minimus* (in N England) are here, along with the LOs of *Grantarhabdus coronadventis* and *Zeugrhabdotus diplogrammus* (in S England), and *Zeugrhabdotus noeliae*.

UC13 Nannofossil Zone

Author. Burnett, herein.

Definition. FO of *Arkhangelskiella cymbiformis sensu* Burnett, 1998b to the FO of *Broinsonia parca parca* (= *Aspidolithus parcus parcus* of some authors).

Range. Lower Lower Campanian (granulata-quadrata or pilula MFZ to lingua/quadrata or pilula MFZ).

Remarks. Whilst the following zones remain virtually globally applicable, the subzonation becomes divided into three discrete components to compensate for provincialism.

UC13a^{BP} Nannofossil Subzone

Author. Burnett, herein.

Definition. FO of *Arkhangelskiella cymbiformis sensu* Burnett, 1998b to the consistent FO of *Orastrum campanensis*.

Range. Lower Lower Campanian (granulata-quadrata or pilula MFZ).

Remarks. *O. campanensis* has not been found at low, or high-southern, palaeolatitudes. In the North Sea area, it seems to have a rare and short-lived occurrence well below the Campanian but then 'disappears' until its higher occurrence, as used here. Although rare and sporadic, its occurrence through the Campanian is still considered to be useful.

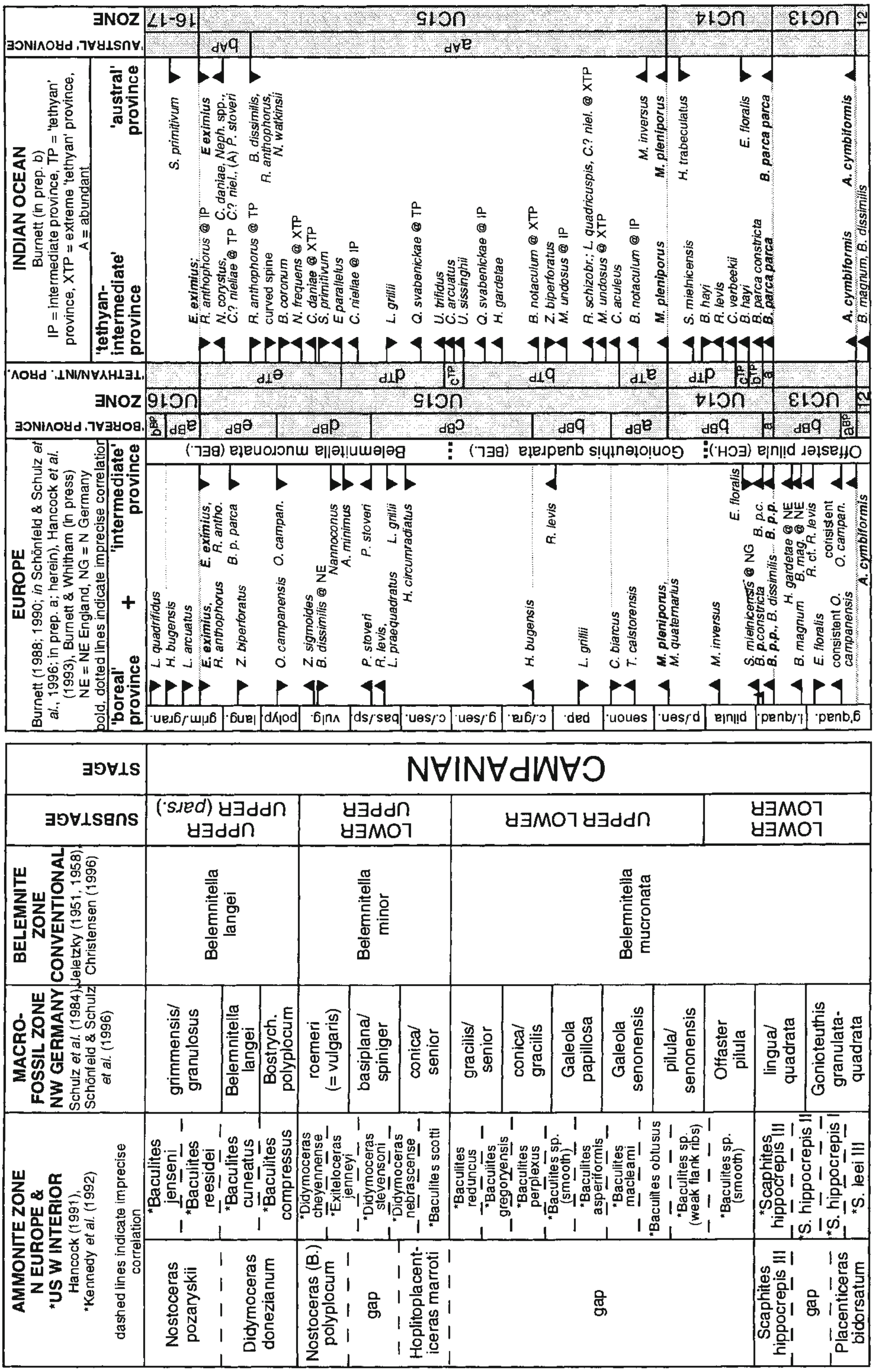


Fig. 6.5 Comparison of Campanian (*pars.*) biozonations with new data which has been correlated with macrofossil zones. Stages appear in quotation marks because no precise correlation of nannofossil data with the stages was attempted by the original authors.

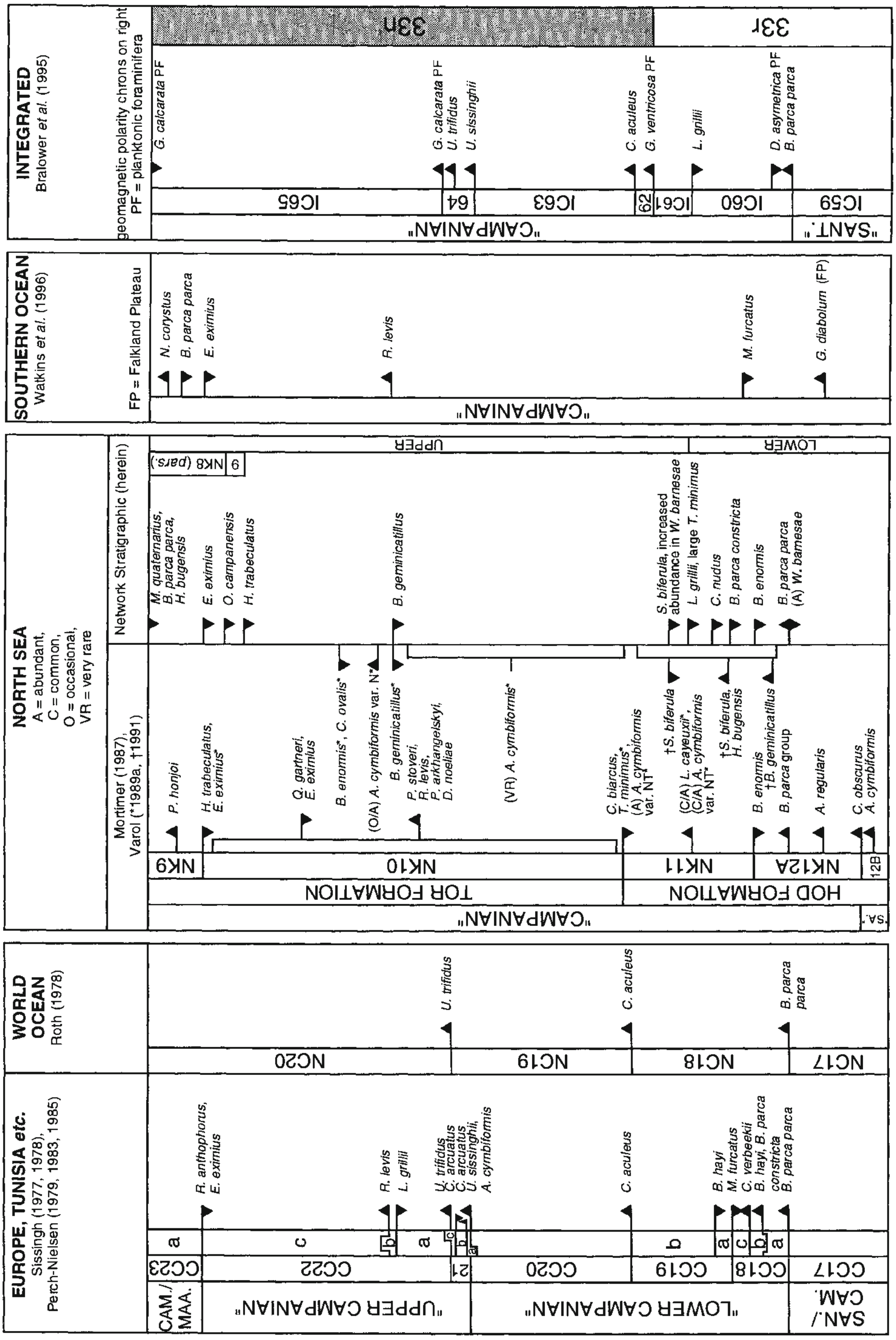


Fig. 6.5 (continued)

UC13b^{BP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of consistent *Orastrum campanensis* to the FO of *Broinsonia parca parca* (= *Aspidolithus parcus parcus* of some authors).
Range. Lower Lower Campanian (granulata-quadrata or pilula MFZ to lingua/quadrata or pilula MFZ).
Remarks. This subzone was found to be fairly condensed in the oceanic settings studied. At 'boreal/intermediate' locations, it contains the LO of rare *Eprolithus floralis* and the FOs of *B. magnum* and *H. gardetae* (the latter appearing much earlier in S England). The FO of *R.* cf. *R. levis* was found in S England.

UC14 Nannofossil Zone

Author. Burnett, herein.
Definition. FO of *Broinsonia parca parca* to the FO of *Misceomarginatus pleniporus.*
Range. Lower Lower (lingua/quadrata or pilula MFZ) to upper Lower Campanian (pilula/ senonensis or ?quadrata MFZ).
Remarks. *M. pleniporus* is difficult to distinguish from *M. quaternarius* in less than well-preserved material, and it is possible that the two are synonymous anyway. *M. pleniporus* was originally believed to be a high-palaeolatitude form but it has since been observed in a variety of locations at different palaeolatitudes. The LOs of *E. floralis* and *Helicolithus trabeculatus* occur here in 'austral' locations but no subzonation was erected for this region.

UC14a Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Broinsonia parca parca* to the FO of *Broinsonia parca constricta* (= *Aspidolithus parcus constrictus* of some authors).
Range. Lower Lower Campanian (lingua/quadrata or pilula MFZ).
Remarks. This subzone is common to all palaeolatitudes except the 'austral' region, where *B. parca constricta* was not identified.

UC14b^{BP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Broinsonia parca constricta* to the FO of *Misceomarginatus pleniporus.*
Range. Lower Lower (lingua/quadrata or pilula MFZ) to upper Lower Campanian (pilula/ senonensis or ?quadrata MFZ).
Remarks. *E. floralis* LOs in this subzone at intermediate and 'austral' locations. *Staurolithites mielnicensis* and *Markalius inversus* FO here in N Germany.

UC14b^{TP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Broinsonia parca constricta* to the FO of *Bukryaster hayi.*
Range. Approximately lower Lower to upper Lower Campanian.
Remarks. *B. hayi* is rare at most locations outside very low palaeolatitudes and is absent from high, and most intermediate, palaeolatitudes.

UC14c^{TP} Nannofossil Subzone

Author. Equivalent to subzone CC18b of Perch-Nielsen (1985a).
Definition. FO of *Bukryaster hayi* to the FO of *Ceratolithoides verbeekii.*
Range. Approximately lower Lower to upper Lower Campanian.
Remarks. *C. verbeekii* is often rare but consistently present at lower palaeolatitudes.

UC14d^{TP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Ceratolithoides verbeekii* to the FO of *Misceomarginatus pleniporus.*
Range. Approximately lower Lower to upper Lower Campanian.
Remarks. Contains the FOs of *Reinhardtites levis* and *S. mielnicensis*, and the LO of *B. hayi*. This low FO of *R. levis* was also noted by Bralower and Siesser (1992) in the Indian Ocean, thus confirming its non-utility as a global marker.

UC15 Nannofossil Zone

Author. Burnett, herein.
Definition. FO of *Misceomarginatus pleniporus* to the LO of *Eiffellithus eximius.*
Range. Upper Lower (pilula/senonensis or ?quadrata MFZ) to upper Upper Campanian (grimmensis/granulosus or mucronata MFZ).
Remarks. This extraordinarily long zone reflects the correlation problems caused by the enhanced biogeographic differentiation which prevailed in the Campanian. However, it was possible to produce a workable subzonation for all but the 'austral' region.

UC15a^{BP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Misceomarginatus pleniporus* to the LO of *Cylindralithus biarcus.*
Range: Upper Lower Campanian (pilula/senonensis MFZ to senonensis MFZ).
Remarks. *Tortolithus caistorensis* first occurs here.

UC15b^{BP} Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Cylindralithus biarcus* to the FO of *Heteromarginatus bugensis*.
Range. Upper Lower Campanian (senonensis MFZ to conica/gracilis MFZ).
Remarks. *L. grillii* last occurs, and *R. levis* first occurs, here.

UC15c^{BP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Heteromarginatus bugensis* to the FO of *Prediscosphaera stoveri.*
Range. Upper Lower to lower Upper Campanian (conica/gracilis MFZ to basiplana/spiniger or mucronata MFZ).
Remarks. *R. levis* first occurs with *Lithraphidites praequadratus* in this subzone in N Germany. At slightly lower palaeolatitudes, *Haquis circumradiatus* and *L. grillii* last occur here.

UC15d^{BP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Prediscosphaera stoveri* to the LO of *Orastrum campanensis.*
Range. Lower Upper to upper Upper Campanian (basiplana/spiniger or mucronata MFZ to polyplocum or mucronata MFZ).
Remarks. *A. minimus*, *Nannoconus* spp. and *B. dissimilis* (the latter in NE England) last occur here, with the FO of *Zeugrhabdotus sigmoides*. It is possible that very rare and sporadic *O. campanensis* occurs above this in the North Sea.

UC15e^{BP} Nannofossil Subzone

Author. Equivalent to the Eiffellithus eximius Zone of Crux (1991a).
Definition. LO of *Orastrum campanensis* to the LO of *Eiffellithus eximius.*
Range. Upper Upper Campanian (polyplocum or mucronata MFZ to grimmensis/granulosus or mucronata MFZ).
Remarks. *Zeugrhabdotus biperforatus* last occurs here in N Germany. *B. parca parca* last occurs here at lower palaeolatitudes. The LO of *R. anthophorus* is virtually coincident with the top of this zone in the 'boreal' region but can be difficult to recognize in even moderately-preserved material.

UC15a^{TP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Misceomarginatus pleniporus* to the FO of *Ceratolithoides aculeus.*
Range. Approximately upper Lower Campanian (pilula/senonensis or ?quadrata MFZ to ? – not identified in an MF-dated sequence).
Remarks. At intermediate palaeolatitudes, *Biscutum notaculum* first occurs here.

UC15b^{TP} Nannofossil Subzone

Author. Equivalent to zone CC20 of Sissingh (1977).
Definition. FO of *Ceratolithoides aculeus* to the FO of *Uniplanarius sissinghii*.
Range. Approximately upper Lower Campanian (not identified in a MF-dated sequence).
Remarks. *Retecapsa schizobrachiata*, *Lithastrinus quadricuspis*, *Cylindralithus*? *nieliae* (all at very low palaeolatitudes), *Quadrum svabenickae* (at intermediate palaeolatitudes) and *Microrhabdulus undosus* and *Biscutum notaculum,* have FOs here. *Z. biperforatus* last occurs in this subzone.

UC15c^{TP} Nannofossil Subzone

Author. Equivalent to zone CC21 of Sissingh (1977).
Definition. FO of *Uniplanarius sissinghii* to the FO of *Uniplanarius trifidus*.
Range. Approximately lower Upper Campanian (not identified in an MF-dated sequence).
Remarks. This subzone contains the FO of *Ceratolithoides arcuatus*, as noted by Sissingh (1977), but not the LO (see Burnett, 1998a).

UC15d^{TP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Uniplanarius trifidus* to the FO of *Eiffellithus parallelus*.
Range. Approximately lower Upper Campanian (not identified in an MF-dated sequence).
Remarks. Contains the LO of *L. grillii,* and FOs of *Quadrum svabenickae* (at low-palaeolatitudes) and *C.* ? *nieliae* at intermediate palaeolatitudes.

UC15e^{TP} Nannofossil Subzone.

Definition. FO of *Eiffellithus parallelus* to the LO of *Eiffellithus eximius*.

Range. Approximately lower to upper Upper Campanian (not identified in an MF-dated sequence).

Remarks. Contains the FOs of *Cribrosphaerella daniae*, *Nephrolithus frequens* (at very low palaeolatitudes), *Nephrolithus corystus* and *C.*? *nieliae* (at low palaeolatitudes), and the LOs of *Seribiscutum primitivum*, *B. coronum*, long, curved spines (which probably belong to *R. anthophorus*), and *R. anthophorus* (at low palaeolatitudes). It is likely that the Indian Ocean contains anomalously low FOs of *Nephrolithus* and *C. daniae*.

UC15a^{AP} Nannofossil Subzone

Author. Burnett, herein.

Definition. FO of *Misceomarginatus pleniporus* to the LO of *Biscutum dissimilis*.

Range. Upper Lower (pilula/senonensis or ?quadrata MFZ) to approximately upper Upper Campanian (not identified in MF-dated sequence).

Remarks. *B. dissimilis* ranges above this at northern high-latitudes. This event co-occurs with the LOs of *R. anthophorus* and *Neocrepidolithus watkinsii*.

UC15b^{AP} Nannofossil Subzone

Author. Burnett, herein.

Definition. LO of *Biscutum dissimilis* to the LO of *Eiffellithus eximius*.

Range. Approximately upper Upper Campanian (? – not identified in an MF-dated sequence – to grimmensis/granulosus or mucronata MFZ).

Remarks. Contains the FOs of *Nephrolithus* spp., *C. daniae*, *C.*? *nieliae* and abundant *P. stoveri*.

UC16 Nannofossil Zone

Author. Approximately equivalent to subzone CC23a of Sissingh (1977).

Definition. LO of *Eiffellithus eximius* to the LO of *Broinsonia parca constricta*.

Range. Upper Upper Campanian (grimmensis/granulosus or mucronata MFZ to lanceolata MFZ).

Remarks. Since the base of the Maastrichtian has recently been defined using the FO of the ammonite, *Pachydiscus neubergicus*, nannofossil relationships have shown that the base of the lanceolata MFZ (which previously marked the base of the Maastrichtian in the 'boreal' region) now technically lies in the top of the Campanian (see Burnett, Hancock *et al.*, 1992 and Cunha *et al.*, 1997, for further discussion). No subzonation was possible outside the 'boreal' province.

UC16a^{BP} Nannofossil Subzone

Author. Burnett, herein.

Definition. LO of *Eiffellithus eximius* to the LO of *Heteromarginatus bugensis*.

Range. Upper Upper Campanian (grimmensis/granulosus or mucronata MFZ).

Remarks. *Lucianorhabdus arcuatus* last occurs here.

UC16b^{BP} Nannofossil Subzone

Author. Burnett, herein.

Definition. LO of *Heteromarginatus bugensis* to the LO of *Tortolithus caistorensis*.

Range. Upper Upper Campanian (grimmensis/granulosus or mucronata MFZ to lanceolata MFZ).

Remarks. *Uniplanarius gothicus* last occurs here (stratigraphically higher elsewhere) and *Neocrepidolithus cohenii* becomes more frequent. This taxon has been found as low as UC13 (lowest Campanian) in the Indian Ocean.

UC16c^{BP} Nannofossil Subzone

Author. Burnett, herein.

Definition. LO of *Tortolithus caistorensis* to the LO of *Monomarginatus quaternarius*.

Range. Upper Upper Campanian (lanceolata MFZ).

UC16d^{BP} Nannofossil Subzone

Author. Burnett, herein.

Definition. LO of *Monomarginatus quaternarius* to the LO of *Broinsonia parca constricta*.

Range. Upper Upper Campanian (lanceolata MFZ).

UC17 Nannofossil Zone

Author. Equivalent to CC23b of Sissingh (1977).

Definition. LO of *Broinsonia parca constricta* to the LO of *Tranolithus orionatus* (= *Tranolithus phacelosus* of some authors).

Range. Upper Upper Campanian (lanceolata MFZ) to upper Lower Maastrichtian (sumensis MFZ or Brachiopod Zone 4).

Remarks. The LO of *B. parca constricta* was not identified at 'austral' locations. *B. dissimilis* last occurs here in N Germany. The FOs of *N. frequens* and *C. daniae* and the LOs of *U. trifidus* and *U. gothicus* occur here at low palaeolatitudes. At intermediate palaeolatitudes, the LO of *U. trifidus* coincides with the top of the zone, as does the LO of *Acuturris scotus* at low palaeolatitudes.

UC18 Nannofossil Zone

Author. Equivalent to zone CC24 of Sissingh (1977).
Definition. LO of *Tranolithus orionatus* (= *Tranolithus phacelosus* of some authors) to the LO of *Reinhardtites levis*.
Range. Upper Lower Maastrichtian (sumensis MFZ or Brachiopod Zones 4 to 5).
Remarks. *B. magnum* LOs around the LO of *R. levis*, generally below the datum at low-latitudes and above at high-latitudes. *M. pleniporus* also LOs here at low palaeolatitudes.

UC18a^{AP} Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Tranolithus orionatus* to the LO of *Biscutum coronum*.
Extrapolated range. Upper Lower Maastrichtian (sumensis MFZ).
Remarks. Contains the LO of *S. primitivum*.

UC18b^{AP} Nannofossil Subzone

Author. Burnett, herein.
Definition. LO of *Biscutum coronum* to the LO of *Reinhardtites levis*.
Extrapolated range. Upper Lower Maastrichtian (sumensis MFZ).
Remarks. The LO of *M. pleniporus* coincides with the top of the zone.

UC19 Nannofossil Zone

Author. Equivalent to subzone CC25a of Perch-Nielsen (1985a).
Definition. LO of *Reinhardtites levis* to the FO of *Lithraphidites quadratus*.
Range. Upper Lower (sumensis MFZ or Brachiopod Zone 5) to lower Upper Maastrichtian (tegulatus/junior MFZ or Brachiopod Zone 8).
Remarks. The top of this zone cannot be determined at 'austral' locations. The zone is characterized by low-diversity assemblages at all palaeolatitudes.

UC20 Nannofossil Zone

Author. Burnett, herein.
Definition. FO of *Lithraphidites quadratus* to the LO of unreworked, non-survivor Cretaceous taxa.
Range. Lower Upper Maastrichtian (tegulatus/junior MFZ or Brachiopod Zone 8) to the Cretaceous/Tertiary boundary.
Remarks. No useful events were identified in this zone at 'austral' locations. It seems that the FOs of *Neobiscutum* and small forms of *Cruciplacolithus primus* may occur in this zone. Romein *et al.* (1996) and Burnett *in* Herngreen *et al.* (1998) have found these forms in the Maastrichtian of the type-region (The Netherlands), and they may also occur below the K/T boundary at El Kef (Tunisia) (K. Perch-Nielsen and J. Bergen, per. comms, 1997). This should be taken into account when applying the earliest Tertiary biozones.

UC20a^{BP} Nannofossil Subzone

Author. Equivalent to the Lithraphidites quadratus Zone of Doeven (1983).
Definition. FO of *Lithraphidites quadratus* to the FO of *Nephrolithus frequens*.
Range. Lower Upper Maastrichtian (tegulatus/junior MFZ or Brachiopod Zone 8 to argentea/junior MFZ or Brachiopod Zone 8).
Remarks. *N. frequens* has a well-documented diachronous FO (Pospichal and Wise, 1990). This datum is youngest at northern high-latitudes.

UC20b^{BP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Nephrolithus frequens* to the FO of *Arkhangelskiella maastrichtiana*.
Range. Lower Upper Maastrichtian (argentea/junior MFZ or Brachiopod Zone 8).

UC20c^{BP} Nannofossil Subzone

Author. Burnett, herein.
Definition. FO of *Arkhangelskiella maastrichtiana* to the FO of *Cribrosphaerella daniae*.
Range. Lower Upper to upper Upper Maastrichtian (argentea/junior MFZ or Brachiopod Zone 8 to baltica/danica MFZ or Brachiopod Zone 10).
Remarks. The top of this zone can also be recognized at intermediate palaeolatitudes.

UC20d^{BP} Nannofossil Subzone

Author. Burnett, herein.

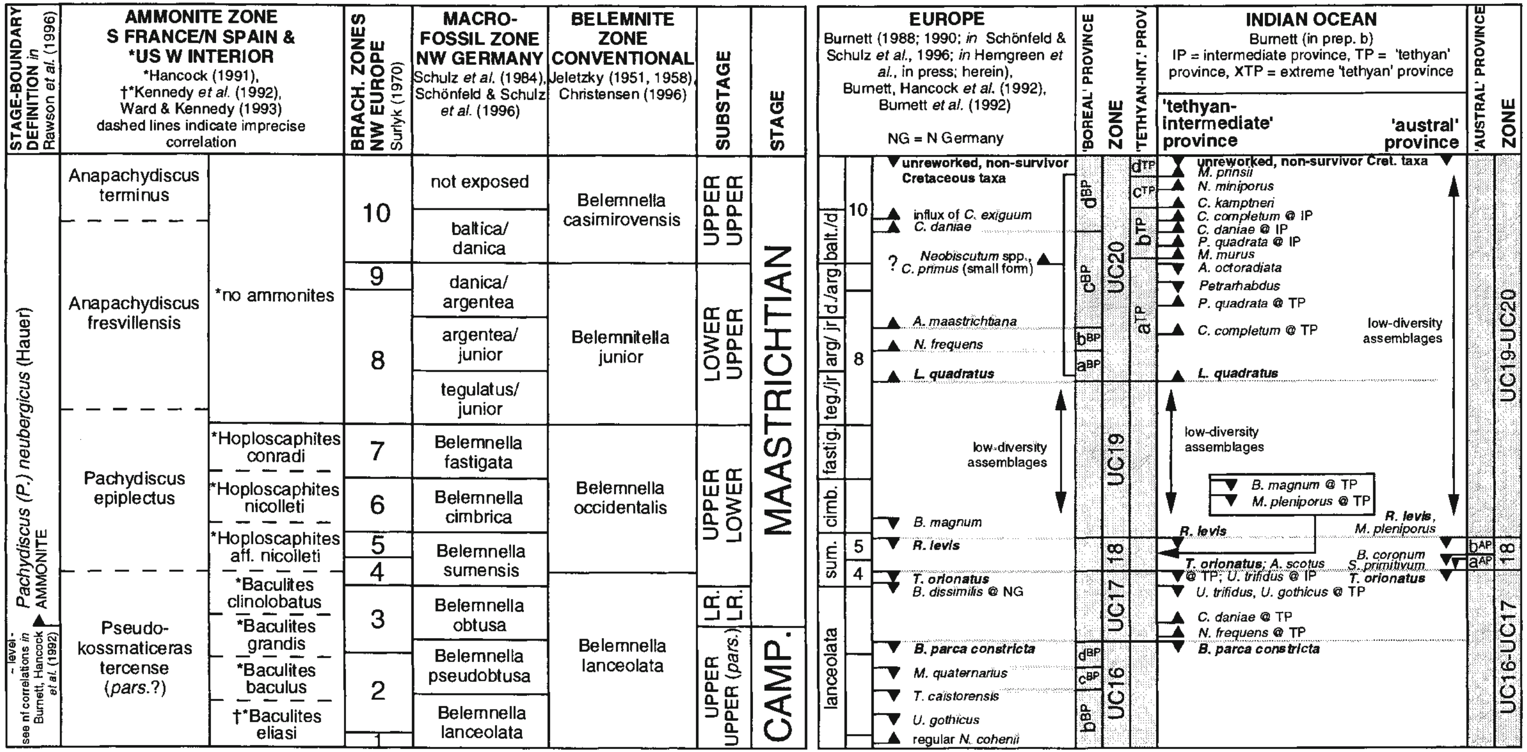


Fig. 6.6 Comparison of uppermost Campanian-Maastrichtian biozonations with new data which has been correlated with macrofossil zones. Stages appear in quotation marks because no precise correlation of nannofossil data with the stages was attempted by the original authors.

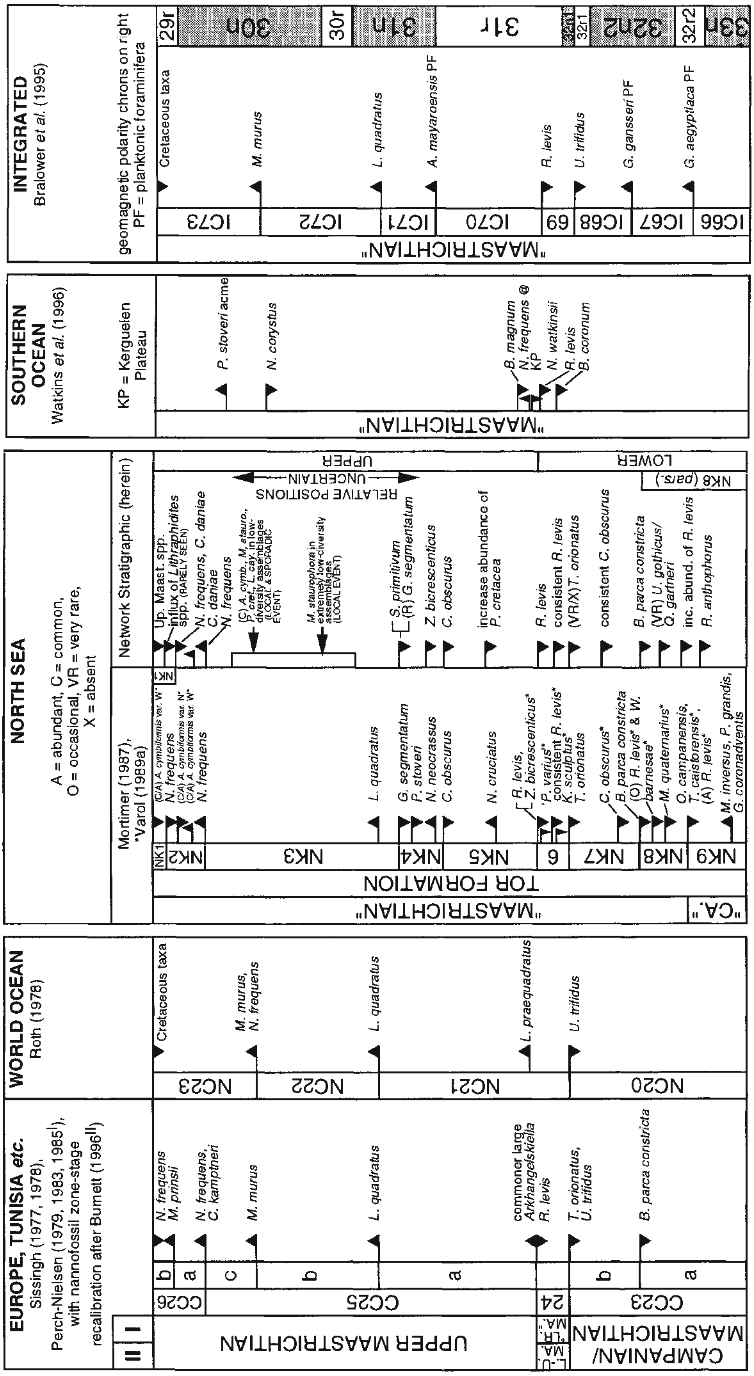


Fig. 6.6 (continued)

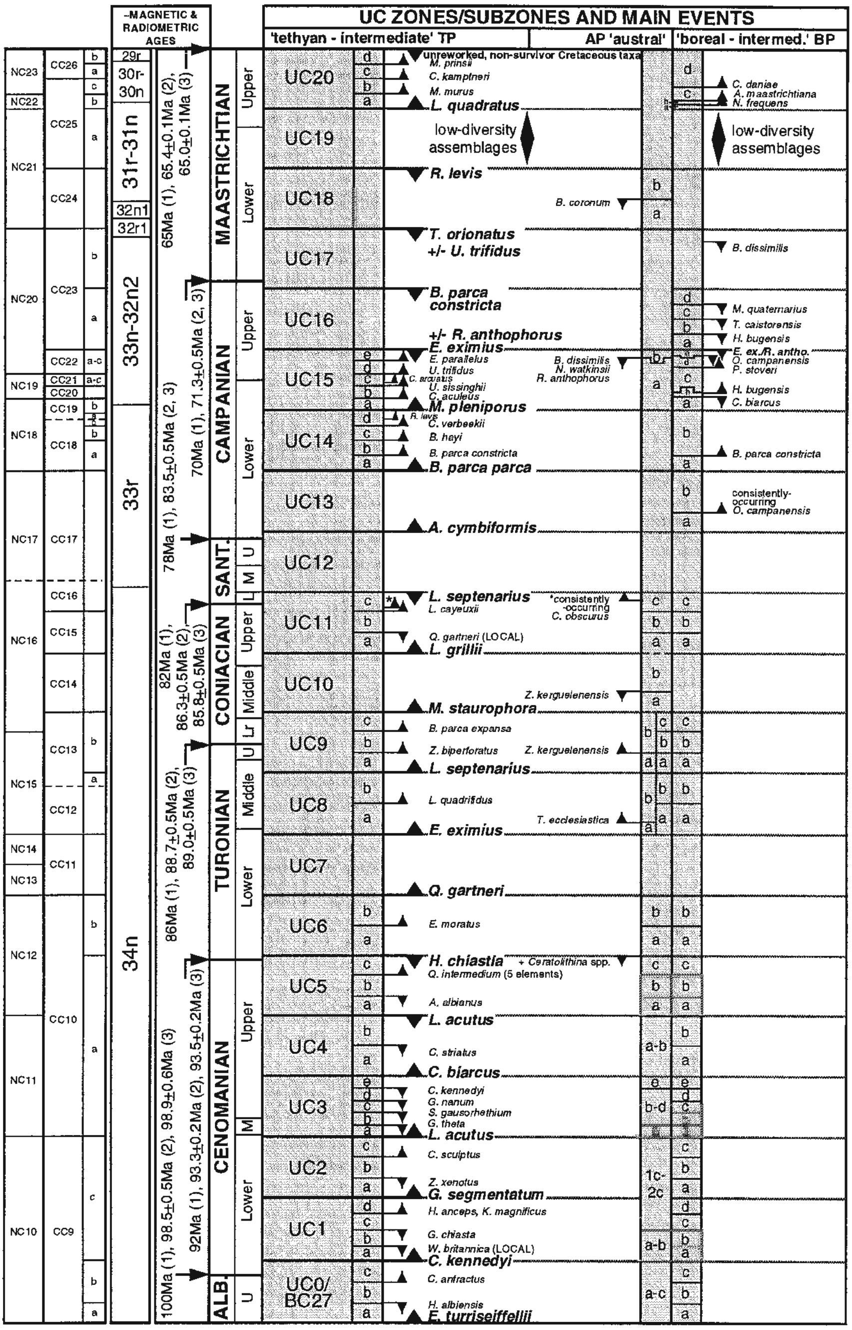


Fig. 6.7 Summary of the new Upper Cretaceous nannofossil biozonation shown against the CC zones of Sissingh (1977, 1978) and Perch-Nielsen (1979, 1983, 1985), NC zones of Roth (1978) and magnetostratigraphy of Bralower *et al.* (1995). Approximate radiometric dates for the stage boundaries after (1) van Hinte (1976), (2) Obradovich (1993) and (3) Gradstein *et al.* (1994).

Definition. FO of *Cribrosphaerella daniae* to the LO of unreworked, non-survivor Cretaceous taxa.
Range. Upper Upper Maastrichtian (baltica/ danica MFZ or Brachiopod Zone 10) to the Cretaceous/Tertiary boundary (casimirovensis MFZ or Brachiopod Zone 10).
Remarks. An influx of *Corollithion exiguum* may be seen in this subzone in well-preserved material.

UC20a^{TP} Nannofossil Subzone

Author. Equivalent to subzone CC25b of Perch-Nielsen (1985a).
Definition. FO of *Lithraphidites quadratus* to the FO of *Micula murus*.
Extrapolated range. Lower Upper Maastrichtian (tegulatus/junior MFZ) to upper? Upper Maastrichtian (not identified in an MF-dated sequence).
Remarks. Contains the FOs of *Corollithion completum* and *Pseudomicula quadrata* at 'tethyan' locations, and the LOs of *Petrarhabdus* and *A. octoradiata*.

UC20b^{TP} Nannofossil Subzone

Author. Approximately equivalent to subzone CC25c of Perch-Nielsen (1985a).
Definition. FO of *Micula murus* to the FO of *Ceratolithoides kamptneri.*
Extrapolated range. Upper Upper Maastrichtian (not identified in an MF-dated sequence).
Remarks. The FOs of *P. quadrata*, *C. daniae* and *C. completum* occur here at intermediate palaeo-latitudes.

UC20c^{TP} Nannofossil Subzone

Author. Approximately equivalent to subzone CC26a of Perch-Nielsen (1985a).
Definition. FO of *Ceratolithoides kamptneri* to the FO of *Micula prinsii*.
Extrapolated range. Upper Upper Maastrichtian (not identified in an MF-dated sequence).
Remarks. Contains the FO of *Nephrolithus miniporus*.

UC20d^{TP} Nannofossil Subzone

Author. Approximately equivalent to subzone CC26b of Perch-Nielsen (1985a).
Definition. FO of *Micula prinsii* to the LO of unreworked, non-survivor Cretaceous taxa.
Extrapolated range. Uppermost Maastrichtian.

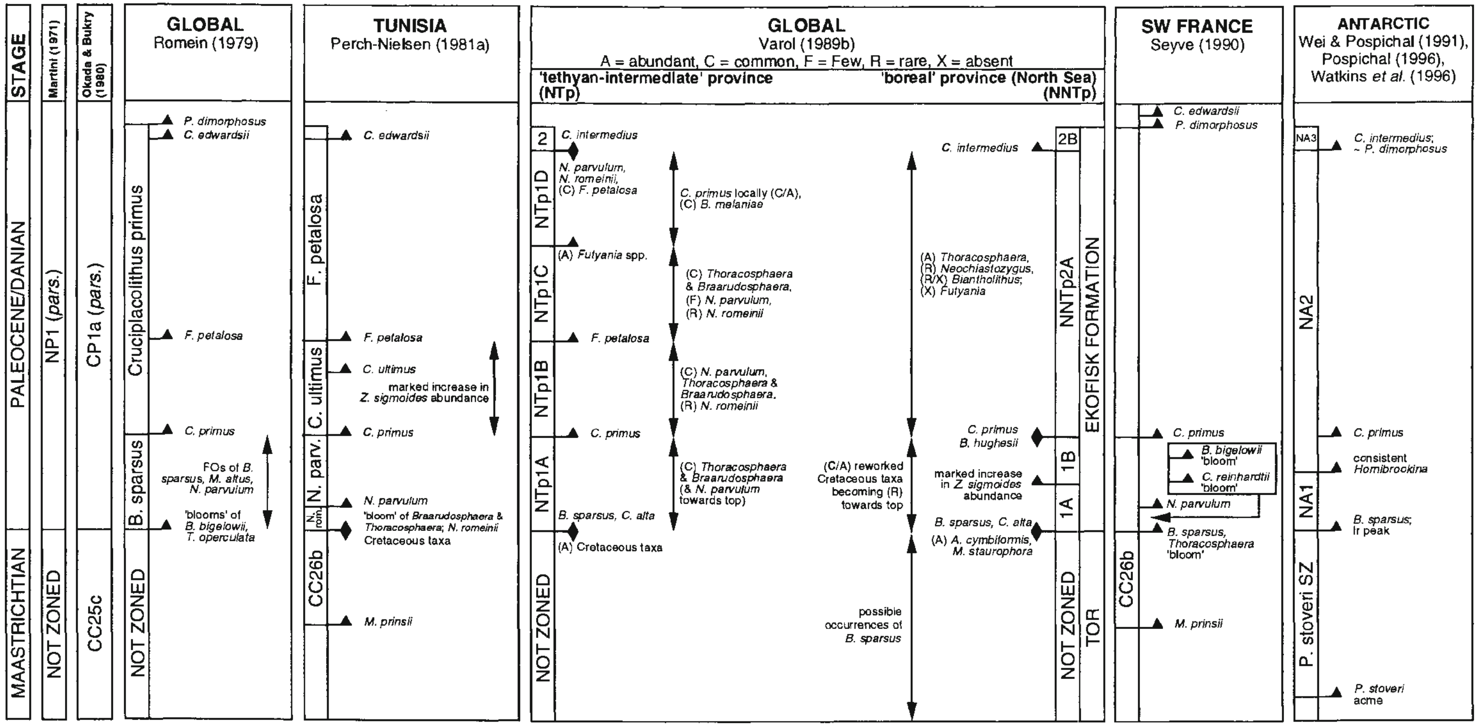
6.4.5 The K/T boundary

Although the K/T boundary represents a dramatic interlude in the history of this group, it is surprisingly not always easy to identify, since the boundary can be associated with significant bioturbation and reworking. Pospichal *et al.* (1990) provided a case study of the problems associated with this phenomenon. Indeed, in the North Sea, reworked Cretaceous taxa can be used as a biostratigraphic tool in the Tertiary (Young, 1995). In some locations the boundary interval contains a hiatus (e.g. Verbeek, 1986), and the boundary clay is often carbonate-poor and can be barren. Thus, defining the K/T boundary on the LO of unreworked, non-survivor Cretaceous taxa is technically correct and applicable in certain locations, but it is not necessarily a practical definition and care should be exercised when making this interpretation.

This boundary has been zoned by numerous workers, but the events they use are basically similar. Figure 6.8 provides an overview and comparison of these biozones. Recent works (Romein *et al.*, 1996; Herngreen *et al.*, 1998) have implied that *Neobiscutum romeinii*, *Neobisc-utum parvulum* and *Cruciplacolithus primus*, all of which are believed to have evolved in the Tertiary, were present, albeit in low abundances, in the latest Maastrichtian, based on associations with other fossil groups and lithostratigraphy.

6.4.6 Global correlation

A wealth of research has meant that global nannofossil biostratigraphic correlation of the Cenomanian to Santonian is generally fairly well-established and has a reasonably high resolution. Pronounced endemism has caused global correlation problems particularly through the Campanian and Maastrichtian. This problem is now gradually being overcome. However, a problem with correlation which is often not appreciated is that which involves intercorrelation between different fossil groups. Schönfeld and Burnett (1991) elegantly illustrated such a problem which arose whilst attempting to correlate from low- to northern high-latitudes using nannofossils, foraminifera and macrofossils, i.e. the Upper Campanian in nannofossil terms appeared to be the Lower



SURVIVOR CRETACEOUS TAXA

compiled from

Perch-Nielsen (1981b), Varol (1989b), Burnett *in* Hemgreen *et al.* (in press), Mai *et al.* (in press), Burnett (pers. obs.)

Biantholithus sparsus?
Biscutum melaniae
Braarudosphaera bigelowii, B. turbinea
Chiastozygus ultimus
Cruciplacolithus primus?
Cyclagelosphaera margerelii, C. monocava, C. reinhardtii, ?C. rotaclypeata
Goniolithus fluckigeri
Lapideacassis
Markalius inversus
Neobiscutum parvulum, N. romeinii
Neocrepidolithus cohenii, N. cruciatus, N. dirimosus, N. neocrassus
Octolithus multiplus
Scapholithus fossilis
Semihololithus
Sollasites?
Thoracosphaera
Zeugrhabdotus sigmoides

Fig. 6.8 Comparison of K/T boundary biozones. Note that the term 'bloom', as used in this context, implies a virtually monospecific assemblage but has no implications for the length of time during which such assemblages were deposited.

Maastrichtian in macrofossil terms, when using a foraminiferal event as a link between the two. Apparent diachroneity is often a function of correlation and is always entirely relative. Similar apparent discrepancies can occur through bad correlation practice or our blind faith in the non-diachroneity of benthic or nekto-benthic bioevents to define our time-scales. In short, an apparently diachronous nannofossil event may in fact represent diachroneity in the event being used to relate this event to a standard time-scale, commonly a macrofossil event. There are very few proven and well-documented diachronous nannofossil events in the Upper Cretaceous, the most well-known being the FO of *Nephrolithus frequens*, the diachroneity of which can be proved because the event transgresses across a number of other nannofossil events (Worsley, 1974; Pospichal and Wise, 1990).

It is important to note that reversed bioevents of certain potentially biostratigraphically-useful taxa seem to be commonplace in the Campanian and, to some extent, in the Maastrichtian. The explanation for this is biogeographic. Burnett (in prep. b), in mapping Late Cretaceous biogeographic zones through time, has illustrated that the boundaries between these zones oscillate, the zones themselves expanding or contracting in response to climatic fluctuations. During the Campanian, the boundaries between the zones becomes diffuse so that, at a low stratigraphic resolution, the biogeographic zones appear to be separated by a zone of mixing. This zone of mixed endemic taxa possibly represents relatively rapidly-oscillating biogeographic boundaries. A sedimentary sequence from this mixed zone would thus record the invasions and retreats of endemic taxa.

6.5 BIOGEOGRAPHY

Provincialism in the Late Cretaceous first became evident when Thierstein (1976), attempting to erect a global biozonation, recognized that certain taxa displayed palaeoenvironmental restrictions which caused them to display diachroneity. He listed some taxa which were affected by latitude, and some which were apparently dependent on marginal oceanic conditions. Around this time, drilling in the Southern Ocean had revealed an abundance of southern high-latitude taxa which had not been reported from elsewhere (Wise and Wind, 1977; Wise, 1983), and sparked a line of research which has produced a number of publications which interpret the biogeography in terms of differences in palaeotemperature and palaeoclimate. In 1981, Thierstein graphically illustrated the predominantly latitudinal nature of the distributions of certain endemic Campanian–Maastrichtian taxa, and the apparent bipolarity of the distributions of high-latitude taxa was confirmed from studies of northern high-latitude locations by Crux (1982) and Burnett (1988). During this time, the Sissingh/Perch-Nielsen and Roth global zonations were published and being successfully used in many locations. However, as research on high latitudes progressed, it became obvious that endemism was too pronounced in the Campanian (and to some extent the Maastrichtian) for the published biozonations to work globally, resulting in the publication of zonations for the higher latitudes (Burnett, 1990 for the 'boreal' region; and Pospichal and Wise, 1990; Crux, 1991a, b; and Watkins *et al.*, 1996 for the 'austral' region). It is now clear that, although high-latitude endemism has certain bipolar elements, the datums supplied by certain taxa are not always coeval between northern and southern high latitudes. Consequently, Burnett's (1990) scheme does not work in the Southern Ocean, and the Watkins *et al.* (1996) scheme does not work in the North Sea! This is probably because certain bipolar taxa are also affected by nutrient distributions, which were locally specific during that interval, being affected by differences in continental distribution and oceanography.

Thierstein's (1981) illustrations generated the idea that Late Cretaceous nannofossil latitudinal biogeographic distributions were primarily dependent upon temperature, and this idea has been persistent in the literature since then, despite the fact that it has not been rigorously tested against $\partial^{18}O$-isotopic evidence, and that it is known that Present Day latitudinal distribution is dependent partly on temperature and partly on other characteristics of the water-mass. Indeed, Hay (1995) has intimated that Late Cretaceous biogeographic patterns can be primarily attributed to water-masses, which also have latitudinal restrictions. It has to be borne in mind that, during the Late Cretaceous, the global temperature gradient was much shallower than it is at present, with no evidence for anything other than perhaps seasonal ice at the poles, and thus, assuming the same pattern of biogeographic zones for the Late Cretaceous as the Present Day, a simple interpretation based on temperature sensitivity might imply that Late Cretaceous endemic nannofossils had a greater degree of sensitivity than extant taxa.

There are a number of lists of apparently endemic taxa which have been assigned to ephemeral biogeographic regions (e.g. Thierstein, 1976, 1981; Perch-Nielsen, 1979a; Wind, 1979; Roth and Bowdler, 1981; Crux, 1991a, b; Burnett, in prep b). These comprise taxa which are either strictly limited to one realm, although these taxa may not be abundant (e.g. *Bukryaster*, *Ceratolithoides*, *Uniplanarius trifidus* and *U. sissinghii* – low palaeolatitude-restricted; *Ceratolithina, Heteromarginatus bugensis*, *Neocrepidolithus watkinsii, Zeugrhabdotus kerguelenensis* – high palaeolatitude-restricted), or they are taxa which, although virtually globally distributed, show an obvious preference for a particular province by displaying high abundances. The most oft-quoted of these are, at high latitudes, large *Biscutums*, *Kamptnerius*, *Nephrolithus*, *Repagulum parvidentatum*, *Seribiscutum primitivum*, and at low latitudes, *Micula murus*.

Burnett (in prep. b) determined >80 taxa with endemic characteristics and used these to define palaeobiogeographic zones in terms of palaeolatitude. She also observed that these zones are not static, i.e. they can be seen to expand and contract spatially through time, in response to changing palaeoceanographic conditions. She interpreted these fluctuations in terms of palaeoclimate change through the Late Cretaceous (Burnett *et al.*, in press). Similar interpretations have been made by, for example, Wind (1979), Wise (1988), Shafik (1990), Huber and Watkins (1992) and Watkins *et al.* (1996).

6.6 ATLAS OF SPECIES

Most Upper Cretaceous calcareous nannofossils are listed and illustrated in Plates 6.1 to 6.15. Taxa are listed according to the classification of Bown and Young (1997), firstly by order and secondly by family. Light micrographs are uniformly enlarged at x2300. Stratigraphic information is given as stages (L=Lower, U=Upper); question marks indicate a degree of uncertainty. Photographs are identified by a UCL number (film and frame) and are stored in the Postgraduate Unit of Micropalaeontology, University College London. The photographs come primarily from the research of J.A. Burnett but also include contributions from the research of J.A. Crux and A. Farhan.

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The new data presented in this chapter could not have been produced without the contributions of sample material and macrofossil data from Profs Jim Kennedy, Andy Gale and Jake Hancock, among others and samples kindly supplied by the DSDP and ODP. The data was produced over a number of years and the work has been variously funded by the NERC and by University College London.

Plate 6.1

Order EIFFELLITHALES Rood, Hay and Barnard, 1971

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

Central-area axial cross

Figs 1–2. ***Ahmuellerella octoradiata.*** XPL, DSDP Site 258 (E Indian Ocean) (1), Con. and DSDP Site 249 (W Indian Ocean) (2), Camp., UCL-5656-27/5659-9. A similar, possibly ancestor, form (*Ahmuellerella* cf. *A. octoradiata*) with less-distinctive bars and a more-complete cross has been recorded from the Alb.–Cen.. Range: Cen.–Maast.

Fig. 3. ***Ahmuellerella regularis.*** XPL, DSDP Site 217 (N Indian Ocean), Camp./Maast., UCL-5657-14. Range: Tur.–Maast.

Figs 4a–c. ***Bukrylithus ambiguus.*** XPL, The Warren, Folkestone, Kent (UK) (a), Cen. and near Portland, Dallas County, Alabama (USA) (b, c rotated), Camp., UCL-5737-10/5703-6/5. Range: Berr.–?Camp.

Figs 5, 10. ***Heteromarginatus bugensis.*** XPL (10 rotated), Trunch BH, Norfolk (UK), Camp., UCL-5665-2/1. Range: Camp.

Not figured. ***Heteromarginatus wallacei.*** Axial cross; bars attached to midpoints of cross bars form diamond shape enclosing centre of cross. Range: Camp.

Figs 6–8. ***Misceomarginatus pleniporus.*** XPL (6, 7 rotated), PC (8), ODP Hole 758A (N Indian Ocean), Camp., UCL-5703-27/28/29. Sometimes difficult to distinguish from *M. quaternarius* in the LM. Range: Camp.–Maast.

Not figured. ***Monomarginatus pectinatus.*** More perforations adjacent to rim than *Monomarginatus quaternarius*. Range: Camp.–Maast.

Fig. 9. ***Monomarginatus quaternarius.*** XPL, Zoe C BH (S Africa), Camp., UCL-5764-22. Range: Camp.

Figs 11–12. ***Staurolithites integer.*** XPL (12 rotated), DSDP Hole 758A (N Indian Ocean), Camp., UCL-5703-23/22. Range: Camp.–Maast.

Figs 13–15. ***Staurolithites mielnicensis.*** XPL (14 rotated), DSDP Site 249 (W Indian Ocean), Camp., UCL-5660-18/19/5659-16. Range: San.–Maast.

Figs 16–17. ***Staurolithites imbricatus.*** XPL (17 rotated), near Portland, Dallas County, Alabama (USA), Camp., UCL-5734-24/23. Range: San.?–Maast.

Figs 18a–20b. ***Staurolithites zoensis.*** XPL, Zoe C BH (S Africa) (18a, b rotated), Camp., near Plymouth Bluff, Lowndes County, Mississippi (USA) (19a, b rotated), San. and Poricy Brook, Monmouth County, New Jersey (USA) (20a, b rotated), Maast., UCL-5657-32/33/5730-9/8/5731-28/29. Range: San.–Maast.

Figs 21–22. ***Staurolithites elongatus.*** XPL (21 rotated), ODP Hole 738C (S Indian Ocean), Maast., UCL-5756-16/17. Range: San.–Maast.

Figs 23a–b. ***Staurolithites ellipticus.*** XPL, Chattahoochee River, Quitman County, Georgia (USA) (a), Maast. and Zoe C BH (S Africa) (b), Maast., UCL-5731-21/5655-17. Range: Alb.?–Maast.

Fig. 24. ***Staurolithites dorfii.*** XPL, near Cottinton, Russel County, Alabama (USA), Camp., UCL-5732-12. Usually has a more-circular outline. Range: ?Camp.

Figs 25a–b. ***Staurolithites flavus.*** XPL, Clay County, Mississippi (USA) (a), Maast. and DSDP Site 217 (N Indian Ocean) (b), Maast., UCL-5732-28/5599-7. Range: Cen.–Maast.

Figs 25c–d. ***Staurolithites laffittei.*** XPL (d rotated), Zoe C BH (S Africa), Maast., UCL-5660-2/3. Range: Alb.?–Maast.

Fig. 26. ***Staurolithites glaber***. XPL, The Warren, Folkestone, Kent (UK), Cen., UCL-5737-20. Range: Apt.–Cen.

Figs 27a–c. ***Staurolithites* cf. *S. mutterlosei***. XPL, Clay County, Mississippi (USA) (a, b rotated), Maast. and Black Mesa, Arizona (USA) (c), Tur., UCL-5732-13/14/5739-10. Range: Alb.–Maast.

Figs 27d–e. ***Staurolithites minutus***. XPL (d rotated), Chattahoochee River, Quitman County, Georgia (USA), Maast., UCL-5731-18/19. Range: Cen.?–Maast.

Figs 28a–b. ***Staurolithites*? *aenigma***. XPL (b rotated), Mont Risou, Drôme (SE France), Cen., UCL-5733-34/35. Range: Alb.–Cen.

Fig. 28c. ***Staurolithites aachenus***. XPL, near Portland, Dallas County, Alabama (USA), Camp., UCL-5759-1. Axial cross composed of inner core of laths sandwiched between blocks which thicken towards rim. Range: San.–Camp.

Figs 29a–30. ***Staurolithites gausorhethium***. XPL (29b rotated), The Warren, Folkestone, Kent (UK), Cen., UCL-5737-25/26/5666-3. Range: Alb.–Cen.

Not figured. ***Staurolithites angustus***. Wide central-area; axial cross aligned at slight angle to ellipse axes. Range: Alb.–Cen.; ***Staurolithites crux***. Commonly used as 'bin' name for unidentifiable *Staurolithites* species but herein restricted to single-cycle forms with a simple cross. Range: Haut.?–Maast.; ***Staurolithites dentatus***. Axial cross with teeth arranged perpendicular to it. Range: Camp.; ***Staurolithites parma***. Small; blocky inner cycle; axial cross composed of calcite laths; bars terminate short of rim. Range: San.–Maast.

Plate 6.2

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

Central-area transverse bar

Figs 1a–3. ***Amphizygus brooksii***. XPL, near Portland, Dallas County, Alabama (USA) (1a, b rotated), Camp. and near Plymouth Bluff, Lowndes County, Mississippi (USA) (2, 3 rotated), San., UCL-5758-24/5730-30/31. Range: Alb.–Maast.

Fig. 4a. ***Amphizygus minimus***. XPL, Zoe C BH (S Africa), Maast., UCL-5655-22. Range: San.–Maast.

Figs 4b–c. ***Tranolithus gabalus***. PC (b), XPL (c), Abbots Cliff, Folkestone, Kent (UK) (b), Cen. and Mont Risou, Drôme (SE France) (c), Cen., UCL-1044-18/5733-36. Range: Cen.–Maast.

Figs 5a–d. ***Tranolithus minimus***. XPL, Brezno (Czech Republic) (a), Con., DSDP Site 258 (E Indian Ocean) (b), Con., Norwegian Sector (North Sea) (c), Camp. and DSDP Site 249 (W Indian Ocean) (d), Camp., UCL-5740-32/5656-19/5738-32/5659-13. Range: Val.?–Maast.

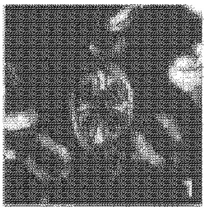
Not figured. ***Tranolithus macleodiae***. Pierced, rhomb-shaped blocks at each end of ellipse; spine. Possible synonym of *T. minimus*, *T. macleodiae* being a well-preserved form, *T. minimus* having blocks overgrown with calcite. Range: Camp.?–Maast.

Figs 6a–7b. ***Tranolithus orionatus***. XPL, Mont Risou, Drôme (SE France) (6a, b rotated, 7a), Cen. and Brezno (Czech Republic) (7b), Con., UCL-5733-9/8/5667-6/5740-30. 6b shows proximal bars which are often not visible or missing. 7b shows almost completely etched blocks. Range: Alb.–Maast.

Figs 8a–9. ***Reinhardtites levis***. XPL, ODP Hole 758A (N Indian Ocean) (8a, b rotated), Camp. and DSDP Site 217 (N Indian Ocean) (9), Camp./Maast., UCL-5703-24/25/5657-8. Range: Camp.–Maast.

Figs 10, 14a. ***Reinhardtites anthophorus***. XPL, DSDP Site 249 (W Indian Ocean) (10), Camp. and near Plymouth Bluff, Lowndes County, Mississippi (USA) (14a), San., UCL-5658-25/5730-35. Range: Tur.?–Camp.

Fig. 11. ***Zeugrhabdotus biperforatus***. XPL, near Plymouth Bluff, Lowndes County, Mississippi (USA), San., UCL-5730-11. Range: Tur.–Camp.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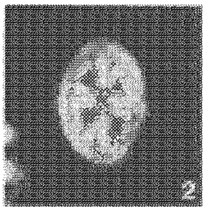
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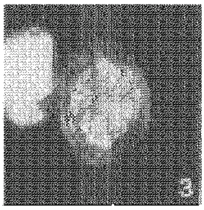
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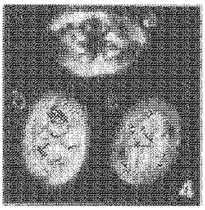
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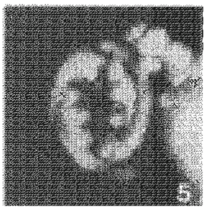
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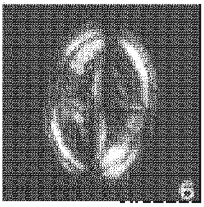
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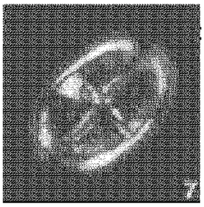
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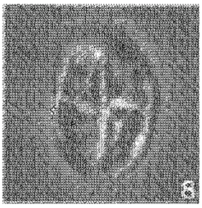
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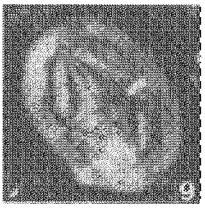
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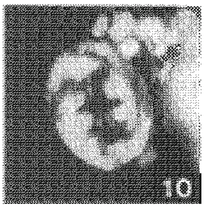
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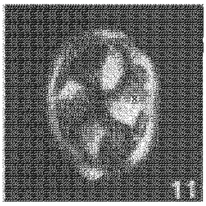
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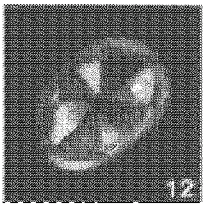
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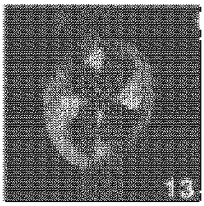
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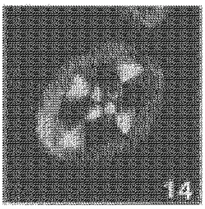
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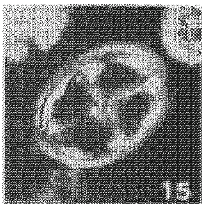
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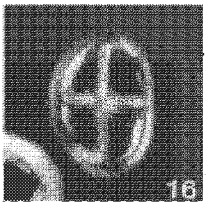
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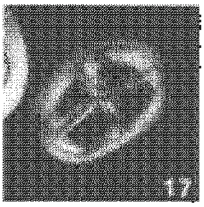
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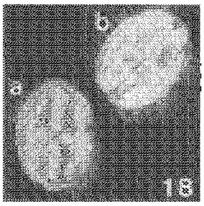
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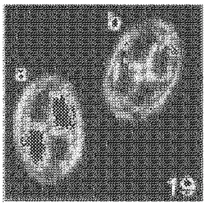
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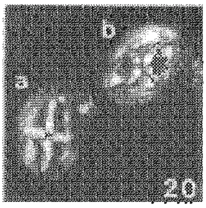
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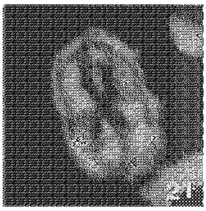
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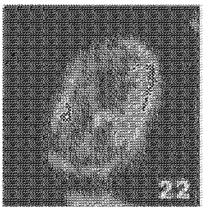
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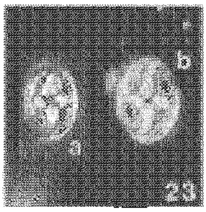
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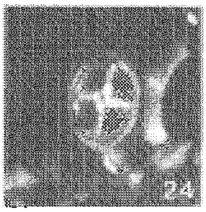
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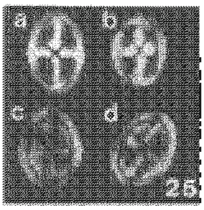
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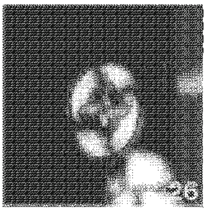
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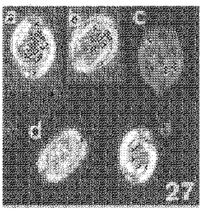
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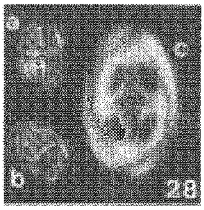
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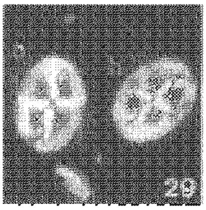
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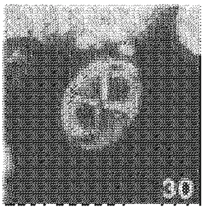
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Figs 12a–c. ***Zeugrhabdotus bicrescenticus***. XPL, DSDP Site 258 (E Indian Ocean) (a, b), Con. and DSDP Site 217 (N Indian Ocean) (c), Camp., UCL-5656-14/36/5653-24. Range: Alb.–Maast.

Figs 13a–b. ***Zeugrhabdotus diplogrammus***. XPL (b rotated), DSDP Site 249 (W Indian Ocean), Camp., UCL-5658-7/8. Range: Val.–Camp.

Figs 14b–15, 20. ***Zeugrhabdotus scutula***. XPL, near Plymouth Bluff, Lowndes County, Mississippi (USA) (14b), San. and Langdon Stairs, Dover, Kent (UK) (15, 20 rotated), Tur., UCL-5730-35/5666-17/16. Range: Haut.–San.

Fig. 16a. ***Gorkaea operio***. XPL, The Warren, Folkestone, Kent (UK), Cen., UCL-5662-6. Range: Alb.–Cen.

Fig. 16b. ***Zeugrhabdotus* sp.**. XPL, near Portland, Dallas County, Alabama (USA), Camp., UCL-5703-13. Range: ?–Camp.

Fig. 17. ***Zeugrhabdotus* cf. *Z. kerguelenensis***. XPL, DSDP Site 258 (E Indian Ocean), Con., UCL-5656-29. Range: Tur.–Con.

Fig. 18. ***Zeugrhabdotus kerguelenensis***. XPL, DSDP Site 258 (E Indian Ocean), Con., UCL-5762-25. Range: Tur.–Con.

Figs 19a–b. ***Zeugrhabdotus noeliae***. XPL (b rotated), The Warren, Folkestone, Kent (UK), Cen., UCL-5737-18/19. Range: Jur.?–San.

Figs 21–22. ***Gorkaea obliqueclausus***. XPL (22 rotated), near Portland, Dallas County, Alabama (USA), Camp., UCL-5703-9/7. Range: Camp.

Not figured. ***Gorkaea pseudanthophorus***. Large; four ?blocks form disjunct bar. Range: Camp.?–Maast.

Figs 23–24. ***Zeugrhabdotus embergeri***. XPL (24 rotated), Abbots Cliff, Folkestone, Kent (UK), Cen., UCL-5755-21/20. Range: Tith.–Maast.

Fig. 25a. ***Zeugrhabdotus burwellensis***. XPL, Mont Risou, Drôme (SE France), Alb., UCL-5187-32. Range: Alb.–Cen.

Figs 25b–c. ***Zeugrhabdotus xenotus***. XPL (c rotated), The Warren, Folkestone, Kent (UK), Alb., UCL-5763-7/8. Range: Val.–Cen.

Fig. 26a. ***Placozygus fibuliformis***. XPL, DSDP Site 217 (N Indian Ocean), Maast., UCL-5599-3. Range: Tur.?–Maast.

Figs 26b–27b. ***Placozygus* cf. *P. fibuliformis***. XPL, near Plymouth Bluff, Lowndes County, Mississippi (USA) (26b), San., The Warren, Folkestone, Kent (UK) (26c, d rotated), Cen., DSDP Site 258 (E Indian Ocean) (27a), Con. and Lydden Spout, Folkestone, Kent (UK) (27b), Cen., UCL-5730-20/5665-34/33/5656-32/5662-23. Range: Alb.–Maast.

Fig. 27c. ***Placozygus* cf. *P. fibuliformis* rim**? XPL, near Portland, Dallas County, Alabama (USA), Camp., UCL-5734-26. Range: Camp.–Maast.

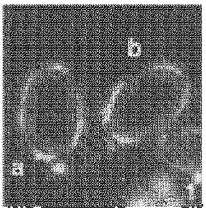
Fig. 28. ***Zeugrhabdotus spiralis***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-5659-28. Range: Con.–Maast.

Figs 29a-b. ***Zeugrhabdotus praesigmoides***. XPL (b rotated), DSDP Site 249 (W Indian Ocean), Camp./Maast., UCL-5795-3/5. Range: San.–Maast.

Fig. 29c. ***Zeugrhabdotus sigmoides***. XPL, DSDP Site 217 (N Indian Ocean), Maast., UCL-5764-32. Range: Camp.–Pal.

Figs 30a–b. ***Zeugrhabdotus trivectis***. XPL (a rotated), Zoe C BH (S Africa), Maast., UCL-5660-35/36. Range: Val.–Maast.

Figs 30c–d. ***Zeugrhabdotus erectus***. XPL, Pd-1 Brezno BH (Czech Republic) (c), Con. and The Warren, Folkestone, Kent (UK) (d), Cen., UCL-5757-3/5662-8. Range: Pliens.–Maast.



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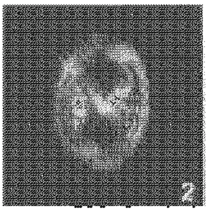
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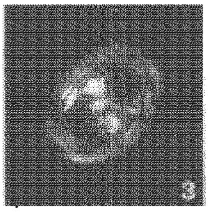
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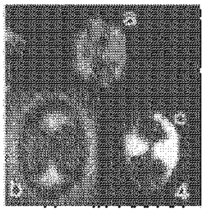

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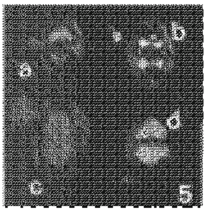

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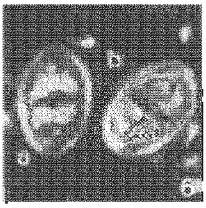

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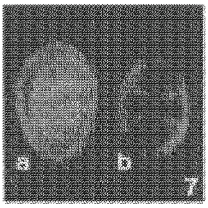

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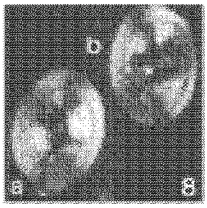

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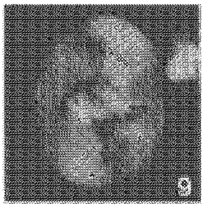
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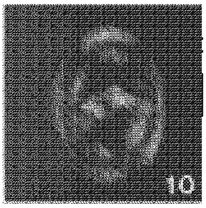
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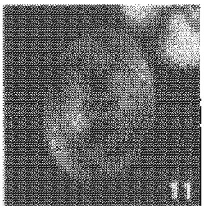
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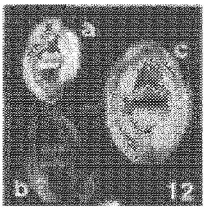

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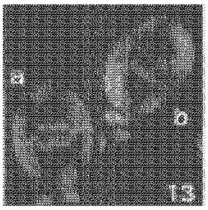

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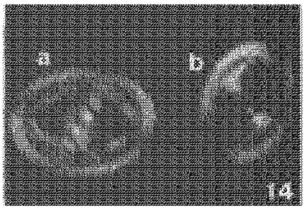

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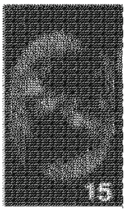
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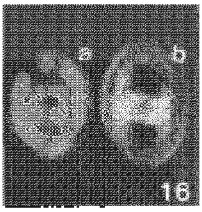

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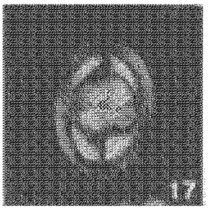
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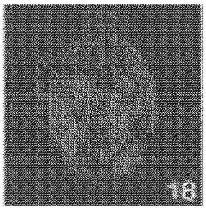
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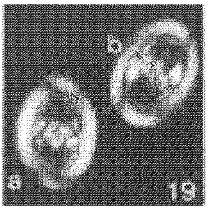

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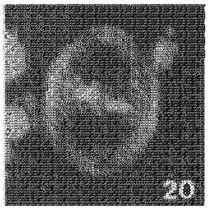
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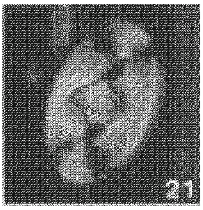
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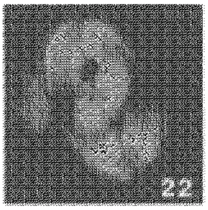
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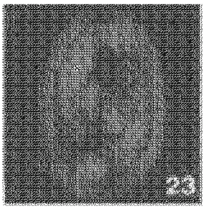
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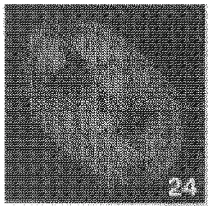
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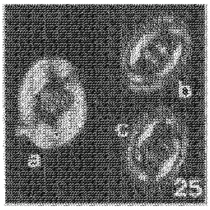

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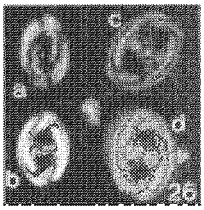

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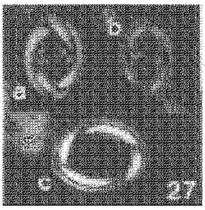

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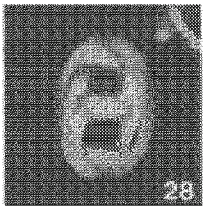
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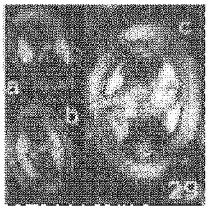

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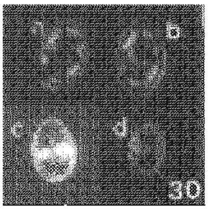

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Plate 6.3

Family CHIASTOZYGACEAE Rood *et al.*, 1973 emend. Varol and Girgis, 1994
Central-area diagonal cross
Figs 1a-b. ***Chiastozygus platyrhethus***. XPL (b rotated), Lydden Spout, Folkestone, Kent (UK), Cen., UCL-5762-31/32. Range: Apt.?–Con.

Figs 2a–b. ***Chiastozygus trabalis***. XPL (b rotated), near Plymouth Bluff, Lowndes County, Mississippi (USA), San., UCL-5730-15/12. Range: Alb.–Maast.

Figs 3a–b. ***Tegumentum stradneri***. XPL, The Warren, Folkestone, Kent (UK), Cen., UCL-5737-27/5662-3. Range: Val.–Maast.

Figs 4a–b. ***Chiastozygus bifarius***. XPL, Mont Risou, Drôme (SE France) (b rotated), Cen., UCL-5734-16/17. Range: Alb.–Maast.

Fig. 5. ***Chiastozygus litterarius***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-5659-6. Range: Barr.–Maast.

Figs 6a–b. ***Chiastozygus antiquus***. XPL (b rotated), Zoe C BH (S Africa), Maast., UCL-5655-31/30. Range: Maast.

Figs 7a–b. ***Chiastozygus* cf. *C. amphipons***. XPL, Clay County, Mississippi (USA) (b rotated), Maast., UCL-5732-15/16. *C. amphipons* has a simple, bright cross. Range: Camp.–Maast. (*C. amphipons* range: San.–Maast.)

Fig. 7c. ***Chiastozygus quadriperforatus***. XPL, near Portland, Dallas County, Alabama (USA), Camp., UCL-5734-35. Range: Camp.–Maast.

Figs 8a–b. ***Chiastozygus synquadriperforatus***. XPL, DSDP Site 217 (N Indian Ocean) (a), Maast. and Zoe C BH (S Africa), Camp., UCL-5763-30/5663-7. Range: Alb.–Maast.

Figs 9a–b. ***Chiastozygus stylesii***. XPL (b rotated), DSDP Site 258 (E Indian Ocean), Con., UCL-5759-9/10. Range: Con.

Not figured. ***Chiastozygus garrisonii***. Subcircular; narrow rim; cross thin, highly-birefringent, composed of laths; large perforations; spine. Range: Camp.–Maast.; ***Chiastozygus propagulis***. 'H'-shaped cross, opposing bars offset from one another. Range: San.–Camp.

Central area closed or open with variable bars or grills
Fig. 10. ***Neocrepidolithus ruegenensis***. XPL, Rügen (E Germany), Maast., UCL-5757-15. Range: Maast.

Figs 11a–b. ***Neocrepidolithus cohenii***. XPL (b rotated), Rügen (E Germany), Maast., UCL-5757-11/12. Range: Camp.–Pal.

Figs 11c–d. ***Neocrepidolithus cruciatus***. XPL (c rotated), Rügen (E Germany), Maast., UCL-5757-18/17. Range: Tur.?–Pal.

Figs 12–13. ***Neocrepidolithus watkinsii***. XPL (13 rotated), DSDP Site 249 (W Indian Ocean), Camp., UCL-5659-35/34. Range: Camp.–Maast.

Central-area net or vacant
Fig. 14. ***Loxolithus armilla***. XPL, Clay County, Mississippi (USA), Maast., UCL-5732-23. Range: Haut.–Maast.

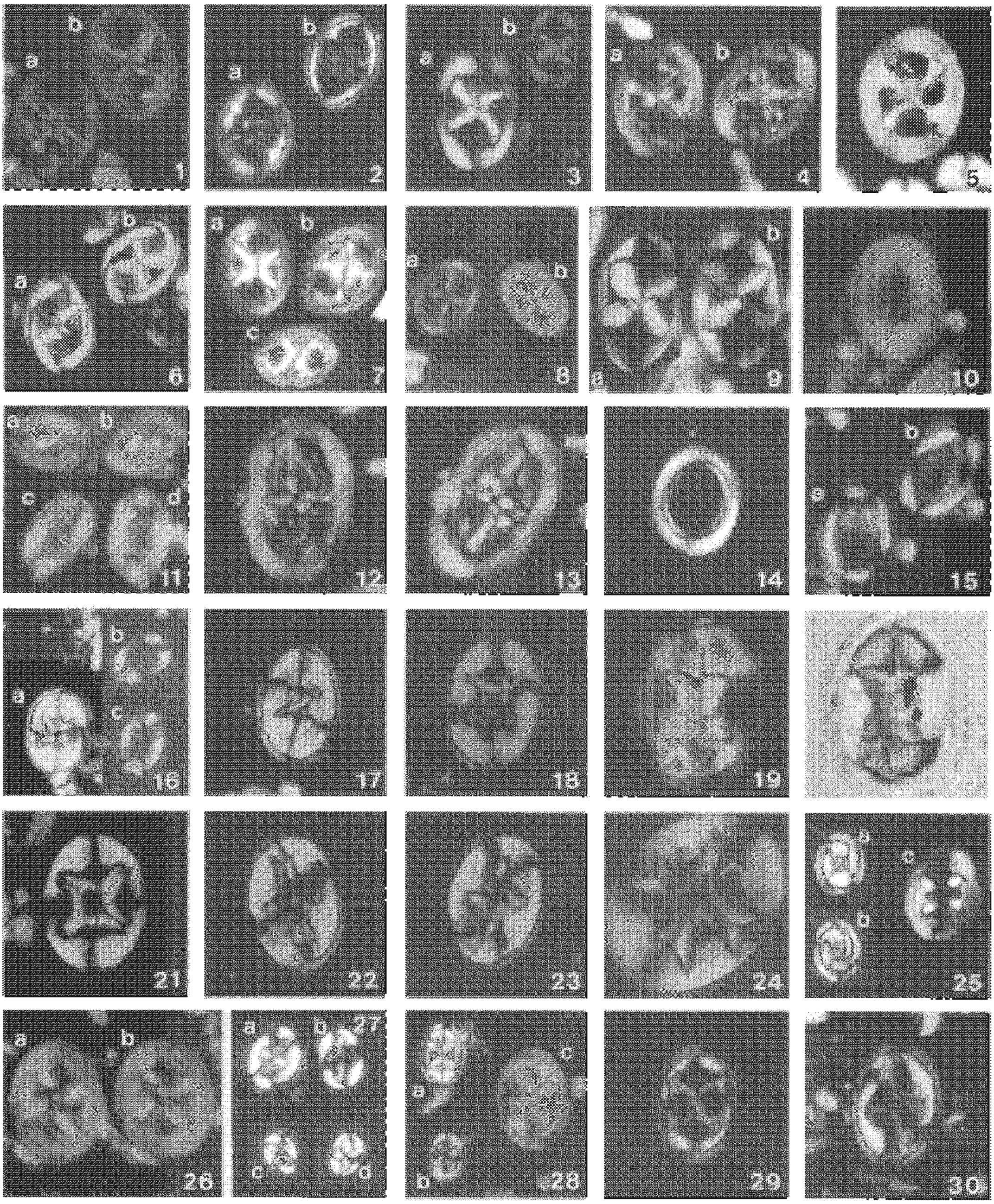
Family EIFFELLITHACEAE Reinhardt, 1965
Figs 15a–b. ***Diloma galei***. XPL (b rotated), Abbots Cliff, Folkestone, Kent (UK), Cen., UCL-5755-26/25. Range: Cen.

Figs 16a–17. ***Eiffellithus gorkae***. XPL, The Warren, Folkestone, Kent (UK) (16a, b rotated), Cen. and Zoe C BH (S Africa), Camp. (16c), Maast. (17), UCL-5764-16/15/5664-21/5655-1. Large forms, such as 17, may actually be *E turriseiffelii* with an overgrown inner cycle. Range: Alb.–Maast.

Fig. 18. ***Eiffellithus turriseiffelii***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5667-2. Range: Alb.–Maast.

Figs 19–20. ***Eiffellithus pospichalii***. XPL (19), PC (20), DSDP Site 217 (N Indian Ocean), Camp., UCL-5599-2/1. Range: Camp.

Fig. 21. ***Eiffellithus parallelus***. XPL, Zoe C BH (S Africa), Maast., UCL-5655-13. Range: Camp.–Maast.



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Figs 22–24. ***Eiffellithus eximius.*** XPL (23 rotated), Zoe C BH (S Africa), Camp., UCL-5664-27/26/5663-24. In some specimens, the cross forms a slight angle with the ellipse axes. Range: Tur.–Camp.

Not figured. ***Eiffellithus monechiae***. Similar to *Eiffellithus eximius*. Range: Alb.–Cen.

Figs 25a–b. ***Eiffellithus? hancockii.*** XPL, Lydden Spout, Folkestone, Kent (UK), Cen., UCL-5762-28/29. Range: Alb.–Cen.

Figs 25c–26b. ***Helicolithus anceps.*** XPL, ODP Hole 765C (E Indian Ocean) (25c), Camp. and ODP Hole 761B (E Indian Ocean) (26a, b rotated), Maast., UCL-5704-33/5199-15/16. Range: Cen.–Maast.

Figs 27a–d. ***Helicolithus compactus.*** XPL, The Warren, Folkestone, Kent (UK) (a, b), Cen. and Mont Risou, Drôme (SE France) (c, d rotated), Cen., UCL-5661-36/5665-36/5734-2/1. Range: Cen.–?San.

Figs 28a–29. ***Helicolithus trabeculatus***. XPL, Zoe C BH (S Africa) (28a), Maast., The Warren, Folkestone, Kent (UK) (28b), Cen., Black Mesa, Arizona (USA) (28c), Tur. and near Plymouth Bluff, Lowndes County, Mississippi (USA) (29), San., UCL-5656-2/5665-4/5739-11/5730-26. The cross is etched in 29. Range: Alb.–Maast.

Fig. 30. ***Helicolithus turonicus.*** XPL, Brezno (Czech Republic), Con., UCL-5740-33. Range: Tur.–Con.

Plate 6.4

Family RHAGODISCACEAE Hay, 1977

Figs 1a–2b. ***Calcicalathina alta.*** XPL, Mont Risou, Drôme (SE France) (1a, 2a, 2b rotated), Cen. and Zoe A BH (S Africa) (1b), Cen., UCL-5667-31/5740-19/5734-10/11. Range: Alb.–Cen.

Fig. 3. ***Percivalia fenestrata.*** XPL, near Portland, Dallas County, Alabama (USA), Camp., UCL-5734-29. Range: Berr.?–Camp.

Fig. 4. ***Percivalia hauxtonensis.*** XPL, Mont Risou, Drôme (SE France), Alb., UCL-5187-31. Range: Alb.–Cen.

Figs 5a–b. ***Percivalia* sp.**. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5667-26/5666-19. Range: Cen.

Figs 6–7b. ***Podorhabdus? elkefensis.*** XPL, Zoe C BH (S Africa), Maast., UCL-5655-36/16/35. Not a podorhabdid; affinity uncertain but shares some features common to other members of the Rhagodiscaceae. Range: Maast.

Figs 8–9. ***Percivalia imperfossa***. XPL (9 rotated), Mont Risou, Drôme (SE France), Cen., UCL-5734-6/5. Range: Haut.–Cen.

Not figured. ***Percivalia pontilitha***. Thick, short-axis bar formed of numerous laths. Range: Camp.; ***Percivalia porosa***. Two cycles of central-area perforations separated by elliptical cycle of laths; small axial cross within inner cycle; small spine. Range: Camp.

Fig. 10. ***Rhagodiscus achlyostaurion***. XPL, The Warren, Folkestone, Kent (UK), Cen., UCL-5665-6. Range: Apt.–Con.

Fig. 11. ***Rhagodiscus asper***. XPL, Mont Risou, Drôme (SE France), Alb., UCL-5187-34. Range: Tith.–Cen.

Figs 12a, 15. ***Rhagodiscus splendens***. XPL, Zoe C BH (S Africa) (12a), Maast. and Chattahoochee River, Quitman County, Georgia (USA) (15), Maast., UCL-5655-29/5731-24. Range: Apt.–Maast.

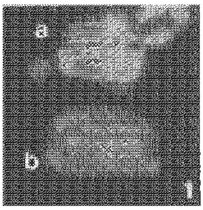
Figs 12b–c. ***Rhagodiscus angustus***. XPL, Poricy Brook, Monmouth County, New Jersey (USA) (b), Maast. and Zoe C BH (S Africa) (c), Maast., UCL-5731-32/5655-33. Range: Apt.–Maast.

Figs 13a–b. ***Rhagodiscus plebeius***. XPL (b rotated), DSDP Site 217 (N Indian Ocean), Maast., UCL-5599-5/4. Range: Cen.–Maast.

Figs 13c–d. ***Rhagodiscus gallagheri.*** XPL, Mont Risou, Drôme (SE France), Cen., UCL-5187-12/5734-15. Range: Apt.–Cen.

Fig. 14. ***Rhagodiscus reniformis.*** XPL, DSDP Site 217 (N Indian Ocean), Maast., UCL-5653-7. Range: Tur.–Maast.

Fig. 19. ***Rhagodiscus indistinctus.*** XPL, DSDP Site 217 (N Indian Ocean), Maast., UCL-5654-13. Range: Camp.–Maast.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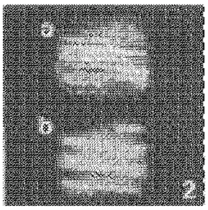
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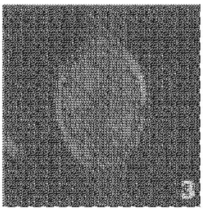
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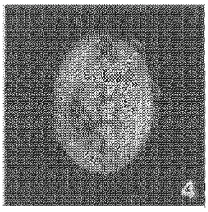
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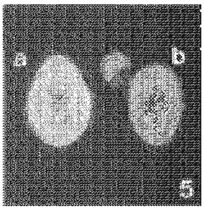
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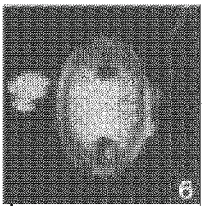
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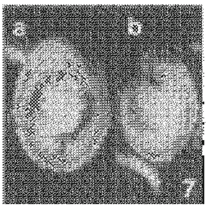
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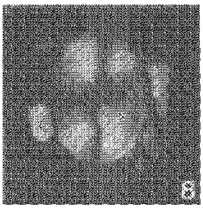
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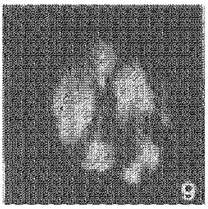
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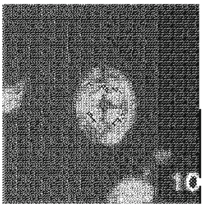
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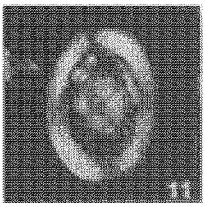
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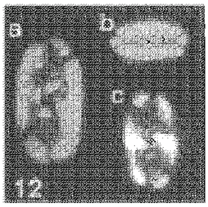
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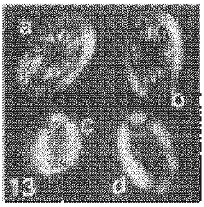
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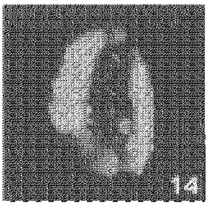
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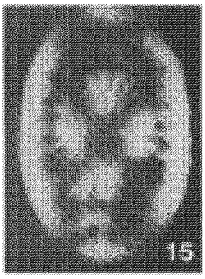
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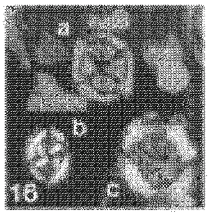
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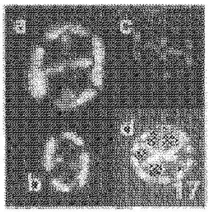
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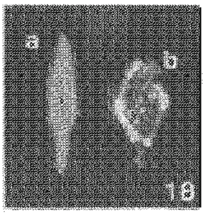
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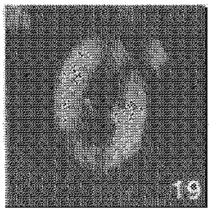
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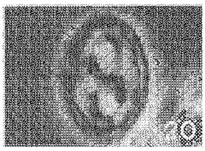
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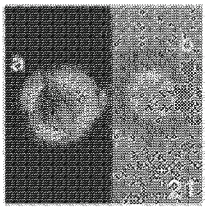
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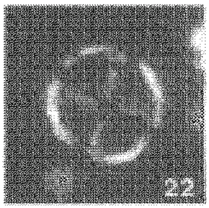
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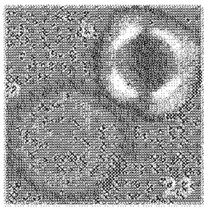
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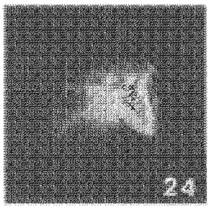
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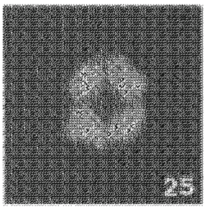
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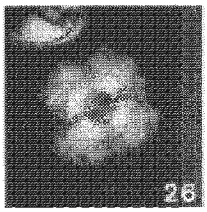
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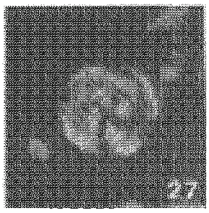
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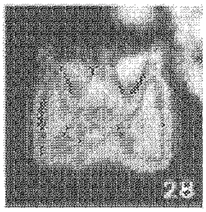
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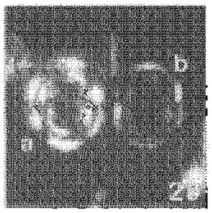
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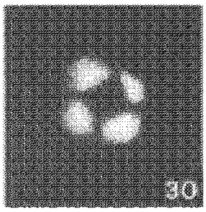
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Fig. 20. ***Rhagodiscus infinitus***. PC, Abbots Cliff, Folkestone, Kent (UK), Cen., UCL-1088-10. Range: Val.?–?Maast.

Order STEPHANOLITHIALES Bown and Young, 1997

Family CALCIOSOLENIACEAE Kamptner, 1927

Fig. 18a. ***Scapholithus fossilis***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5666-36. Range: Haut.–PD

Not figured. ***Scapholithus stegnus***. Broad rim; extremely restricted central-area. Range: San.

Family STEPHANOLITHIACEAE Black, 1968

Fig. 16a. ***Corollithion kennedyi***. XPL, Lydden Spout, Folkestone, Kent (UK), Cen., UCL-5662-32. Range: Cen.

Fig. 16b. ***Corollithion? madagaskarensis***. XPL, DSDP Site 241 (W Indian Ocean), Camp., UCL-5202-33. Range: Cen.–Maast.

Fig. 16c. ***Corollithion completum***. XPL, DSDP Site 217 (N Indian Ocean), Maast., UCL-5796-26. Range: Camp.–Maast.

Figs 17a–b. ***Corollithion signum***. XPL, Waxahachie Dam Spillway, Ellis County, Texas (USA) (a), Camp. and near Plymouth Bluff, Lowndes County, Mississippi (USA) (b), San., UCL-5730-5/5730-25. Range: Alb.–Maast.

Figs 17c–d. ***Corollithion exiguum***. XPL, near Cottinton, Russel County, Alabama (USA) (c), Camp. and Clay County, Mississippi (USA) (d), Maast., UCL-5732-5/18. Range: Tur.–Maast.

Fig. 18b. ***Rhombolithion rhombicum***. XPL, Zoe C BH (S Africa), Maast., UCL-5655-27. Range: Jur.?–Maast.

Not figured. ***Corollithion acutum***. Elliptical; four bars form low-angled cross about short ellipse axis. Range: Apt.–Camp.; ***Corollithion ellipticum***. Elliptical; six bars. Range: Camp.; ***Corollithion fractum***. Subcircular; six bars. Range: Alb.–Cen.

Figs 21a–b. ***Rotelapillus crenulatus***. XPL (a), PC (b), near Portland, Dallas County, Alabama (USA) (a), Camp. and DSDP Hole 550B (NE Atlantic Ocean), Camp., UCL-5758-16/2261-17. Range: Tith.–Maast.

Not figured. ***Rotelapillus applegatei***. Subelliptical; six bars; short, thick spine. Range: San.

Fig. 22. ***Stoverius achylosus***. XPL, Abbots Cliff, Folkestone, Kent (UK), Cen., UCL-2376-8. Range: Apt.?–Tur.

Fig. 23. ***Cylindralithus biarcus***. PC (a), XPL (b), DSDP Hole 550B (NE Atlantic Ocean), Camp. and DSDP Site 258 (E Indian Ocean), Con., UCL-2261-8/5759-11. Range: Cen.–Maast.

Fig. 24. ***Cylindralithus*** **side-view**. XPL, ODP Hole 765C (E Indian Ocean), Camp., UCL-5704-30. Typical side-view of *C. asymmetricus*, *C. biarcus*, *C. coronatus*, *C. nudus*, *C. serratus*.

Fig. 25. ***Cylindralithus nudus***. XPL, Zoe C BH (S Africa), Camp., UCL-5661-22. Range: Alb.–Maast.

Figs 26–28. ***Cylindralithus sculptus***. XPL, near Plymouth Bluff, Lowndes County, Mississippi (USA) (26, distal view), San., DSDP Site 217 (N Indian Ocean) (27, proximal view), Maast. and ODP Hole 765C (E Indian Ocean) (28, side-view), Camp., UCL-5730-18/5599-36/5704-31. Range: Cen.–Maast.

Figs 29a–b. ***Cylindralithus? nieliae***. XPL (a focused on distal end, b focused on proximal end), ODP Hole 761B (E Indian Ocean), Maast., UCL-5704-17/19. Range: Camp.–Maast.

Fig. 30. ***Cylindralithus serratus***. XPL, Clay County, Mississippi (USA), Maast., UCL-5732-21. Range: Alb.?–Maast.

Not figured. ***Cylindralithus asymmetricus***. Straight rather than curved bars as in *C. biarcus*; often indistinguishable from *C. biarcus*. Range: San.–Camp.; ***Cylindralithus coronatus***. Bars form 90° angle and thicken at rim. Range: Cen.–Camp.; ***Cylindralithus duplex***. Distal and proximal cycles extend (distally and proximally) beyond central structure. Range: Maast.

Not figured. ***Darwinilithus pentarhethum***. Similar to *Cylindralithus* but processes extend proximally from central area. Range: Cen.

Not figured. ***Perchnielsenella stradneri***. Superficially similar to proximal views of *C. sculptus* in the LM but distinctive in side-view. Range: Camp.–Maast.

Plate 6.5

Order PODORHABDALES Rood, Hay and Barnard, 1971 emend. Bown, 1987

Family AXOPODORHABDACEAE Bown and Young, 1997
Figs 1–2. ***Axopodorhabdus albianus***. XPL (2 rotated), The Warren, Folkestone, Kent (UK), Cen., UCL-5665-28/29. Range: Alb.–Cen.

Not figured. ***Axopodorhabdus dietzmannii***. More elongated than *A. albianus*. Range: Berr.?–Cen.

Figs 3–6. ***Cribrosphaerella ehrenbergii***. XPL (3, 5), PC (4, 6), DSDP Site 217 (N Indian Ocean), Camp./Maast. (3, 4) and Maast. (5, 6), UCL-5599-18/19/5654-6/7. Includes forms with varying rim:central area width ratios and outlines. Forms with both one and two distal shields have been observed but it is believed that this is a preservational effect, whereby the distal shields, which possess the same crystallographic orientation, become fused by calcite overgrowth (T. Ehrendorfer, pers. comm., 1994). Range: Alb.–Maast.

Figs 7–8. ***Psyktosphaera firthii***. XPL, Zoe C BH (S Africa), Maast., UCL-5655-9/5656-1. Range: Camp.?–Maast.

Fig. 9. ***Cribrosphaerella daniae* rim.** XPL, ODP Hole 738C (S Indian Ocean), Maast., UCL-5756-21. Range: Camp.–Maast.

Fig. 10. ***Perissocyclus fenestratus***. XPL, DSDP Site 217 (N Indian Ocean), Camp./Maast., UCL-5657-11. Plate perforated by two cycles of holes around large spine. Range: Barr.?–Maast.

Fig. 11. ***Nephrolithus corystus***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-5659-3. Range: Camp.–Maast.

Figs 12a–b, 13c–d. ***Nephrolithus frequens***. XPL (12a, b, 13c), PC (13d), Tombigbee River, Sumter County, Alabama (USA) (12a), Maast., Zoe C BH (S Africa) (12b), Maast. and ODP Hole 738C (S Indian Ocean) (13c, d), Maast., UCL-5732-34/5660-7/5756-12/13. Range: Camp.–Maast.

Figs 13a–b. ***Nephrolithus miniporus***. XPL (a), PC (b), ODP Hole 738C (S Indian Ocean), Maast., UCL-5756-15/14. Range: Maast.

Figs 14a–b. ***Cribrocorona gallica***. XPL (a, side-view), DSDP Site 217 (N Indian Ocean), Maast., UCL-5796-25/22 Range: Con.–Maast.

Figs 15a–b, 20. ***Tetrapodorhabdus decorus***. XPL (15a, 20), PC (15b), Tombigbee River, Sumter County, Alabama (USA) (15a, b), Maast. and DSDP Site 249 (W Indian Ocean) (20), Camp., UCL-5732-36/5333-1/5659-14. Range: Berr.?–Maast.

Not figured. ***Hemipodorhabdus gorkae***. Podorhabdid rim; two large perforations; short-axis bar, perforated near rim. Range: Berr.?–?Tur.

Figs 16–17. ***Octocyclus reinhardtii***. XPL (16), PC (17), The Warren, Folkestone, Kent (UK), Cen., UCL-5737-13/14. Range: Alb.–Maast.

Figs 18–19. ***Dodekapodorhabdus noeliae***. XPL (18), PC (19), DSDP Hole 550B (NE Atlantic Ocean), Camp., UCL-2275-30/29. Plate perforated by single ring of 12 holes around large spine. Range: ?Cen.

Not figured. ***Teichorhabdus ethmos***. Plate perforated by three cycles of perforations. Range: Maast.

Family BISCUTACEAE Black, 1971a
Figs 21a–c. ***Biscutum ellipticum***. XPL, Shakespeare Cliff, Dover, Kent (UK) (a), Tur. and Mont Risou, Drôme (SE France), Cen., UCL-5661-24/5733-17/18. Range: Bath.–Maast.

Figs 21d–f. ***Gephyrobiscutum diabolum***. PC (d, e rotated), XPL (f), DSDP Site 511 (S Atlantic Ocean), Camp., UCL-5737-32/33/31. Range: Camp.

Figs 22–23. ***Biscutum* cf. *B. ellipticum***. XPL (23 rotated), near Portland, Dallas County, Alabama (USA), Camp., UCL-5703-15/16. Much larger than *B. ellipticum*. Range: Alb.–Maast.

Figs 24a–c. ***Biscutum notaculum***. PC (a), XPL (b, c rotated), DSDP Site 217 (N Indian Ocean), Maast., UCL-5653-17/15/16. Range: Camp.–Maast.

Figs 25a–b. ***Biscutum hattneri***. XPL (b rotated), Tombigbee River, Sumter County, Alabama (USA), Maast., UCL-5732-33/31. Range: Con.–Maast.

Figs 26–27. ***Biscutum dissimilis***. XPL, DSDP Site 217 (N Indian Ocean) (26), Camp. and DSDP Site 249 (W Indian Ocean) (27), Camp., UCL-5653-35/5658-30. Range: Alb.–Maast.

Figs 28–30a. ***Biscutum magnum***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-5658-9/5659-5/7. Central-area shows variable degrees of closure. Range: San.–Maast.

Figs 30b. ***Biscutum thurowii***. XPL, Mont Risou, Drôme (SE France), Alb., UCL-3842-30. Range: Alb.–Cen.

Plate 6.6

Figs 1–2. ***Biscutum coronum***. XPL, DSDP Site 258 (E Indian Ocean) (1), Con. and DSDP Site 249 (W Indian Ocean) (2), Camp., UCL-5656-22/5658-11. Range: Tur.?–Maast.

Figs 3–4. ***Biscutum melaniae***. XPL, Sewerby Cliff-Danes Dyke, Humberside (UK), Camp., UCL-5764-4/5. Range: Tur.–Pal.

Not figured. ***Biscutum arrogans***. Small; circular central perforation appears bright in XPL. Range: Maast.; ***Biscutum boletum***. Small; collar projects from distal surface. Range: Maast.; ***Biscutum dekaenelii***. Axial cross; possibly = spineless *Boletuvelum candens*. Range: Con.–San.; ***Biscutum virginica***. Similar to *B. dissimilis* but with more rim elements; longer, wider central-area filled with elements. Range: Con.–San.; ***Biscutum zulloii***. Small-medium; distinctive inner cycle; forms coccocylinders. Range: Tur.–Camp.

Not figured. ***Boletuvelum candens***. Large, flaring, bulbous spine unmistakable in side-view. Range: Con.?–Maast.

Fig. 5. ***Seribiscutum gaultensis***. XPL, Mont Risou, Drôme (SE France), Alb., UCL-5153-12. Range: Apt.–?Cen.

Fig. 6a. ***Discorhabdus ignotus***: XPL, Waxahachie Dam Spillway, Ellis County, Texas (USA), Camp., UCL-5730-4. Range: Oxf.–Maast.

Figs 6b–7. ***Discorhabdus* cf. *D. ignotus***. XPL, Zoe C BH (S Africa) (6b), Maast., DSDP Site 249 (W Indian Ocean) (6c), Camp. and ODP Hole 761B (E Indian Ocean) (7), Camp., UCL-5655-32/5660-16/5066-9. Range: Camp.?–Maast.

Fig. 8. ***Gaarderella granulifera*?** XPL, The Warren, Folkestone, Kent (UK), Alb., UCL-5796-29. Range: Alb.–?Maast.

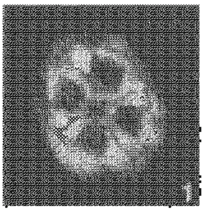
Fig. 9. ***Seribiscutum primitivum***. XPL, DSDP Site 258 (E Indian Ocean), Cen., UCL-5759-13. Range: Alb.–Camp.

Figs 10a–b. ***Seribiscutum* cf. *S. gaultensis***. XPL (b rotated), Pd-1 Brezno BH (Czech Republic), Con., UCL-5756-34/35. Range: Apt.–?Con.

Fig. 14. ***Crucibiscutum hayi***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5667-27. Range: Alb.–Cen.

Figs 15a–b. ***Sollasites horticus***. PC (a), XPL (b), near Portland, Dallas County, Alabama (USA), Camp., UCL-5734-33/32. Range: Oxf.?–Camp.

Not figured. ***Sollasites lowei***. Axial cross; cycle of elements half-way between rim and centre bisect each bar of the cross. Range: Con.–Camp.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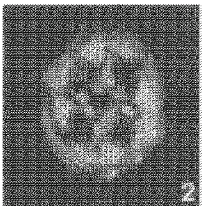
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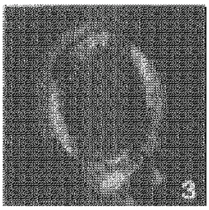
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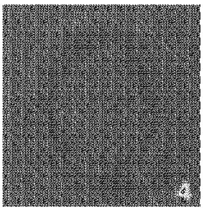
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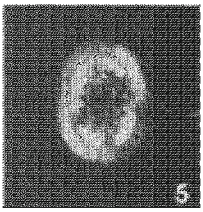
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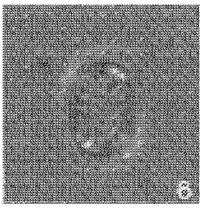
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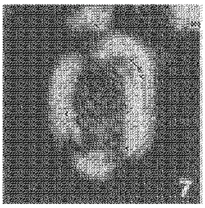
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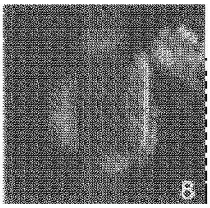
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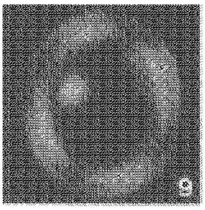
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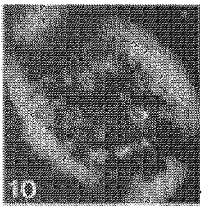
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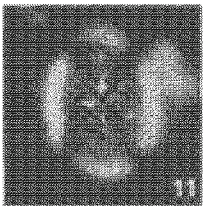
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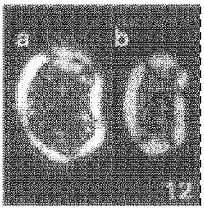
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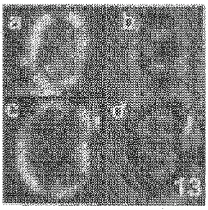
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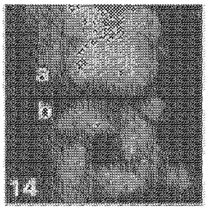
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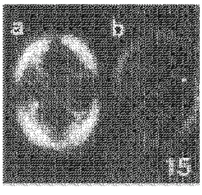
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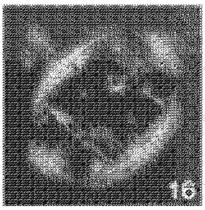
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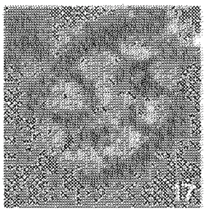
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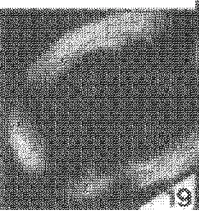
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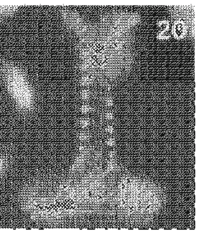
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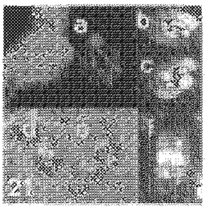
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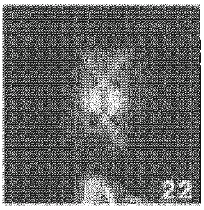
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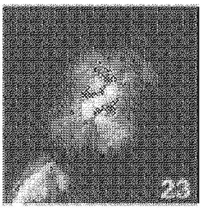
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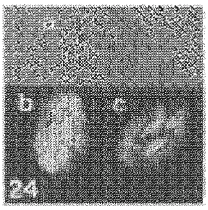
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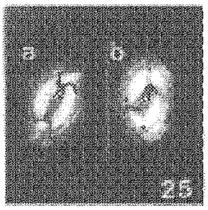
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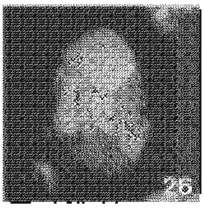
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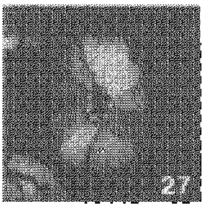
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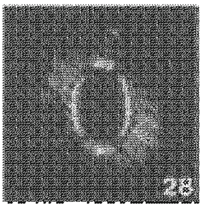
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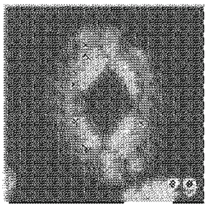
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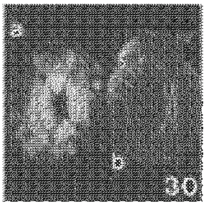
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Family PREDISCOSPHAERACEAE Rood, Hay and Barnard, 1971
Figs 11–12, 16, 18. ***Petrarhabdus copulatus***. XPL, DSDP Site 249 (W Indian Ocean) (11 focused on spine, 12 focused on coccolith, 16 side-view), Camp./Maast. and DSDP Site 217 (N Indian Ocean) (18), Camp., UCL-5659-27/26/5795-14/5654-36. Range: Camp.–Maast.

Fig. 13. ***Petrarhabdus vietus***. XPL, DSDP Site 217 (N Indian Ocean), Maast., UCL-5599-9. Range: San.–Maast.

Fig. 17. ***Prediscosphaera cretacea*** or ***Prediscosphaera ponticula* side-view**. XPL, DSDP Site 249 (W Indian Ocean), Camp./Maast., UCL-5795-11.

Figs 19a–b. ***Prediscosphaera microrhabdulina***. XPL, ODP Hole 738C (S Indian Ocean) (a), Camp. and DSDP Site 217 (N Indian Ocean) (b, spine), Maast., UCL-5756-20/5599-13. Spines easier to distinguish than coccoliths, which might be confused with *P. cretacea*. Range: San.–Maast.

Figs 20, 25. ***Prediscosphaera majungae***. XPL (20), PC (25), DSDP Site 401 (NE Atlantic Ocean), Maast., UCL-2471-24/23. Short spine easy to recognise in side-view; coccoliths similar to *P. microrhabdulina* and often mistaken for *P. cretacea*. Range: Camp.–Maast.

Fig. 21. ***Prediscosphaera grandis***. XPL, DSDP Site 249 (W Indian Ocean), Camp./Maast., UCL-5795-26. Range: Tur.?–Maast.

Figs 22a–b. ***Prediscosphaera cretacea***. XPL, DSDP Site 249 (W Indian Ocean) (a), Camp./Maast. and near Plymouth Bluff, Lowndes County, Alabama (USA) (b), San., UCL-5795-2/5730-19. Arkhangelsky's (1912) original drawings are small and *elliptical*, with a cross aligned at 45° to the ellipse axes. Range: Cen.–Maast.

Fig. 23a–b. ***Prediscosphaera columnata***. XPL, Mont Risou, Drôme (SE France), Cen. and The Warren, Folkestone, Kent (UK), Cen., UCL-5734-12/5763-5. Herein, includes all small, circular forms, i.e. *P. avitus* (Black, 1973) Perch-Nielsen, 1984 and *P. cantabrigensis* (Black, 1967) Reinhardt, 1970. Range: Alb.–Tur.

Fig. 23c. ***Prediscosphaera ponticula***. XPL, DSDP Site 249 (W Indian Ocean), Camp./Maast., UCL-5796-34. Presence of secondary bars on cross cannot routinely be reliably and consistently distinguished. Range: Alb.–Maast.

Fig. 24. ***Prediscosphaera serrata***. PC, DSDP Hole 550B (NE Atlantic Ocean), San., UCL-2261-27. Range: San.–Maast.

Fig. 26. ***Prediscosphaera* cf. *P. grandis***. XPL, near Plymouth Bluff, Lowndes County, Mississippi (USA), San., UCL-5730-34. Smaller than *P. grandis*. Range: San.–Maast.

Figs 27–28. ***Prediscosphaera arkhangelskyi***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-5658-13/5703-18. Range: San.–Maast.

Fig. 29. ***Prediscosphaera incohatus***. XPL, DSDP Site 258 (E Indian Ocean), Con., UCL-5657-3. Range: Tur.–Maast. (*Prediscosphaera incohatus* (Stover, 1966) Burnett comb. nov.: *Discolithus incohatus* Stover, 1966, p.143, pl.2, figs 23 (holotype), 24, pl.8, fig.17. Cretaceous coccoliths and associated nannofossils from France and the Netherlands. *Micropaleontology*, **12** (2), 133–167.)

Figs 30a–b. ***Prediscosphaera spinosa***. XPL, The Warren, Folkestone, Kent (UK) (a), Cen. and near Portland, Dallas County, Alabama (USA) (b), Camp., UCL-5665-9/5703-10. Has a range of sizes. Range: Apt.–Maast.

Figs 31a–b. ***Prediscosphaera stoveri***. XPL, ODP Hole 738C (S Indian Ocean) (a, empty rims), Camp. and ODP Hole 761B (E Indian Ocean) (b), Camp., UCL-5738-3/5065-30. Range: Camp.–Maast.

Not figured. ***Prediscosphaera bukryi***. Small; small central area; axial cross; less distinctive inner cycle than *P. stoveri*. Range: Alb.–Maast.; ***Prediscosphaera rhombica***. Axial cross; further bars form diamond around centre of cross. Range: Camp.–Maast.

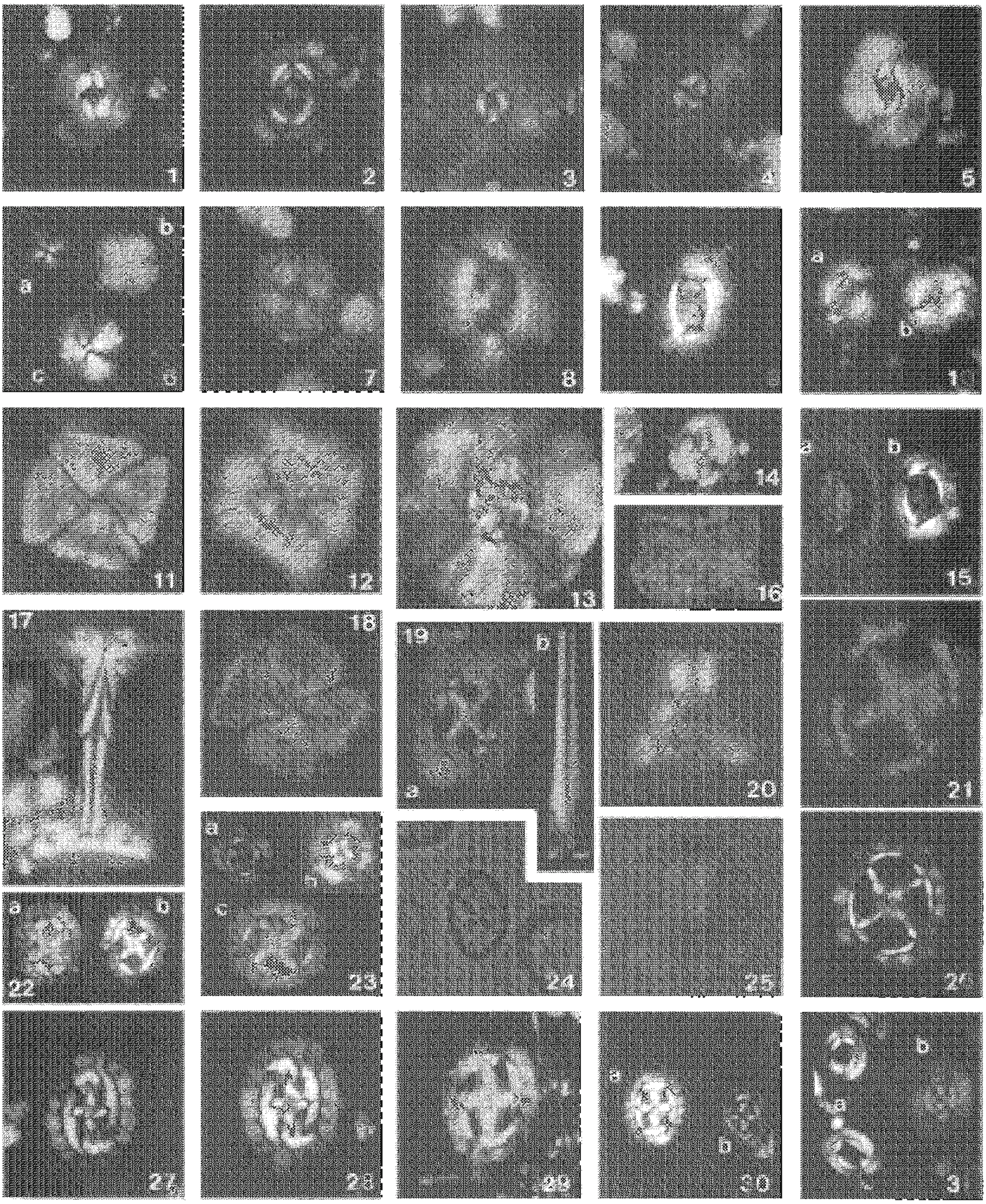
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Plate 6.7

Family CRETARHABDACEAE Thierstein, 1973
Figs 1–2. ***Cretarhabdus conicus***. XPL (1), PC (2), DSDP Site 217 (N Indian Ocean), Maast., UCL-5653-20/21. Range: Kimm.–Maast.

Figs 3–4. ***Cretarhabdus striatus***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5667-21/5184-16. Range: Apt.–Cen.

Fig. 5. ***Retecapsa schizobrachiata***. XPL, ODP Hole 758A (N Indian Ocean), Camp., UCL-5703-26. Range: Camp.–Maast.

Fig. 6. ***Retecapsa angustiforata***. XPL, near Plymouth Bluff, Lowndes County, Alabama (USA), San., UCL-5730-21. Range: Berr.–Maast.

Fig. 7. ***Retecapsa crenulata***. XPL, Poricy Brook, Monmouth County, New Jersey (USA), Maast., UCL-5732-3. Range: Berr.?–Maast.

Fig. 8. ***Retecapsa ficula***. XPL, DSDP Site 217 (N Indian Ocean), Maast., UCL-5654-20. Range: Tur.–Maast.

Figs 9–10. ***Retecapsa surirella***. XPL (9), PC (10), DSDP Hole 550B (NE Atlantic Ocean), Camp., UCL-2276-30/29. Range: Berr.?–Maast.

Figs 11–12. ***Flabellites oblongus***. XPL (12 rotated), Mont Risou, Drôme (SE France), Cen., UCL-5667-17/18. Range: Barr.–San.

Figs 13–14. ***Helenea chiastia***. XPL, The Warren, Folkestone, Kent (UK) (13), Cen. and Mont Risou, Drôme (SE France) (14), Cen., UCL-5665-24/5733-12. Range: Tith.–?Tur.

Fig. 15. ***Grantarhabdus coronadventis***. XPL, DSDP Site 258 (E Indian Ocean), Con., UCL-5796-21. Range: Apt.?–Camp.

Family TUBODISCACEAE Bown and Rutledge *in* Bown and Young, 1997
Fig. 16. ***Manivitella pemmatoidea***. XPL, DSDP Site 217 (N Indian Ocean), Maast., UCL-5599-14. Range: Tith.–Maast.

Order WATZNAUERIALES Bown, 1987

Family WATZNAUERIACEAE Rood, Hay and Barnard, 1971
Fig. 17. ***Cyclagelosphaera argoensis***. XPL, DSDP Site 217 (N Indian Ocean), Maast., UCL-5599-11. Range: Tith.–Maast.

Fig. 18. ***Cyclagelosphaera reinhardtii***. XPL, The Warren, Folkestone, Kent (UK), Cen., UCL-5737-15. Range: Alb.–Pal.

Fig. 19. ***Cyclagelosphaera margerelii***. XPL, Trunch BH, Norfolk (UK), San., UCL-2334-19. Range: Baj.–Pal.

Fig. 20. ***Cyclagelosphaera rotaclypeata***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-5763-31. Range: Alb.–Pal.

Not figured. ***Cyclagelosphaera deflandrei***. Rare; very large; very highly-birefringent. Range: Tith.?–Maast.

Figs 21–22, 26. ***Watznaueria biporta***. XPL, The Warren, Folkestone, Kent (UK) (21), Cen., DSDP Site 258 (E Indian Ocean) (22), Con. and near Portland, Dallas County, Alabama (USA) (26), Camp., UCL-5665-19/5656-34/5758-33. Range: Alb.?–Maast.

Fig. 23. ***Watznaueria britannica***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5667-19. Range: Baj.–?Con.

Fig. 24. ***Watznaueria fossacincta***. XPL, Lydden Spout, Folkestone, Kent (UK), Cen., UCL-5762-26. Range: Baj.–Maast.

Fig. 25. ***Watznaueria ovata***. XPL, DSDP Hole 550B (NE Atlantic Ocean), San., UCL-2269-24. Range: Alb.?–Maast.

Fig. 27. ***Watznaueria manivitiae***. XPL, The Warren, Folkestone, Kent (UK), Cen., UCL-5737-24. Range: Call.–Maast.

Fig. 28. ***Watznaueria barnesae***. XPL, DSDP Site 258 (E Indian Ocean), Con., UCL-5255-6. Range: Baj.–Maast.

Figs 29–30. ***Watznaueria quadriradiata***. XPL, Zoe C BH (S Africa), Camp., UCL-5660-12/5664-22. Range: San.–Maast.

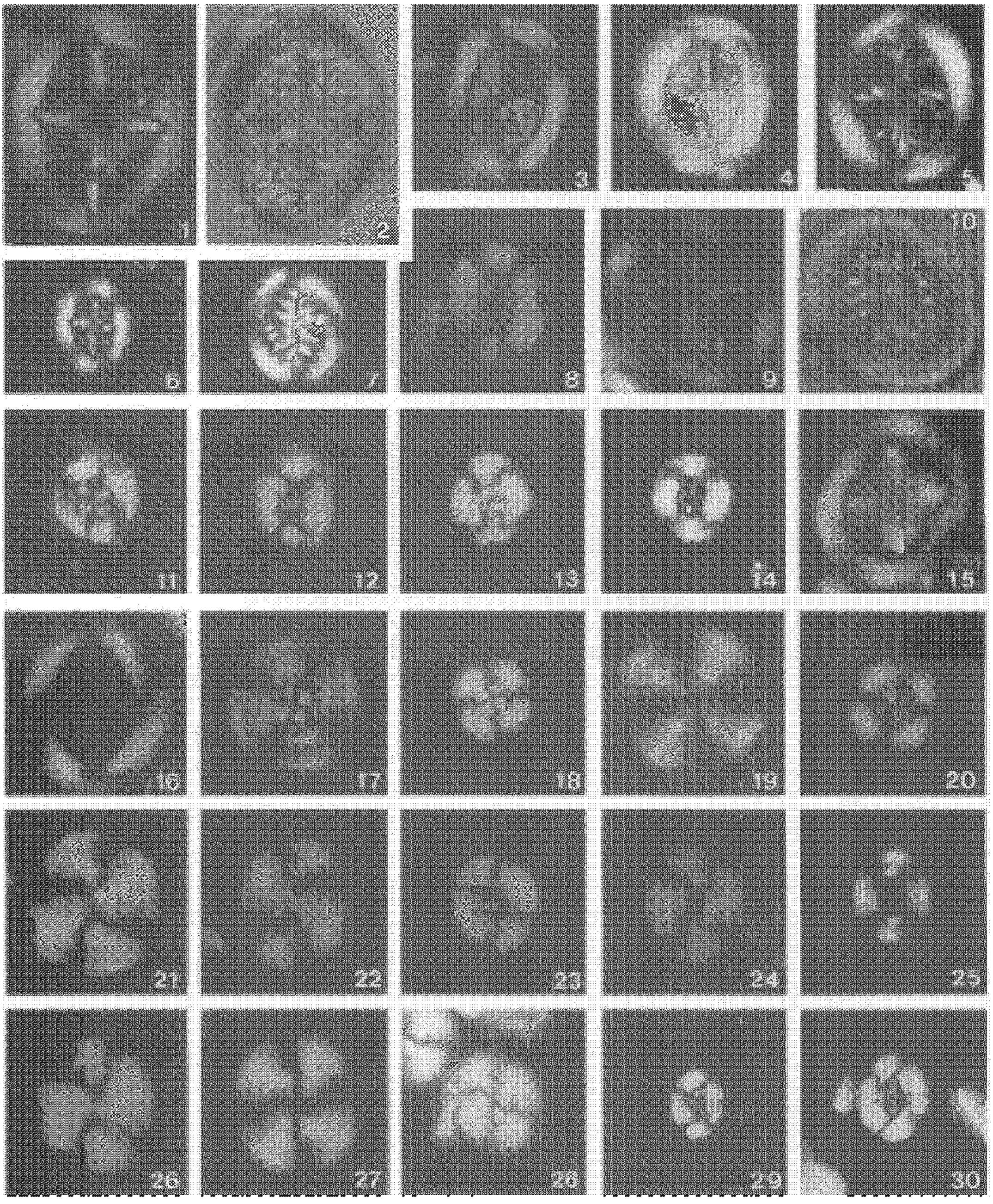
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Plate 6.8

Order ARKHANGELSKIALES Bown and Hampton *in* Bown and Young, 1997
Family ARKHANGELSKIELLACEAE Bukry, 1969 emend. Bown and Hampton *in* Bown and Young, 1997
Fig. 1. ***Arkhangelskiella antecessor***. XPL, Mont Risou, Drôme (SE France), Alb., UCL-5183-4. Range: Alb.

Figs 2–4, 8–9. ***Arkhangelskiella cymbiformis***. SEM (2, x2600), XPL (3, 4 rotated, 8, 9), Keswick, Norfolk (UK) (2), Camp., Zoe C BH (S Africa), Maast. (3, 4), Camp. (9) and DSDP Site 249 (W Indian Ocean) (8), Camp., UCL-926-9/5655-11/10/5658-14/5657-36. Large-very large; narrow rim; = Varol's (1989a) var. NT. LM differentiation between *Arkhangelskiella* and *Broinsonia* sometimes difficult: 2 and 12 show distinctions between rims. Range: Camp.–Maast.

Figs 5, 10. ***Arkhangelskiella maastrichtiana*** XPL (10 rotated), DSDP Site 217 (N Indian Ocean), Maast., UCL-5660-28/29. Large-very large; broad rim; = Varol's (1989a) var. W. Range: Maast.

Figs 6a–7. ***Arkhangelskiella confusa***. XPL, Zoe C BH (S Africa) (6a), Maast., DSDP Site 217 (N Indian Ocean) (6b), Camp. and DSDP Site 249 (W Indian Ocean) (7), Camp./Maast., UCL-5660-34/5653-31/5795-20. Small-medium; narrow rim; in LM, smaller forms easily confused with *Broinsonia enormis*, medium forms with *Broinsonia parca expansa*; partly = Varol's (1989a) var. N. Range: Con.–Maast.

Not figured. ***Arkhangelskiella paucipunctata***. Medium-very large; very convex; four rim-tiers; possibly = *A. cymbiformis* as used herein. Range: Maast.; ***Arkhangelskiella specillata***. Highly-perforate central plate. Range: Camp.–Maast.

Broinsonia Bukry, 1969 has seniority over ***Aspidolithus*** Noël, 1969 because it was published first. Noël (1970, p.75) placed the genera in synonymy herself. However, *Broinsonia* may be used for forms with an axial cross, *Aspidolithus* for those with a plate. *Broinsonia*'s central-area plate/cross is divided into quadrants by axial sutures and does not bear a spine. Perforations are not believed to be of primary importance in the species-level classification of this genus (nor in *Arkhangelskiella*), since they cannot be consistently observed.

Fig. 11. ***Broinsonia parca expansa***. XPL, Trunch BH, Norfolk (UK), Camp., UCL-2374-23. Range: Con.–Camp.

Figs 12–13. ***Broinsonia parca parca***. SEM (12, x8523), XPL (13), DSDP Site 241 (W Indian Ocean), Camp. and Hatcher's Bluff, Dallas County, Alabama (USA), Camp., UCL-5046-18/5757-30. Range: Camp.

Figs 14–15. ***Broinsonia parca constricta***. XPL, Hatcher's Bluff, Dallas County, Alabama (USA) (14), Camp. and DSDP Site 249 (W Indian Ocean) (15), Camp., UCL-5757-36/5660-20. Includes forms in which central-area closes up completely. Range: Camp.

Figs 16a–17b. ***Broinsonia verecundia***. XPL (16b and 17b rotated), DSDP Site 241 (W Indian Ocean), Camp. and Hatcher's Bluff, Dallas County, Alabama (USA), Camp., UCL-5255-35/36/1427-5/4. Range: Camp.–Maast.

Figs 18a–19. ***Broinsonia enormis***. XPL (18a rotated), Mont Risou, Drôme (SE France), Cen., UCL-5734-4/3/5733-31. Range: Alb.–?Maast.

Fig 20. ***Broinsonia furtiva***. XPL, Akers Steps, Dover, Kent (UK), Tur., UCL-5737-29. Range: Tur.–?San.

Fig. 21. ***Broinsonia? sp.***. XPL, Zoe C BH (S Africa), Camp., UCL-5664-16. Range: Camp.

Figs 22a–b, 24–25. ***Broinsonia signata***. XPL (22b, 26 rotated), Zoe C BH (S Africa), Camp. (22a, b), Maast. (24, 25), UCL-5663-19/18/5661-13/14. Rim wider than in *B. matalosa* (22); cross less distinctive than in *B. matalosa* (24, 25). Range: Apt.?–Maast.

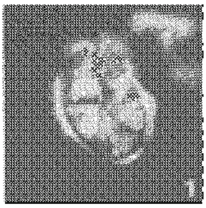
Figs 23a–b. ***Broinsonia* cf. *B. matalosa*** XPL (b rotated), Mont Risou, Drôme (SE France), Cen., UCL-5733-15/16. Cross fills central area. Range: Alb.–?Camp.

Figs 26a–c. ***Broinsonia matalosa***. PC (a), XPL (b, c rotated), The Warren, Folkestone, Kent (UK), Cen., UCL-5763-4/3/2. Range: Barr.–Camp.

Not figured. ***Broinsonia dentata***. Axial cross; teeth extend laterally from bars. Range: Camp.

Fig. 27. ***Acaenolithus cenomanicus***. XPL, Mont Risou, Drôme (SE France), Alb., UCL-5187-27. Similar to *Broinsonia* but with a spine or knob. Range: Alb.–Cen.

Figs 28–29. ***Thiersteinia ecclesiastica***. XPL (30 rotated), DSDP Site 258 (E Indian Ocean), Con., UCL-5656-25/24. Range: Tur.–Con.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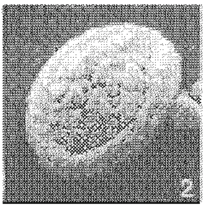
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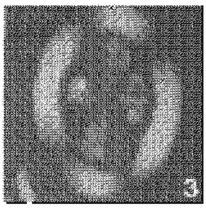
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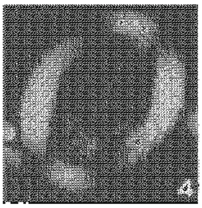
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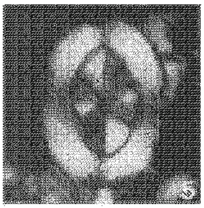
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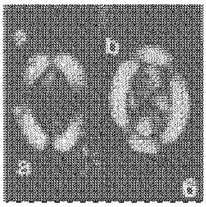
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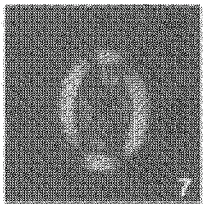
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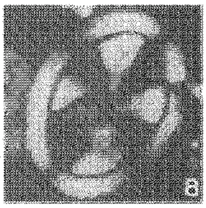
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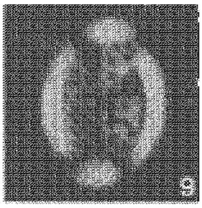
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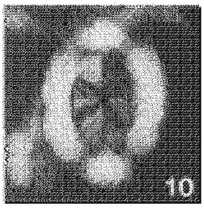
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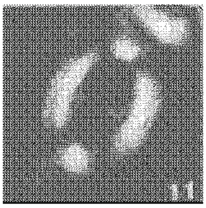
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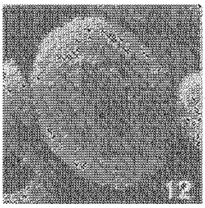
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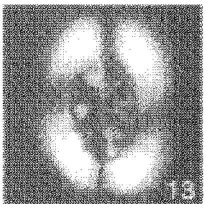
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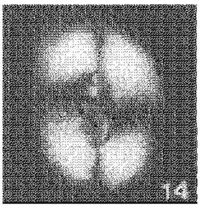
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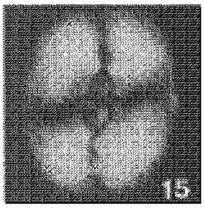
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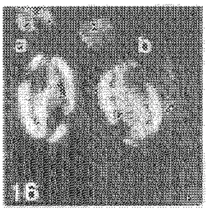
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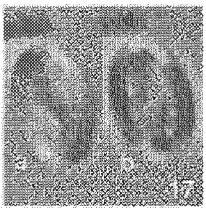
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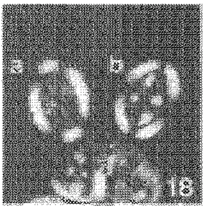
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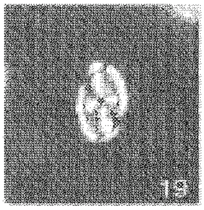
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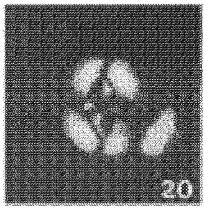
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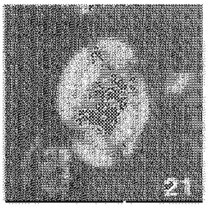
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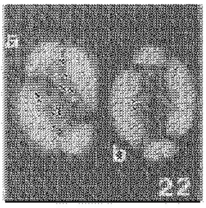
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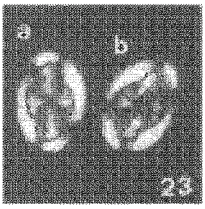
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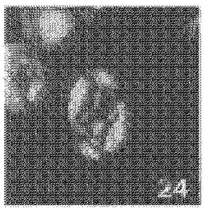
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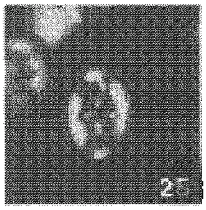
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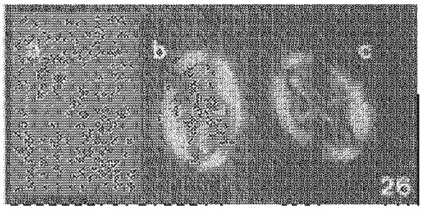
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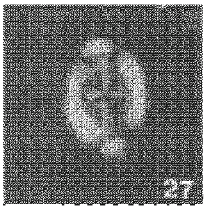
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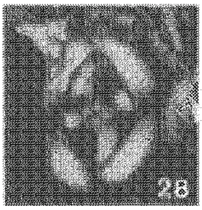
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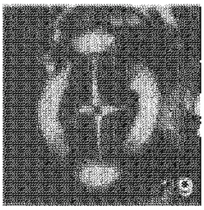
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Plate 6.9

Family KAMPTNERIACEAE Bown and Hampton *in* Bown and Young, 1997
Fig. 1. ***Crucicribrum anglicum***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5187-23. Range: Alb.–Cen.

Fig. 2. ***Gartnerago chiasta***. XPL, The Warren, Folkestone, Kent (UK), Cen., UCL-5763-9. Range: Alb.–Cen.

Fig. 3. ***Gartnerago obliquum***. XPL, DSDP Site 258 (E Indian Ocean), Cen., UCL-5796-13. Wide, perforate central plate bears subaxial cross. Range: Cen.–Con.

Figs 4–5. ***Gartnerago praeobliquum***. XPL (4), PC (5), DSDP Site 258 (E Indian Ocean), Cen., UCL-5294-13/14. Range: Alb.–Cen.

Figs 6–10. ***Gartnerago segmentatum***. PC (6), XPL (7–10), ODP Hole 738C (S Indian Ocean) (6), Maast., Waxahachie Dam Spillway, Ellis County, Texas (USA) (7), Camp., Langdon Stairs, Dover, Kent (UK), Cen. (8), Tur. (9) and Shakespeare Cliff, Dover, Kent (UK) (10), Cen., UCL-5756-23/5730-3/5666-13/5757-34/5661-26. Preservational morphotypes display distinctive overgrowth on the innermost distal cycle; often erroneously recorded as *G. obliquum*. Range: Cen.–Maast.

Figs 11–12. ***Gartnerago nanum***. XPL, The Warren, Folkestone, Kent (UK), Cen., UCL-5662-2/5665-8. Small axial cross. Range: Alb.–Cen.

Figs 13–14. ***Gartnerago theta***. XPL, Lydden Spout, Folkestone, Kent (UK), Cen., UCL-5662-21/5762-27. Central-area grill often missing. Range: Cen.

Not figured. ***Gartnerago costatum***. Perforate, cruciform central-area; perforations spanned by bars. Range: San.–Camp.

Figs 15–17. ***Kamptnerius magnificus***. XPL (15, 16), PC (17), Clay County, Mississippi (USA) (15), Maast. and Hatcher's Bluff, Dallas County, Alabama (USA), Camp., UCL-5732-30/5758-1/2. Herein includes forms with perforate central areas, i.e. *K. punctatus*, and varying degrees of central axial-cross development, i.e. *K. sculptus*. Range: Cen.–Maast.

Heterococcoliths of uncertain affinities - muroliths
Figs 18–19. ***Angulofenestrellithus snyderi***. XPL (18), PC (19), Poricy Brook, Monmouth County, New Jersey (USA), Maast., UCL-5731-34/35. Range: Camp.–Maast.

Not figured. ***Laguncula dorotheae***. Bulbous; narrow neck. Range: Alb.–?Cen.

Fig. 20. ***Laguncula montrisouensis***. XPL, Mont Risou, Drôme (SE France), Alb., UCL-5733-10. Range: Alb.–Cen.

Fig. 21. ***Tortolithus caistorensis***. XPL, Trunch BH, Norfolk (UK), Con., UCL-2373-1. Range: Con.–Camp.

Fig. 22. ***Tortolithus polygonatus***: SEM (x13182), DSDP Site 258 (E Indian Ocean), Con., UCL-5008-29. Range: Con.–Camp.

Figs 23a–b. ***Tortolithus hallii***. XPL (a), PC (b), Caistor St. Edmund, Norfolk (UK), Camp., UCL-1012-32/33. Similar to *T. pagei* but with inner rim-cycle of elongated elements. Range: Camp.

Figs 24–25. ***Tortolithus pagei***: XPL (24), PC (25), ODP Hole 738C (S Indian Ocean), Camp., UCL-5738-1/2. Range: Camp.–Maast.

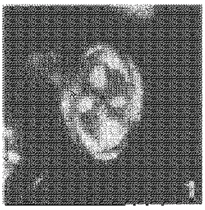
Not figured. ***Tortolithus furlongii***. Elongate; central-area filled with overlapping elements. Range: Camp.

Heterococcoliths of uncertain affinities - placoliths
Fig. 26. ***Haqius circumradiatus***. XPL, DSDP Site 258 (E Indian Ocean), Con., UCL-5759-8. Range: Berr.–Camp.

Fig. 27. ***Markalius inversus***. XPL, Curfs Quarry (The Netherlands), Maast., UCL-5731-7. Camp.–Pal.

Figs 28–29. ***Prolatipatella multicarinata***. XPL (29 rotated), near Portland, Dallas County, Alabama (USA), Camp., UCL-5703-11/12. Range: Camp.–Maast.

Figs 30a–b. ***Repagulum parvidentatum***. XPL, DSDP Site 258 (E Indian Ocean), Con., UCL-5656-23/15. Range: Haut.–Maast.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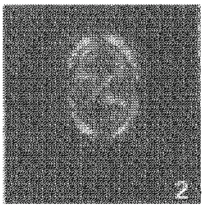
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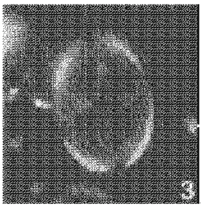
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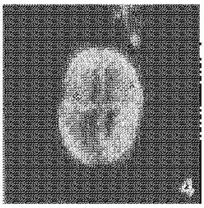
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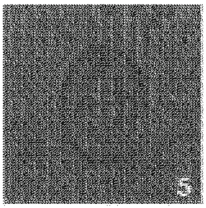
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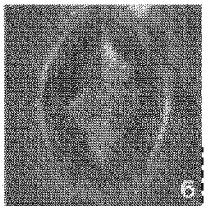
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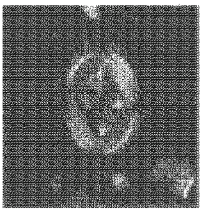
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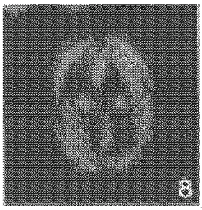
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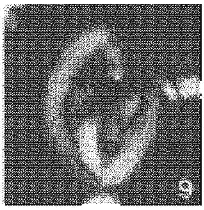
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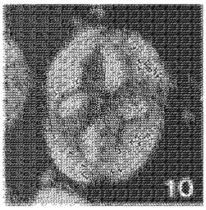
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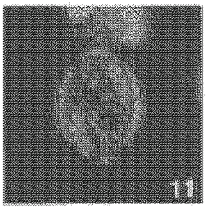
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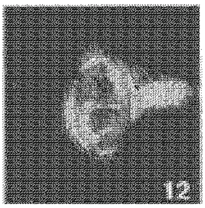
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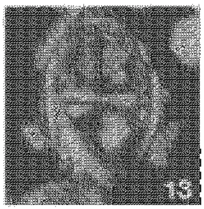
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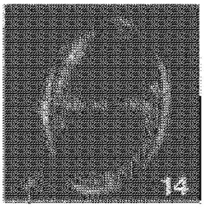
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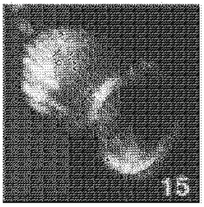
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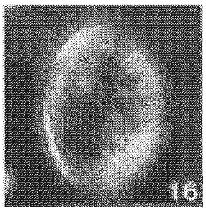
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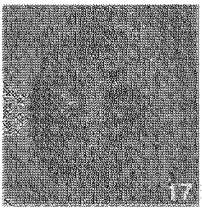
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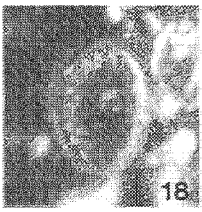
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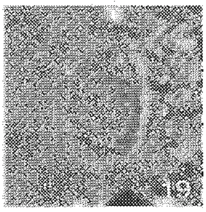
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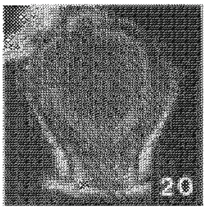
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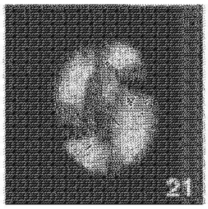
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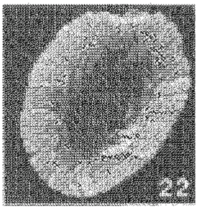
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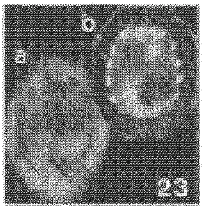
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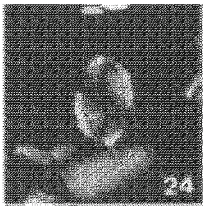
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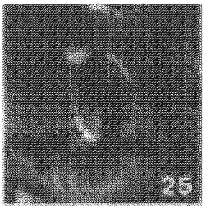
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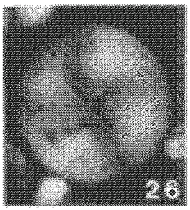
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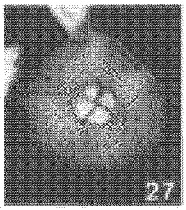
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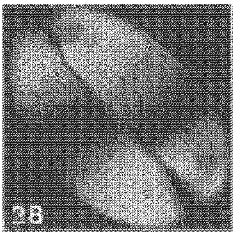
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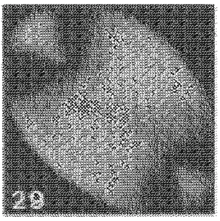
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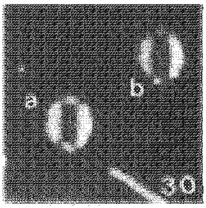
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Plate 6.10

HOLOCOCCOLITHS
Family CALYPTROSPHAERACEAE Boudreaux and Hay, 1969
Cavate with 3/4 proximal blocks
Figs 1–2. ***Acuturris scotus***. XPL, Zoe C BH (S Africa), Camp., UCL-5657-34/5664-17. Range: Cen.?–Maast.

Figs 3a–4. ***Isocrystallithus compactus***. XPL (3a rotated), Mont Risou, Drôme (SE France), Cen., UCL-5666-33/35/5667-11. Range: Alb.–Cen.

Figs 5a–c. ***Isocrystallithus* cf. *I. compactus***. XPL (c rotated), Zoe A BH (S Africa), Cen., UCL-5740-5/6/7. Range: Cen.

Figs 6a–b. **'*Owenia hillii*'**. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5666-28/5187-3. Basal plate of *I. compactus*. Range: Alb.–Cen.

Figs 7, 11–12, 16. ***Lucianorhabdus cayeuxii***. XPL, Zoe C BH (S Africa) (7, 12), Camp., near Portland, Dallas County, Alabama (USA) (11), Camp. and Trunch BH, Norfolk (UK), Camp., UCL-5659-1/5703-3/5664-3/5665-3. Possesses a variety of straight or curved shapes. Overgrowth results in specimens which appear like 16. Range: Con.–Maast.

Fig 8a. ***Calculites obscurus* side-view**. XPL, near Portland, Dallas County, Alabama (USA), Camp., UCL-5703-1. *C. obscurus* may or may not have a spine. Range: Con.?–Maast.

Fig. 8b. ***Lucianorhabdus* cf. *L. maleformis***. XPL, Black Mesa, Arizona (USA), Tur., UCL-5739-23. Range: Tur.

Figs 9a–b. ***Petrobrasiella venata***. XPL (9), PC (10), near Cottinton, Russel County, Alabama (USA), Camp., UCL-5732-7/10. Range: San.–Camp.

Figs 10a–b. ***Petrobrasiella? bownii***. XPL (a, distal view), PC (b, side-view), DSDP Site 249 (W Indian Ocean), Camp./Maast., UCL-5795-31/24. Range: Camp.?–Maast.

Fig. 13. ***Lucianorhabdus quadrifidus***. XPL, ODP Hole 761B (E Indian Ocean), Con./San., UCL-5065-13. Range: Tur.–Camp.

Figs 14–15. ***Lucianorhabdus arcuatus***. XPL, near Plymouth Bluff, Lowndes County, Mississippi (USA) (14), San. and Zoe C BH (S Africa) (15), Camp., UCL-5730-23/5664-24. Range: Con.–Camp.

Figs 17a–c. ***Lucianorhabdus maleformis***. XPL, Hatcher's Bluff, Dallas County, Alabama (USA) (a, b rotated, short), Camp. and Langdon Stairs, Dover, Kent (UK) (c, long), Con., UCL-5757-35/34/5764-10. Range: Tur.–Maast.

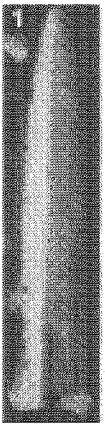
Fig. 18. ***Lucianorhabdus? cubiterminalis***. PC, Hatcher's Bluff, Dallas County, Alabama (USA), Camp., UCL-1359-2. Range: Camp.–Maast.

Figs 19–20, 24–25. ***Lucianorhabdus windii***. XPL, Zoe C BH (S Africa), Camp., UCL-5663-13/5664-7/5663-12/5664-6. Range: Camp.–?Maast.

Figs 21–22. ***Lucianorhabdus lageniformis***. XPL (21), PC (22), Hatcher's Bluff, Dallas County, Alabama (USA), Camp., UCL-1358-15/12. Range: Camp.

Fig. 23. ***Lucianorhabdus inflatus***. XPL, near Portland, Dallas County, Alabama (USA), Camp., UCL-5734-20. Range: Camp.

Not figured. ***Lucianorhabdus arborius***. Flared, fluted spine ends in small projections. Range: Maast.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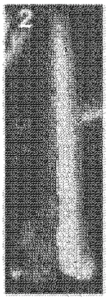
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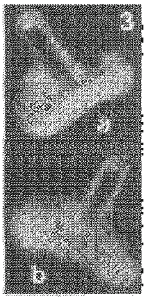
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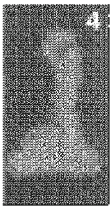
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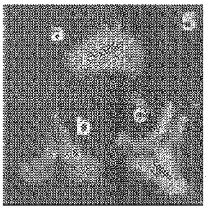
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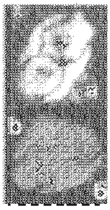
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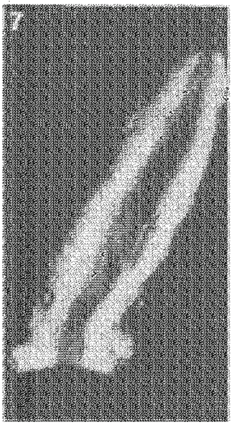
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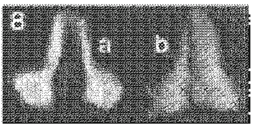
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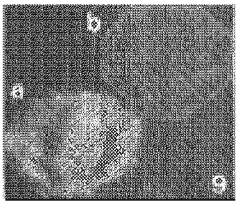
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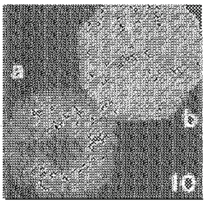
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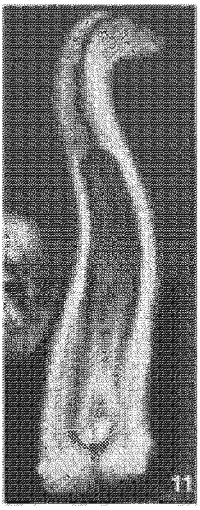
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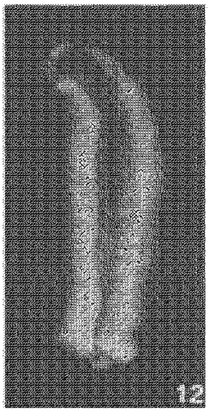
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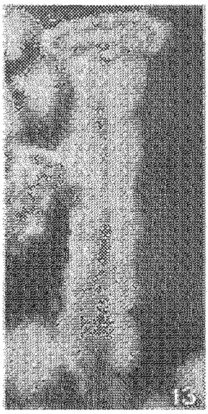
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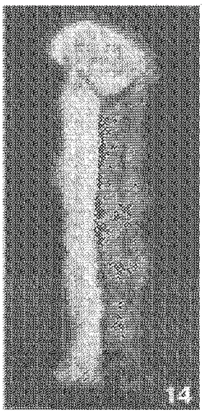
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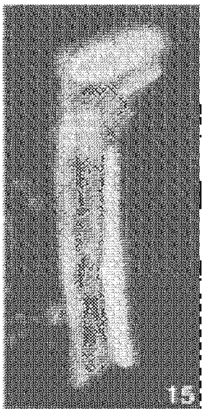
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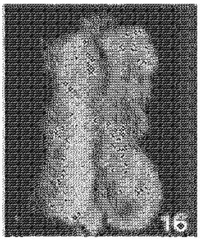
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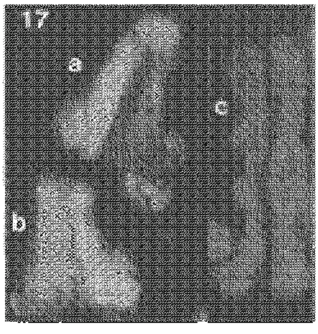
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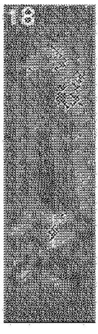
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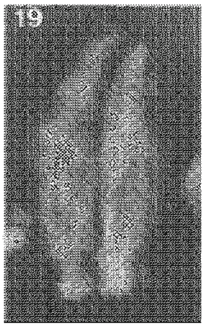
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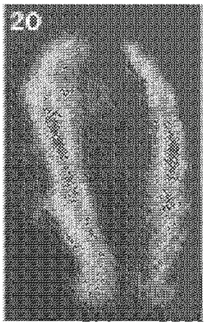
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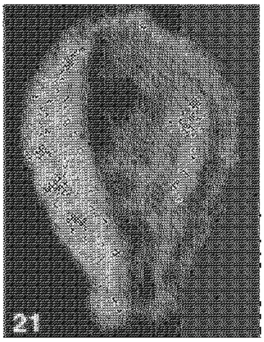
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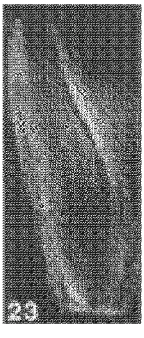
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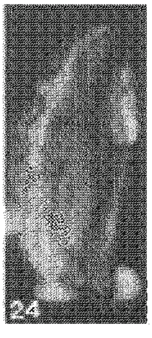
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Plate 6.11

Family CALYPTROSPHAERACEAE Boudreaux and Hay, 1969
Cavate with 3/4 proximal blocks and Rim formed from numerous small blocks with variable central structures
Upper Cretaceous holococcolith taxonomy desperately needs revision. However, this needs to be carried out in tandem with SEM analyses of the morphologies of the existing genera.

Figs 1a–b. ***Calculites additus***. XPL (b rotated), Zoe C BH (S Africa), Camp., UCL-5663-4/5. Range: Camp.?–Maast.

Figs 2a–c. ***Calculites obscurus***. XPL, Zoe C BH (S Africa) (a), Camp., near Portland, Dallas County, Alabama (USA) (b), Camp. and Norwegian Sector (North Sea) (c), Camp., UCL-5660-32/5734-19/5759-28. Range: Tur.?–Maast.

Figs 3a–b. ***Calculites ovalis***. XPL, Zoe C BH (S Africa) (a), Camp. and Coon Creek, McNairy County, Tennessee (USA) (b), Maast., UCL-5664-34/5731-15. Range: Con.?–Maast.

Figs 4a–d. ***Calculites percenis***. XPL, Black Mesa, Arizona (USA) (a, b rotated), Tur. and Zoe A BH (S Africa) (c, d rotated), Cen., UCL-5739-24/25/5740-10/9. Range: Alb.–Maast.

Not figured. ***Calculites anfractus***. Zig-zag sutures. Range: Alb.–Cen.

Figs 5a–d. ***Russellia laswellii***. XPL (b, d rotated), Zoe C BH (S Africa), Maast., UCL-5656-4/5/5655-7/6. Range: Maast.

Figs 6a–b. ***Russellia bukryi***. XPL (b rotated), Zoe C BH (S Africa), Maast., UCL-5655-3/2. Range: Maast.

Figs 7a–b. ***Octolithus* cf. *O. multiplus***. XPL (b rotated), Zoe C BH (S Africa), Maast., UCL-5660-30/31. Range: Maast.

Figs 7c–8e. ***Octolithus multiplus***. XPL, near Portland, Dallas County, Alabama (USA) (7c, 7d rotated), Camp., El Kef (Tunisia) (8a, 8b and 8c rotated), Maast. and Rügen (E Germany) (8d, 8e rotated), Maast., UCL-5758-34/35/5703-32/31/33/5757-19/20. Range: Camp.–Pal.

Figs 9a–c. ***Owenia* cf. '*O. hillii*'**. XPL, Black Mesa, Arizona (USA) (a), Tur. and Zoe A BH (S Africa) (b, c rotated), Cen., UCL-5739-4/5740-17/18. Range: Alb.–Tur.

Figs 10a–d. ***Munarinus marszalekii***? XPL, Zoe A BH (S Africa) (a, b rotated), Cen. and Black Mesa, Arizona (USA) (c, d), Tur., UCL-5739-29/30/21/9. Range: Cen.–Maast.

Figs 11a–d. ***Munarinus* cf. *M. lesliae***. XPL, Mont Risou, Drôme (SE France) (a, b rotated), Cen. and Zoe A BH (S Africa) (c, d rotated), Cen., UCL-5733-14/13/5740-12/13. Range: Cen.–?Maast.

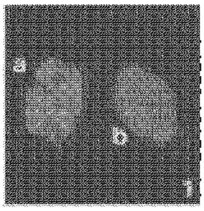
Figs 12a–b. **Holococcolith sp.1**. XPL (b rotated), near Portland, Dallas County, Alabama (USA), Camp., UCL-5734-32/33. Range: Camp.

Figs 12c–d. **Holococcolith sp.2**. XPL (d rotated), Zoe A BH (S Africa), Cen., UCL-5739-34/35. Range: Cen.

Figs 13a–d. ***Ottavianus* cf. *O. terrazetus***. XPL, Mont Risou, Drôme (SE France) (a, b rotated), Cen. and Zoe A BH (S Africa) (c, d rotated), Cen., UCL-5667-3/4/5740-3/4. Range: Cen.

Figs 14a–d. ***Ottavianus terrazetus***. XPL (a and c rotated), Zoe C BH (S Africa), Camp., UCL-5661-17/16/8/9. Range: Camp.–Maast.

Figs 15a–b. ***Orastrum* cf. *O. perspicuum***. XPL (b rotated), Zoe A BH (S Africa), Cen., UCL-5740-27/26. Range: Cen.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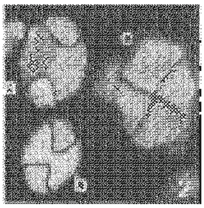
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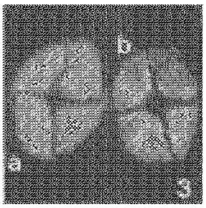
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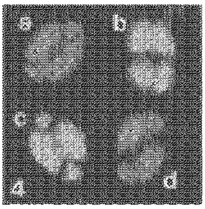
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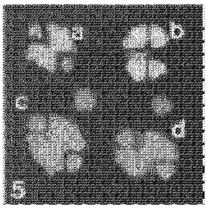
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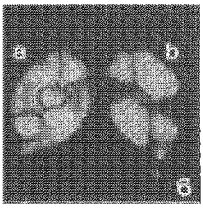
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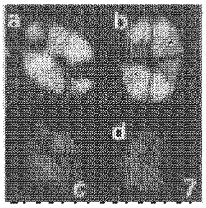
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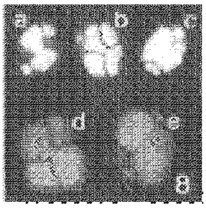
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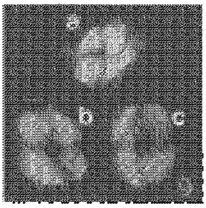
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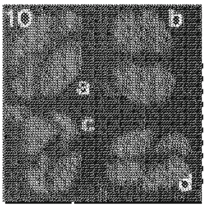
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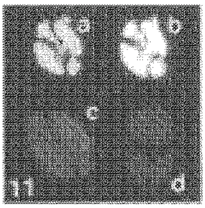
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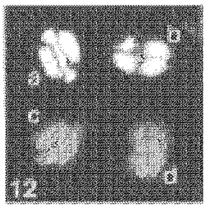
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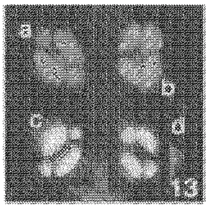
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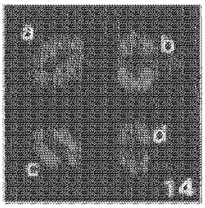
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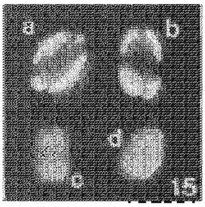
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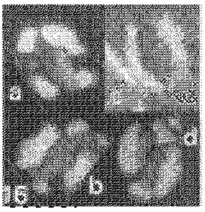
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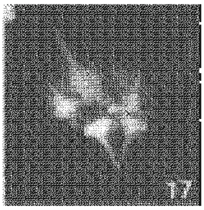
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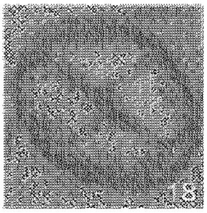
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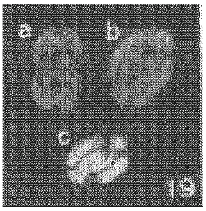
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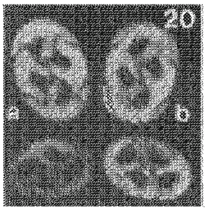
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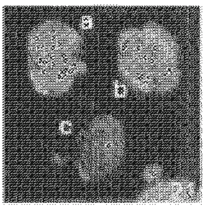
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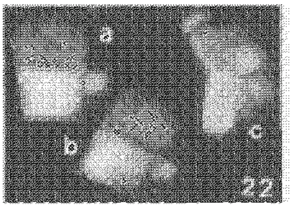
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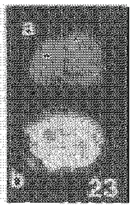
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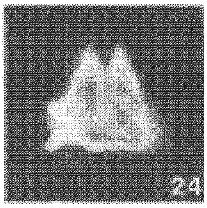
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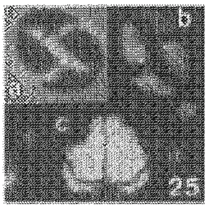
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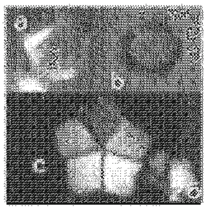
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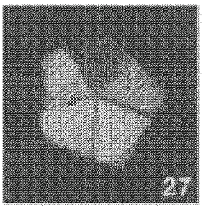
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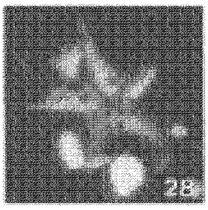
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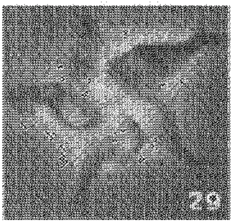
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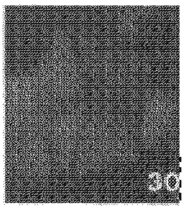
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Figs 15c–d, 21a–c. ***Orastrum perspicuum***. XPL, Zoe A BH (S Africa) (15c, d rotated), Cen. and Mont Risou, Drôme (SE France) (21a–c, 21b rotated), Cen., UCL-5740-27/26/5667-13/12/5666-27. Range: Alb.–Cen.

Not figured. ***Multipartis ripliensis***. ~Seven rim elements; ?infilled central area. Range: Maast.; ***Munarinus keadyi***. Range: Maast.; ***Ottavianus giannus***. Two central-area pores. Range: Camp.–Maast.; ***Pharus simulacrum***. Easily identifiable; low-birefringence; appears as one block with two pores. Range: Maast.; ***Ramsaya swanseana***. Short-axis bar. Range: Maast.; ***'Tetralithus' mississippiensis***. Small; divides into four blocks in one orientation, with a further two segments appearing at the ends of the ellipse in a different orientation. Range: Maast.

Figs 16a–d. ***Saepiovirgata biferula***. XPL (a, b, d rotated), PC (c rotated), Norwegian Sector (North Sea), Camp., UCL-5759-29/34/33/32. Range: Camp.

Fig. 17. **Holococcolith sp.3**. XPL, near Plymouth Bluff, Lowndes County, Mississippi (USA), San., UCL-5731-1. Range: San.

Not figured. ***Orastrum asarotum***. Medium; thin rim; central-area divides into four blocks; central pore. Range: Maast.

Fig. 18. ***Orastrum campanensis***. PC, Trunch BH, Norfolk (UK), Camp., UCL-2461-19. Range: San.?–Camp.

Figs 19a–b. ***Okkolithus australis***. XPL (b rotated), Zoe C BH (S Africa), Camp., UCL-5661-19/18. Range: Camp.–Maast.

Fig. 19c. ***Okkolithus* cf. *O. australis***. XPL, Zoe C BH (S Africa), Maast., UCL-5656-3. Range: Maast.

Figs 20a–b. ***Orastrum colligatum***. XPL (b rotated), Kiev (CIS), Cen., UCL-5660-26/27. Range: Alb.–Cen.

Figs 22a–c. ***Bifidalithus geminicatillus***. XPL (b rotated, c side-view), Norwegian Sector (North Sea), Camp., UCL-5759-20/19/21. Range: Camp.

Figs 23a–b. ***Semihololithus bicornus***. XPL (b proximal view), Zoe C BH (S Africa), Maast., UCL-5655-15/34. Range: Maast.

Fig. 24. ***Semihololithus dens***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-4054-20. Range: Cen.?–Maast.

Figs 25a–b. ***Orastrum porosuturalis***. PC (a), XPL (b), Hatcher's Bluff, Dallas County, Alabama (USA), Camp., UCL-1427-16/15. Range: San.–Camp.

Fig. 25c. ***Semihololithus priscus***. XPL, Zumaya (N Spain), Maast., UCL-5738-19. Range: Maast.–Eoc.

NANNOLITHS

Family GONIOLITHACEAE Deflandre, 1957
Figs 26a–b. ***Goniolithus fluckigeri***. XPL (a), PC (b), Tombigbee River, Sumter County, Alabama (USA), Maast., UCL-5733-4/6. Range: Con.?–Tert.

Family BRAARUDOSPHAERACEAE Deflandre, 1947
Fig. 26c. ***Braarudosphaera africana***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5733-32. Range: Alb.–Cen.

Fig. 27. ***Braarudosphaera bigelowii***. XPL, Zoe C BH (S Africa), Camp., UCL-5657-31. Range: Cen.–PD

Not figured. ***Braarudosphaera turbinea***. Pentaliths appear to 'twist' and overlap. Range: Maast.

Figs 28–29. ***Bukryaster hayi***. XPL (28), PC (29, with feet), DSDP Site 241 (W Indian Ocean) (28), Camp. and Hatcher's Bluff, Alabama (USA) (29), Camp., UCL-4050-21/1427-26. Range: Camp.

Fig. 30. ***Micrantholithus quasihoschulzii***. XPL, Langdon Stairs, Dover, Kent (UK), Con., UCL-5764-9. Range: Con.

Plate 6.12

Family LAPIDEACASSACEAE Bown and Young, 1997
Fig. 1. ***Lapideacassis asymmetrica***. XPL, Tombigbee River, Sumter County, Alabama (USA), Maast., UCL-5732-35. Range: San.–Pal.

Fig. 2. ***Lapideacassis blackii***. SEM (x3182), DSDP Site 249 (W Indian Ocean), Camp./Maast., UCL-5046-21. Range: Tur.–Pal.

Figs 3–4. ***Lapideacassis* cf. *L. bispinosa***. XPL (3), SEM (4, x11400), DSDP Site 258 (E Indian Ocean), Con., UCL-5255-3/5013-4. Range: Con.–Pal.

Fig. 5. ***Lapideacassis mariae***. XPL, The Warren, Folkestone, Kent (UK), Alb., UCL-5763-6. Range: Alb.–Maast.

Figs 6–7. **'*Pervilithus varius*'**. XPL (6), PC (7), Trunch BH, Norfolk (UK), Tur., UCL-2348-12/13. Equivalent to the larger (distal) tier of a lapideacassid. Range: Cen.–Maast.

Figs 8, 12. **Distal tier of *Lapideacassis***. SEM (x30000 and x21818, side-view), DSDP Site 401 (NE Atlantic Ocean), Camp., UCL-2473-34/33. Range: Cen.–Maast.

Fig. 9. ***Lapideacassis cornuta***. XPL, near Portland, Dallas County, Alabama (USA), Camp., UCL-5758-31. Range: Alb.–Camp.

Figs 10–11. ***Lapideacassis glans***. XPL (10), SEM (11, x16875), Abbots Cliff, Folkestone, Kent (UK) (10), Cen. and ODP Hole 765C (E Indian Ocean) (11), Con./San., UCL-5755-35/5040-16. Range: Alb.–Con./San.

Not figured. ***Lapideacassis magnifica***. Apical process ends in three/four, horizontal spines. Range: Con.?–Pal.; ***Lapideacassis tricornus***. Three vertical apical spines. Range: Alb.–Maast.; ***Lapideacassis trispina***. Three horizontal apical spines. Range: Tur.–Pal.

Family MICRORHABDULACEAE Deflandre, 1963
Figs 13, 24. ***Pseudomicula quadrata***. XPL, DSDP Site 217 (N Indian Ocean) (13), Maast. and Zumaya (N Spain) (24), Maast., UCL-5764-11/5738-11. Range: Maast.

Figs 14–15. ***Lithraphidites acutus***. XPL (14), SEM (15, x5547), Lydden Spout, Folkestone, Kent (UK) (14), Cen. and DSDP Hole 550B (NE Atlantic Ocean), Cen., UCL-5762-22/2061-23. Range: Cen.

Figs 16–18. ***Lithraphidites carniolensis***. XPL (16), SEM (17, x10500, 18, x13600), Abbots Cliff, Folkestone, Kent (UK), Cen. and DSDP Hole 550B (NE Atlantic Ocean) (17, 18), Camp., UCL-5755-31/2430-9/2434-27. Range: Berr.–Maast.

Figs 19–20. ***Lithraphidites praequadratus***. SEM (19, x12069), XPL (20), DSDP Site 401 (NE Atlantic Ocean) (19), Maast. and ODP Hole 761B (E Indian Ocean), (20), Maast., UCL-2473-22/5199-5. Range: Camp.–Maast.

Fig. 21. ***Lithraphidites pseudoquadratus***. PC, Abbots Cliff, Folkestone, Kent (UK), Cen., UCL-1044-17. Range: Cen.–Tur.

Figs 22–23. ***Lithraphidites quadratus***. SEM (22, x16406), XPL (23), DSDP Hole 550B (NE Atlantic Ocean) (22), Maast. and Zoe C BH (S Africa) (23), Maast., UCL-2184-30/5764-21. Range: Maast.

Fig. 25. ***Lithraphidites kennethii***. SEM (x15500), Tombigbee River, Sumter County, Alabama (USA), Maast., UCL-1346-1. Range: Maast.

Not figured. ***Lithraphidites alatus***. Closed-umbrella-shaped outline. Range: Alb.–Cen.; ***Lithraphidites grossopectinatus***. Long, serrated blades. Range: Maast.

Figs 26–27. ***Microrhabdulus helicoideus***. SEM (26, x7308), XPL (27), DSDP Hole 550B (NE Atlantic Ocean) (26), Camp. and Waxahachie Dam Spillway, Ellis County, Texas (USA) (27), Camp., UCL-2434-1/5730-6. Range: Con.–Maast.

Figs 28–31. ***Microrhabdulus belgicus***. XPL (28, 29 rotated), SEM (30, x14000, 31, x31500), DSDP Site 249 (W Indian Ocean) (28, 29), Camp./Maast. and DSDP Hole 550B (NE Atlantic Ocean), San. (30), Camp. (31), UCL-5795-18/17/2436-29/2434-19. Range: Alb.–Maast.

Figs 32–34. ***Microrhabdulus decoratus***. SEM (32, x21539, 33, x5667), XPL (34), DSDP Site 401 (NE Atlantic Ocean) (32, 33), Maast. and DSDP Site 249 (W Indian Ocean) (34), Camp./Maast., UCL-2470-24/22/5659-15. A thin, possibly precursor form, *Microrhabdulus* cf. *M. decoratus*, occurs sporadically in the Alb. and Cen.. Range: Cen.–Maast.

Figs 35–37. ***Microrhabdulus undosus***. XPL (36 and 37 rotated), Clay County, Mississippi (USA), Maast., UCL-5732-25/26/27. Range: Camp.–Maast.

Family NANNOCONACEAE Deflandre, 1959
Fig. 38. ***Nannoconus dislocatus***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5733-24. Range: Haut.–Cen.

Fig. 39. ***Nannoconus elongatus***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5733-25. Range: Barr.–Camp.

Fig. 40. ***Nannoconus multicadus***. TL, DSDP Hole 550B (NE Atlantic Ocean), Camp., UCL-2271-14. Range: Alb.–Camp.

Fig. 41. ***Nannoconus truitti frequens***. XPL, Mont Risou, Drôme (SE France), Cen., UCL-5187-18. Range: Apt.–Camp.

Fig. 43. ***Nannoconus truitti rectangularis***. PC, DSDP Site 549 (NE Atlantic Ocean), Cen., UCL-2240-17. Range: Alb.–Camp.

Fig. 42. ***Nannoconus vocontiensis***. PC, DSDP Site 549 (NE Atlantic Ocean), Alb., UCL-2239-30. Range: Apt.–Cen.

Fig. 44. ***Nannoconus* sp. cross-section**. XPL, DSDP Hole 550B (NE Atlantic Ocean), Camp., UCL-2262-15.

Not figured. ***Nannoconus dauvillieri***. Thin; elongated; flared at one end. Range: Alb.–Camp. ***Nannoconus farinacciae***. Pear-shaped; narrow canal. Range: Con.–Camp. ***Nannoconus minutus***. Small; rectangular; canal-width = wall-thickness. Range: Haut.–Camp.; ***Nannoconus regularis***. Elongated dome-shaped; narrow canal. Range: Alb.–Camp.; ***Nannoconus truitti truitti***. Bulging-rectangle-shaped; narrow canal. Range: Apt.–Camp.

Plate 6.13

Family POLYCYCLOLITHACEAE Forchheimer, 1972 emend. Varol, 1992
Figs 1–2. ***Eprolithus apertior***. PC (1), XPL (2, side-view), Copt Point, Folkestone, Kent (UK) (1), Alb. and The Warren, Folkestone, Kent (UK) (2), Cen., UCL-2449-3/5665-23. Range: Apt.–Tur.

Figs 3a–b. ***Eprolithus floralis***. XPL (b side-view), Pd-1 Brezno BH (Czech Republic), Con., UCL-5756-28/31. Range: Apt.–?Camp.

Figs 4a–b. ***Eprolithus octopetalus***. XPL, BMS-4 BH, Arizona (USA), Tur., UCL-5737-3/7. Range: Tur.

Figs 5a–6. ***Eprolithus moratus***. XPL, BMS-4 BH, Arizona (USA) (5a, b), Tur. and ODP Hole 761B (E Indian Ocean) (6), Con./San., UCL-5737-4/5/5065-10. Range: Tur.–?San. (*Eprolithus moratus* (Stover, 1966) Burnett comb. nov.: *Lithastrinus moratus* Stover, 1966, p.149, pl.7, fig.20. Cretaceous coccoliths and associated nannofossils from France and the Netherlands. *Micropaleontology*, **12** (2), 133–167.)

Fig. 7. ***Lithastrinus septenarius***. XPL, DSDP Site 258 (E Indian Ocean), Con., UCL-5255-6. Range: Tur.–San.

Fig. 8. ***Eprolithus rarus***? XPL, ODP Hole 765C (E Indian Ocean), Camp., UCL-5704-35. Range: Tur.–?Camp.

Figs 9a–b. ***Lithastrinus grillii***. XPL, near Plymouth Bluff, Lowndes County, Mississippi (USA) (a focused on lower cycle, b focused on upper cycle), San., UCL-5730-32/33. Range: Con.–Camp.

Figs 10a–b. ***Lithastrinus quadricuspis***. XPL, near Portland, Dallas County, Alabama (USA) (a), Camp. and DSDP Site 249 (W Indian Ocean) (b), Camp., UCL-5703-2/5659-25. Range: Camp.–?Maast.

Not figured. ***Lithastrinus pentabrachius***. Five-rayed form. Range: Camp.

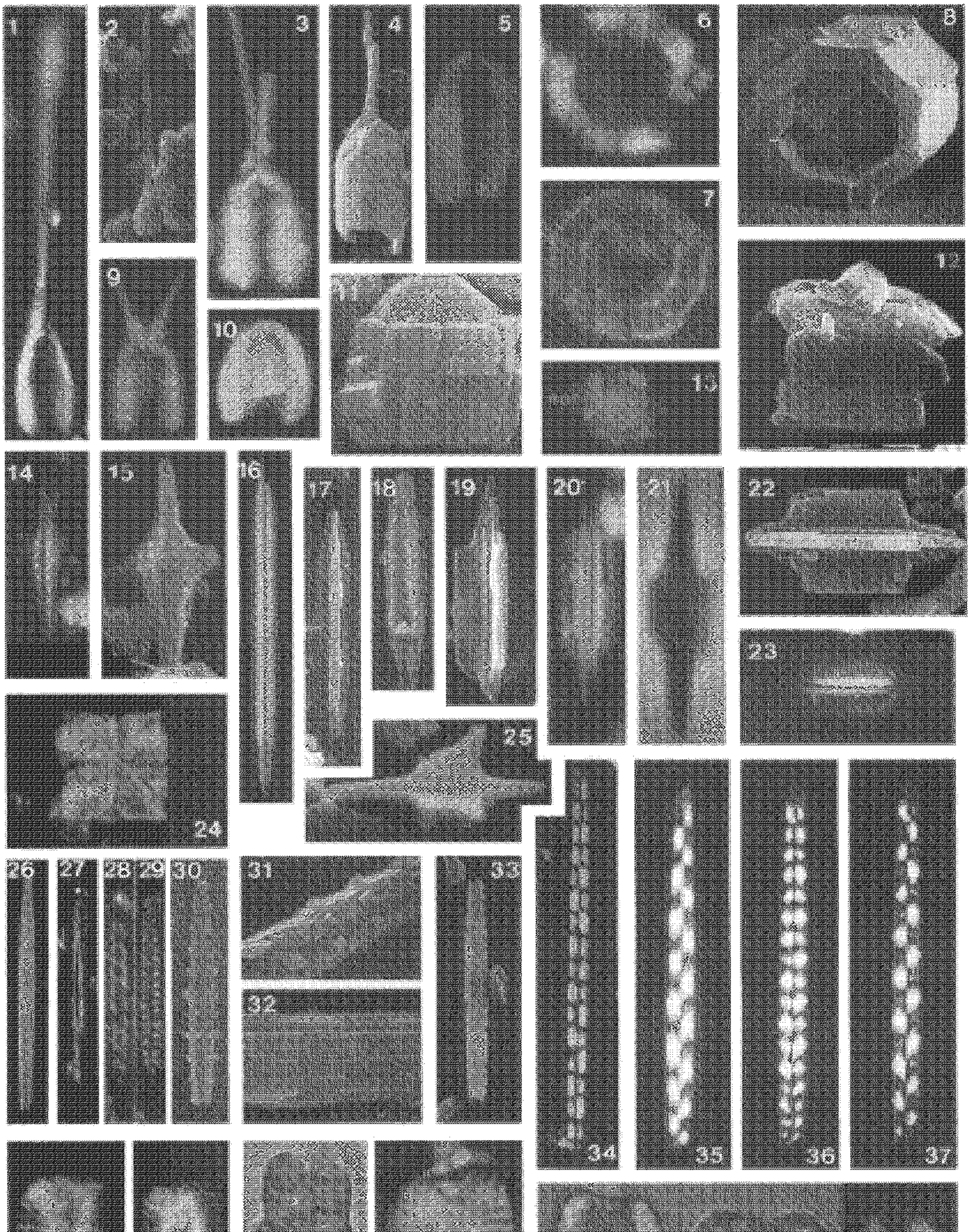
Not figured. ***Radiolithus hollandicus***. >Nine elements. Range: Apt.?–Cen.

Fig. 11. ***Radiolithus planus***. XPL, S-13 BH, Tarfaya (Morocco), Tur., UCL-5756-24. Range: Alb.–Tur.

Figs 12a–b. ***Quadrum gartneri***. XPL, DSDP Site 217 (N Indian Ocean) (a), Camp. and DSDP Site 258 (E Indian Ocean) (b), Con., UCL-5653-28/5656-20. Range: Tur.–?Maast.

Figs 12c–d. ***Quadrum intermedium***. PC (c, 5 elements), XPL (d, 7 elements), Akers Steps, Dover, Kent (UK) (c), Tur. and Norwegian Sector (North Sea) (d), Tur., UCL-949-18/5759-36. Five to eight elements per cycle, one to three of which are smaller and inserted between the regular elements. Range: Cen.–Tur.

Fig. 13. ***Quadrum giganteum***. XPL, Norwegian Sector (North Sea), Tur., UCL-5759-34. Range: Tur.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Not figured. ***Quadrum eneabrachium***. Nine regularly-spaced elements per cycle. Range: Alb.–San.; ***Quadrum eptabrachium***. Seven regularly-spaced elements per cycle. Range: Tur.–San.; ***Quadrum octobrachium***. Eight regularly-spaced elements per cycle. Range: Tur.

Figs 14–15. ***Uniplanarius gothicus***. XPL, ODP Hole 761B (E Indian Ocean) (14), Camp. and DSDP Site 241 (W Indian Ocean) (15), Camp., UCL-5704-27/5255-32. Range: San.–Maast.

Figs 16–17. ***Uniplanarius sissinghii***. XPL, DSDP Site 241 (W Indian Ocean), Camp./Maast. (16), Camp. (17), UCL-5202-28/4050-6. Range: Camp.–?Maast.

Figs 18–19b. ***Uniplanarius trifidus***. XPL, DSDP Site 217 (N Indian Ocean) (18), Camp./Maast., near Portland, Dallas County, Alabama (USA) (19a), Camp. and DSDP Site 241 (W Indian Ocean) (19b), Camp., UCL-5657-9/5734-34/5796-31. Range: Camp.–Maast.

Fig. 20. ***Uniplanarius* cf. *U. trifidus***. XPL, Trunch BH, Norfolk (UK), Camp., UCL-2340-2. Range: Camp.

Figs 21–22a. ***Quadrum svabenickae***. XPL, DSDP Site 249 (W Indian Ocean) (21), Camp. and ODP Hole 761B (E Indian Ocean) (22), Camp., UCL-4055-9/5704-24. Range: Con.–Maast.

Figs 22b–c. ***Quadrum bengalensis***. XPL (c rotated), DSDP Site 217 (N Indian Ocean), Maast., UCL-5763-25/24. Range: Maast.

Fig. 23a. ***Micula cubiformis***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-5659-8. Holococcolith. Range: Con.–Maast.

Figs 23b–c. ***Micula concava***. TL (b), XPL (c), DSDP Hole 550B (NE Atlantic Ocean), Camp., UCL-2506-28/29. Holococcolith. Range: Con.–Maast.

Figs 24a–c. ***Micula adumbrata***. PC (a, b rotated), XPL (c), Pd-1 Brezno BH (Czech Republic), Con., UCL-5757-8/9/6. Range: Con.

Fig. 25. ***Micula staurophora***. XPL, near Ripley, Tippah County, Mississippi (USA), Camp., UCL-5731-13. Range: Con.–Maast.

Fig. 26. ***Micula swastica***. XPL, ODP Hole 761B (E Indian Ocean), Maast., UCL-5200-24. Range: Con.–Maast.

Figs 27a–b. ***Micula praemurus***. XPL, DSDP Site 217 (N Indian Ocean) (a), Maast. and near Portland, Dallas County, Alabama (USA) (b), Camp., UCL-5599-25/5703-17. Range: Camp.–Maast.

Figs 28–29. ***Micula murus***. XPL, ODP Hole 761B (E Indian Ocean) (28), Maast. and DSDP Site 217 (N Indian Ocean) (29), Maast., UCL-5199-30/5704-15. Range: Maast.

Fig. 30. ***Micula prinsii***. XPL, Clay County, Mississippi (USA), Maast., UCL-5732-29. Range: Maast.

Plate 6.14

Uncertain 'polycycloliths'

Fig. 2c. ***Hexalithus gardetae***. XPL, DSDP Site 401 (NE Atlantic Ocean), Camp., UCL-2468-35. Range: San.–Camp.

Fig. 1a. ***Rucinolithus hayi***. XPL, Norwegian Sector (North Sea), Camp., UCL-5738-31. Range: San.–Camp.

Figs 2a–b. ***Rucinolithus? magnus***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-5658-24/17. Range: Camp.–Maast.

Fig. 1b. ***Rucinolithus? sp.***. XPL, DSDP Site 249 (W Indian Ocean), Camp., UCL-5763-33. Range: Camp.

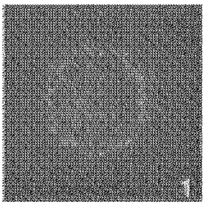
Unclassified nannoliths

Fig. 5. ***Ceratolithina naturalisteplateauensis***. XPL, DSDP Site 258 (E Indian Ocean), Cen., UCL-5759-15. Range: Alb.–?Tur.

Fig. 6. ***Ceratolithina duplex duplex***. XPL, DSDP Site 258 (E Indian Ocean), Alb./Cen., UCL-5251-21. Range: Alb.–Cen.

Fig. 10. ***Ceratolithina copis***. XPL, DSDP Site 258 (E Indian Ocean), Alb./Cen., UCL-5250-35. Range: Alb.–?Tur.

Fig. 4. ***Ceratolithina cruxii capitanea***. XPL (x940), DSDP Site 258 (E Indian Ocean), Alb./Cen., UCL-5601-16. Range: Alb.?–Cen.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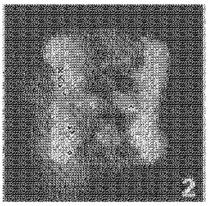
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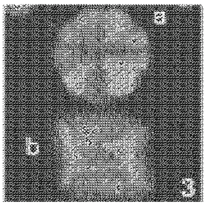

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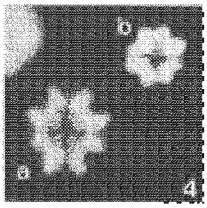

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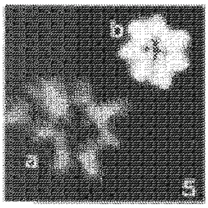

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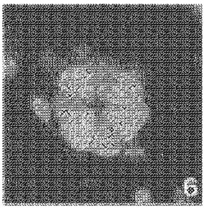
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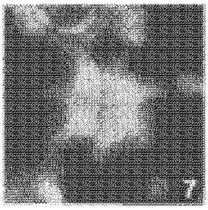
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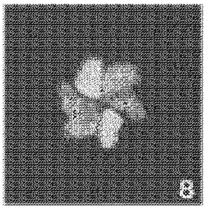
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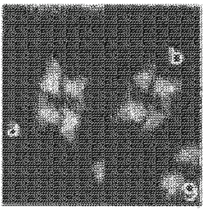

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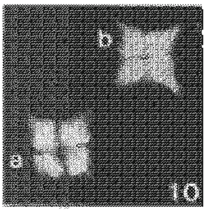

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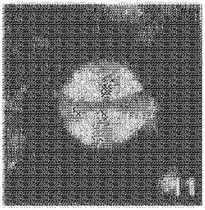
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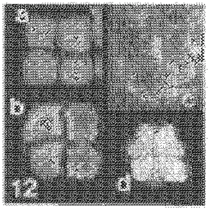

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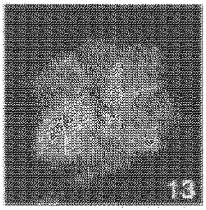
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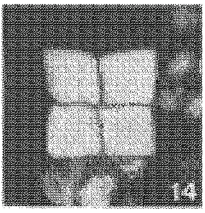
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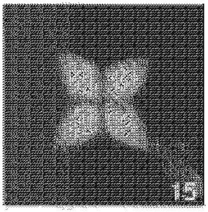
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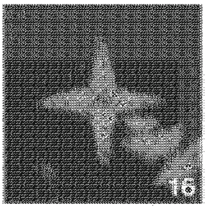
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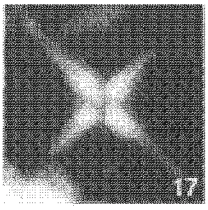
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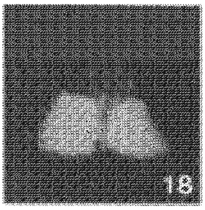
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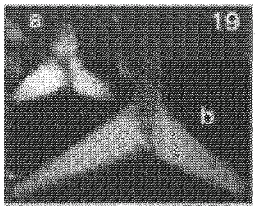

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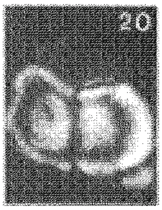
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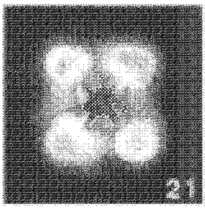
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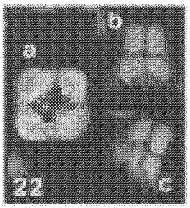

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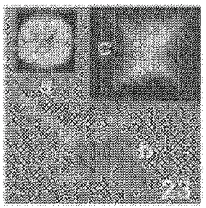

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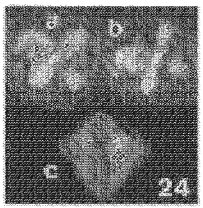

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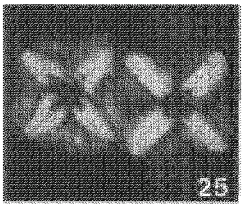
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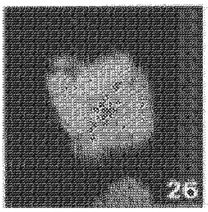
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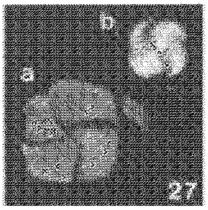

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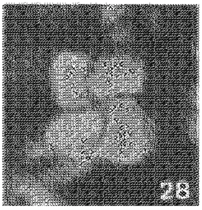
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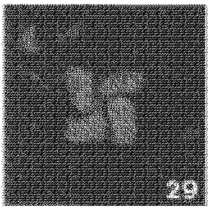
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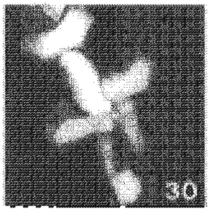
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Fig. 7. ***Ceratolithina cruxii cruxii***. XPL, DSDP Site 258 (E Indian Ocean), Alb./Cen., UCL-5601-6. Range: Alb.–Cen.

Fig. 9. ***Ceratolithina duplex gemina***. XPL (x940), DSDP Site 258 (E Indian Ocean), Cen., UCL-5250-27. Range: Cen.

Fig. 3. ***Ceratolithina hamata falcata***. XPL, DSDP Site 258 (E Ind. Ocean), Cen., UCL-5601-30. Range: Alb.–?Tur.

Fig. 8. ***Ceratolithina hamata hamata***. XPL, DSDP Site 258 (E Indian Ocean), Cen., UCL-5796-15. Range: Alb.–?Tur.

Not figured. ***Ceratolithina bicornuta***. 'H'-shaped; two horns. Range: Alb.

Fig. 11a, 12a–b. ***Ceratolithoides aculeus***. XPL, near Portland, Dallas County, Alabama (USA) (11a), Camp. and DSDP Site 217 (N Indian Ocean), Camp., UCL-5703-4/5653-22/23. Range: Camp.–Maast.

Fig. 11b. ***Ceratolithoides kamptneri***. XPL, El Kef (Tunisia), Maast., UCL-5704-11. Range: Maast.

Figs 13a–b. ***Ceratolithoides prominens***. XPL (b rotated), DSDP Site 249 (W Indian Ocean), Camp., UCL-5658-15/16. Range: Camp.–Maast.

Figs 14a–b. ***Ceratolithoides brevicorniculans***. XPL (b rotated), DSDP Site 249 (W Indian Ocean), Camp./Maast., UCL-5659-10/11. Range: Camp.–Maast.

Figs 15a–b. ***Ceratolithoides verbeekii***. XPL (b rotated), DSDP Site 249 (W Indian Ocean), Camp., UCL-5763-34/35. Range: Camp.

Fig. 16a. ***Ceratolithoides arcuatus***. XPL, DSDP Site 241 (W Indian Ocean), Camp., UCL-5255-33. Range: Camp.–?Maast.

Fig. 16b. ***Ceratolithoides quasiarcuatus***. XPL, DSDP Site 241 (W Indian Ocean), Camp., UCL-4050-10. Range: Camp.–Maast.

Figs 17a–b. ***Ceratolithoides sesquipedalis***. XPL, DSDP Site 241 (W Indian Ocean), Camp., UCL-5255-34/4050-2. Range: Camp.–Maast.

Figs 18a–b. ***Ceratolithoides indiensis***. XPL (b rotated), DSDP Site 217 (N Indian Ocean), Maast., UCL-5599-27/28. Range: Camp.–Maast.

Figs 19a–b. ***Ceratolithoides longissimus***. XPL (b rotated), ODP Hole 761B (E Indian Ocean), Camp., UCL-5201-22/21. Range: Camp.–Maast.

Figs 21a–b. ***Ceratolithoides amplector***. XPL (b rotated), ODP Hole 761B (E Indian Ocean), Maast., UCL-5201-12/13. Range: Camp.–Maast.

Figs 22a–b. ***Ceratolithoides pricei***. XPL (b rotated), ODP Hole 761B (E Indian Ocean), Maast., UCL-5201-5/4. Range: Camp.–Maast.

Figs 23a–b. ***Ceratolithoides self-trailiae***. XPL (b rotated), DSDP Site 217 (N Indian Ocean), Maast., UCL-5653-4/3. Range: Camp.–Maast.

Figs 24a–b. ***Ceratolithoides ultimus***. XPL (b rotated), DSDP Site 217 (N Indian Ocean), Maast., UCL-5763-29/28. Range: Maast.

Not figured. ***Ceratolithoides* sp.**. Conical; >six horns. Range: Camp.–?Maast.

Not figured. ***Liliasterites angularis***. Six pointed rays alternating on two levels; Range: Tur.

Figs 20, 25. ***Marthasterites furcatus***. PC (20), SEM (25, x21818), DSDP Site 258 (E Indian Ocean) (20), Con. and DSDP Hole 550B (NE Atlantic Ocean) (25), San., UCL-5759-7/2436-33. Range: Tur.–Camp.

Figs 26a–27. ***Marthasterites crassus***. XPL (26a), PC (26b), SEM (27, x27000), Waxahachie Dam Spillway, Ellis County, Texas (USA) (26a), Camp., Brezno (Czech Republic) (26b), Con. and DSDP Hole 550B (NE Atlantic Ocean) (27), San., UCL-5730-7/5740-35/2435-4. Range: Tur.–Camp.

Fig. 28a. ***Marthasterites inconspicuus***. PC, Brezno (Czech Republic), Con., UCL-5755-9. Range: Con.–San.

Figs 28b–29. ***Marthasterites simplex***. PC (28b), SEM (29, x17368), Brezno (Czech Republic) (28b), Con. and DSDP Hole 550B (NE Atlantic Ocean) (29), San., UCL-5755-6/2508-8. Range: Tur.–Camp.

Not figured. ***Watkinsia pedalion***. Elliptical base; looks like a boat's rudder in side-view. Range: San.

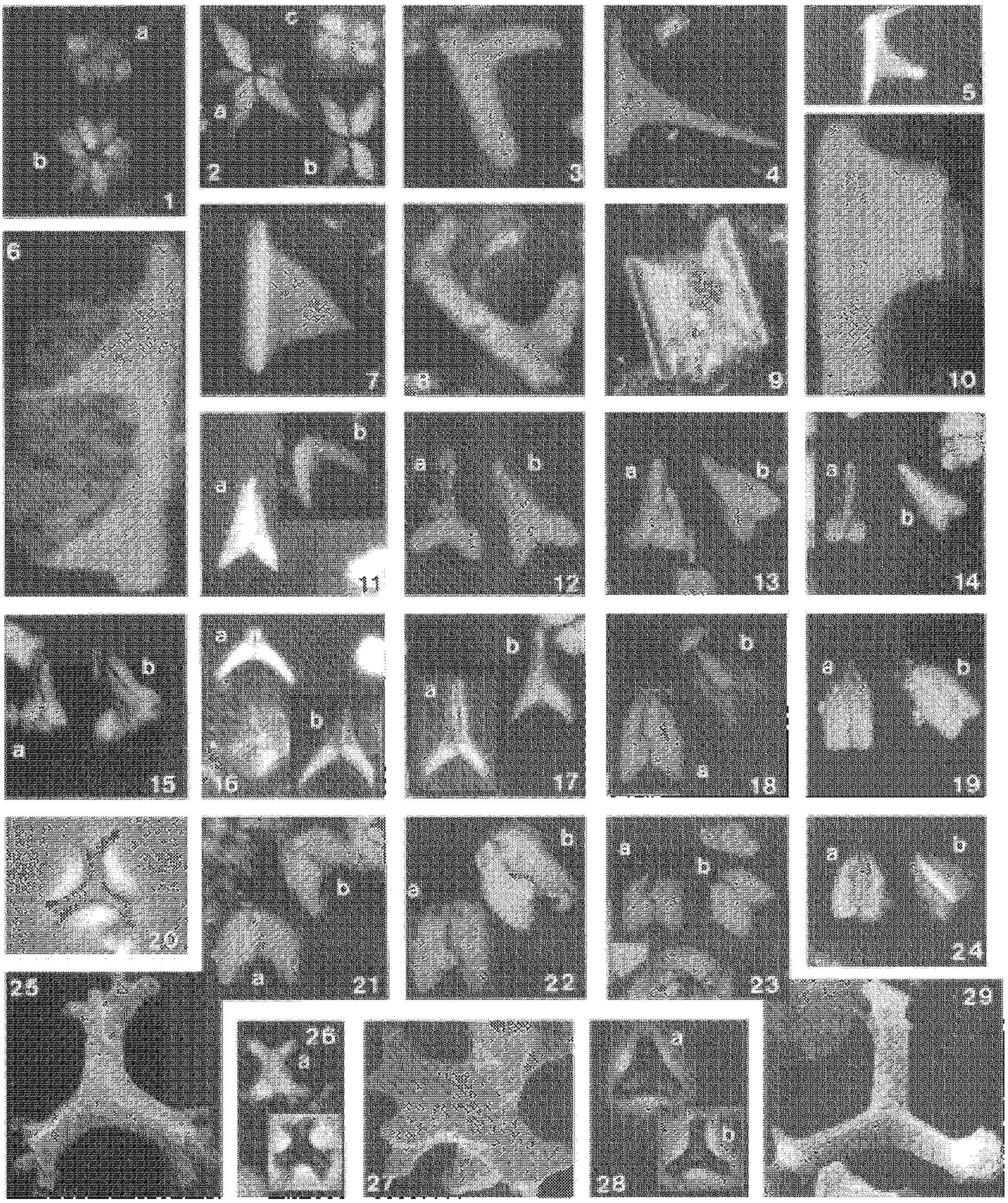
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Plate 6.15

K/T BOUNDARY TAXA

Survivors

Figs 1a–b. ***Biscutum melaniae***. XPL (b rotated), Sewerby Cliff-Danes Dyke, Humberside (UK), Camp., UCL-5764-4/5.

Fig. 2. ***Markalius inversus***. XPL, DSDP Site 217 (N Indian Ocean), Pal. (NP1), UCL-5764-27.

Figs 3a–b. ***Neocrepidolithus cohenii***. XPL (b rotated), DSDP Site 217 (N Indian Ocean), Pal. (NP1), UCL-5764-33/34.

Figs 4a–b. ***Neocrepidolithus neocrassus***. XPL, El Kef (Tunisia) (a), Pal. (high NP1) and DSDP Site 217 (N Indian Ocean) (b), Pal. (NP1), UCL-5704-10/5764-36.

Fig. 5. ***Zeugrhabdotus sigmoides***. XPL, DSDP Site 217 (N Indian Ocean), Pal. (NP1), UCL-5764-32.

Figs 6–7. ***Braarudosphaera bigelowii***. XPL (6, coccosphere), SEM (7), W Africa (6), Camp. and El Kef (Tunisia) (7), Pal. (low NP1), UCL-5764-24/5375-24.

Fig. 15a. **'*Thoracosphaera*' sp. fragment**. XPL, El Kef (Tunisia), Pal. (low NP1), UCL-5703-36.

Incoming taxa

Fig. 8. ***Neochiastozygus* sp.**. SEM (distal view), El Kef (Tunisia), Pal. (low NP1), UCL-5374-33. Bicyclic rim; axial cross slightly rotated.

Fig. 9. **?*Chiastozygus ultimus***. SEM (distal view), El Kef (Tunisia), Pal. (high NP1), UCL-5374-13. Reduced or absent inner rim-cycle; rotated axial cross with lateral teeth.

Fig. 10. ***Neochiastozygus* sp.**. SEM (distal view), El Kef (Tunisia), Pal. (low NP1), UCL-5375-21. Bicyclic rim; low-angled cross about short ellipse axis.

Figs 16e–f. ***Neochiastozygus* sp.**. XPL, El Kef, (Tunisia), Pal. (low NP1), UCL-5553-19/20.

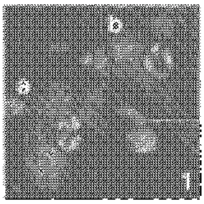
Figs 11-13, 17a–b. ***Cruciplacolithus primus***. SEM (11-12, distal views; 13, proximal view showing complex, layered construction of proximal shield typical of Cenozoic placoliths of the Coccolithaceae (see Young, 1992)), XPL (17a-b), El Kef (Tunisia) (11-13, 17a), Pal. (high NP1) and DSDP Site 217 (N Indian Ocean) (17b), Pal. (NP1), UCL-5374-16/5375-7/6/5704-3/5764-30.

Fig. 14. ***Biantholithus sparsus***. XPL, DSDP Site 217 (N Indian Ocean), Pal. (NP1), UCL-5764-31.

Figs 16a–b, 18–19, 22–23. ***Futyania petalosa***. XPL (16a, plan view, 16b, side-views), SEM (18, coccosphere, 19, side-view (1μm=9mm), 22, coccosphere close-up showing coccoliths with/without spines, 23, close-up of inner coccosphere surface showing proximal coccolith views), El Kef (Tunisia), Pal. (high NP1), UCL-5704-7/4+3/5375-9/5734-3/5374-36/5376-6.

Fig. 24. ***Praeprinsius dimorphosus***. SEM (close-up of proximal coccoliths on coccosphere, showing similarity to *Futyania*), El Kef (Tunisia), Pal. (high NP1), UCL-5374-18.

Figs 15b, 16c–d, 20–21, 25–26. ***Neobiscutum parvulum***. XPL (15b and 16c, coccospheres), PC (16d, two specimens), SEM (20 and 21, coccospheres, 25 and 26, respective close-ups), El Kef (Tunisia) (15b, 16d, 20-21, 25-26), Pal. (low NP1) and Chattahoochee River, Quitman County, Georgia (USA) (16c), Maast., UCL-5703-36/5731-20/5565-19/5375-26/16/29/17.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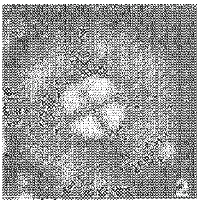
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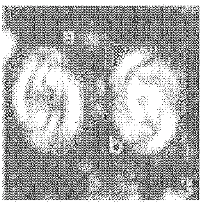
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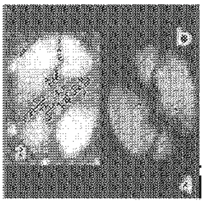
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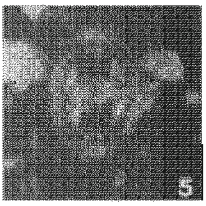
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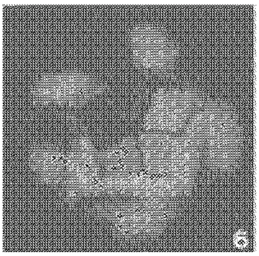
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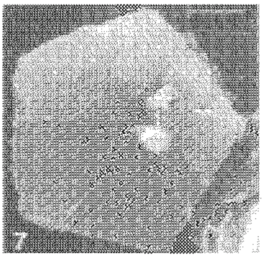
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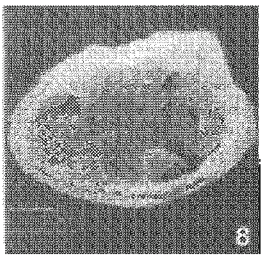
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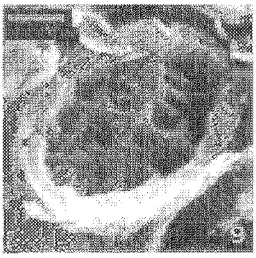
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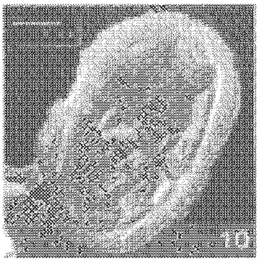
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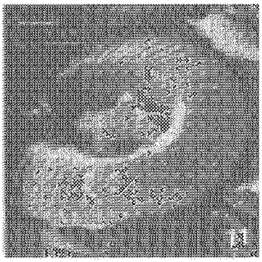
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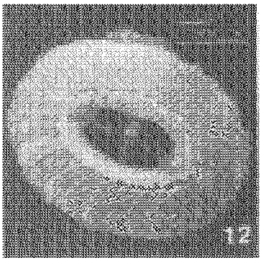
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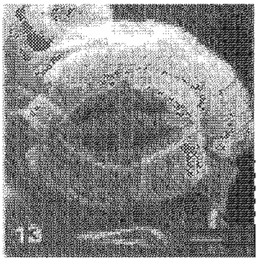
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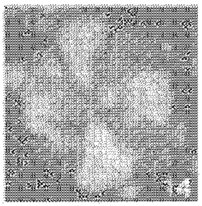
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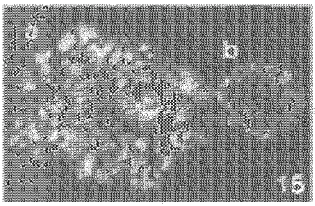
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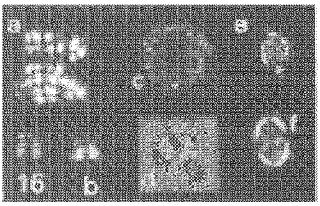
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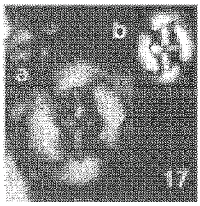
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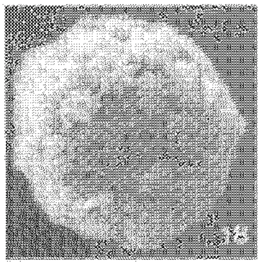
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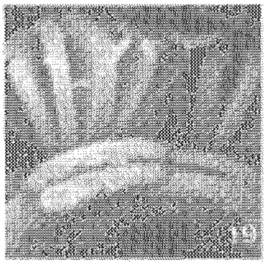
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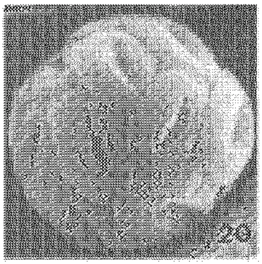
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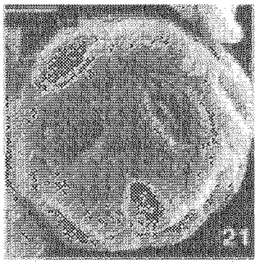
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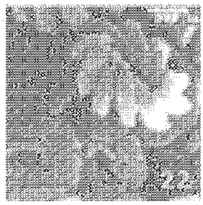
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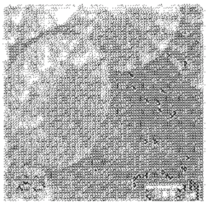
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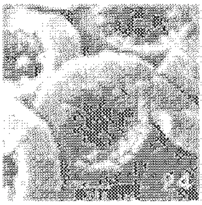
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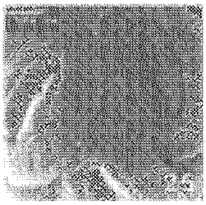
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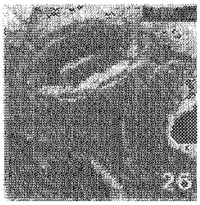
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7

Palaeogene

O. Varol

7.1 INTRODUCTION

Intense hydrocarbon exploration within the Ekofisk Formation (Paleocene) in the North Sea area has provided the impetus for new nannofossil zonations which are more refined than those provided by the standard 'global' schemes of Martini (1971) and Okada and Bukry (1980). The demand for precise correlation of reservoirs, and for biostratigraphically controlled horizontal drilling (in order to increase the commerciality of thin reservoirs which are not commercial under normal drilling methods or to appraise the hydrocarbon field) has increased the urgency even further for a practical, high-resolution biostratigraphic scheme. Moreover, several studies have revealed that the stratigraphic ranges of several marker taxa in the North Sea area are different from those in the standard zonation schemes, owing to biogeographic variation, local, adverse environmental conditions and/or poor preservation.

North Sea zonation schemes for the Paleocene have already been proposed by Perch-Nielsen (1979b), van Heck and Prins (1987), Varol (1989b) and Gallagher (1990). The zonation scheme of Varol (1989b) is the most suitable for industrial applications because the zonal boundaries are based on LOs and acme tops. These criteria are essential when dealing with ditch cutting samples.

The recent recovery of hydrocarbons in sediments younger than Paleocene, and the application of seismic sequence stratigraphy in order to explore stratigraphic traps, has also led to demand for a high-resolution biostratigraphic scheme for the Eocene and Oligocene.

The zonation scheme of Gallagher (1990) includes the Eocene and Oligocene but it is not sufficiently refined (eight zones within the Eocene to Oligocene), and several zones are difficult to detect when using ditch-cutting samples. However, the scheme provides valuable information concerning the distribution of the standard zonal markers in the North Sea area, allowing correlation with the zonation schemes of Martini (1971) and Okada and Bukry (1980).

In the present study, a new zonation scheme for the Palaeogene of the North Sea area is proposed to suit the requirements of the oil industry. The zonation comprises 36 zones and 38 subzones.

7.2 STUDY MATERIAL

The results are mainly based on the analyses of ditch-cuttings, sidewall core and core samples from over one hundred well sections in the British, Danish, Norwegian and Dutch sectors of the North Sea. Field samples were also examined from Denmark: Dania Quarry, Kjølby Gaard, Klintholm, Lundsgaard Cliff (Kerteminde), Lellinge Creek, Sovind, Rojle and Olst.

7.3 PALAEOGENE CHRONOSTRATIGRAPHY AND IMPORTANT REFERENCES

The Palaeogene System was introduced by Naumann (1866) and currently includes the Paleocene, Eocene and Oligocene Series. The Palaeogene stratotypes are relatively small outcrops scattered mainly throughout NW Europe, in Belgium, Denmark, England, France and Germany. The stratotype of the Upper Eocene

Priabonian Stage is in Italy. The lack of continuous exposures, combined with lateral and vertical facies variations of marine, marginal marine and non-marine facies makes inter-basinal and global correlation difficult. In many cases, it is also difficult to define the stages by means of the lower boundaries of the stratotypes. The improvement of calcareous nannofossil and planktonic foraminiferal biostratigraphy has, however, enabled more widespread correlation.

The standard Palaeogene chronostratigraphy based upon Curry *et al.* (1978) and Jenkins and Luterbacher (1992), and the stratigraphic ranges of the Palaeogene stratotypes, are presented in Figs 7.1–7.2. Nannofossil studies of Palaeogene type sections are summarized below.

Denmark: Perch-Nielsen (1969, 1971a, b, 1979 b, c), Mikkelsen (1975), Martini (1971), Romein (1979), Perch-Nielsen and Hansen (1981) Thomson and Heilman-Clausen (1985) and Varol (1989b).

Belgium: Achuthan and Stradner (1969), Martini (1969a, 1971), Martini and Moorkens (1969), Müller (1970a), Roth (1970), Müller and Willems (1981), Steurbaut (1986a, b), Steurbaut and Nolf (1986), Verbeek *et al. in* Vinken (1988), Steurbaut (1990) and Steurbaut and King (1993).

Germany: Martini (1958, 1959a, b, 1964, 1969 b), Martini and Ritzkowski (1968, 1969, 1970), Müller (1970a, b, 1974c), Roth (1970), Martini and Müller (1971, 1975), Locker (1972), von Benedek and Müller (1974, 1976, 1986) and Köthe (1986).

England: Bramlette and Sullivan (1961), Bigg (1982), Hamilton and Hojjatzadeh (1982), Aubry (1983, 1986), Siesser *et al.* (1987) and Knox *et al.* (1994).

France: Bramlette and Sullivan (1961), Bouche (1962a, b), Hay and Mohler (1967), Lezaud (1967), Bignot and Lezaud (1969), Chang (1969), Martini (1969a, 1970a,b, 1971), Hodson and West (1970), Bybell and Gartner (1972), Kapellos and Schaub (1973), Lezaud *in* Blondeau *et al.* (1976), Aubry *in* Cavelier *et al.* (1977), Aubry (1983, 1986) and Janin and Bignot (1993).

7.3.1 Paleocene

The Paleocene Series was defined by Schimper (1874) from the Paris Basin. It is subdivided into Danian, Selandian and Thanetian Stages following Jenkins and Luterbacher (1992).

(a) Danian

Desor (1847) introduced the Danian Stage for the limestones in Stevns Klint and Fakse in Denmark. The Danian Stage has been extended to include limestones above the Maastrichtian white chalk exposed at Stevns Klint and below clastic sediments of the Selandian.

Perch-Nielsen (1979b) and Varol (1989b) identified Subzones D1 to D10 and Zones NNTp1 to NNTp5 respectively from the Danian chalk exposed in Denmark. These zones are equivalent to NPl to NP4 (*pars*) of Martini (1971). Zones NNTp6 to NNTp7 were not recognized in Denmark due to the unconformity between the Danian limestone and Selandian clastics. Zones NNTp1 to NNTp5 were recognized in the limestones of the Ekofisk Formation (North Sea offshore equivalent) (Varol, 1989b). The Danian Stage, therefore, includes Zones NTpl to Ntp7 (NPl to NP4 (*pars*)).

Danian chalk from Denmark has also been studied by Perch-Nielsen (1969), Martini (1971) and Romein (1979).

(b) Selandian

The Selandian Stage was introduced by Rosenkrantz (1924) based on the Lelinge Greensand and Kerteminde Marl in Denmark. The Vestre Gasvaerk section in the Copenhagen area was regarded as a type section for the Selandian (Perch-Nielsen and Hansen, 1981). Currently, a broad definition of the Selandian includes the clastic sediments above the Danian chalk and below the clay with volcanic ash beds (Mo-clay).

Varol (1989b) recorded Zones NNTp8 to NNTpl0 from the Selandian of Denmark. Zones NNTp6 to NNTpl0 were identified in the clastic sediments of the Maureen Formation (North Sea offshore equivalent). The base of the Selandian stage, as used herein, therefore includes Zone NNTp6.

Perch-Nielsen (1971a, b, 1979b) and Perch-Nielsen and Hansen (1981) also studied the Selandian of Denmark.

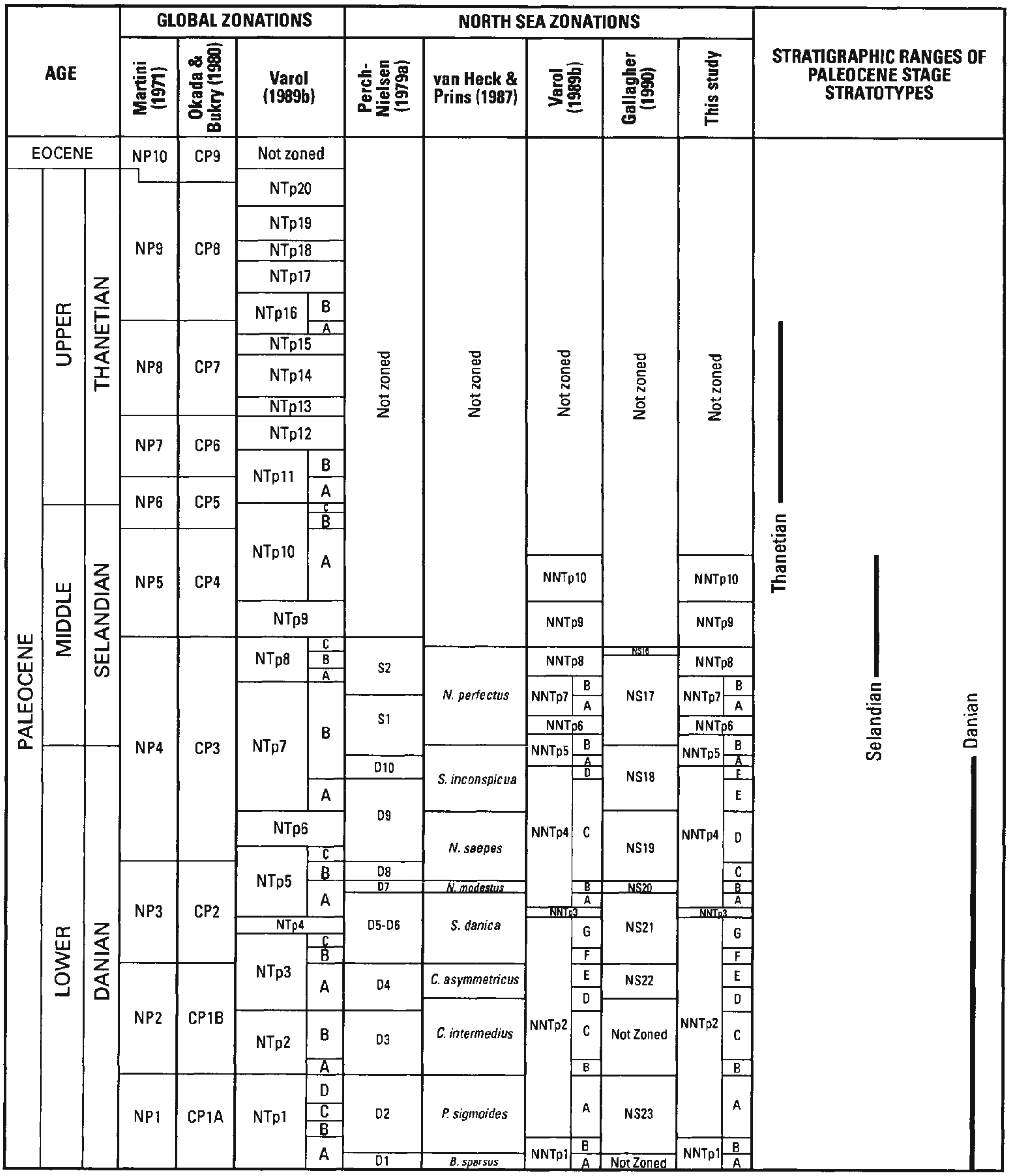


Fig. 7.1 Correlation of Paleocene nannofossil zonation schemes and stratigraphic extent of Paleocene stage stratotypes.

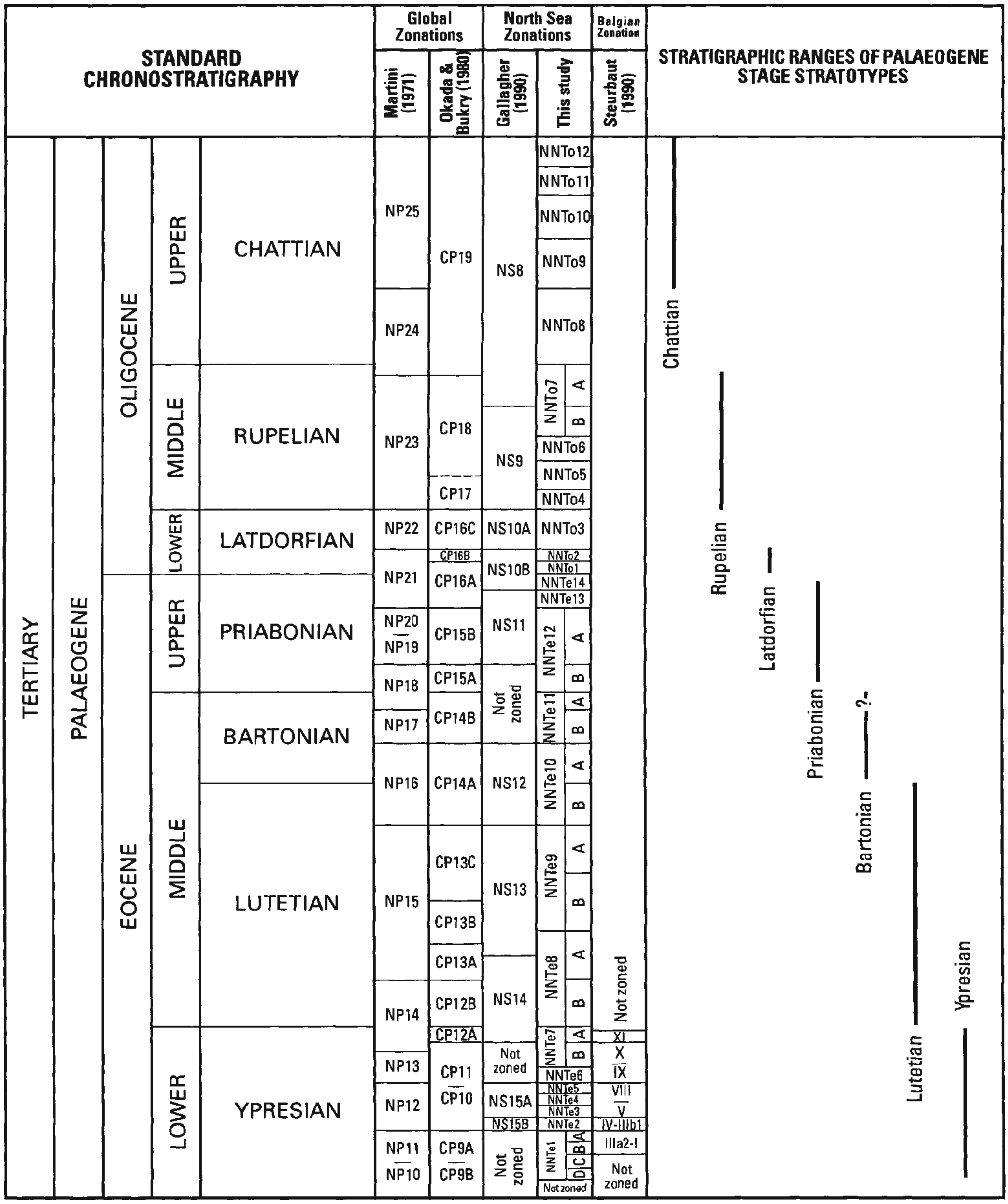


Fig. 7.2 Correlation of Eocene and Oligocene nannofossil zonation schemes and stratigraphic extent of stage stratotypes.

(c) Thanetian

The term 'Thanet Sands' was introduced by Prestwich (1850). Subsequently, Renevier (1873) established the Thanetian Stage for the Thanet Formation, Woolwich Bottom Bed and Oldhaven Beds in Kent, England. Curry (1981b) designated the cliffs at Pegwell Bay and Herne Bay-Reculver as the stratotype. This definition, however, excludes the Woolwich Bottom Bed and Oldhaven Beds.

Siesser *et al.* (1987) assigned the Thanet Formation to zones NP6/7 to NP8, whereas the Woolwich Bottom Bed at Clarendon Hill were attributed to NP9. In the present study (and see Knox *et al.*, 1994) the base of the Thanetian Stage occurs within NP6 (top NTpl0), and is correlated with the 58.5Ma sea level fall of Haq *et al.* (1987). According to Haq *et al.* (1987), the 58.5Ma event corresponds to the top of Planktonic Foraminiferal Zone P3, and they correlated this to within Nannofossil Zone NP5. Conversely, we believe that the top of zone P3 correlates to a level within NP6, marked by the LO of *Fasciculithus pileatus* and/or *Fasciculithus janii* (NTpl0).

The Thanetian stage-stratotype has also been studied by Bramlette and Sullivan (1961), Hay and Mohler (1967), Martini (1971), Hamilton (*in* Hamilton and Hojjatzadeh, 1982), Aubry (1983, 1986), Godfrey and Lord (1984) and Knox *et al.* (1994).

7.3.2 Eocene

Lyell (1833) introduced the Eocene Series and included the Ypresian, Lutetian, Bartonian and Priabonian Stages (Jenkins and Luterbacher, 1992).

(a) Ypresian

This stage was established by Dumont (1849) based on the Ieper Clay and overlying sands (Belgium). Steurbaut and Nolf (1986) redefined the Ieper Formation to include the Orchies Clay Member, the Raubaix Clay Member, the Aalbeke Clay Member, the Kortemark Silt Member, the Egem Sand Member and the Merelbeke Clay Member. Steurbaut and Nolf (1986) also designated neostratotypes for each member (holo-, lecto- and neostratotypes).

Steurbaut and Nolf (1986) studied nannofossils from the Belgian stratotype and recognized zones NP11 to lower NP14 (NNTe1-NNTe7). The lower boundary of the Ypresian elsewhere is equivalent to the top of NP9 (NTp20). Its upper boundary is approximated by the LO of *Discoaster kuepperi* (NNTe7), within NP14.

The Ypresian type area has also been studied by Martini (1971), Müller and Willems (1981) and Steurbaut (1990).

(b) Lutetian

This stage was defined by de Lapparent (1883) for the Calcaire Grossier in the Paris Basin. The neostratotype of the Lutetian Stage at St Leu d'Esserent (lower Lutetian) and St. Vaast-les-Mello (middle and upper Lutetian) was designated by Blondeau (1981).

Aubry (1983, 1986) studied nannofossils from the neostratotype and correlatable sections in the Paris Basin and recognized zones upper NP14 to lower NP16. In the present study, the LO of *Discoaster kuepperi* (top NNTe7), within NP14, and the FO of *Helicosphaera compacta* (top NNTe10A), within NP16, are taken to approximate the base and top of the Lutetian Stage, respectively.

The Lutetian type area has also been studied by Hay and Mohler (1967), Bigg (1982) and Bouche (1962a, b).

(c) Bartonian

This stage was established by Mayer-Eymar (1858). The cliffs near Barton in Hampshire (England) were designated the stratotype, with a parastratotype at Alum Bay, Isle of Wight (England) (Curry, 1981a).

Zones NP16 (upper) to NP17 were identified by Aubry (1983, 1986) in the stratotype section, and Aubry (1986) suggested that the lower part of NP18 might also be present. In the present study, the LO of *Chiasmolithus grandis* and/or *Neococcolithes* spp. (top NNTe11), within the basal part of NP18, is taken to approximate the boundary between the Bartonian and Priabonian Stages. This is consistent with results obtained from the stratotypes of the respective stages.

Martini (1971) also studied the Bartonian stratotype.

(d) Priabonian

Munier-Chalmas and de Lapparent (1893) introduced the Priabonian Stage for the marls at Granella, Priabona and Brendola in Italy.

Zones NP18 (*pars*) to lower NP21 were identified in the stratotype and parastratotype by Verhallen and Romein (1983). The upper boundary of the Priabonian Stage is approximated by the LO of *Pemma basquense* and/or *Pemma papillatum* (top NNTe14), within NP21.

The Priabonian stratotype has also been studied by Cita (1969), Proto-Decima (1969), Roth *et al.* (1971), Proto-Decima *et al.* (1975), Jossen (1982) and Barbin (1989).

7.3.3 Oligocene

This series was introduced by Beyrich (1854) and includes the Lattorfian, Rupelian and Chattian stages.

(a) Latdorfian

Mayer-Eymar (1893) introduced the term Latdorfian for the Latdorf Sands in Germany. The type locality is the former lignite open-cast mine (CARL) near Latdorf on the Saale, Germany.

Martini and Ritzkowski (1969) and Roth (1970) recognized NP21 in the stratotype section. The upper part of this stage also includes NP21 (*pars*) and NP22 (NNTo1 to NNTo3).

Martini (1969b) and Martini and Ritzkowski (1968) also studied the stratotype.

(b) Rupelian

This stage was introduced by Dumont (1849) to include a lowermost sandy unit (subsequently named the Ruisbroch Sand in West Belgium and Berg Sand in East Belgium), or locally sandy clay (Kleine Spouwen Clay), and an uppermost unit, the Boom Clay (Vandenberghe and van Echelpoel, 1988). The Bilzen area in the Belgian East-Limburg region was considered as the stratotype for the lower Rupelian, with the upper Rupelian based on many clay pits and brick works along the Rupel and Schelde rivers. No formal stratotype has been designated.

Roth (1970) studied the stratotype area and identified zone NP23. The Rupelian also includes NP23 and lower NP24 (NNTo4 to NNTo7). The LO of *Helicosphaera compacta* and/or *Helicosphaera bramlettei* approximates the top of the Rupelian Stage.

Steurbaut (1992) identified NP22 (based on the occurrence of *Reticulofenestra umbilica*) in the Ruinsbroch Sands, underlying the Boom Clay, in the type area. This occurrence may represent reworking since the background assemblage does not support the NP22 zonal assignment.

(c) Chattian

Fuchs (1894) established the Chattian Stage for the Cassel Sands in Germany. A stratotype was designated by Goerges (1957) at Doberg Hill near Bunde in Westphalia.

Martini and Müller (1975) identified zones NP24 (*pars*) to NP25 in the stratotype section. In the present study, zones NNTo8 to NNTo12 (upper NP24 to lower NN1) are included in the Chattian Stage.

The stratotype Chattian was also studied by Müller (1970a), Haq (1971), Anderson *et al.* (1971) and Martini *et al.* (1975).

7.4 BIOSTRATIGRAPHY

The proposed zonation scheme is largely based upon North Sea ditch-cutting samples, supplemented by core, sidewall core and Danish field samples. The zones are given the prefix NNTp, e or o, for ease of use. (North Sea Nannofossil Tertiary Paleocene, Eocene or Oligocene). Zonal boundaries are based upon the LOs (= first downhole occurrences) of selected species and their acmes. This enables application of the zones to ditch-cutting samples. FOs (= last downhole occurrences) of selected species and their acmes have been used to define subzonal boundaries, and are additionally applicable when working with sidewall core, core or field sample material.

The stratigraphic ranges of the species used has been determined in a number of different ways, including calibration against the standard nannofossil zonation schemes (Martini, 1971; Okada and Bukry, 1980), planktonic foraminiferal zones (Blow, 1979) and unpublished palynological events.

The scheme incorporates the North Sea Paleocene zonation of Varol (1989b), with minor modification. Many of the zonal and subzonal markers have been used in previous schemes or have been suggested in the literature to have stratigraphic significance. The majority of the bioevents used are only consistently recognizable in the North Sea area and Denmark.

This work has benefited greatly from the results of the following studies: Bramlette and Sullivan (1961), Hay *et al.* (1967), Hay and Mohler (1967), Martini (1971), Edwards (1971), Bukry (1973a, 1975), Perch-Nielsen (1979b), Okada and Bukry (1980), Aubry (1983, 1986), Varol (1989b), Steurbaut (1990) and Gallagher (1990).

Correlation between the proposed zonation scheme and other North Sea area zonations is presented in Figs 7.1–7.2. These figures also provide correlations with the standard zonation schemes of Martini (1971), Okada and Bukry (1980) and Varol (1989b).

The zonal markers have well-defined local stratigraphic tops, are easily recognizable under the LM, are widely distributed throughout the North Sea area and are present in relatively frequent numbers. The names of the authors who first established the zonal boundaries are given in square brackets. Subzone is abbreviated to SZ.

The following relative abundance categories were applied:

Rare – ≤1/10 FOV
Common – >1/10 FOV
Abundant – >1/3 FOV
Influx – usually >50% of total assemblage

7.4.1 Paleocene

Ten zones and 19 subzones have been defined for the Lower to Middle Paleocene (Danian to Selandian) (Fig. 7.3). The detection of these zones and subzones requires a close sampling interval (<5m).

No zones have been established for the Upper Paleocene (Thanetian) as most North Sea sediments of this age are barren of nannofossils and not routinely studied. However, in the Central Graben area, a few wells have yielded *Fasciculithus tympaniformis, Fasciculithus thomasii* and *Heliolithus kleinpellii.* This evidence suggests that an applicable zonation scheme could be possible if detailed studies were undertaken.

The North Sea zonation scheme of Varol (1989b) is applied here, with minor modification: Subzone NNTp4C of Varol (1989b) has been further divided using the FO of *Neochiastozygus eosaepes* and the LO of *Neocrepidolithus fossus* or FO of *Neochiastozygus saepes.*

NNTp1 Biantholithus hughesii Zone
Base. LO of *Arkhangelskiella cymbiformis* and *Micula decussata* (= *M. staurophora*) [Varol, 1989b] and/or the FO of *Biantholithus sparsus* [Romein, 1979] and/or the FO of *Cyclagelosphaera alta* [Varol, 1989b].
Top. LO of *Biantholithus hughesii* [Varol, 1989b] and/or the FO of *Cruciplacolithus primus* [Romein, 1979].
Range. Danian (lower NP1).
Remarks. When dating ditch-cutting samples it is best to use the LO of common *A. cymbiformis* and *M. decussata* (= *M. staurophora*) to mark the base of this zone. This zone commonly includes abundant and consistently-occuring reworked Campanian nannofossils (see also section 6.4.5 and Fig. 6.8).

NNTp1A Biantholithus sparsus SZ
Base. LO of common *Arkhangelskiella cymbiformis* and common *Micula decussata* [Varol, 1989b] and/or the FO of *Biantholithus sparsus* [Romein, 1979] and/or the FO of *Cyclagelosphaera alta* [Varol, 1989b].
Top. FO of *Placozygus sigmoides* (= *Zeugrhabdotus sigmoides*) [Perch-Nielsen, 1979b].
Range. Danian (lowermost NP1).
Remarks. The persistent FO of *Neocrepidolithus cruciatus* is recorded in this subzone.

NNTp1B Placozygus sigmoides SZ
Base. FO of *Placozygus sigmoides* [Perch-Nielsen, 1979b].
Top. LO of *Biantholithus hughesii* [Varol, 1989b] and/or the FO of *Cruciplacolithus primus* [Romein, 1979].
Range. Danian (lower NP1).
Remarks. Typical specimens of *P. sigmoides* (= *Zeugrhabdotus sigmoides*) are not observed below this subzone, although this is clearly a local feature. Extremely rare occurrences of minute specimens of *Neochiastozygus* species with asymmetrical bars were recorded in this subzone.

NNTp2 Cyclagelosphaera alta Zone
Base. LO of *Biantholithus hughesii* [Varol, 1989b] and/or the FO of *Cruciplacolithus primus* [Romein, 1979].
Top. LO of *Hornibrookina edwardsii* [Varol, 1989b] and /or *Cyclagelosphaera alta* [herein].
Range. Danian (NP1–NP3).

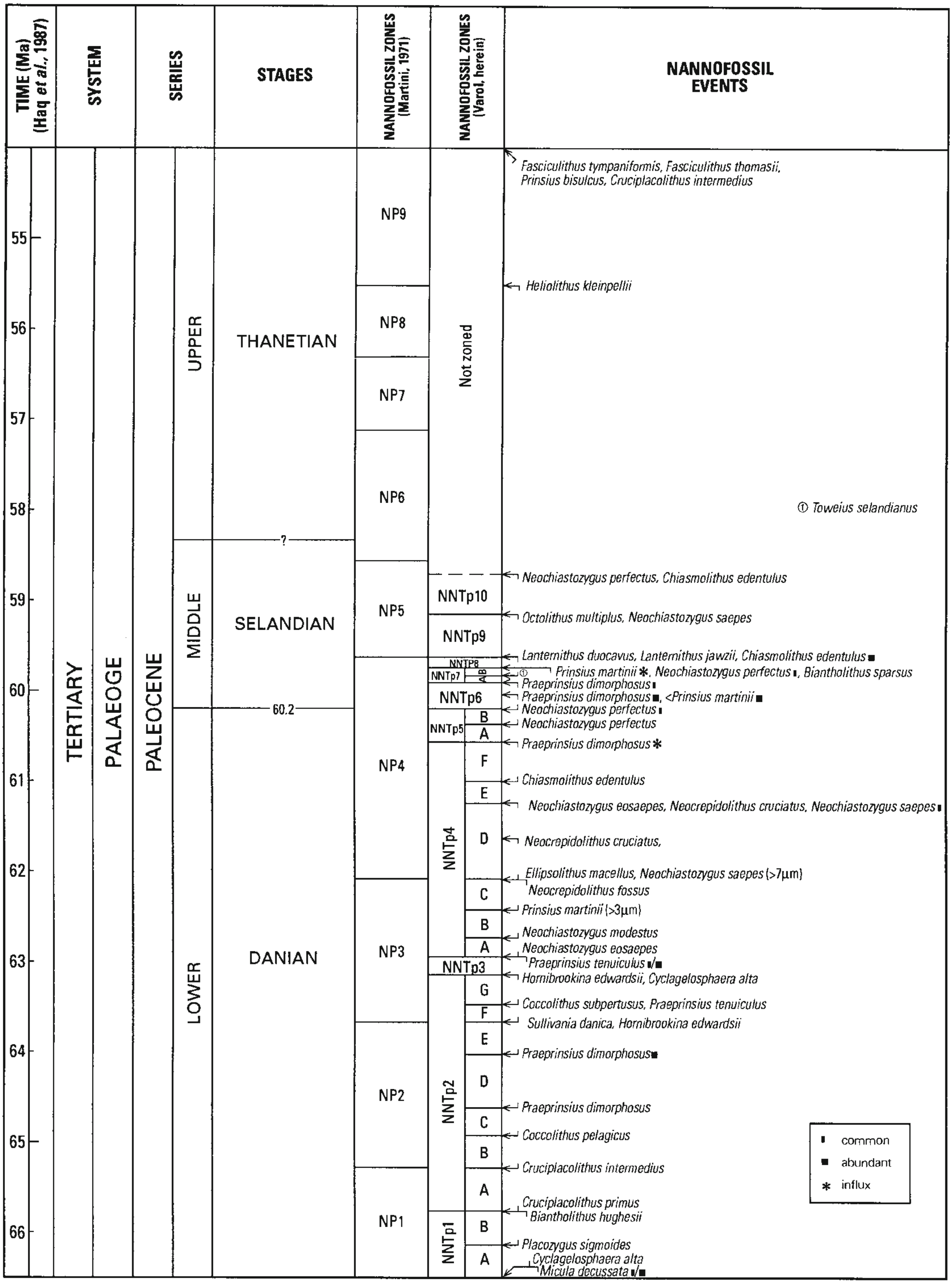


Fig. 7.3 Paleocene nannofossil zones and events for the North Sea area.

Remarks. *Thoracosphaera* spp. are common to abundant within this zone and above. Assemblages are usually dominated by *Coccolithus pelagicus* and, to a lesser extent, by *Praeprinsius dimorphosus* in the upper part of the zone. The LO of *C. alta* is found within this zone (only forms with a five-sided plug are assigned to this species).

NNTp2A Cruciplacolithus primus SZ
Base. LO of *Biantholithus hughesii* [Varol, 1989 b] and/or the FO of *Cruciplacolithus primus* [Romein, 1979].
Top. FO of *Cruciplacolithus intermedius* [Mohler and Hay *in* Hay *et al.*, 1967].
Range. Danian (upper NP1).

NNTp2B Cruciplacolithus intermedius SZ
Base. FO of *Cruciplacolithus intermedius* [Mohler and Hay *in* Hay *et al.*, 1967].
Top. FO of *Coccolithus pelagicus* (*sensu lato*) [Varol, 1989b].
Range. Danian (lower NP2).

NNTp2C Coccolithus pelagicus SZ
Base. FO of *Coccolithus pelagicus* (*sensu lato*) [Varol, 1989b].
Top. FO of *Praeprinsius dimorphosus* [Perch-Nielsen, 1979b].
Range. Danian (within NP2).

NNTp2D Praeprinsius dimorphosus SZ
Base. FO of *Praeprinsius dimorphosus* [Perch-Nielsen, 1979b].
Top. FO of abundant *Praeprinsius dimorphosus* [Varol, 1989b].
Range. Danian (within NP2).
Remarks. A rare occurrence of *Praeprinsius tenuiculus* (*sensu lato*) has been observed in this subzone.

NNTp2E Neocrepidolithus cruciatus SZ
Base. FO of abundant *Praeprinsius dimorphosus* [Varol, 1989b].
Top. FO of *Sullivania danica* [Martini, 1970a] and/or *Hornibrookina edwardsii* [Varol, 1989b].
Range. Danian (upper NP2).
Remarks. *P. dimorphosus* dominates these assemblages, and those to the top of Zone NNTp4.

NNTp2F Hornibrookina edwardsii SZ
Base. FO of *Sullivania danica* [Martini, 1970a] and/or *Hornibrookina edwardsii* [Varol, 1989b].
Top. FO of *Coccolithus subpertusus* [Varol, 1989b] and/or the FO of common *Praeprinsius tenuiculus* [Varol, 1989b].
Range. Danian (lower NP3).

NNTp2G Coccolithus subpertusus SZ
Base. FO of *Coccolithus subpertusus* [Varol, 1989b] and/or the FO of common *Praeprinsius tenuiculus*.
Top. LO of *Hornibrookina edwardsii* [Varol, 1989b] and/or *Cyclagelosphaera alta* [herein].
Range. Danian (lower NP3).
Remarks. Assemblages are dominated by *P. dimorphosus* and, to a lesser extent, by *P. tenuiculus.*

NNTp3 Praeprinsius tenuiculus Zone
Base. LO of *Hornibrookina edwardsii* [Varol, 1989b] and/or *Cyclagelosphaera alta* [herein].
Top. LO of common to abundant *Praeprinsius tenuiculus* [Varol, 1989b].
Range. Danian (within NP3).
Remarks. The FO of *Cruciplacolithus latipons* was recognized in the uppermost part of this zone. Rounded forms of *P. dimorphosus* dominate the assemblages, although *P. tenuiculus* is common to abundant. Small *Neochiastozygus* (*saepes* group) with an axial cross which fills the central area are persistently observed in this zone.

NNTp4 Coccolithus cavus Zone
Base. LO of common to abundant *Praeprinsius tenuiculus* [Varol, 1989b].
Top. The top of an influx (first downhole influx) of *Praeprinsius dimorphosus* [Varol, 1989b].
Range. Danian (NP3–NP4).
Remarks. *P. dimorphosus* dominates over *Prinsius martinii.*

NNTp4A Neocrepidolithus dirimosus SZ
Base. LO of common to abundant *Praeprinsius tenuiculus* [Varol, 1989b].
Top. FO of *Neochiastozygus modestus* [Perch-Nielsen, 1979b].
Range. Danian (within NP3).
Remarks. The FO of *N. eosaepes* is observed at the base of this subzone.

NNTp4B Neochiastozygus modestus SZ
Base. FO of *Neochiastozygus modestus* [Perch-Nielsen, 1979b].
Top. FO of *Prinsius martinii* [Edwards, 1971].
Range. Danian (within NP3).
Remarks. Specimens of *Prinsius martinii* <3µm are present in this subzone.

NNTp4C Prinsius martinii SZ
Base. FO of *Prinsius martinii* [Edwards, 1971].
Top. FO of *Neochiastozygus saepes* (>7µm) [Perch-Nielsen, 1979b].
Range. Danian (upper NP3).
Remarks. The lower boundary of this subzone is marked by the FO of *P. martinii* whose size is >3µm. *Cruciplacolithus* spp. and *Chiasmolithus* spp. numerically dominate over *Coccolithus* spp. Small forms of *N. saepes* (<7 µm) are observed within this subzone. The LO of *Neocrepidolithus fossus* was noted at the top of this subzone.

NNTp4D Neochiastozygus eosaepes SZ
Base. FO of *Neochiastozygus saepes* (>7µm) [Perch-Nielsen, 1979b].
Top. LO of *Neochiastozygus eosaepes* [Varol, 1989b].
Range. Danian (lower NP4).
Remarks. *C. pelagicus* usually dominates the assemblages. The FO of *Ellipsolithus macellus* in the Central North Sea was found at the base of this subzone but it is extremely rare. The FO of *Cruciplacolithus subrotundus* and the FO of common *Coccolithus cavus* and common *Octolithus multiplus* are also recorded within this subzone. The LO of small *Neochiastozygus* spp. (with asymmetrical cross) is recorded at the base of this subzone, the LO of *N. cruciatus* in the upper part.

NNTp4E Cruciplacolithus subrotundus SZ
Base. LO of *Neochiastozygus eosaepes* [Varol, 1989b].
Top. FO of *Chiasmolithus edentulus* [Perch-Nielsen, 1979b].
Range. Danian (within NP4).

NNTp4F Chiasmolithus edentulus SZ
Base. FO of *Chiasmolithus edentulus* [Perch-Nielsen, 1979b].
Top. The top of an influx (first downhole influx) of *Praeprinsius dimorphosus* [Varol, 1989b].
Range. Danian (within NP4).
Remarks. The LO of persistent *N. saepes* is observed at the base of this subzone. *Chiasmolithus* spp. and *Cruciplacolithus* spp. dominate over *Coccolithus* spp. Common to abundant forms recorded include *P. sigmoides* and *O. multiplus. Chiasmolithus edentulus* is abundant in the upper part of the subzone.

NNTp5 Markalius apertus Zone
Base. The top of an influx (first downhole influx) of *Praeprinsius dimorphosus* [Varol, 1989b].
Top. LO of abundant *Praeprinsius dimorphosus* [Varol, 1989b].
Range. Danian (within NP4).
Remarks. Nannofloral assemblages are dominated by *P. martinii* and, to a lesser extent, by *P. dimorphosus* and *C. edentulus.*

NNTp5A Chiasmolithus inconspicuus SZ
Base. The top of an influx (first downhole influx) of *Praeprinsius dimorphosus* [Varol, 1989b].
Top. FO of *Neochiastozygus perfectus* [Perch-Nielsen, 1979b].
Range. Danian (within NP4).
Remarks. According to Varol (1989b), *Neochiastozygus imbriei* persistently occurs in this subzone; it is here believed to be reworked or the result of contamination: *N. imbriei* has its LO at the top of NNTp4D.

NNTp5B Neochiastozygus perfectus SZ
Base. FO of *Neochiastozygus perfectus* [Perch-Nielsen, 1979b].
Top. LO of abundant *Praeprinsius dimorphosus* [Varol, 1989b].
Range. Danian (within NP4).
Remarks. The top of this zone is coincident with the top of the Ekofisk Formation, and marks the boundary between the Danian and Selandian stages. The FO of common *Neochiastozygus perfectus* occurs within this zone and may have local correlative value.

NNTp6 Neocrepidolithus neocrassus Zone
Base. LO of abundant *Praeprinsius dimorphosus* [Varol, 1989b].
Top. LO of common *Praeprinsius dimorphosus* [Varol, 1989b].
Range. Selandian (within NP4).

NNTp7 Prinsius bisulcus Zone

Base. LO of common *Praeprinsius dimorphosus* [Varol, 1989b].
Top. LO of common *Neochiastozygus perfectus* [Varol, 1989b] and/or the top of an influx (first downhole influx) of *Prinsius martinii* [Varol, 1989b].
Range. Selandian (within NP4).
Remarks. Rare occurrences of *Sphenolithus primus* and *Fasciculithus chowii* were observed at the top of the zone.

NNTp7A Cruciplacolithus frequens SZ

Base. LO of common *Praeprinsius dimorphosus* [Varol, 1989b].
Top. FO of *Toweius selandianus* [Perch-Nielsen, 1979b].
Range. Selandian (within NP4).

NNTp7B Toweius selandianus SZ

Base. FO of *Toweius selandianus* [Perch-Nielsen, 1979b].
Top. LO of common *Neochiastozygus perfectus* [Varol, 1989b] and/or the top of an influx (first downhole influx) of *Prinsius martinii* [Varol, 1989b].
Range. Selandian (within NP4).

NNTp8 Lanternithus duocavus Zone

Base. LO of common *Neochiastozygus perfectus* [Varol, 1989b] and/or the top of an influx (first downhole influx) of *Prinsius martinii* [Varol, 1989b].
Top. LO of *Lanternithus duocavus* [Varol, 1989 b] and/or *Lanternithus jawzii* [herein].
Range. Selandian (uppermost NP4).
Remarks. The last abundant occurrence of *C. edentulus* also approximates the top of this zone.

NNTp9 Octolithus multiplus Zone

Base. LO of *Lanternithus duocavus* [Varol, 1989 b] and/or *Lanternithus jawzii* [herein].
Top. LO of *Octolithus multiplus* [Varol, 1989b].
Range. Selandian (lower NP5).
Remarks. Varol (1989b) used the LO of *N. saepes* as an alternative marker for the top of this zone. Above Zone NNTp4, *N. saepes* is sparsely present, possibly as a result of reworking.

NNTp10 Toweius pertusus Zone

Base. LO of *Octolithus multiplus* [Varol, 1989 b].
Top. LO of *Neochiastozygus perfectus* [Varol, 1989b].
Range. Selandian (within NP5).
Remarks. Extensive reworking usually dilutes or completely masks the *in situ* assemblages through this interval.

7.4.2 Eocene

Fourteen zones and 16 subzones are proposed for the Eocene (Ypresian to Priabonian) (Fig. 7.4).

NNTe1 Sphenolithus radians Zone

Base. FO of *Tribrachiatus orthostylus* [Edwards, 1971].
Top. LO of *Ellipsolithus macellus* [Steurbaut and Nolf, 1986] and/or the FO of *Discoaster lodoensis* [Hay and Mohler *in* Hay *et al.*, 1967].
Range. Ypresian (NP10–NP11).
Remarks. Poorly preserved and low diversity nannofossil assemblages are usually recorded in this zone. *Toweius* spp. dominate.

NNTe1A Toweius rotundus SZ

Base. FO of *Tribrachiatus orthostylus* [Edwards, 1971].
Top. FO of *Imperiaster obscurus* [Aubry, 1983].
Range. Ypresian (NP10–NP11).
Remarks. *T. rotundus* and *Toweius oztunalii* dominate.

NNTe1B Toweius crassus SZ

Base. FO of *Imperiaster obscurus* [Aubry, 1983].
Top. FO of *Neococcolithes* spp. [herein].
Range. Ypresian (NP10–NP11).
Remarks. *T. crassus* persistently occurs in this subzone.

NNTe1C Neococcolithes protenus SZ

Base. FO of *Neococcolithes* spp. [herein].
Top. FO of *Discoaster kuepperi* [Edwards, 1971].
Range. Ypresian (NP10–NP11).
Remarks. *Toweius occultatus* is dominant. The FOs of *Rhabdosphaera perlonga, Rhabdosphaera pinguis, Lophodolithus nascens* and *Discoaster binodosus* were noted within this subzone.

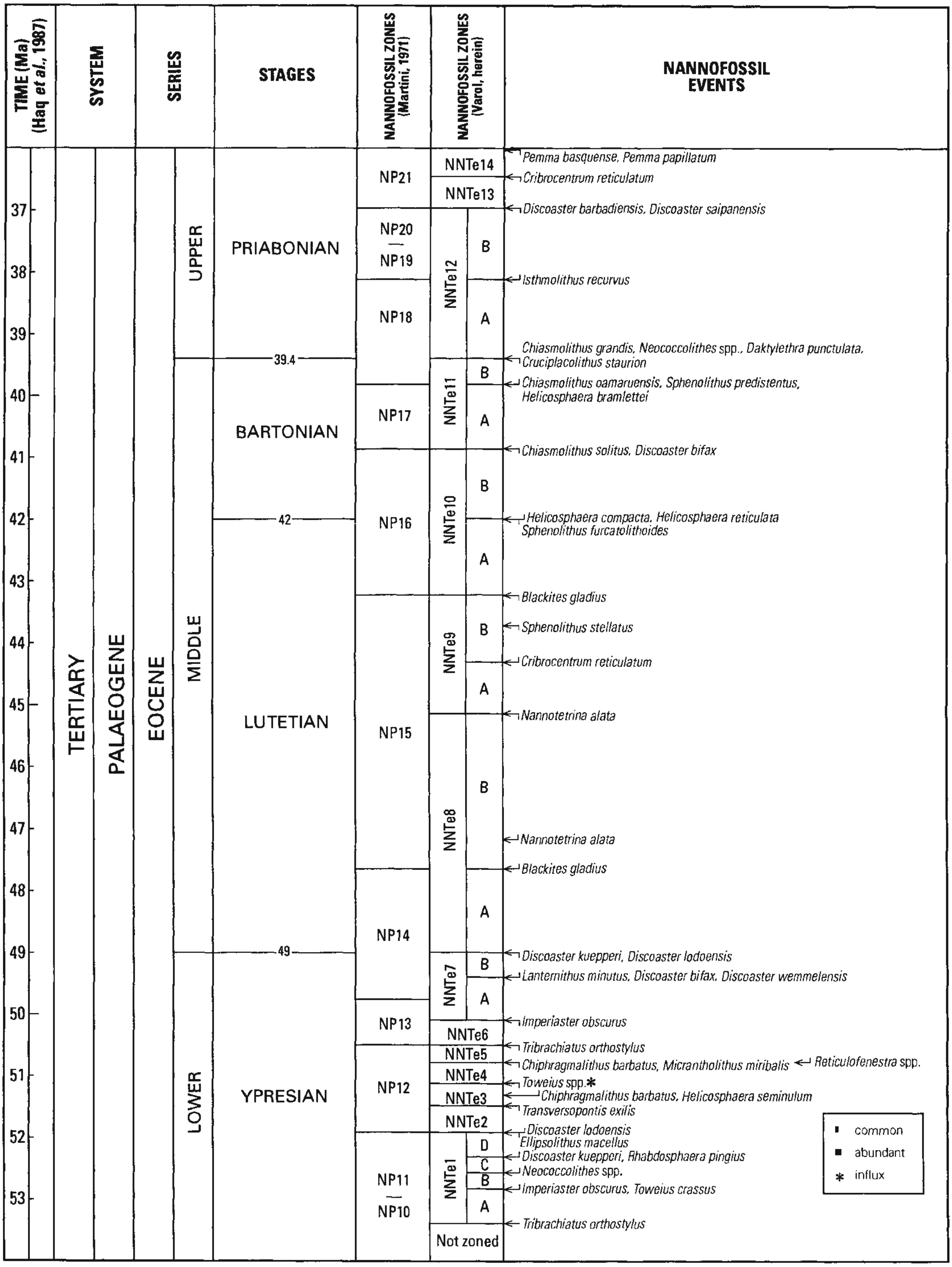


Fig. 7.4 Eocene nannofossil zones and events for the North Sea area.

NNTe1D Rhabdosphaera pinguis SZ

Base. FO of *Discoaster kuepperi* [Edwards, 1971].
Top. LO of *Ellipsolithus macellus* [Steurbaut and Nolf, 1986] and/or the FO of *Discoaster lodoensis* [Mohler and Hay *in* Hay *et al.*, 1967].
Range. Ypresian (NP10–NP11).
Remarks. *Chiasmolithus eograndis* has its FO here but is rare. *T. crassus* is common. The assemblages recovered from the type Cuisian by Aubry (1986) are typical for this subzone. A sample examined from the Rosneas Clay, above ash band 118 and the glauconitic horizon at, Olst (Denmark) yielded a nannofloral assemblage assignable to this subzone.

NNTe2 Discoaster lodoensis Zone

Base. LO of *Ellipsolithus macellus* [Steurbaut and Nolf, 1986] and/or the FO of *Discoaster lodoensis* [Hay and Mohler *in* Hay *et al.*, 1967].
Top. LO of *Transversopontis exilis* [Steurbaut, 1988].
Range. Ypresian (lower NP12).
Remarks. *Cyclicargolithus luminis* and *Chiasmolithus grandis* have their FOs within this zone. *Toweius* spp. dominate.

NNTe3 Toweius occultatus Zone

Base. LO of *Transversopontis exilis* [Steurbaut, 1988].
Top. The top of an influx (first downhole influx) of *Toweius* spp. [herein].
Range. Ypresian (within NP12).
Remarks. Assemblages are usually dominated by *T. occultatus, T. pertusus* and *C. pelagicus* and, to a lesser extent, *D. kuepperi, D. lodoensis, Geminilithella bramlettei* and *T. orthostylus.* The FOs of *Chiphragmalithus barbatus* and *Helicosphaera seminulum* are observed within this zone.

A sample from the Rosneas Clay at Rojle (Denmark) is assigned to this zone.

NNTe4 Micrantholithus mirabilis Zone

Base. The top of an influx (first downhole influx) of *Toweius* spp. [herein].
Top. LO of *Chiphragmalithus armatus* and/or *Micrantholithus mirabilis* [herein].
Range. Ypresian (within NP12).
Remarks. Well preserved and high diversity assemblages are usually obtained from this zone. In some of the study sections an overlap in the ranges of *C. armatus* and/or *M. mirabilis* and *Reticulofenestrata* spp. was observed, but it was so short as to be difficult to detect. For practical reasons, the two LOs can be taken to approximate the upper limit of this zone.

NNTe5 Tribrachiatus orthostylus Zone

Base. LO of *Chiphragmalithus armatus* and/or *Micrantholithus mirabilis* [herein].
Top. LO of *Tribrachiatus orthostylus* [Brönnimann and Stradner, 1960].
Range. Ypresian (upper NP12).
Remarks. The FO of *Helicosphaera lophota* was recorded within this zone. Specimens of *Reticulofenestra* spp. are small and usually rare, whereas the abundance of *Neococcolithes* spp. increases.

NNTe6 Imperiaster obscurus Zone

Base. LO of *Tribrachiatus orthostylus* [Brönnimann and Stradner, 1960].
Top. LO of *Imperiaster obscurus* [herein].
Range. Ypresian (lower NP13).
Remarks. This and the following zone are not usually recovered. The major sea level fall at 49Ma (Haq *et. al.*, 1987) is thought to have been responsible for a period of non-deposition and/or erosion of sediments in many parts of the North Sea area.

Poorly preserved and low diversity assemblages are obtained when this zone is present.

NNTe7 Discoaster kuepperi Zone

Base. LO of *Imperiaster obscurus* [herein].
Top. LO of *Discoaster kuepperi* [Edwards, 1971] and/or *Discoaster lodoensis* [herein].
Range. Ypresian (upper NP13–lower NP14).
Remarks. See NNTe6. The LO of *T. pertusus* is observed at the top of this zone.

NNTe7A Transversopontis pulcher SZ

Base. LO of *Imperiaster obscurus* [herein].
Top. FO of *Lanternithus minutus* [Aubry, 1983].
Range. Ypresian (upper NP13–lower NP14).
Remarks. Typified by sparse assemblages.

NNTe7B Discoaster wemmelensis SZ

Base. FO of *Lanternithus minutus* [Aubry, 1983].
Top. LO of *Discoaster kuepperi* [Edwards, 1971] and/or *Discoaster lodoensis* [herein].
Range. Ypresian (within NP14).

Remarks. The FOs of *Discoaster bifax* and *D. wemmelensis* were recorded at the base of this subzone but they are extremely rare.

NNTe8 Nannotetrina alata Zone

Base. LO of *Discoaster kuepperi* [Edwards, 1971] and/or *Discoaster lodoensis* [herein].
Top. LO of *Nannotetrina alata* [Perch-Nielsen, 1985b] and/or *Nannotetrina pappii* [herein].
Range. Lutetian (upper NP14–lower NP15).
Remarks. This zone is well developed in the Central North Sea and onshore Denmark, but is absent in the South Viking Graben area due to an unconformity.

NNTe8A Helicosphaera lophota SZ

Base. LO of *Discoaster kuepperi* [Edwards, 1971] and/or *Discoaster lodoensis* [herein].
Top. FO of *Blackites gladius* [Martini, 1970a].
Range. Lutetian (upper NP14).
Remarks. *Helicosphaera seminulum, H. lophota, Cruciplacolithus staurion, Chiasmolithus solitus* and *Reticulofenestra* spp. are the most prominent species.

NNTe8B Cruciplacolithus staurion SZ

Base. FO of *Blackites gladius* [Martini, 1970a] and/or *Nannotetrina alata* [Hay *in* Hay *et al.*, 1967].
Top. LO of *Nannotetrina alata* [Perch-Nielsen, 1985b].
Range. Lutetian (lower NP15).
Remarks. The FO of *Discoaster distinctus, Daktylethra punctulata* and *Helicosphaera dinesenii* are observed in this subzone. The FO of *Sphenolithus furcatolithoides* was also recorded in this zone but, according to Gallagher (1990), this species has an earlier FO than that of *Blackites gladius*, an observation not substantiated in the course of this study. In some areas, the FO of *N. alata* is younger than the FO of *B. gladius.*

NNTe9 Blackites gladius Zone

Base. LO of *Nannotetrina alata* [Perch-Nielsen, 1985b] and/or *Nannotetrina pappii* [herein].
Top. LO of *Blackites gladius* [Martini, 1970a].
Range. Lutetian (upper NP15).
Remarks. Well developed throughout the North Sea area. The FOs of *Rhabdosphaera pseudomorionum* and *Pontosphaera formosa* are observed in the lower part of this zone.

NNTe9A Corannulus germanicus SZ

Base. LO of *Nannotetrina alata* [Perch-Nielsen, 1985b] and/or *Nannotetrina pappii* [herein].
Top. FO of *Cribrocentrum reticulatum* [herein].
Range. Lutetian (within NP15).
Remarks. The FOs of abundant *Reticulofenestra umbilica* and FO of *Dictyococcites stavensis* are usually recorded within this subzone. Samples examined from the Sovind Marl (below the glauconitic horizon), near Vissing in Denmark, are assigned to this subzone.

NNTe9B Sphenolithus stellatus SZ

Base. FO of *Cribrocentrum reticulatum* [herein].
Top. LO of *Blackites gladius* [Martini, 1970a].
Range. Lutetian (upper NP15).
Remarks. The LOs of *H. dinesenii* and *Sphenolithus stellatus* and the FO of *Helicosphaera salebrosa* are observed in the upper part of this subzone. The FO of *Cribrocentrum reticulatum* was recorded above the LO of *B. gladius* by Aubry (1983) and Wei and Wise (1989), at a level which is much younger than the findings of this study. The stratigraphic occurrence of *C. reticulatum* below the LO of *B. gladius* has also been confirmed in field samples from the Sovind Marl, Denmark. A sample examined 13 feet below the top of the pit at Sovind yielded common *B. gladius* and *C. reticulatum.*

NNTe10 Chiasmolithus solitus Zone

Base. LO of *Blackites gladius* [Martini, 1970a].
Top. LO of *Chiasmolithus solitus* [Martini, 1970a].
Range. Lutetian–Bartonian (NP16).
Remarks. Assemblages are moderately well preserved and of high diversity, usually dominated by *Reticulofenestra* spp. The LO of *S. furcatolithoides* is within this zone.

NNTe10A Helicosphaera seminulum SZ

Base. LO of *Blackites gladius* [Martini, 1970a].
Top. FO of *Helicosphaera compacta* [Aubry, 1983].
Range. Lutetian (lower NP16).

NNTe10B Birkelundia arenosa SZ

Base. FO of *Helicosphaera compacta* [Aubry, 1983].
Top. LO of *Chiasmolithus solitus* [Martini, 1970a].

Range. Bartonian (upper NP16).
Remarks. The LO of *D. distinctus* was observed at the top of this subzone by Aubry (1983), whereas Gallagher (1990) recorded it just above the LO of *C. solitus.* In this study, the LO of this species was found as high as Subzone NNTe11B, where there is no obvious reworking.

NNTe11 Chiasmolithus grandis Zone

Base. LO of *Chiasmolithus solitus* [Martini, 1970a].
Top. LO of *Chiasmolithus grandis* [Bukry, 1973 a] and/or *Neococcolithes* spp. [Edwards, 1971].
Range. Bartonian (NP17–lower NP18).
Remarks. The most widely recognized zone in the North Sea area. *D. distinctus, H. seminulum* and *Campylosphaera dela* have their LOs, whereas *Cyclicargolithus floridanus* has its first consistent occurrence within this zone.

NNTe11A Daktylethra punctulata SZ

Base. LO of *Chiasmolithus solitus* [Martini, 1970a].
Top. FO of *Chiasmolithus oamaruensis* [Martini, 1970a].
Range. Bartonian (NP17).

NNTe11B Neococcolithes dubius SZ

Base. FO of *Chiasmolithus oamaruensis* [Martini, 1970a].
Top. LO of *Chiasmolithus grandis* [Bukry, 1973 a] and/or *Neococcolithes* spp. [Edwards, 1971].
Range. Bartonian (lower NP18).
Remarks. The LO of *D. punctulata* and *C. staurion* are observed at the top of this subzone. *Helicosphaera bramlettei* and *Sphenolithus predistentus* have their FO at the base.

A sample examined 3 feet below the top of the Sovind Marl pit in Sovind (Denmark) was assigned to this subzone.

NNTe12 Discoaster barbadiensis Zone

Base. LO of *Chiasmolithus grandis* [Bukry, 1973a] and/or *Neococcolithes* spp. [Edwards, 1971].
Top. LO of *Discoaster barbadiensis* and/or *Discoaster saipanensis* [Hay *et al.*, 1966].
Range. Priabonian (upper NP18–NP20).
Remarks. Poorly developed in the Central North Sea but found in the South Viking Graben area and Dutch North Sea. The top of the zone is considered to be coincident with the top of Planktonic Foraminiferal Zone P16 of Blow (1979).

NNTe12A Helicosphaera bramlettei SZ

Base. LO of *Chiasmolithus grandis* [Bukry, 1973a] and/or *Neococcolithes* spp. [Edwards, 1971].
Top. FO of *Isthmolithus recurvus* [Hay *in* Hay *et al.*, 1967].
Range. Priabonian (upper NP18).
Remarks. *R. umbilica* is common to abundant but its abundance is much reduced above this subzone.

NNTe12B Discoaster saipanensis SZ

Base. FO of *Isthmolithus recurvus* [Hay *in* Hay *et al.*, 1967].
Top. LO of *Discoaster barbadiensis* and/or *Discoaster saipanensis* [Hay *et al.*, 1966].
Range. Priabonian (NP19/NP20).
Remarks. *D. saipanensis* is rare whilst *I. recurvus* and *C. reticulatum* are usually common in the upper part.

NNTe13 Cribrocentrum reticulatum Zone

Base. LO of *Discoaster barbadiensis* and/or *Discoaster saipanensis* [Hay *et al.*, 1966].
Top. LO of *Cribrocentrum reticulatum* [Müller, 1978].
Range. Priabonian (lower NP21).
Remarks. *L. minutus* and *Clausicoccus* spp. are usually common.

NNTe14 Pemma basquense Zone

Base. LO of *Cribrocentrum reticulatum* (Müller, 1978).
Top. LO of *Pemma basquense* and/or *Pemma papillatum* [herein].
Range. Priabonian (upper NP21).
Remarks. Due to poor preservation, usually only isolated elements of *Pemma* spp. are observed. *P. basquense* is more common than *P. papillatum.* The top of this zone is considered to be coincident with the top of Planktonic Foraminiferal Zone P17 of Blow (1979) and is taken to approximate the top of the Upper Eocene, Priabonian Stage.

7.4.3 Oligocene

Twelve zones and three subzones are proposed for the Oligocene (Fig. 7.5).

NNTo1 Clausicoccus fenestratus Zone
Base. LO of *Pemma basquense* and/or *Pemma papillatum* [herein].
Top. LO of abundant *Clausicoccus* spp. [Bukry, 1973a].
Range. Latdorfian (lower NP21).
Remarks. The LO of common *L. minutus* is observed in this zone.

NNTo2 Coccolithus formosus Zone
Base. LO of abundant *Clausicoccus* spp. [Bukry, 1973a].
Top. LO of *Coccolithus formosus* [Martini, 1970 a].
Range. Latdorfian (upper NP21).

NNTo3 Reticulofenestra umbilica Zone
Base. LO of *Coccolithus formosus* [Martini, 1970a].
Top. LO of *Reticulofenestra umbilica* [Bramlette and Wilcoxon, 1967a].
Range. Latdorfian (upper NP22).
Remarks. It is usually difficult to separate *R. umbilica* from *Reticulofenestra hillae* due to the presence of intermediate forms. The LOs of both species are very close to each other, therefore, for practical reasons, the LO of *R. hillae* can also be used to identify the upper boundary of this zone.

NNTo4 Isthmolithus recurvus Zone
Base. LO of *Reticulofenestra umbilica* [Martini, 1970a].
Top. LO of *Isthmolithus recurvus* [Edwards, 1971].
Range. Rupelian (lower NP23).
Remarks. This zone is characterized by common reworked components. The last persistent occurrence of *Blackites tenuis* and *Blackites spinosus* were recorded in this zone.

NNTo5 Lanternithus minutus Zone
Base. LO of *Isthmolithus recurvus* [Edwards, 1971].
Top. LO of *Lanternithus minutus* [herein].
Range. Rupelian (within NP23).
Remarks. This short zone is only detected when sampling intervals are close. Assemblages differ from those of the underlying zone by the absence of *I. recurvus*. The last persistent occurrence of *C. luminis* was observed here.

NNTo6 Dictyococcites scrippsae Zone
Base. LO of *Lanternithus minutus* [herein].
Top. LO of *Chiasmolithus oamaruensis* [Edwards, 1971].
Range. Rupelian (within NP23).
Remarks. *Reticulofenestra* spp. usually dominate.

NNTo7 Helicosphaera compacta Zone
Base. LO of *Chiasmolithus oamaruensis* [Edwards, 1971].
Top. LO of *Helicosphaera compacta* [Haq, 1971] and/or *Helicosphaera bramlettei* [herein].
Range. Rupelian (within NP23–lower NP24).
Remarks. *H. compacta* and *H. bramlettei* are rare but occur persistently in the study area. The top of this zone is considered to approximate the top of the Middle Oligocene, Rupelian Stage.

NNTo7A Dictyococcites bisectus SZ
Base. LO of *Chiasmolithus oamaruensis* [Edwards, 1971].
Top. FO of *Cyclicargolithus abisectus* [Waghorn *in* Perch-Nielsen, 1985b].
Range. Rupelian (within NP23).
Remarks. The LO of *D. scrippsae* is observed in this subzone.

NNTo7B Cyclicargolithus abisectus SZ
Base. FO of *Cyclicargolithus abisectus* [Waghorn *in* Perch-Nielsen, 1985b].
Top. FO of *Helicosphaera truncata* [Bramlette and Wilcoxon, 1967a].
Range. Rupelian (upper NP23).
Remarks. *Dictyococcites* spp., *Reticulofenestra* spp., *Chiasmolithus altus* and *C. floridanus* are common. *Sphenolithus moriformis* is rare but other species of *Sphenolithus* are absent (see also Gallagher, 1990).

NNTo7C Helicosphaera perch-nielseniae SZ
Base. FO of *Helicosphaera truncata* [Bramlette and Wilcoxon, 1967a].
Top: LO of *Helicosphaera compacta* [Haq, 1971] and/or *Helicosphaera bramlettei* [herein].

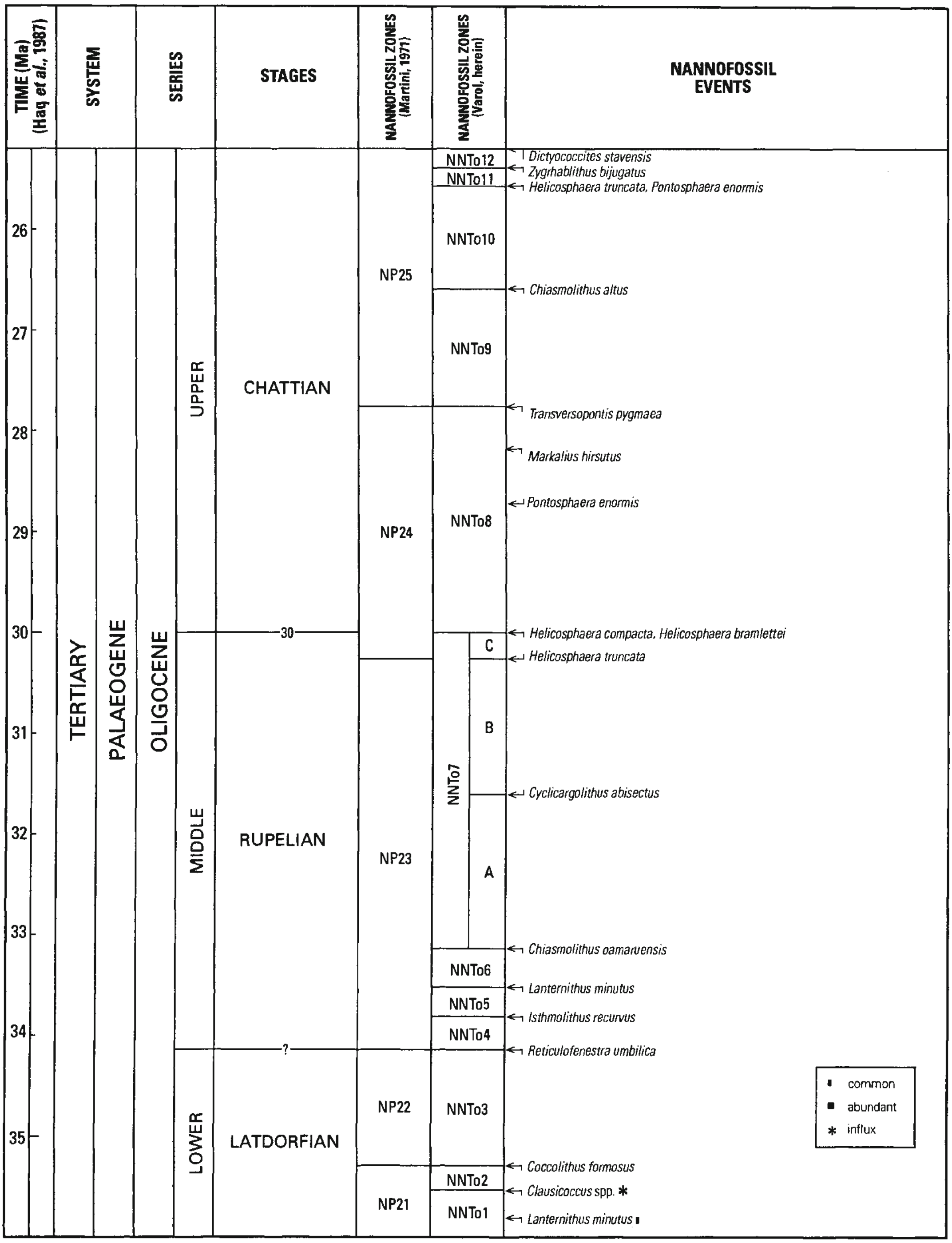


Fig. 7.5 Oligocene nannofossil zones and events for the North Sea area.

Range. Rupelian (lower NP24).
Remarks. The FOs of *H. perch-nielseniae* and *Helicosphaera obliqua* are observed at the base of this subzone. *C. altus* sometimes dominates assemblages.

NNTo8 Transversopontis pygmaea Zone

Base. LO of *Helicosphaera compacta* [Haq, 1971] and/or *Helicosphaera bramlettei* [herein].
Top. LO of *Transversopontis pygmaea* [herein] and/or *Pontosphaera enormis* [Martini, 1981].
Range. Chattian (~upper NP24).
Remarks. The occurrence of *Rhabdosphaera pannonica* was noted in this zone. The last persistent occurrence of *Markalius hirsutus* Varol comb. nov. (Basionym: *Cyclococcolithus hirsutus* Müller, 1970a (*Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **135**, 82-101, Pl. 9, figs 1-4 (holotype 1, 2)), last common *C. abisectus* and LO of *C. luminis* were recorded within this zone.

NNTo9 Chiasmolithus altus Zone

Base. LO of *Transversopontis pygmaea* [herein] and/or the FO of *Pontosphaera enormis* [Martini, 1981].
Top. LO of *Chiasmolithus altus* [Waghorn *in* Perch-Nielsen, 1985b].
Range. Chattian (lower NP25).

NNTo10 Pontosphaera enormis Zone

Base. LO of *Chiasmolithus altus* [Waghorn *in* Perch-Nielsen, 1985b].
Top. LO of *Helicosphaera truncata* [Bramlette and Wilcoxon, 1967a] and/or *Pontosphaera enormis* [herein].
Range. Chattian (within NP25).
Remarks. *H. truncata* is usually rare with the exception of the Dutch North Sea area.

NNTo11 Zygrhablithus bijugatus Zone

Base. LO of *Helicosphaera truncata* [Bramlette and Wilcoxon, 1967a] and/or *Pontosphaera enormis* [herein].
Top. LO of *Zygrhablithus bijugatus* [Edwards, 1971].
Range. Chattian (within NP25).

NNTo12 Dictyococcites stavensis Zone

Base. LO of *Zygrhablithus bijugatus* [Edwards, 1971].
Top. LO of *Dictyococcites stavensis* [Bukry, 1973a].
Remarks. Typically yields poorly preserved and low diversity assemblages. Species include *D. stavensis* (>10µm), *D. bisectus* (<10µm = *Dictyococcites antarcticus*), *Discoaster deflandrei, Reticulofenestra* spp. and *C. floridanus.*

Acknowledgement
I would like to express my gratitute to Dr. T. Romein and Dr. E. Steurbaut for their constructive review of the manuscript.

All specimens figured from North Sea well sections. Scale bars = 10μm.

Plate 7.1

Figs **1–2** *Cyclagelosphaera alta*; **3–5** *Hornibrookina edwardsii*; **6** *Cyclagelosphaera* cf *C. alta*; **7** *Octolithus multiplus*; **8** *Lanternithus* sp.; **9–10** *Lanternithus duocavus*; **11** *Neocrepidolithus cruciatus*; **12** *Neocrepidolithus* sp.; **13** *Neocrepidolithus dirimosus*; **14** *Neocrepidolithus neocrassus*; **15** *Neocrepidolithus fossus*; **16–17** *Lanternithus minutus*; **18–19** *Neochiastozygus saepes*; **20** *Neochiastozygus saepes* (small form); **21** *Transversopontis pygmaea*; **22** *Birkelundia arenosa*; **23** *Neochiastozygus perfectus*; **24** *Neochiastozygus modestus*; **25** *Neochiastozygus eosaepes*; **26** *Clausicoccus vanheckiae*; **27** *Clausicoccus fenestratus*; **28** *Clathrolithus ellipticus*; **29** *Clathrolithus spinosus*; **30** *Nannotetrina alata.*

Plate 7.2

Fig. **1** *Cyclicargolithus floridanus*; **2** *Cyclicargolithus abisectus*; **3** *Dictyococcites scrippsae*; **4** *Dictyococcites bisectus*; **5** *Dictyococcites stavensis* (Levin and Joerger, 1976) comb. nov. Basionym: *Coccolithus stavensis* Levin and Joerger, 1967 (*Micropaleontology*, **13**, 163–182, p. 165, pl. 1, figs 7a–d); **6** *Cyclicargolithus luminis*; **7** *Reticulofenestra dictyoda*; **8–10** *Cribrocentrum reticulatum*; **11–12** *Toweius occultatus*; **13** *Toweius crassus*; **14–15** *Toweius rotundus*; **16–17** *Toweius selandianus*; **18–19** *Prinsius martinii*; **20** *Toweius pertusus*; **21–22** *Prinsius martinii* (small forms); **23–25** *Praeprinsius dimorphosus*; **26–28** *Praeprinsius tenuiculus*; **29–30** *Praeprinsius dimorphosus* (round forms).

Plate 7.3

Figs **1–2** *Biscutum harrisonii*; **3** *Placozygus sigmoides*; **4** *Markalius astroporus*; **5** *Markalius apertus*; **6** *Coccolithus subpertusus*; **7** *Coccolithus pelagicus*; **8** *Coccolithus formosus*; **9–10** *Cruciplacolithus staurion*; **11–12** *Cruciplacolithus primus*; **13–15** *Cruciplacolithus intermedius*; **16–20** *Cruciplacolithus tenuis*; **21–22** *Cruciplacolithus asymmetricus*; **23–25** *Sullivania danica*; **26–28** *Chiasmolithus solitus*; **29** *Chiasmolithus modestus*; **30** *Chiasmolithus altus.*

Plate 7.4

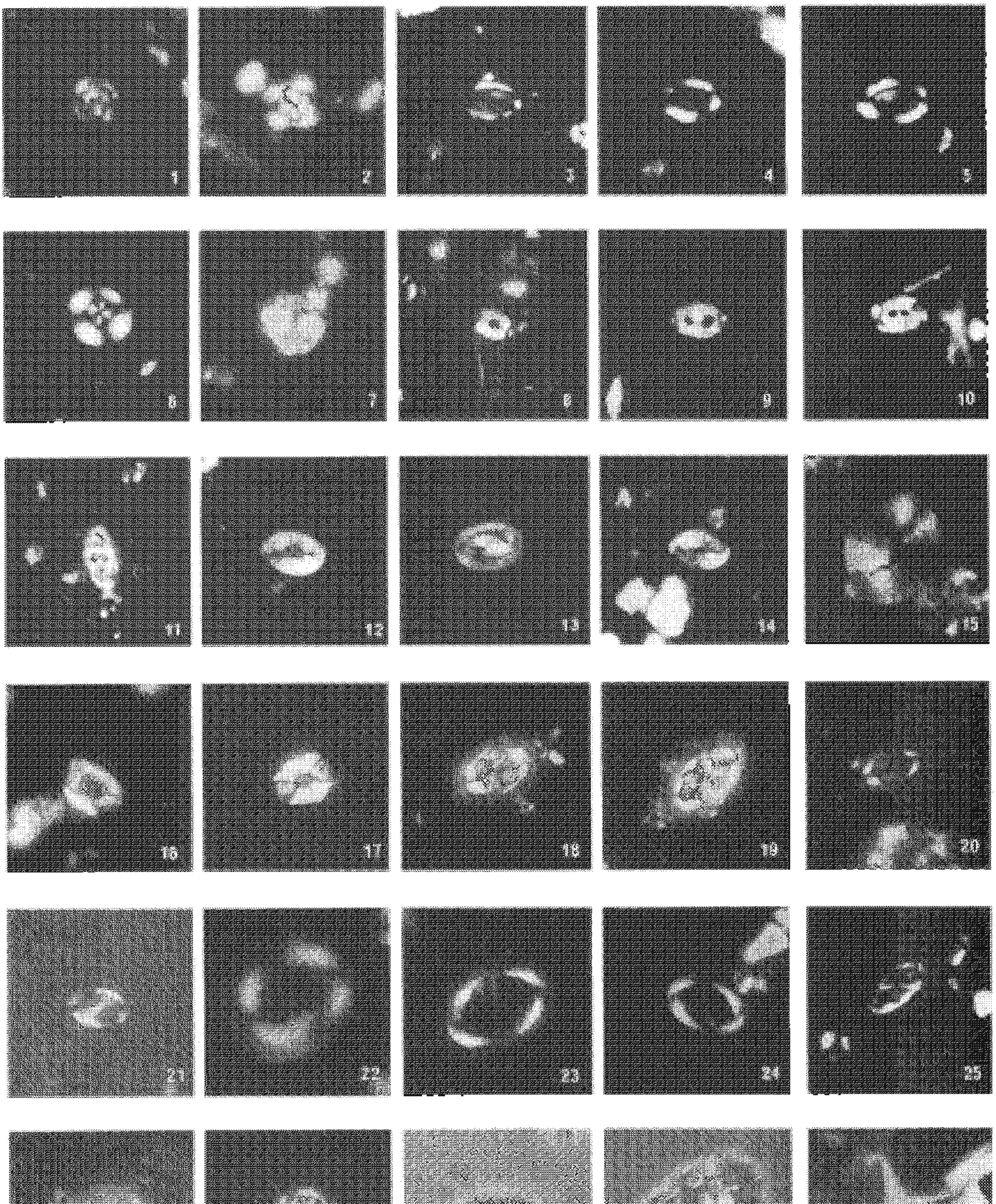
Fig. **1** *Pontosphaera enormis*; **2** *Daktylethra punctulata*; **3–5** *Chiphragmalithus armatus*; **6** *Neococcolithes dubius*; **7** *Neococcolithes protenus*; **8–9** *Isthmolithus recurvus*; **10** *Pemma papillatum*; **11–12** *Sphenolithus stellatus*; **13–14** *Sphenolithus obtusus*; **15** *Pemma basquense*; **16** *Sphenolithus furcatolithoides*; **17** *Sphenolithus spiniger*; **18** *Sphenolithus orphanknollensis*, **19–20** *Sphenolithus predistentus*; **21** *Discoaster barbadiensis*; **22** *Discoaster saipanensis*; **23–24** *Discoaster distinctus*; **25** *Tribrachiatus orthostylus*; **26–27** *Discoaster kuepperi*; **28–29** *Corannulus germanicus*; **30** *Hayella situliformis.*

Plate 7.5

Figs **1–3** *Petasus faviformis*; **4–5** *Goniolithus fluckigeri*; **6** *Ellipsolithus macellus*; **7–8** *Blackites gladius*; **9** *Rhabdosphaera pseudomorionum*; **10** *Rhabdosphaera pinguis*; **11** *Helicosphaera seminulum*; **12** *Helicosphaera lophota*; **13** *Helicosphaera bramlettei*; **14** *Helicosphaera truncata*; **15** *Helicosphaera reticulata*; **16** *Helicosphaera compacta*; **17** *Helicosphaera perch-nielseniae*; **18** *Biantholithus hughesii*; **19** *Biantholithus sparsus*; **20** *Thoracosphaera operculata*; **21–22** *Chiasmolithus medius*; **23** *Chiasmolithus expansus*; **24** *Zygrhablithus bijugatus*; **25–26** *Pontosphaera formosa*; **27** *Reticulofenestra umbilica.*

Plate 7.6

Figs **1–4** *Imperiaster obscurus*; **5–6** *Micrantholithus mirabilis*; **7** *Nannotetrina alata*; **8–9** *Discoaster lodoensis*; **10** *Reticulofenestra umbilica*; **11** *Chiasmolithus oamaruensis*; **12** *Chiasmolithus grandis.*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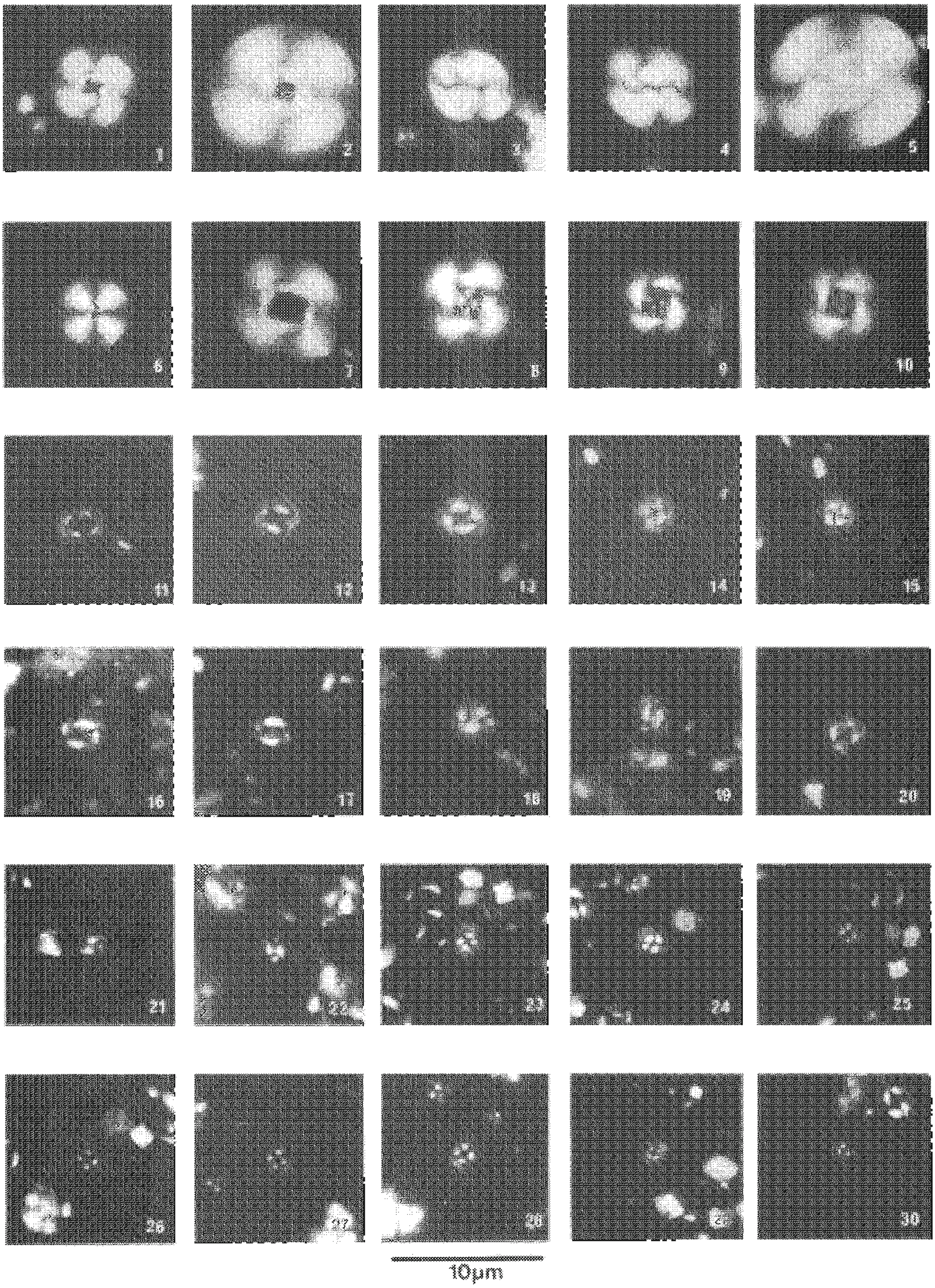
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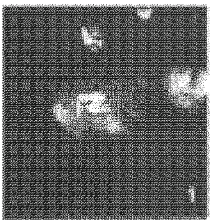
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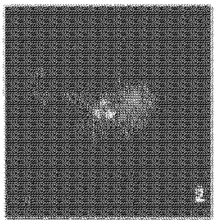
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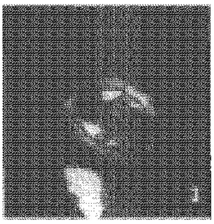
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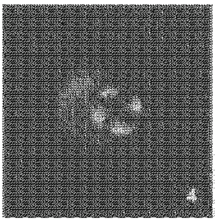
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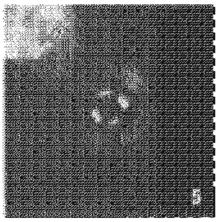
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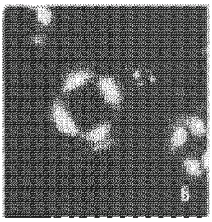
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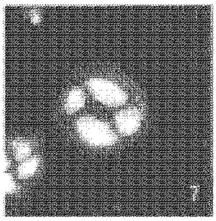
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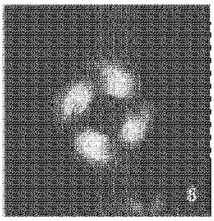
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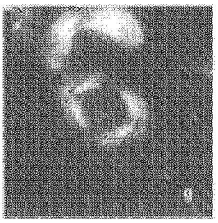
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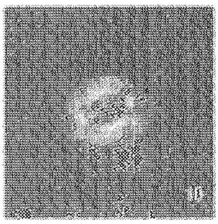
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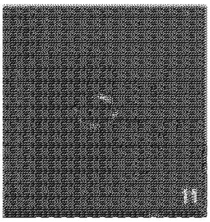
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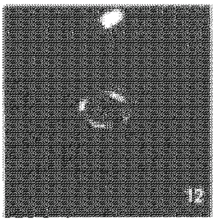
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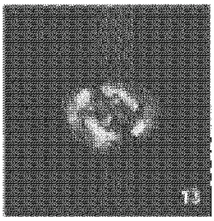
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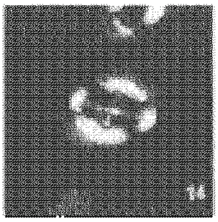
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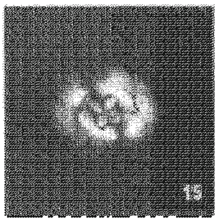
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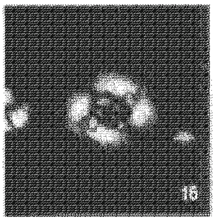
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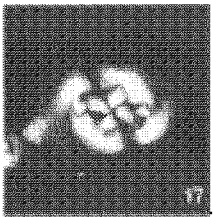
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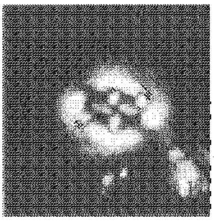
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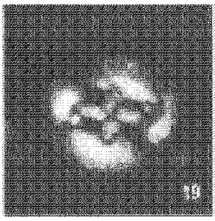
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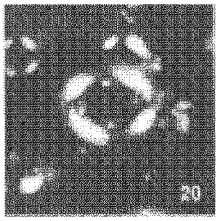
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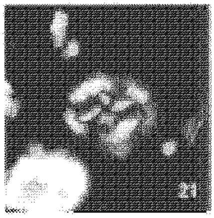
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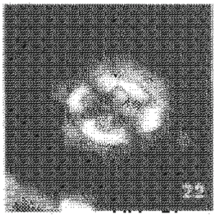
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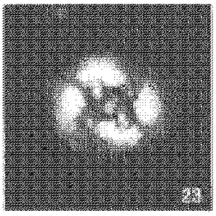
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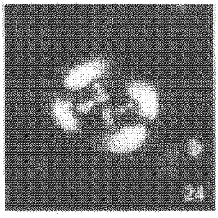
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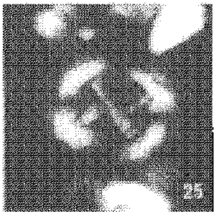
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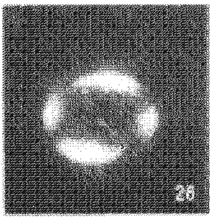
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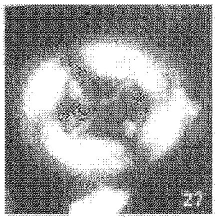
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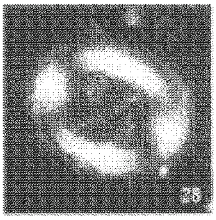
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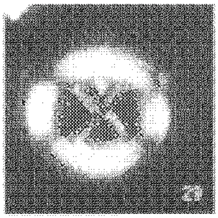
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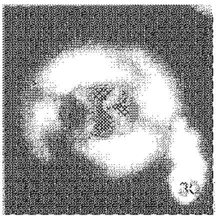
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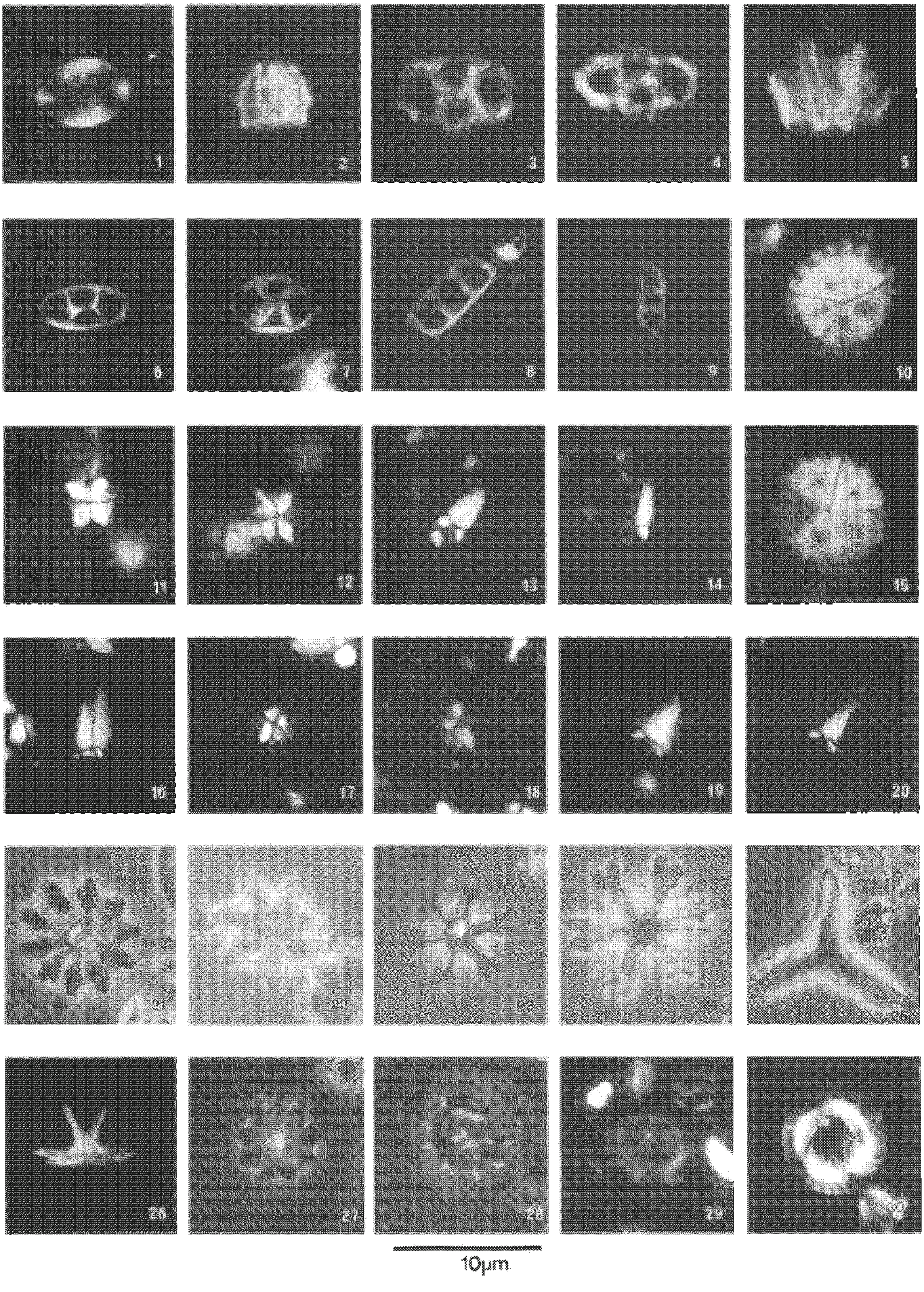
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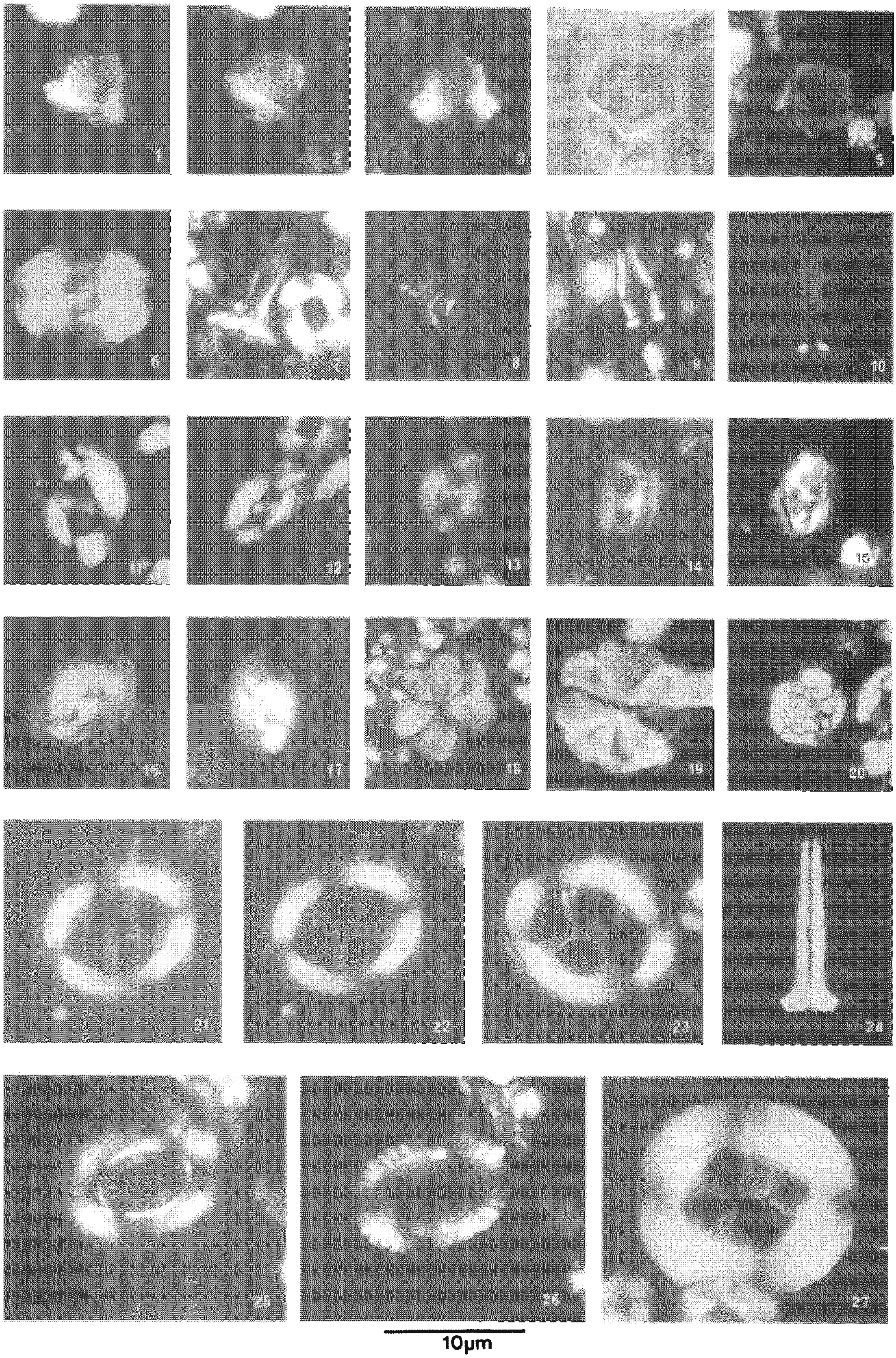
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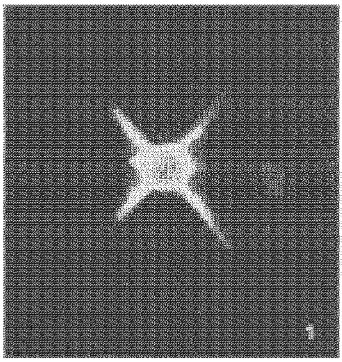

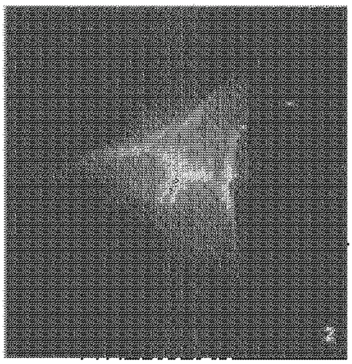

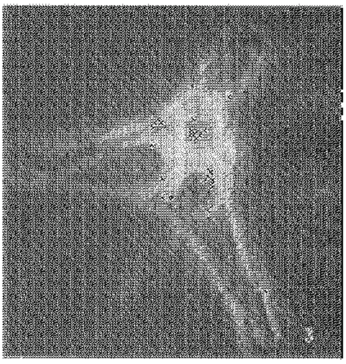

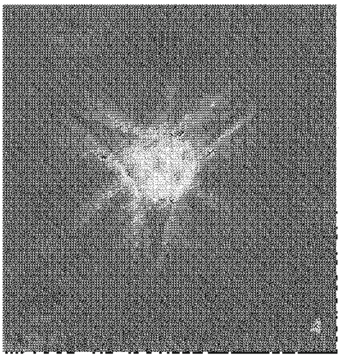

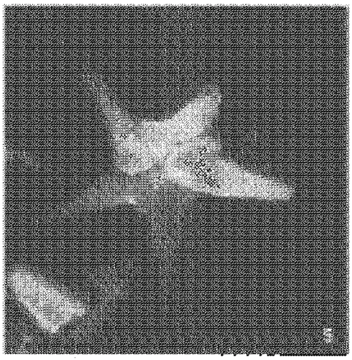

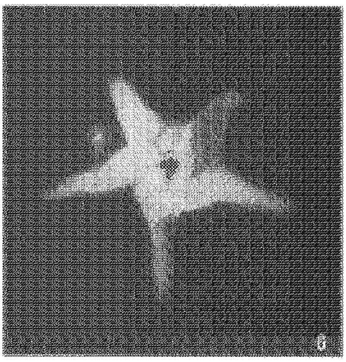

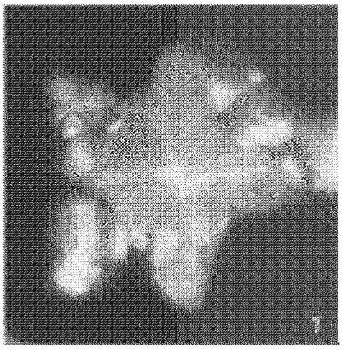

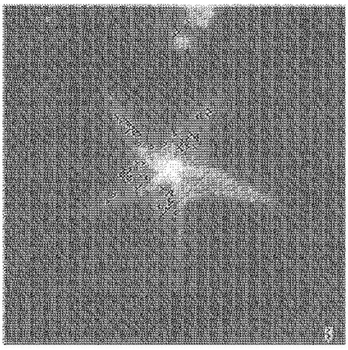

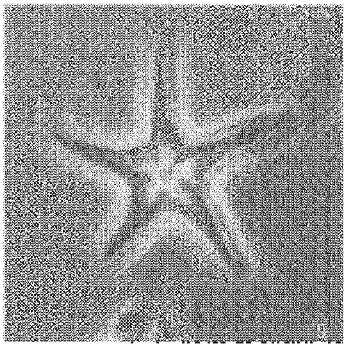

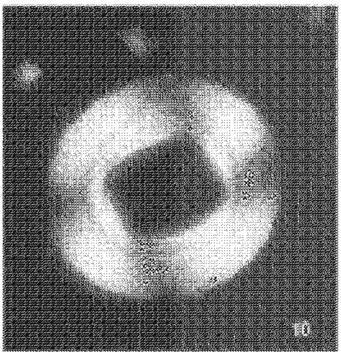

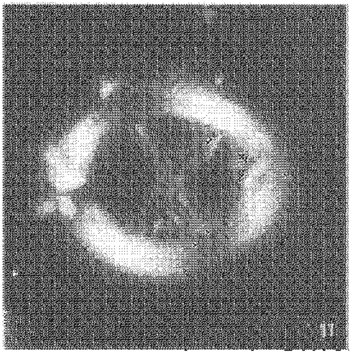

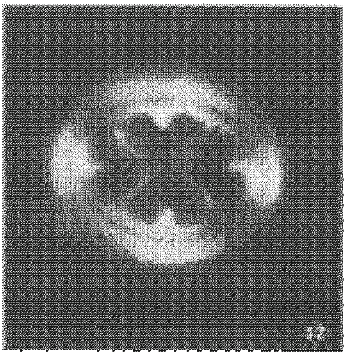

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8

Neogene

J.R. Young

8.1 INTRODUCTION

The Neogene comprises the Miocene and Pliocene, that is, the 22 million years of Earth history between the Oligocene and Pleistocene. Throughout this interval nannofossils provide a high-resolution biostratigraphy and are the prime tool for long distance biostratigraphic correlation. Thus they play an essential role in modern academic research and hydrocarbon exploration. Neogene marine sediments are extremely widespread offshore; the ODP and DSDP have recovered long Neogene sequences from hundreds of sites around the world, and these are matched by commercial drilling in provinces such as the US Gulf Coast and South East Asia. Conversely, good marine Neogene successions are rather rare onshore; most outcropping Neogene successions are in basin-margin facies, in tectonically active areas or on oceanic islands.

8.2 IMPORTANT REFERENCES

The relative shortage of readily available open marine sections meant that studies of Neogene nannofossils started slowly, with very few studies before the 1960s, and the most important of these were based on a single sample from Rotti in Indonesia (Tan, 1927a, b; Kamptner, 1955). Modern studies arguably began with the work of Martini and Bramlette (1963) on the Mohole cores, including description of several key marker -species. Subsequently, studies developed rapidly based initially on material from other deep-sea samples, and from the oceanic sediments of Trinidad, then after the late 1960s from the Deep Sea Drilling Project. Martini and Worsley (1970) published a standard zonation for the Neogene and from then on nannofossils have formed a prime tool for the dating and correlation of Neogene sediments. Indeed, there are now several thousand publications and unpublished reports detailing studies of Neogene nannofossils, the vast majority comprising applied biostratigraphic work.

The most important single published source are the DSDP and ODP report volumes, most of which contain chapters on Neogene nannofossils including many major papers, such as Perch-Nielsen (1972, Leg 12), Bukry (1973b, Leg 16), Müller (1974a, Leg 25), Edwards and Perch-Nielsen (1975, Leg 29), Perch-Nielsen (1977, Leg 39), Bukry (1981a, Leg 63), Bergen (1984, Leg 78A), Pujos (1985, Leg 80), Rio *et al.* (1990a, b, Legs 107 and 115), Raffi and Flores (1995, Leg 138) and de Kaenel and Villa (1996, Leg 149). Most of these contain zonal discussions, detailed distribution charts, illustration of key taxa and often new taxonomy. Other essential papers dealing with Neogene taxonomy and biostratigraphy include Backman (1980), Backman and Shackleton (1983), Berggren *et al.* (1995), Bramlette and Riedel (1954), Bramlette and Wilcoxon (1967), Bukry (1971a, b), Bukry and Bramlette (1968, 1969), Gartner (1967a, b, 1992), Gartner and Bukry (1975), Haq (1973), Haq and Berggren (1978), Hay *et al.* (1967), Martini (1971), Martini and Bramlette (1963), Müller (1974b), Okada and Bukry (1980), Raffi and Rio (1979), Theodoridis (1984), Martini and Müller (1986), Varol (1989d), Young (1990), Raffi *et al.* (1995), Fornaciari and Rio (1996), Fornaciari *et al.* (1996) and Su (1996).

There are, however, surprisingly few syntheses of this work, in fact the only comprehensive overview is provided by Perch-Nielsen (1985b). For taxonomic research the catalogues of Aubry (1984, 1988, 1989a, 1990) and Farinacci (1969 *et seq.*) and the Nannobase database (Bybell, 1994) are invaluable, but they are not suitable as routine identification guides.

The objective of this chapter is to provide an up-to-date guide to Neogene nannofossil taxonomy and biostratigraphy in a succinct and useful format. About 150 species are included here with brief identification notes, complimented by light micrograph illustrations and range charts. Range charts, plates and text are arranged essentially on the same taxonomic basis to ease cross reference between them.

8.3 BIOSTRATIGRAPHY

The basis of Neogene nannofossil zonation was worked out during the 1960s by, in particular, Bramlette and Wilcoxon (1967a), Hay *et al.* (1967), Hay and Schmidt (1968) and Gartner (1969c). This work was synthesized into a Standard Neogene Calcareous Nannoplankton Zonation by Martini and Worsley (1970) and described in detail by Martini (1971). They numbered the zones NN1–21, without subzones (Fig. 8.1). In parallel Bukry (1973a, 1975, 1981a) reformulated the same zonation as a Low Latitude Coccolith Zonation, with some additional events. Okada and Bukry (1980) numbered these zones CN1–15, with many subzones (e.g. CN1a–c). The co-existence of two virtually identical zonations is an unfortunate accident, with little objective justification. However, European workers have mostly used the NN zones and American workers the CN zones, with the result that neither system has predominated. I primarily use the NN zonation here. For convenience the single references Martini (1971) and Okada and Bukry (1980) are used in the text when referring to these zonations.

These zonations have served nannofossil workers extremely well but it may be noted that there are several problems with them: zones are of rather random duration (0.1 to 4Ma); several very poor events are used as markers (e.g. FO of *Discoaster kugleri*, FCO of *D. asymmetricus*); some good events are not used in the zonations (e.g. LO of *Reticulofenestra bisecta*, FO of *Amaurolithus amplificus*). Consequently various authors have suggested modifications to the zonations (e.g. Varol, 1989d; Raffi *et al.*, 1995; de Kaenel and Villa, 1996), whilst for the Mediterranean area reformulated zonations have been proposed by Theodoridis (1984) and by Rio and co-workers (Raffi and Rio, 1979; Fornaciari and Rio, 1996; Fornaciari *et al.*, 1996).

8.3.1 Biozonation overview

For discussion purposes the Neogene is here subdivided into eight intervals (A–H) of 1–5Ma duration, based on the most important events. This is the most consistently obtainable level of zonation, and in clastic sediments with poor preservation this is frequently the level of resolution which is achieved, even after considerable time and effort has been expended. Similarly a novice should expect to be able to reliably achieve this resolution. With well preserved nannofossil oozes experienced workers can obtain this resolution after examination of one field or two fields of view, and usually will obtain significantly higher resolution after careful study. Additional events are discussed in the text and summarized in Fig. 8.1.

The following standardized abbreviations are used in this section: *Coccolithus-C.*, *Calcidiscus-Cd.*, *Catinaster-Ct.*, *Ceratolithus-Cr.*, *Clausicoccus-Cl.*, *Coronocyclus-Co.*, *Cyclicargolithus-Cy.*, *Discoaster-D.*, *Helicosphaera-H.*, *Hughesius-Hu.*, *Orthorhabdus-Or.*, *Reticulofenestra-R.*, *Sphenolithus-S.*, *Triquetrorhabdulus-Tq.*, *Umbilicosphaera-U.*

The stratigraphic ranges of marker and selected other species are graphically represented in Figs 8.2–8.4. Photographic illustrations are presented in Plates 8.1–8.11.

Interval A (LO *S. ciperoensis* to FO *S. belemnos* NN1–2/CN1a–c)

This is a negatively-defined interval, between the LOs of typical Oligocene species *(R. bisecta, Zygrhablithus bijugatus, S. ciperoensis, Cl. fenestratus, H. recta)* and the FO of *S. belemnos*. Nannofloras are of low diversity with many typical Neogene elements rare or absent, e.g. *Calcidiscus, U. jafari, U. rotula, D. exilis-variabilis* group.

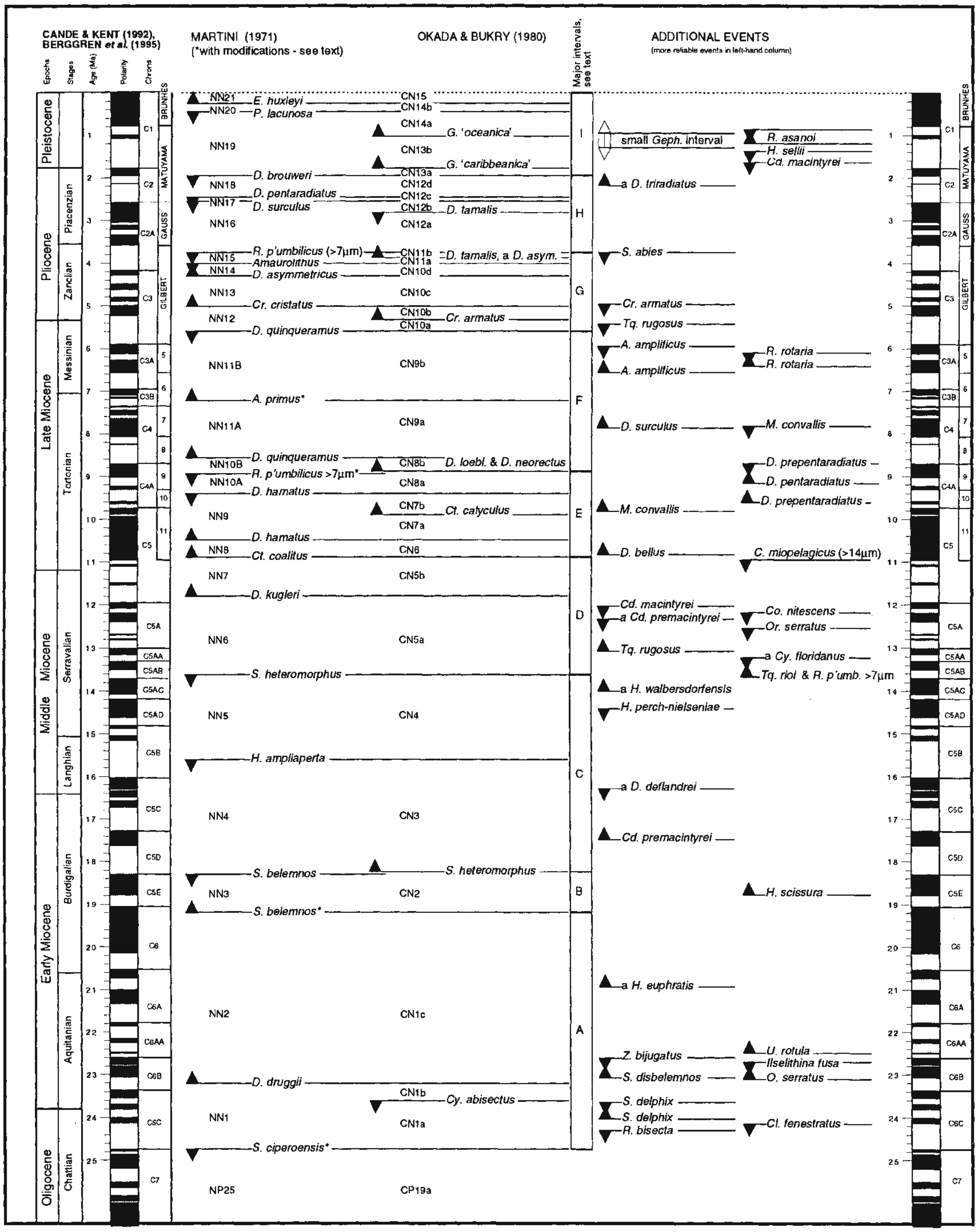

Fig. 8.1 Summary of Neogene nannofossil biostratigraphic zonation schemes and bioevents (a = acme).

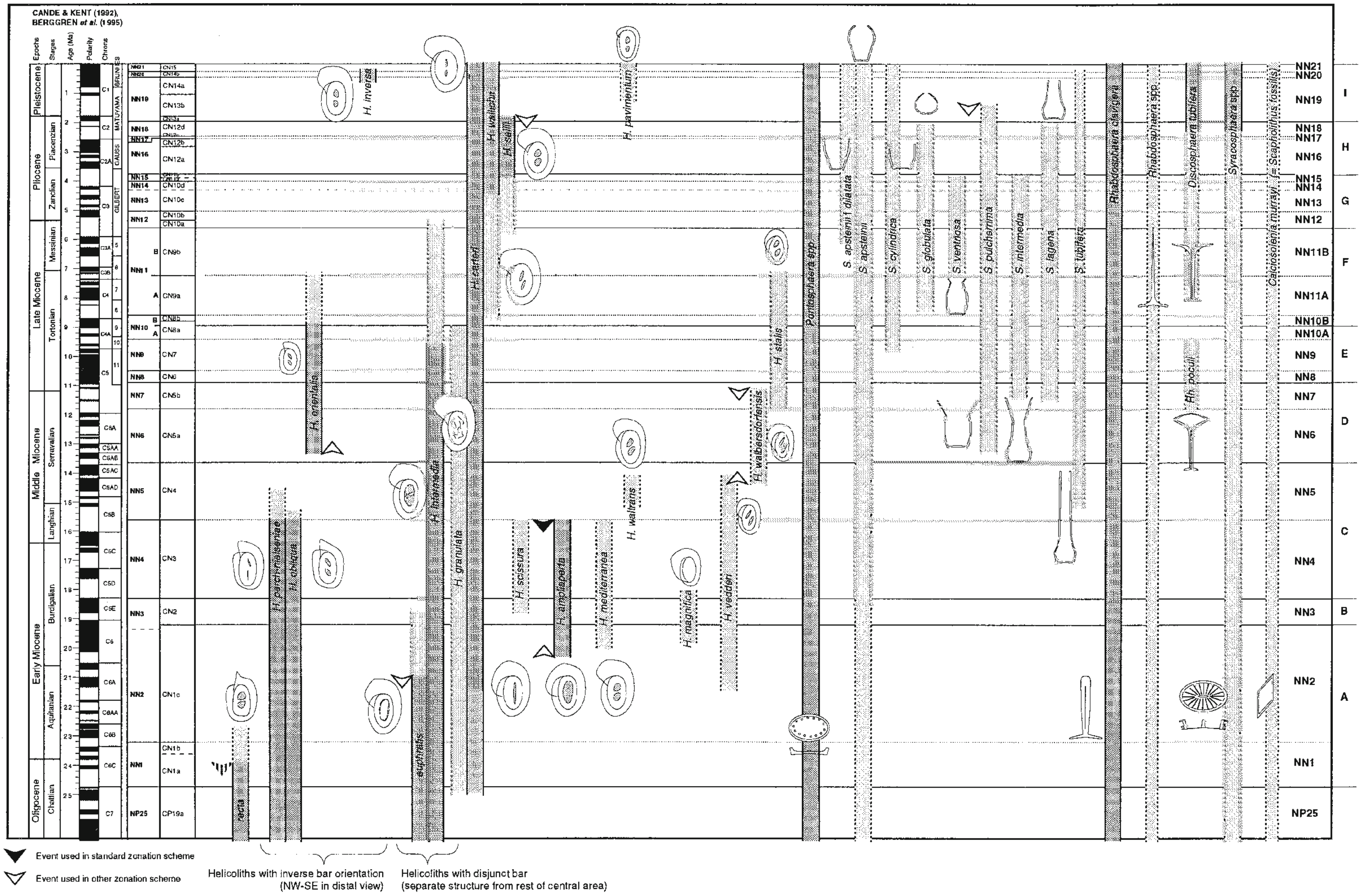

Fig. 8.2 Stratigraphic distribution of Neogene Helicosphaeraceae, Syracosphaeraceae and Pontosphaeraceae, based on literature data supplemented by results of the author. Darker shaded range-bars with solid lines indicate well-established, dependable ages, paler-shaded range bars with dotted edges indicate less-reliably established ranges. Close spacing of range-bars indicates likely evolutionary relationship and, when adjacent, indicate intergradational morphotypes. Helicoliths are drawn in distal view but with an indication of the flange origin (proximal feature).

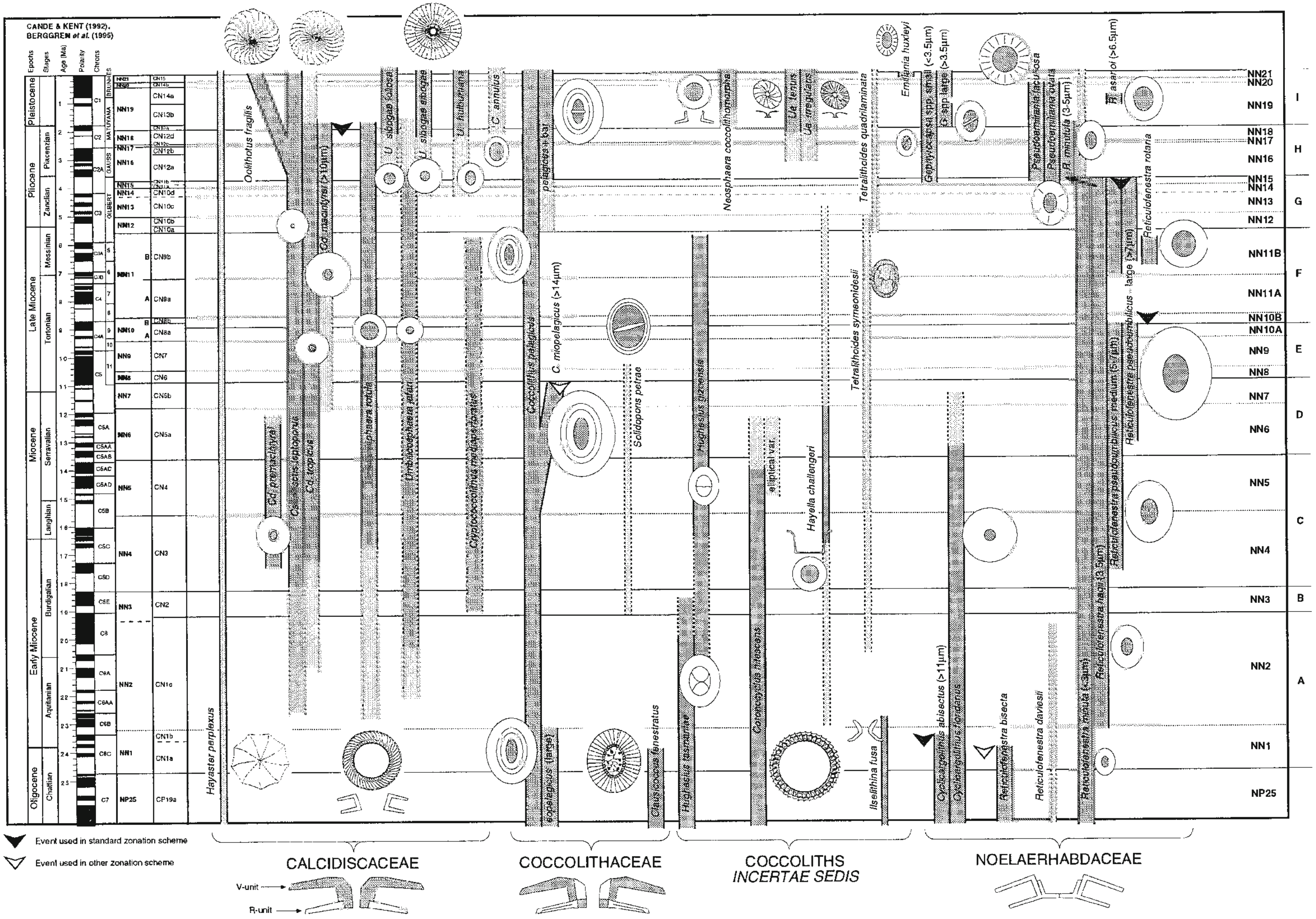

Fig. 8.3 Stratigraphic distribution of Neogene Calcidiscaceae, Coccolithaceae and Noelaerhabdaceae and other placolith coccoliths. Conventions as per Fig. 8.2.

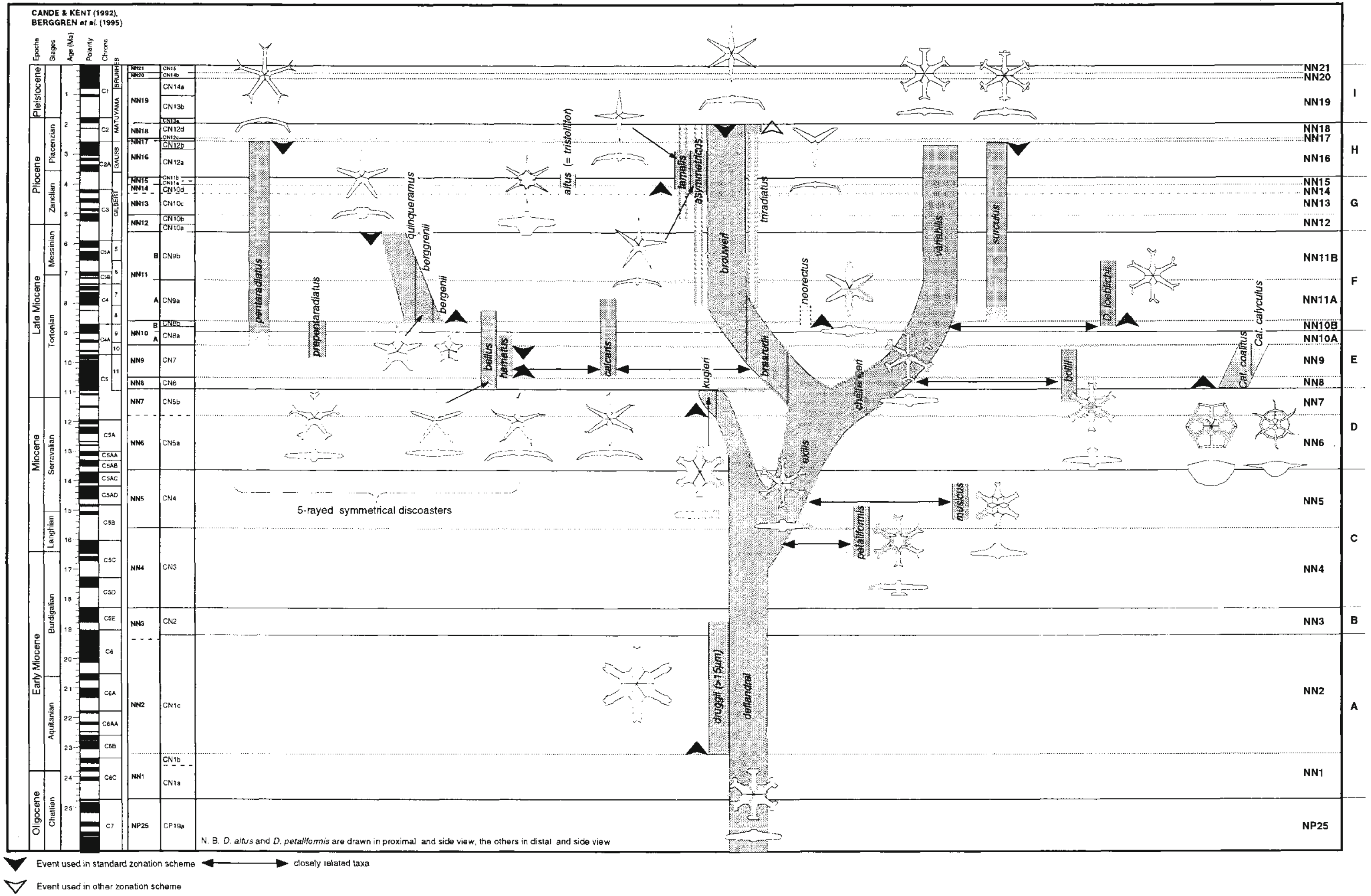

Fig. 8.4 Stratigraphic distribution of Neogene Discoasteraceae. Species are illustrated in distal and side view, except *D. altus* and *D. petaliformis* which are shown in proximal view. Double-headed horizontal arrows indicate close affinities not shown by placement of the range-bars. Other conventions as per Fig. 8.2. NB. Treatment of the *exilis-challengeri-variabilis* group varies between authors.

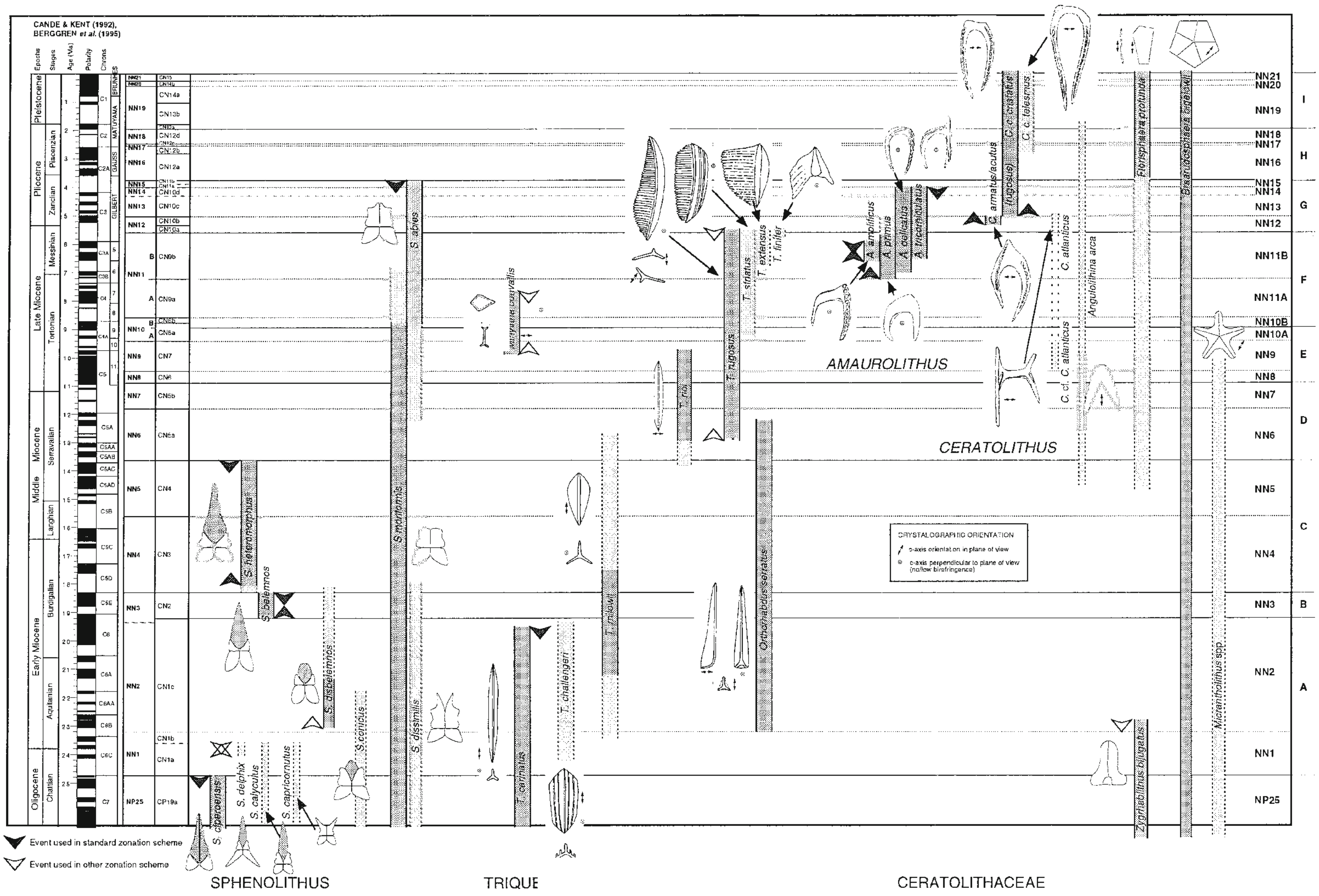

Fig. 8.5 Stratigraphic distribution of Neogene Sphenolithaceae, Triquetrorhabdul[illegible] n the sphenolith sketches, the shaded part is in extinction when the specimen is orientated N-S in XPL. In other sketches the small double-headed arrow and circle with dot indicates c-axis orientation. Other conventions are as per Fig. 8.2.

Most common species. *Cy. floridanus, C. pelagicus, D. deflandrei, S. moriformis, S. dissimilis, Helicosphaera* spp. This rather resembles an impoverished Oligocene assemblage. The best positive indication of Neogene age is often the presence of *H. carteri,* although its FO is gradational and inconsistent in precise placement. In addition, *D. deflandrei* is typically more abundant and diverse than in Oligocene assemblages. *Tq. challengeri* is essentially confined to this interval, but only sporadically present.

Base. The Oligo-Miocene transition is characterized by a succession of last occurrences: LO *S. ciperoensis*, LCO *R. bisecta*, LO *Z. bijugatus*, LO *H. recta*. The LO of *H. recta* was formally adopted by Martini and Worsley (1970) as the base of zone NN1 but it is now well established that *H. recta* can occur well into the Miocene (e.g. Rio *et al*., 1990b). Consequently, many workers, including Martini (1986), have formally recommended substitution of the LO of *S. ciperoensis* as the base of NN1, as is used in the Okada and Bukry (1980) zonation for the base of CN1. Note, however, that Berggren *et al.* (1995) and Fornaciari *et al.* (1996) suggest redefining the base of NN1 at the LO of *R. bisecta* since it is closer to the Oligo-Miocene boundary.

Subdivision. Both standard zonation schemes use the FO of *D. druggii*; a rare, poorly defined variant of *D. deflandrei*. Recent studies (Rio *et al.*, 1990; Fornaciari and Rio, 1996; de Kaenel and Villa, 1996) have shown that a consistent *D. druggii* FO can be identified within chron C6Br but also that the FO of a distinctive small sphenolith, *S. disbelemnos*, provides a better marker at about the same level. Various other events have also been suggested within this interval, including in stratigraphic sequence: LO *Cl. fenestratus*; FO and LO *S. delphix* (these usefully define a short interval within NN1); LCO *Cy. abisectus* (used as subzonal marker by Okada and Bukry (1980) but a difficult event to define objectively); FO *Or. serratus* (often occurs near the NN1/2 boundary but not consistent); FO *S. disbelemnos*; LO *Ilselithina fusa*; FO *U. rotula*; LO *H. recta* (these last three events appear to occur close together in the lower part of NN2, Chron C6Bn – Gartner, 1992; de Kaenel and Villa, 1996) and LCO *H. euphratis*. The FOs of *Cd. leptoporus*, *Cd. tropicus* and *H. ampliaperta* also occur within NN2 but with less consistency. Extended discussions of the NN1–2 interval are given by Fornaciari *et al.* (1996), and de Kaenel and Villa (1996); see also Theodoridis (1984), Varol (1989d) and Gartner (1992).

Interval B (FO *S. belemnos* to LO *S. belemnos* NN3/CN2)
The assemblages of this interval are similar to those of the NN1–2 interval but with the addition of the distinctive common marker *S. belemnos*. Also *Umbilicosphaera* and *Calcidiscus* are more consistently present.

Base. The base of NN3 was defined as the LO of *Tq. carinatus* with the FO of *S. belemnos* as a secondary marker. *Tq. carinatus* is however only common in well-preserved, open-marine sediments, so the FO of *S. belemnos* is a much better marker. Where both are present, the LO of *Tq. carinatus* is usually slightly above the FO *S. belemnos*.

Subdivision. No events for subdivision of this interval have been identified, except possibly the FO of *H. scissura* (de Kaenel and Villa, 1996).

Interval C (LO *S. belemnos* to LO *S. heteromorphus* NN4–5/CN3–4)
S. heteromorphus characterizes this interval, it is distinctive and abundant, but it should be noted that it is easily reworked. This is also an interval of fairly high diversity: most of the early Miocene taxa, such as *H. obliqua* and *Co. nitescens,* persist and they are joined by a range of new species, including notably, *Cd. premacintyrei* and *D. exilis.*

Most common species. *Cy. floridanus, C. pelagicus, Calcidiscus* spp., *S. moriformis, S. heteromorphus, D. exilis, H. carteri, U. jafari, U. rotula.*

Base. The LO of *S. belemnos* and FO of *S. heteromorphus* are very close and the sequence of these events has been unclear. Olaffson (1991) and Fornaciari and Rio (1996) suggest that there is usually an interval between the LCO of *S. belemnos* and the FCO of *S. heteromorphus* within which the two species co-occur at low abundances. This would fit most observations.

Subdivision. Both Martini (1971) and Okada and Bukry (1980) use the LO of *H. ampliaperta* to subdivide this long interval. Its occurrence, however, is often sporadic, particularly toward its LO, hence it is not an outstandingly reliable marker. Other possible markers include, in order: FO *Cd. premacintyrei* (Gartner, 1992; de Kaenel and Villa, 1996), almost certainly useful; LCO *D. deflandrei* (Bukry, 1973a; Rio *et al.*, 1990; Fornaciari *et al.*, 1996), often a well marked event, but possibly diachronous; *S. heteromorphus* paracme/low abundance interval (Fornaciari *et al.*, 1996), a promising event, but only proven in the the Mediterranean; FO *D. exilis* (Theodoridis, 1984), difficult to define objectively; LO *H. perch-nielseniae* (Theodoridis, 1984; de Kaenel and Villa, 1996), rare toward its LO; FCO *H. walbersdorfensis* (Müller, 1981; Fornaciari *et al.*, 1996), promising.

Interval D (LO *S. heteromorphus* to FO *Catinaster* NN6–7/CN5a–b)

This interval tends to have low diversity as many typical species of earlier assemblages disappear or become very rare, e.g. *Cy. floridanus*, *S. heteromorphus*, *Co. nitescens*, *H. obliqua* and *H. perch-nielseniae*. Conversely, there are relatively few new occurrences. This interval is therefore negatively defined and can also be difficult to subdivide.

Most common species. *R. pseudoumbilicus*, *C. pelagicus*, *Cd. leptoporus*, *D. exilis*, *H. carteri*, *U. jafari*, *U. rotula*. Less common but more useful species include *Tq. rugosus*, *D. kugleri* and *H. orientalis*.

Base. The LO of *S. heteromorphus* is a good marker. The LCO of *C. floridanus* and FO of *Tq. rugosus* and *Tq. rioi* occur slightly later and are useful for general recognition of the interval. The FCO of *R. pseudoumbilicus* (>7µm) is also in this interval but is a gradational size-increase event and not surprisingly is diachronous, occurring slightly above or below the LO of *S. heteromorphus* (Raffi *et al.*, 1995). The LO of *Or. serratus* is also often recorded near the NN5/6 boundary (e.g. de Kaenel and Villa, 1996), but higher by Raffi *et al.* (1995).

Subdivision. The FO of *D. kugleri* is used by both Martini (1971) and Okada and Bukry (1980) to subdivide this interval. This is a difficult event since unambiguous specimens are never common. A number of other events, however, occur slightly below (ca. 0.4 to 0.2Ma earlier): LCO *Cd. premacintyrei*, LO *Co. nitescens*, LO *Cd. premacintyrei* (Raffi *et al.*, 1995). Of these, Fornaciari *et al.* (1996) suggest that the LCO of *Cd. premacintyrei*, which occurs just before the *D. kugleri* FO (e.g. Gartner, 1992), is the best alternative marker. The LO of *Or. serratus* and LO *Co. nitescens* occur close together. The large (>14µm) species, *C. miopelagicus*, is essentially confined to NN7 but its FO is gradational.

Interval E (FO *Catinaster* to base small *Reticulofenestra* interval NN8–10a/CN6–8a)

This interval is characterized by large placoliths, especially *R. pseudoumbilicus*, and rapidly diversifying discoasters, including the first symmetrical 5-rayed discoasters. It has some of the most interesting nannofossil assemblages of the Miocene and could probably be finely subdivided.

Most common species. *R. pseudoumbilicus*, *C. pelagicus*, *Cd. leptoporus*, *D. exilis*, *D. bellus*, *Ct. coalitus*, *Ct. calyculus*, *H. carteri*, *Minylitha convallis*, *U. jafari*, *U. rotula*.

Base. The FO of *Ct. coalitus* is the standard marker, and virtually coincident with this are the LO of *C. miopelagicus* and FO of *D. bellus*.

Subdivision. The FO and LO of *D. hamatus* define zone NN9/CN7. Okada and Bukry (1980) use the FO of *Ct. calyculus* to define subzones CN7a and b. This FO certainly does occur within this interval but its position seems variable (e.g. Peleo-Alampay and Wei, 1995; Peleo-Alampay *et al.*, 1998). The FOs of *D. prepentaradiatus* and *M. convallis* occur just before the LO of *D. hamatus*.

Interval F (base small *Reticulofenestra* interval to LO *D. quinqueramus* NN10b–11/CN8b–9b)

The upper part of this interval is widely represented by thick sequences and has been particularly well studied. Assemblages are generally characterized by small coccoliths, particularly small reticulofenestrids. *Discoaster* assemblages stabilize after the rapid evolution of the preceding interval.

Most common species. Small reticulofenestrids (e.g. *R. haqii), C. pelagicus, Cd. leptoporus, D. quinqueramus, D. variabilis, D. surculus, D. brouweri, D. pentaradiatus, S. abies, H. carteri, U. jafari, U. rotula.*

Base. The base of this interval is marked by the most dramatic nannofossil event in the Neogene *not* included in the standard zonations, the abrupt disappearance of large *Reticulofenestra* specimens. Large *R. pseudoumbilicus* does recur later but reticulofenestrid assemblages above the small *Reticulofenestra* interval are dominated by specimens <5μm long whereas those of NN6-10A are dominated by specimens >5μm. This event was first described by Young (1990) and Rio *et al.* (1990), and has since been widely documented (e.g. Gartner, 1992; Takayama, 1993) and appears to be isochronous (Young *et al.*, 1994; Mock and Bralower, unpubl. data). The event was almost certainly an evolutionary response to change in oceanographic conditions, and associated effects include decrease in size in other coccoliths and increase in abundance of sphenoliths. Zone NN10 is here divided into subzones NN10A and NN10B on the basis of this event. The FO of *D. pentaradiatus* occurs at about this level, and for low-resolution work the occurrence of this unmistakable species can be useful; the LO of *D. prepentaradiatus* is slightly higher.

Subdivision. The FO of *D. quinqueramus* defines the base of NN11 and CN9. This is an excellent marker, but its exact magnetochronostratigraphic correlation is uncertain and it may be diachronous. In addition, *D. quinqueramus* is virtually absent in the Mediterranean. *D. berggrenii* and *D. bergenii* are variants of *D. quinqueramus* with larger central-areas; they have the same FO but become less abundant upwards. *Minylitha convallis* and *D. calcaris* are characteristic of the lower part of NN11 but their LOs do not appear to be reliable events. The first *Amaurolithus* species (*A. primus*) occurs sparsely but reliably midway through NN11/CN9, defining subzones CN9A/B and NN11A/B (Martini and Müller, 1986). Subsequently, *A. amplificus* and *R. rotaria* have valuable short ranges.

Interval G (LO *D. quinqueramus* to LO *R. pseudoumbilicus* NN12–15/CN10a–11b)
This interval approximately corresponds to the Lower Pliocene and is reasonably easy to recognize but often difficult to subdivide.

Most common species. Small reticulofenestrids (e.g. *R. haqii), Cd. leptoporus, D. variabilis, D. surculus, D. brouweri, D. pentaradiatus, S. abies, H. carteri, U. jafari, U. rotula.*

Base. The LO of *D. quinqueramus* is usually a good event but it can be rare towards the top of NN11/CN9. In addition, the LO of *Tq. rugosus* and *Hu. gizoensis* occur near this level. In poor assemblages the presence of *C. pelagicus* specimens with a bar can be a valuable positive indication of Pliocene age; they do not seem to have a sharp FO but typically the largest 5–10% of Lower Pliocene specimens have bars.

Subdivision. Most events are based on ceratoliths: FO and LO *Cr. armatus*; FO *Cr. cristatus*; LO *Amaurolithus tricorniculatus* and *A. delicatus*. These are reliable events when ceratoliths are present but even in nannofossil oozes they are often rare. The FCOs of *D. asymmetricus* and *D. tamalis* are easier to use in some sites but are more diachronous.

Interval H (LO *R. pseudoumbilicus* to LO *D. brouweri* NN16–18/CN12a–d)
A major nannofossil turnover occurs around the Lower/Upper Pliocene boundary so that this interval is easily recognizable.

Most common species. Small reticulofenestrids (e.g. *Pseudoemiliania lacunosa, P. ovata, R. minutula), C. pelagicus, Cd. leptoporus, D. variabilis, D. surculus, D. brouweri, D. pentaradiatus, H. carteri, U. jafari, U. rotula.*

Base. The LOs of *R. pseudoumbilicus* (>7μm) and *S. abies* occur almost synchronously and define the base of NN16. In addition, *Pseudoemiliania* specimens (i.e. reticulofenestrids with slits in the distal shield) have their FO near this level. Indeed *Pseudoemiliania* usually dominates Upper Pliocene assemblages, although large circular *P. lacunosa* specimens do not occur until the Pleistocene. The FO of *Gephyrocapsa* is also near the Lower/Upper Pliocene boundary, and small *Gephyrocapsa* specimens are usually common in the lower part of NN16. They then become rare until near the end of the Pliocene. *C. pelagicus* specimens with bars become much more common in the Upper Pliocene.

Subdivision. Subdivision is essentially based on the successive last occurrences of discoasters, with one FCO: LCO *D. tamalis* and *D. asymmetricus*; LO *D. variabilis* (rather unreliable); LO *D. surculus*; LO *D. pentaradiatus*; FCO *D. triradiatus*; LOs *D. brouweri* and *D. triradiatus*. The timing of these events has been well constrained and they allow precise biostratigraphy of the upper part of this interval. As ever, dating spot samples may be less certain, particularly since any of these species may have absence intervals below their true LOs, and also discoasters are only abundant in oligotrophic environments.

Interval I (LO *Discoaster* to Present NN19–21/CN13a–15)

The Plio-Pleistocene boundary is marked both by the final disappearance of discoasters and by the replacement of *Pseudoemiliania* by *Gephyrocapsa* as the predominant reticulofenestrid. Thus Pleistocene assemblages are unambiguously identifiable. High-resolution subdivision is also possible but this is dependent on careful taxonomy (e.g. Young *et al.*, 1994; Takayama, 1993; Sato and Kameo, 1996; Hine and Weaver (Chapter 9)).

8.4 MAGNETOBIOCHRONOLOGY

The entire Neogene is characterized by a high frequency of magnetic reversals which offer the potential of excellent calibration of biostratigraphic datums. For the Plio-Pleistocene this potential has been largely realized and oxygen isotope stages are enabling even higher-resolution calibration. It is heartening to note that many nannofossil datums, especially last occurrences, have proven virtually isochronous at the available resolution (down to +/-20ka) (Thierstein *et al.*, 1977; Dowsett, 1989b; Wei, 1993).

For the Miocene the situation is less satisfactory. There are no good, long land-sections with both unambiguous magnetostratigraphy and nannofossil stratigraphy. Good deep-sea cores are now being obtained by the ODP but there are still very few of them. As a result many Miocene nannofossil events have only been well correlated against magnetostratigraphy in a few holes and so it is difficult to be certain about isochrony. Spencer-Cervato *et al.* (1994) have suggested that the data indicates significant diachrony in many events, however, their database includes much low-quality data. We agree with Berggren *et al.* (1995), that in the absence of good evidence to the contrary it is likely that the Plio-Pleistocene pattern of high nannofossil event isochrony extends through the Neogene. Raffi *et al.* (1995) suggest, however, that many events display significant latitudinal diachroneity.

Key primary sources for Miocene magnetobiostratigraphic correlations include Rio *et al.* (1990 a, b, Leg 115), Olafsson (1991, Site 608), Gartner (1992, Site 608), Raffi *et al.* (1995, Leg 138). Syntheses are provided by Young *et al.* (1994), Raffi *et al.* (1995) and Berggren *et al.* (1995). Figure 8.1 gives a summary of the results, using the time-scale of Cande and Kent (1992a, 1995) and this framework is used in all other diagrams.

Generally, correlations of the main nannofossil events to magnetostratigraphy now appear robust although further fine calibration is in progress. In addition, it must be noted that calibration of the magnetostratigraphy to radiometric age tie-points is still being actively revised. Consequently, estimates of the ages of events in Ma are still liable to shift significantly, especially in the Lower and Middle Miocene.

8.5 BIOGEOGRAPHY

The standard biostratigraphy as outlined above is based on low latitude sections, whilst at high latitudes there is a marked drop in diversity. In particular, most non-placolith groups diminish in abundance with latitude, e.g. sphenoliths, discoasters and helicoliths. Conversely, *Coccolithus pelagicus* becomes more abundant and reticulofenestrids tend to develop closed central-areas, although there are very few indigenous high latitude species. Latitudinal variations in nannofloras have been usefully summarized by Haq (1980) and Su (1996). Within low/mid latitude floras the strongest control is probably productivity. In particular, discoasters and *Florisphaera* are characteristic of oligotrophic environments, whilst placoliths in general, and especially reticulofenestrids, dominate eutrophic environments.

In Europe, marine Neogene deposits are important in three distinct areas: the Mediterranean, Paratethys and North Sea. Neogene deposits are widespread around the Mediterranean reflecting the tectonic activity of the region. Extensive sequences occur in Italy, Greece, Malta, North Africa and Southern Spain. They have been well-studied, notably by Theodoridis (1984), Driever (1988), Rio *et al.* (1990a, Leg 107), Fornaciari and Rio (1996), Fornaciari *et al.* (1996), and are complimented by deep sea drilling sites from DSDP Leg 13 (Stradner, 1973; Raffi and Rio, 1979) and ODP Leg 107 (Rio *et al.*, 1990b). Mediterranean nannofloras often show some restriction, especially in the late Miocene. In particular, certain marker-species, such as *D. quinqueramus* and *Or. serratus*, are absent from the Mediterranean. Helicoliths, in contrast, are relatively abundant.

More-extreme restricted nannofloras occur in the Paratethyan area, a region of shallow, variable -salinity basins covering much of eastern Europe and extending into southern Germany and the Former Soviet Union. Marine floras, reflecting varying degrees of restriction, occur in Lower and Middle Miocene sediments, especially in the western areas. Upper Miocene and Pliocene sediments, however, are almost entirely nonmarine. These are some of the most accessible Miocene nannofloras in Europe and have been extensively studied (Kamptner, 1948; Báldi-Beke, 1960; Stradner, 1960; Stradner and Papp, 1961; Martini, 1961; Müller, 1974b; Lehotoyova and Priewalder, 1978). Most of this literature, however, is in German or east European languages, and published in regional geological journals, which has inhibited dissemination of the work. This applies significantly to taxonomy. The Paratethyan literature includes many descriptions of new taxa (e.g. *H. walbersdorfensis, D. musicus, U. jafari, U. rotula*) the descriptions of which were initially overlooked by other workers. Very few of these taxa have, however, proven endemic. The principal exceptions are two aberrant endemic reticulofenestrid genera, *Noelaerhabdus* and *Bekelithella*, described from the Upper Miocene, Pannonian Stage (?correlative to NN10/11).

Within the North Sea, Neogene deposits are widespread but economically they are relatively unimportant and have not been extensively studied. In addition, diverse open-marine nannofloras are only consistently developed in the Lower Miocene, and foraminifera have proven of more general value for biostratigraphy. There is only a limited literature on these nannofloras, although they might prove ecologically interesting. A useful summary is provided by Gallagher (1990).

8.6 NOTES ON TAXONOMIC PROBLEMS

8.6.1 *Helicosphaera carteri* (Wallich, 1877) Kamptner, 1954 and *Helicopontosphaera kamptneri* Hay and Mohler *in* Hay *et al.*, 1967

H. carteri is the dominant Neogene and Recent helicolith. Hay *et al.* (1967) proposed the alternative name *H. kamptneri* on the grounds that the type illustration appeared to be of a different coccolithophore. Jafar and Martini (1975) convincingly demonstrated that Wallich's illustration showed the typical features of helicolith coccospheres but some doubt has remained as to whether the species illustrated was the common species with small pores or a different helicolith, since it appears to show unusually large pores (e.g. Perch-Nielsen, 1985b). Wallich's original slides have been relocated in the Natural History Museum and show clearly that the specimens he drew were the common form, with small pores, and identical to the species described by Hay *et al.* (1967) as *H. kamptneri*. The misleading nature of Wallich's illustration is due to the fact that he only illustrated the central-area not the flanges of the coccoliths, a reasonable convention when illustrating coccospheres from light microscopy.

8.6.2 Size-defined taxa in *Reticulofenestra*

The primarily size-defined *Reticulofenestra* species included here are all widely used with these senses. However, numerous other reticulofenestrid taxa have also been used, for instance, many workers use a parallel set of taxa for specimens with closed central-areas. It is likely that these are ecophenotypes of no stratigraphic value (Young, 1990) so they are not recommended. Other workers use other size definitions or different taxon names. Rationalization is difficult because: (1) the reticulofenestrids appear to form a large intergradational group so that any divisions are arbitrary; (2) a very large number of valid names are available, particularly if poorly described taxa are used from the older literature (e.g. Kamptner, 1956). In practice this means that workers should always briefly define the reticulofenestrid taxa they use. See also Backman (1980), Pujos (1987), Driever (1988), Gallagher (1989), Young (1991), Gartner (1992) and Su (1996).

Similar size-defined species are used in other genera, e.g. *Cyclicargolithus*, *Coccolithus* and *Calcidiscus*. These definitions are intrinsically arbitrary but form a useful way of consistently recording major morphotypic variation of stratigraphic value (see also Young, 1991).

8.6.3 *Coccolithus doronicoides* Black and Barnes, 1961

The holotype of this species is a proximal view TEM of a reticulofenestrid coccolith 3.4µm in length, which might be either a *Gephyrocapsa* or a *Reticulofenestra*, as it is not possible to tell if a bridge is present. Re-examination of the type material (Challenger dredging 338) reveals that it contains a Holocene or Late Pleistocene assemblage, with minimal reworking. The assemblage contains abundant *Gephyrocapsa oceanica* but no true *Reticulofenestra* of this size. So, *C. doronicoides* is best regarded as a junior synonym of *G. oceanica* Kamptner, 1943 and the name should certainly not be used for Neogene *Reticulofenestra* specimens.

8.6.4 '*Pyrocyclus*' Hay and Towe, 1962

This genus was described from the Eocene but many authors have ascribed Neogene specimens to it. Backman (1980) described them as coccoliths with a single shield composed of two cycles: a lower cycle of numerous, steeply-imbricate elements and an upper cycle of fewer, tabular elements. In the LM these specimens have a *Reticulofenestra*-type extinction cross but with a bright outer rim (in *Reticulofenestra* the shields are darker than the inner parts of the coccolith, since they are thinner). However, reticulofenestrid coccoliths which have lost most of their shields, leave central cores identical to '*Pyrocyclus*'. Also, '*Pyrocyclus*' coccoliths always occur with reticulofenestrids with central-areas of similar size and shape. This suggests that the '*Pyrocyclus*' specimens are relict reticulofenestrid cores or in some cases proto-coccolith rings. Described 'species' of *Pyrocyclus* include: *P. inversus* Hay and Towe, 1962; *P. hermosus* Roth and Hay *in* Hay *et al.*, 1967 and *P. orangensis* (Bukry, 1971a) Backman, 1980. There is no obvious justification or value in using any of these species.

8.6.5 *Umbilicosphaera* Lohmann, 1902 and *Geminilithella* Backman, 1980

The genus *Geminilithella* is not used here because our observations indicate that there is no significant structural difference between the type species of *Umbilicosphaera* (*U. sibogae*) and *Geminilithella* (*G. rotula*). Like other *Umbilicosphaera* species, *U. rotula* has complex distal shield sutures and the R-unit is confined to the proximal shield. *U. rotula* also has a wide, open central-area and monocyclic proximal shield. In these respects it is, arguably, closer to *U. sibogae* var. *sibogae* than is *U. sibogae* var. *foliosa*. *U. rotula* and *U. jafari* are closely associated species and it is possible that they bore a relationship to each other similar to that between modern *U. s. sibogae* and *U. s. foliosa*. Biometric study of the Late Pliocene/Early Pleistocene transition from *U. jafari* and *U. rotula* to *U. s. sibogae* and *U. s. foliosa* would be worthwhile.

8.6.6 *Cricolithus jonesii* Cohen, 1965

This name is often applied to narrow, ring-shaped elliptical coccoliths showing high birefringence. They are mostly *Coccolithus* proto-coccolith rings and *Syracosphaera* specimens which have lost their central-areas.

8.6.7 *D. altus* Müller, 1974a and *D. tristellifer* Bukry, 1976

D. tristellifer and *D. altus* were both described from the same material, DSDP Site 242, Core 3

Section 1, but without reference to each other. Both species were described as 6-rayed discoasters with very large proximal bosses and complanate rays. Re-examination of this material reveals, unsurprisingly, that it contains only one such species. The description of Bukry (1976), based on light microscopy, is much better since it mentions the smaller, but very distinct, distal knob. The description of Müller (1974), however, has priority so the correct name is *D. altus*.

8.6.8 *D. pentaradiatus* Tan, 1927b and *D. prepentaradiatus* Bukry and Percival, 1971

There are two distinct, symmetrical 5-rayed discoasters with bifurcate tips. Non-birefringent, low convexity forms, ranging from mid NN9 to mid NN10, normally named *D. prepentaradiatus* (Bukry and Percival, 1971), and birefringent, markedly concavo-convex species, ranging from mid NN10 to end NN17, normally named *D. pentaradiatus* (Tan, 1927b). Theodoridis (1984), however, showed that use of the name *D. pentaradiatus* for the curved birefringent morphotype was based on a misconception of Tan's type specimen. He suggested the name *D. misconceptus* as an alternative, however *D. tridenus* Kamptner, 1967 and *D. anconitanus* Cati and Borsetti, 1972 would have priority. I have followed the conventional usage for the sake of nomenclatural stability; the name *D. pentaradiatus* has been used in the conventional sense in thousands of publications.

8.6.9 *Discoaster aster* Bramlette and Riedel, 1954 and other preservational species of discoaster

Throughout the Neogene, discoasters can be found with blunt ray terminations, but otherwise similar morphology to co-occurring, well-formed discoasters. The blunt ray-tip specimens have probably been produced both by diagenetic alteration and by original growth variation. Various species have been described to include these specimens including: *D. aster* Bramlette and Riedel, 1954; *D. adamanteus* Bramlette and Wilcoxon, 1967; *D. chambrayensis* Hojjatzadeh, 1978; *D. zammitmaempeli* Hojjatzadeh, 1978; *D. intercalaris* Bukry, 1971; and *D. toralus* Ellis *et al.*, 1972. It is more sensible to assign these specimens to an explicit category such as 'unidentifiable 6-rayed discoaster'.

8.6.10 *Triquetrorhabdulus*

The genus *Triquetrorhabdulus*, as conventionally used, includes species with two quite different crystallographic structures. The type species, *Tq. carinatus*, and other Early Miocene species, have c-axes parallel to the length of the nannolith. By contrast, *Tq. rugosus* and other Late Miocene species, have c-axes perpendicular to the length of the nannolith. In addition, the Early Miocene species are straight and show high symmetry, whilst the Late Miocene forms are typically curved and asymmetric. Representatives of both groups occur in the Middle Miocene. This degree of difference necessitates a new genus being described for the Late Miocene species (Varol and Young, in prep.). In the interim, the conventional taxonomy is followed here.

8.6.11 *Ceratolithus armatus* Müller, 1974 and *Ceratolithus acutus* Gartner and Bukry, 1974

C. armatus and *C. arcuatus* were both described in 1974 from Indian Ocean sediments of Early Pliocene age (NN12, Sites 242 and 214, respectively). The holotypes and paratypes of the two species are very similar. The *C. armatus* specimens have slightly longer arms and more distinct ornament but this is almost certainly a result of the much better preservation at Site 242. They are clearly synonyms and although most subsequent authors have distinguished them this has not proven of biostratigraphic value. According to the publication dates, *C. armatus* has two months priority (May 1974 *vs*. July 1974).

8.7 ATLAS OF SPECIES

8.7.1 Explanation

In the following section the systematic taxonomy of Neogene nannofossils is outlined with light micrograph illustration of most species. The objectives are to catalogue the diversity of preserved Neogene nannofossils and to outline a taxonomy suitable for widespread use without losing biostratigraphic precision. So, a middle road taxonomy is given here, reflecting general usage, with a slight tendency toward splitting. However, many Neogene taxa show a pattern of gradualistic evolution with successive morphotypes co-existing through long periods of time, as discussed in Aubry (1989b), Young (1990) and Young *et al.* (1994). The number of species recognized is thus intrinsically subjective and varies between workers and according to the purpose of the study; in particular biostratigraphy demands finer splitting than palaeoceanography. As far as possible, gradualistic relationships are indicated on the range charts by placing related taxa together. In addition in the systematic text (opposite the plates) possible subdivisions of the species used are listed. The higher classification used is that of Young and Bown (1997b).

The information given for each 'accepted' species consists of:

Full citation: as recommended by the ICBN, including original author and author of the combination, followed where appropriate by the original generic assignment in square brackets [].

Identification notes: a very brief note of the features which characterize the species, mainly intended as *aide memoires*. There is no space to explain in full the often complex structure and morphology of the coccoliths, and other works should be consulted by novice workers (e.g. Theodoridis, 1984; Aubry, 1984 *et seq.*; Perch-Nielsen, 1985b).

Range: in NN zones.

Synonyms and variants: the two categories are in some respects subjective. Names are listed as *synonyms* when they are used as alternatives to the accepted name, most commonly due to two authors having independently described the same taxon. Only synonyms still commonly encountered are included. Names are listed as *variants* when they are used by some authors to describe particular morphotypes not distinguished here; the notes indicate the difference between them and typical specimens of the species.

Plates: virtually all listed species are illustrated with light micrographs. The main exceptions are very rare species. SEMs are not provided since the majority of practical work is conducted by light microscopy, and because good SEMs of many species were not available. Useful SEMs are provided in many of the references listed in the literature section, notably by Perch-Nielsen (1977), Aubry (1984 *et seq.*) and, for living equivalents, Winter and Siesser (1994).

Each plate consist of 30 figures and, in many cases, individual figures include several sub-figures. Sub-figures are used either: (1) to provide images of a single specimen under different illumination, focal plane or orientation (using mobile mounts); or (2) to illustrate several specimens of a single species from a single sample in the same orientation and illumination. All XPL micrographs are presented in original orientation with the polarizers oriented N–S and E–W. In several XPL micrographs the approximate c-axis orientation is indicated by a white line (based on colour pattern with a gypsum plate). PC and BF micrographs were mostly taken without a polarizer; when a polarizer is present the orientation is variable.

Scale bars at the bottom of each plate apply to most micrographs; any exceptions have 2μm scale bars on the micrograph.

Provenance of the illustrated specimens can be found in Appendix 1.

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APPENDIX – Sample details for specimens figured on the Plates 8.1–8.10

Reference table

Figure	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Plate 1	W	Y	b	Z	R	t	Q	A	F	b	f	f	g	c	J	z3	z3	z2	z2	z	j	y	q	q	z	j	g	g	e	e
Plate 2	P	O	M	O	M	X	R	I	I	t	W	W	P	S	S	Q	Q	O	X	X	P	V	V	M	M	R	M	t	M	x
Plate 3	l	l	l	l	l	j	j	j	f	f	T	T	j	Z	f	Z	Z	Z	Z	p	P	P	P	Q	Q	t	M	M	N	M
Plate 4	b	b	b	H	z2	k	j	j	G	v	t	Q	T	M	M	z2	a	u	B	c	b	b	D	T	T	s	t	t	x	t
Plate 5	x	t	x	t	t	z2	r	T	P	a	h	i	e	b	d	d	d	a	p	c	x	i	q	k	j	x	x	T	a	x
Plate 6	l	T	R	f	j	e	g	a	e	j	e	e	z3	e	i	f	f	f	f	t	j	j	j	j	a	z	w	X	X	z1
Plate 7	g	h	i	a	a	c	a	d	z3	z3	u	u	Z	q	s	R	R	Q	P	U	R	R	Z	Z	X	q	R	R	T	B
Plate 8	n	n	T	P	P	Z	Z	u	Z	Z	o	o	T	T	T	R	P	O	Y	Y	R	a	T	Z	q	L	Z	q	Z	Z
Plate 9	j	f	i	i	j	f	k	j	h	h	c	c	c	f	e	c	d	b	b	b	a	T	T	T	X	Y	U	U	U	T
Plate 10	D	n	C	C	D	T	R	R	R	R	R	R	S	S	R	m	Q	P	R	A	Z	Z	M	x	x	E	K	M	x	x

This table provides a key to the sample localities, e.g. the specimen illustrated in Figure 3 of Plate 2 comes from sample **M**, which, as listed below, is from DSDP Site 242-2-1, 50–51cm, from zone NN18.

Sample details – locality details and age in terms of the Martini (1971) zonation.

A–H DSDP Leg 23, Arabian Sea: **A**, 219-1-3, 53–54cm, NN20; **B**, 219-9-2, 73–74cm, NN11; **C**, 219-10-6, 74–75cm, NN11B; **D**, 219-11-2, 76–77cm, NN11B; **E**, 219-12-6, 74–75cm, NN11; **F**, 219-13, 128–29cm, NN5; **G**, 219-13-5, 74–75cm, NN5; **H**, 223-6-4, 69–70cm, NN15.

I–K DSDP Leg 23, Red Sea: **I**, 227-13-2, 93–94cm, NN13/14; **J**, 227-20-2, 35–36cm, NN13/14; **K**, 229-2-5, 40–45cm, NN21.

L–l DSDP Leg 25, W Indian Ocean: **L**, 239-8-4, 110–11cm, NN9; **M**, 242-2-1, 50–51cm, NN18; N, 242-2-4, 74–75cm, NN17; **O**, 242-3-1, 99–100cm, NN15; **P**, 242-3-3, 102–103cm, NN15; **Q**, 242-3-4, 98–99cm, NN13/14 or 15?; **R**, 242-4-3, 79–80cm, NN13/14; **S**, 242-4-6, 77–78cm, NN12; **T**, 242-5-2, 61–62cm, NN11B; **U**, 242-5-4, 93–94cm, NN11B; **V**, 242-6-2, 96–97cm, NN11B; **W**, 242-6-3, 26–27cm, NN11A; **X**, 242-6-3, 104–105cm, NN11A; **Y**, 242-6-3, 142–143cm, NN10B; **Z**, 242-6-CC, NN9; **a**, 242-7-1, 71–72cm, NN7; **b**, 242-7-4, 47–48cm, NN6; **c**, 242-7-4, 105–106cm, NN6; **d**, 242-7-5, 97–98cm, NN6; **e**, 242-8-1, 86–87cm, NN5; **f**, 242-8-2, 30–31cm, NN3; **g**, 242-8-3, 125–126cm, NN2; **h**, 242-8-4, 81–82cm, NN2; **i**, 242-8-5, 99–100cm, NN2; **j**, 242-9-1, 31–32cm, NN1; **k**, 242-9-4, 130–131cm, NP25; **l**, 242-10-3, 69–70cm, NP24.

m DSDP Leg 26, SW Indian Ocean: **m**, 251A-4-5, 78–79cm, NN15.

n DSDP Leg 26, SE Indian Ocean: **n**, 258A-8-1, 143–144cm, NN11B.

o–s ODP Leg 124, Sulu Sea (W Equatorial Pacific): **o**, 771A-3R-3, 25–26cm, NN11A; **p**, 771A-4R-1, 75–76cm, NN10B; **q**, 771A-6R-3, 25–26cm, NN9; **r**, 771A-8R-CC, 11–12cm, NN6; **s**, 771A-10R-3, 23–24cm, NN5.

t–u ODP Leg 144, Pacific Guyots: **t**, 872-1H-2, 124–126cm, NN19; **u**, 872-5H-5, 122–124cm, NN9.

v–z3 MISCELLANEOUS SAMPLES: **v** Sediment trap sample, 48°N 20°W, N Atlantic, July 1989, 3200m, BOFS C8, modern; **w** Dredge sample, Black Sea, BP-BS, NP19; **x** Dredge sample, HMS Challenger, 3640m, 21°S 14°W, S Atlantic, Ch 338, NN21; **y** Outcrop sample, Cyprus, HJS-Cyp, NN6–7; **z** Outcrop sample, Pre-Betics, S Spain, JH 51, NN6–7; **z1** Piston core sample, Bosphorus M1 CC NN21; **z2**, Outcrop sample, Valea Roduli, Romania; Loc 2b Exc Q of 14th European Micropalaeontological Colloquim, Ro 81 Badenian, NN6–7; **z3**, Outcrop sample, Cipero Formation, Trinidad, Trin 8838, NN4.

Plate 8.1

Order ZYGODISCALES Young and Bown, 1997b
Family HELICOSPHAERACEAE Black, 1971c
Genus HELICOSPHAERA Kamptner, 1954

H. CARTERI GROUP
Figs 1–5. **Helicosphaera carteri** (Wallich, 1877) Kamptner, 1954 [*Coccosphaera*]. The most common *Helicosphaera* species. Medium to large size, flange ends in wing, two pores in central-area. RANGE: NN1–21. SYNONYM: *H. kamptneri* (Hay and Mohler *in* Hay *et al.*, 1967) Locker, 1992 [*Helicopontosphaera*] – see taxonomic notes. VARIANTS: *H. carteri* var. *burkei* (Black, 1971c) Theodoridis, 1984 – central-area closed; *H. carteri* var. *hyalina* (Gaarder, 1970) Jordan and Young, 1990 – central-area closed (Fig. 5); *H. acuta* Theodoridis, 1984 – no true wing, slight inverse orientation of openings; *H. colombiana* (Gartner, 1977) Haq and Berggren, 1978 – smaller wing; *H. neogranulata* (Gartner, 1977) Haq and Berggren, 1978 – central-area with no true pores/granular; *H. paleocarteri* Theodoridis, 1984 – with small pores separated from the extinction line (Figs 3–4).

Fig. 6. **Helicosphaera carteri** var. **wallichii** (Lohmann, 1902) Theodoridis, 1984 [*H. wallichii*]. Like *H. carteri* but central-area with inclined pores. RANGE: NN9–21.

Fig. 7. **Helicosphaera sellii** (Bukry and Bramlette, 1969a) Jafar and Martini, 1975 [*Helicopontosphaera*]. Like *H. carteri* but pores large. RANGE: NN12–19. VARIANT: *H. omanica* Sato *et al.*, 1991 – bar missing, ? dissolved. Also similar to *H. neogranulata.*

Fig. 8. **Helicosphaera inversa** (Gartner, 1980) Theodoridis, 1984 [*Helicopontosphaera*]. Like *H. carteri* but with large pores separated by prominent conjunct sub-horizontal bar usually with inverse orientation. RANGE: NN19–21 (LO low in NN21).

Fig. 9. ***H. granulata*** (Bukry and Percival, 1971) Jafar and Martini, 1975 [*Helicopontosphaera*]. Like *H. carteri* but with central-area showing irregular, granular structure, possibly a preservational variant. RANGE: Palaeogene–NN9.

Figs 11–13. **Helicosphaera euphratis** Haq, 1966. Central-area almost filled by strongly inclined, disjunct bar, often very large. RANGE: Palaeogene–NN4. SYNONYM: *H. parallela* Bramlette and Wilcoxon, 1967a. VARIANT: *H. rhomba* (Bukry, 1971a) Jafar and Martini, 1975 – bar does not fill central-area, transitional to *H. intermedia*.

Figs 10, 14–15. **Helicosphaera intermedia** Martini, 1965. Like *H. euphratis* but central-area open, spanned by curved, disjunct bar. RANGE: NP21–NN12.

Not figured. **Helicosphaera truempyi** Biolzi and Perch-Nielsen, 1982. Like *H. carteri* but central-area open, spanned by horizontal, disjunct bar. RANGE: NP25–lower NN1.

Not figured. *Helicosphaera pavimentum* Okada and McIntyre, 1977. Small- to medium-sized. Flange narrow without distinct wing. Central-area with two small in-line pores. RANGE: NN19?–21.

H. AMPLIAPERTA GROUP
Figs 16–17. **Helicosphaera ampliaperta** Bramlette and Wilcoxon, 1967. Similar to *H. carteri* but central-area open, and wing weaker. RANGE: NN2–4. VARIANT: *H. porosa* Lehotayova, 1985 – with grill in central-area.

Not figured. *Helicosphaera scissura* Miller, 1981. Like *H. ampliaperta* but with slit rather than wide opening in central-area. RANGE: NN3–4.

Not figured. *Helicosphaera mediterranea* Müller, 1981. Like *H. ampliaperta* but with central opening spanned by narrow, conjunct bar. RANGE: NN2–4. SYNONYM: *H. crouchii* Bukry, 1981a.

Fig. 18. **Helicosphaera waltrans** Theodoridis, 1984. Similar to *H. ampliaperta* but with central opening spanned by wide, normally oriented, oblique, conjunct bar, openings triangular. RANGE: NN5.

Plate 8.1 cont'd

H. WALBERSDORFENSIS GROUP
Figs 19–20. ***Helicosphaera walbersdorfensis*** Müller, 1974b. Small- to medium-sized. Flange ends in broad wing. Central-area with two normally oblique pores separated by narrow, conjunct bar. N.B. *H. walbersdorfensis sensu* Varol (1989d) = *H. stalis* of other authors. RANGE: NN5–7. SYNONYM: *H. muellerae* Varol, 1989 – alternative name for *H. walbersdorfensis* based on interpretation that the type specimen is atypical. VARIANTS: *H. californiana* Bukry, 1981a – bar absent, cf. Theodoridis (1984), this is usually a result of dissolution; *H. minuta* Müller, 1981 – without prominent wing, or possibly a senior synonym of *H. stalis*.

Not figured. *Helicosphaera vedderi* Bukry, 1981a. Similar to *H. walbersdorfensis* with wider bar and less distinct wing. RANGE: NN2–5. VARIANT: *H. jakubowskii* Varol, 1989d – granular central-area.

Not figured. *Helicosphaera magnifica* Varol, 1989d. Medium-sized, like *H. walbersdorfensis*, but with closed central-area and wide wing which extends along entire length of helicolith. RANGE: NN2–3.

Figs 22–23. ***Helicosphaera stalis*** Theodoridis, 1984. Small, lenticular or rhomboid outline. No distinct flange ending. Two normally inclined pores in central-area. RANGE: NN6–11. VARIANTS: *H. stalis* ssp. *ovata* Theodoridis, 1984 – outline rounded, lenticular rather than rhombohedral; *H. girgisii* Varol, 1989d – closed central-area.

HELICOSPHAERA RECTA GROUP
Not figured. *Helicosphaera gertae* Bukry, 1981a. Closed central-area. RANGE: NN1–2.

Figs 21, 26. ***Helicosphaera recta*** (Haq, 1966) Jafar and Martini, 1975 [*Helicopontosphaera*]. Large size, sub-rectangular shape. Wing ends in spur, central-area with two large pores separated by narrow, conjunct bar. RANGE: NP24–NN1. SYNONYM: *H. truncata* Bramlette and Wilcoxon, 1967.

Figs 24–25. ***Helicosphaera orientalis*** Black, 1971c. Small species. Flange ends abruptly, no wing or spur. Central-area with inversely oriented pores. RANGE: NN6–11. SYNONYM: *H. philippinensis* Müller, 1981 – described from better preserved material but otherwise identical to *H. orientalis*. VARIANT: *H. pacifica* Müller and Brönnimann, 1974 – central-area granular, without well defined pores.

Figs 27–28. ***Helicosphaera obliqua*** Bramlette and Wilcoxon, 1967. Medium-sized, sub-rectangular shape. Only weakly birefringent. Wing ends in spur, central-area with two prominent pores with inverse orientation. RANGE: NP24–NN6.

Figs 29–30. ***Helicosphaera perch-nielseniae*** (Haq, 1971) Jafar and Martini, 1975 [*Helicopontosphaera*]. Like *H. obliqua* but pores narrower and shape more oblong, less spindle-like (N.B. criteria for separating *H. obliqua* and *H. perch-nielseniae* vary between authors). RANGE: NP23–NN6. VARIANT: *H. elongata* Theodoridis, 1984 – more elongate with more rectangular outline.

Plate 8.2

Family PONTOSPHAERACEAE Lemmermann, 1908
Genus PONTOSPHAERA Lohmann, 1902
Coccoliths are muroliths, central-area with variable number of perforations. V-units form narrow, imbricate outer wall, R-units form inner wall and central-area. Species-level taxonomy is poorly worked out. The species listed below are the established extant taxa and are all frequently cited but some authors also use other taxa (e.g. Varol, 1989d). SYNONYMS: *Crassapontosphaera* Boudreaux and Hay, 1969; *Discolithina* Loeblich and Tappan, 1963; *Discolithus* Huxley, 1868; *Koczyia* Boudreaux and Hay, 1969.

Figs 1–2. ***Pontosphaera multipora*** (Kamptner, 1948) Roth, 1970 [*Discolithus*]. Central-area protrudes above rim, 3 or more cycles of large pores. RANGE: Palaeogene–NN21. SYNONYM: *Pontosphaera indooceanica* Cepek, 1973.

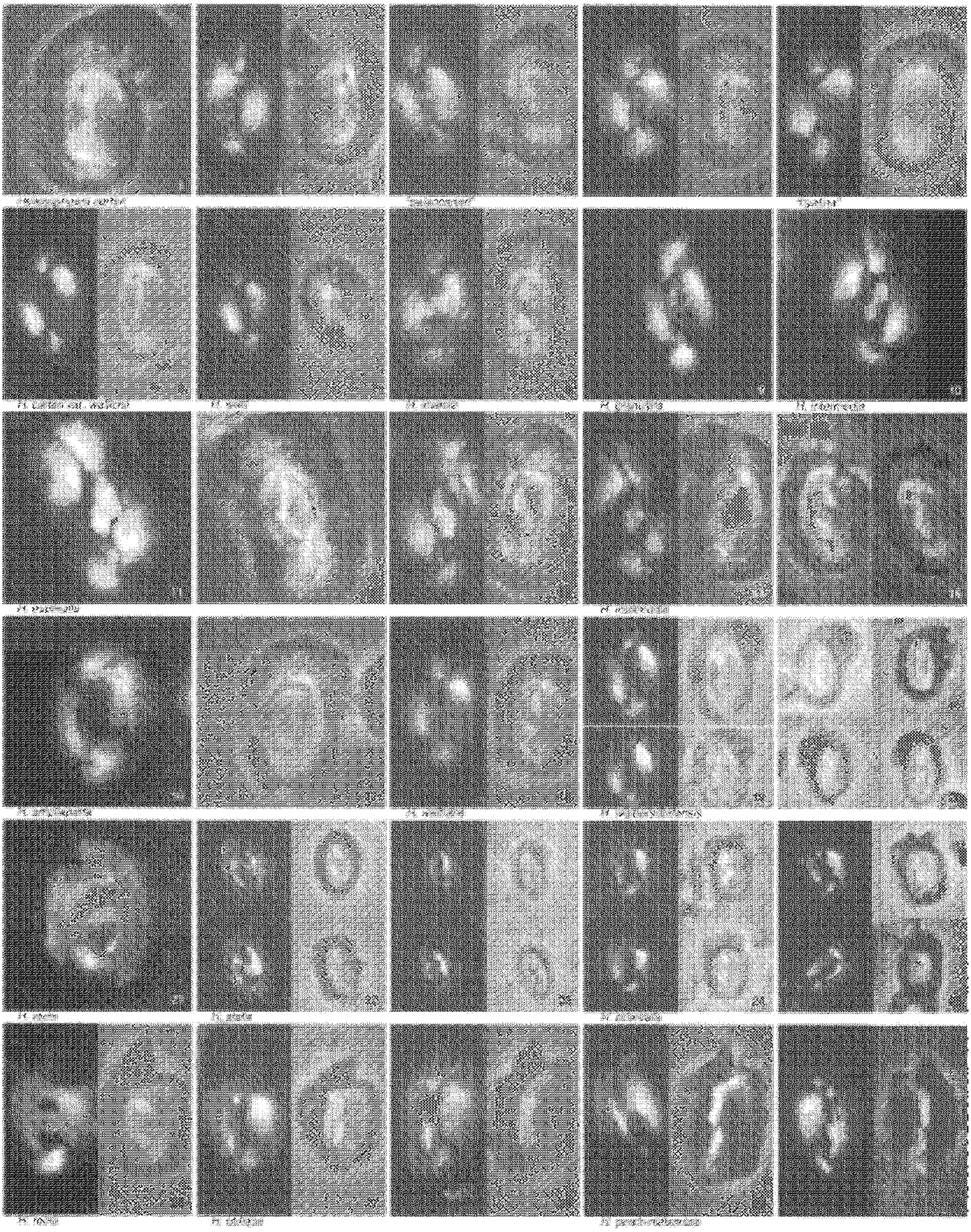

9
10
11
10µm

Plate 8.2 cont'd

Figs 3–5. ***Pontosphaera discopora*** Schiller, 1925. Rim elevated, 3 or more cycles of pores. RANGE: Palaeogene–NN21.

Fig. 10. ***Pontosphaera japonica*** (Takayama, 1967) Nishida, 1971 [*Discolithina*]. Rim flush with central-area, pores very small (<0.1µm) often infilled during diagenesis. RANGE: Palaeogene–NN21. SYNONYM: *Discolithina millepuncta* Gartner, 1967b.

Not figured. *Pontosphaera syracusana* Lohmann, 1902. Central-area is thin plate, rim strongly elevated, numerous small pores. RANGE: ?–NN21.

Genus SCYPHOSPHAERA Lohmann, 1902
Coccospheres with *Pontosphaera*-like body coccoliths and equatorial coccoliths with rims elevated into vase-like structures (lopadoliths). In fossil assemblages, only lopadoliths are assigned to *Scyphosphaera*. Numerous Neogene species have been described, often based on subtle variations in outline, but since the single modern species *S. apsteinii* shows considerable variation in lopadolith outline, a broader species concept is justified. Three main species are certainly separable: *S. apsteinii*, *S. pulcherimma* and *S. globulata*. The listing below also includes a few other apparently different morphotypes. See also Jafar (1975), Perch-Nielsen (1984) and Aubry (1990).

Figs 6–8. ***Scyphosphaera apsteinii*** Lohmann, 1902. Simple, convex outward profile, or somewhat constricted at base. RANGE: Palaeogene–NN21. VARIANTS: *Scyphosphaera ampla* Kamptner, 1955; *S. brevisa* Varol, 1984; *S. globulosa* Kamptner, 1955; *S. graphica* Müller, 1974a (possibly = *Tintinnabuliformis*); *S. inversiconica* Varol, 1984; *S. piriformis* Kamptner, 1955; *S. praeglobulata* Varol, 1989d; *S. procera* Kamptner, 1955; *S. pseudorecurvata* Varol, 1989d; *S. recta* (Deflandre, 1942) Kamptner, 1955 [*S. apsteinii* ssp. *recta*]. *S. recurvata* Deflandre, 1942 – profile concave outwards near base (Fig. 6). Often separated from *S. apsteinii*, but such forms are common on extant *S. apsteinii* coccospheres.

Fig. 9. ***Scyphosphaera apsteinii*** forma ***dilatata*** Gaarder, 1970. With wide distal opening. RANGE: NN11?–21. VARIANTS: *S. antilleana* Boudreaux and Hay, 1969; *S. cohenii* Boudreaux and Hay, 1969; *S. magna* Kamptner, 1967; *S. porosa* Kamptner, 1967.

Figs 11–12. ***Scyphosphaera cylindrica*** Kamptner, 1955. Parallel sided. RANGE: NN9?–21. VARIANTS: *S. aranta* Kamptner, 1967; *S. galeana* Kamptner, 1967; *S. oremesa* Kamptner, 1967; *S. penna* Kamptner, 1955; *S. tora* Kamptner, 1967; ?*S. elegans* (Ostenfeld, 1910) Deflandre, 1942 [*Thorosphaera*] – but type is of uncertain affinities, and possibly not a coccolithophore, see Jordan and Chamberlain (1992).

Figs 14–15, 19–20. ***Scyphosphaera globulata*** Bukry and Percival, 1971. Almost spherical, with narrow opening. Distinctive and common. RANGE: NN11–18.

Figs 16–17. ***Scyphosphaera intermedia*** Deflandre, 1942. Moderately elevated (3–5x as high as wide) with maximum width near base and flaring collar. RANGE: NN7?–15?

Fig. 18. ***Scyphosphaera lagena*** Kamptner, 1955. Moderately elevated (3–5x as high as wide) with maximum width near base. RANGE: NN7?–?18. VARIANTS: *S. aequatorialis* Kamptner, 1963; *S. canescens* Kamptner, 1955; *S. cantharellus* Kamptner, 1955; *S. conica* Kamptner, 1955; *S. turris* Kamptner, 1955.

Figs 21–25. ***Scyphosphaera pulcherrima*** Deflandre, 1942. Opening wide and with well developed collar. RANGE: NN6?–19. VARIANTS: *S. amphora* Deflandre, 1942; *S. campanula* Deflandre, 1942; *S. darraghi* Rade, 1975; *S. halldalii* Deflandre *in* Deflandre and Fert, 1954.

Not figured. *Scyphosphaera tubifera* Kamptner, 1955. Strongly elevated (>5x as high as wide) with maximum width near base; rare. RANGE: NN5?–?21. VARIANTS: *S. martinii* Jafar, 1975; *S. quasitubifera* Varol, 1984 – like *S. tubifera* but with flaring end.

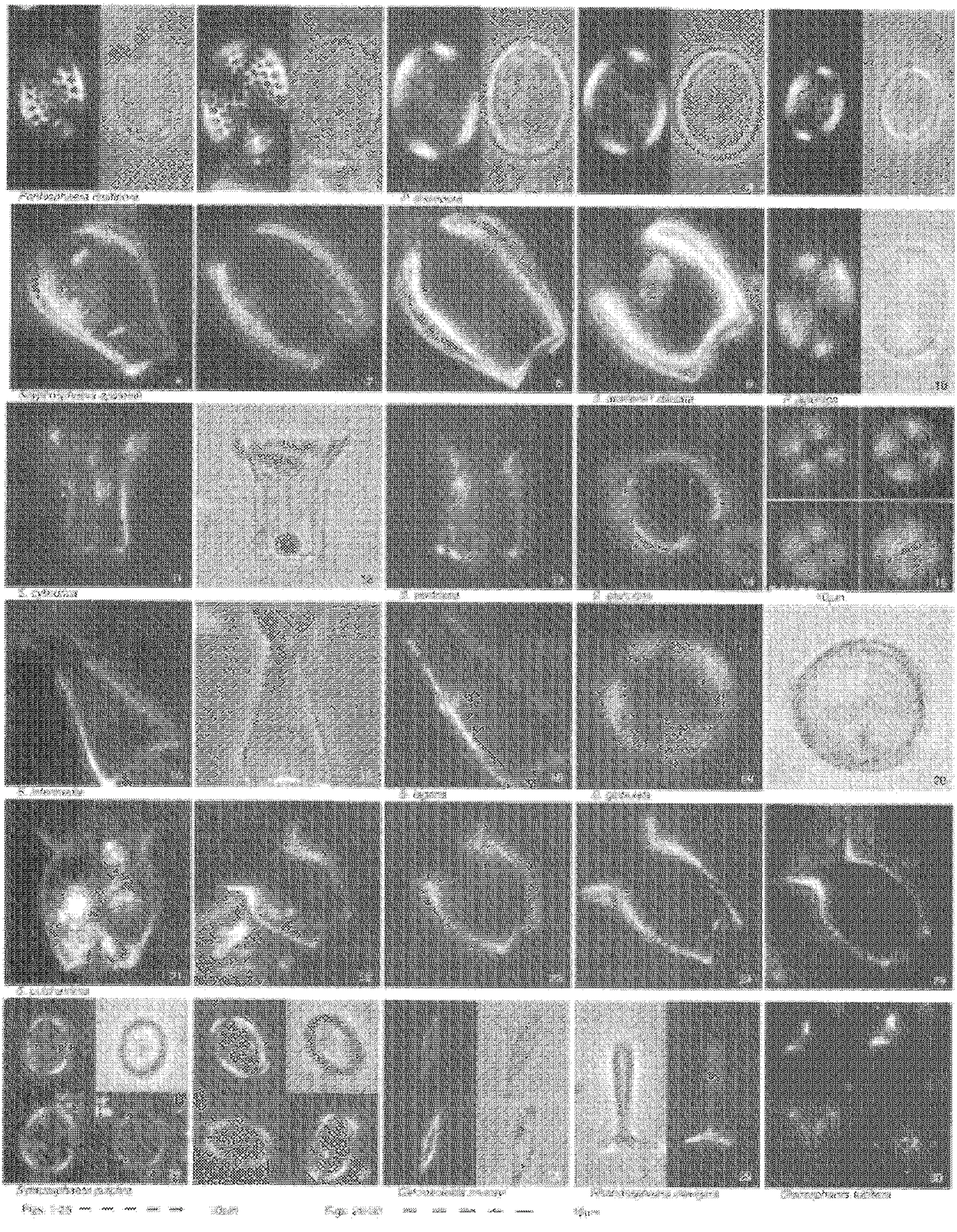

10
15
20
10µm

Plate 8.2 cont'd

Fig. 13. ***Scyphosphaera ventriosa*** Martini, 1968. Similar to *S. apsteinii* but with low collar around opening. RANGE: NN9?–15?. VARIANTS: *S. abelei* Rade, 1975; *S. australensis* Rade, 1975; *S. deflandrei* Müller, 1974a; *S. gladstonensis* Rade, 1975; *S. kamptneri* Müller, 1974; *S. pacifica* Rade, 1975; *S. queenslandensis* Rade, 1975; *S. rottiensis* Jafar, 1975.

Order SYRACOSPHAERALES Hay, 1977
This order is responsible for much of the diversity of modern coccolithophores (>50 species (Jordan and Kleijne, 1994)) but most species produce small coccoliths with low preservation potential and which are difficult to identify in the LM. The restricted list here includes only the common, larger (>3µm) species.

Family CALCIOSOLENIACEAE Kamptner, 1937
Genus CALCIOSOLENIA Gran, 1912
Coccosphere with small rhomb-shaped muroliths (=scapholiths), structure apparently similar to *Syracosphaera*.

Fig. 28. ***Calciosolenia murrayi*** Gran, 1912. Fossil scapholiths are too small to identify confidently but this is the predominant extant species and so a sensible default identification. RANGE: Palaeogene?–NN21. ~SYNONYM: *Scapholithus fossilis* Deflandre *in* Deflandre and Fert, 1954 – widely used by palaeontologists to indicate unidentified scapholith.

Family SYRACOSPHAERACEAE Lemmermann, 1903
Genus SYRACOSPHAERA Lohmann, 1902

Figs 26–27. ***Syracosphaera pulchra*** Lohmann, 1902. Default identification for larger *Syracosphaera* coccoliths. Oblong or irregularly elliptical with bright rim and central-area of radial laths showing tangential c-axis orientation. RANGE: Palaeogene?–NN21.

Family RHABDOSPHAERACEAE Haeckel, 1894
Genus RHABDOSPHAERA Haeckel, 1894
SYNONYM: *Rhabdolithus* Kamptner *ex* Deflandre *in* Grassé, 1952.

Fig. 29. ***Rhabdosphaera clavigera*** Murray and Blackman, 1898. This is the only common, consistently-occurring Neogene rhabdolith. RANGE: Palaeogene–NN21. VARIANTS: *R. clavigera* var. *stylifera* (Lohmann, 1902) Kleijne and Jordan, 1990 – form with narrow, parallel-sided spine; *R. procera* Martini, 1969c – delicate form, similar to *R. c. stylifera*; *R. sicca* (Stradner, 1963).

Not figured. *Rhabdosphaera poculii* (Bona and Kernene, 1966) Müller, 1974b [*Rhabdolithus*]. Similar to *Discosphaera tubifera* but with domal rather than open flaring end; rare. RANGE: NN4–10.

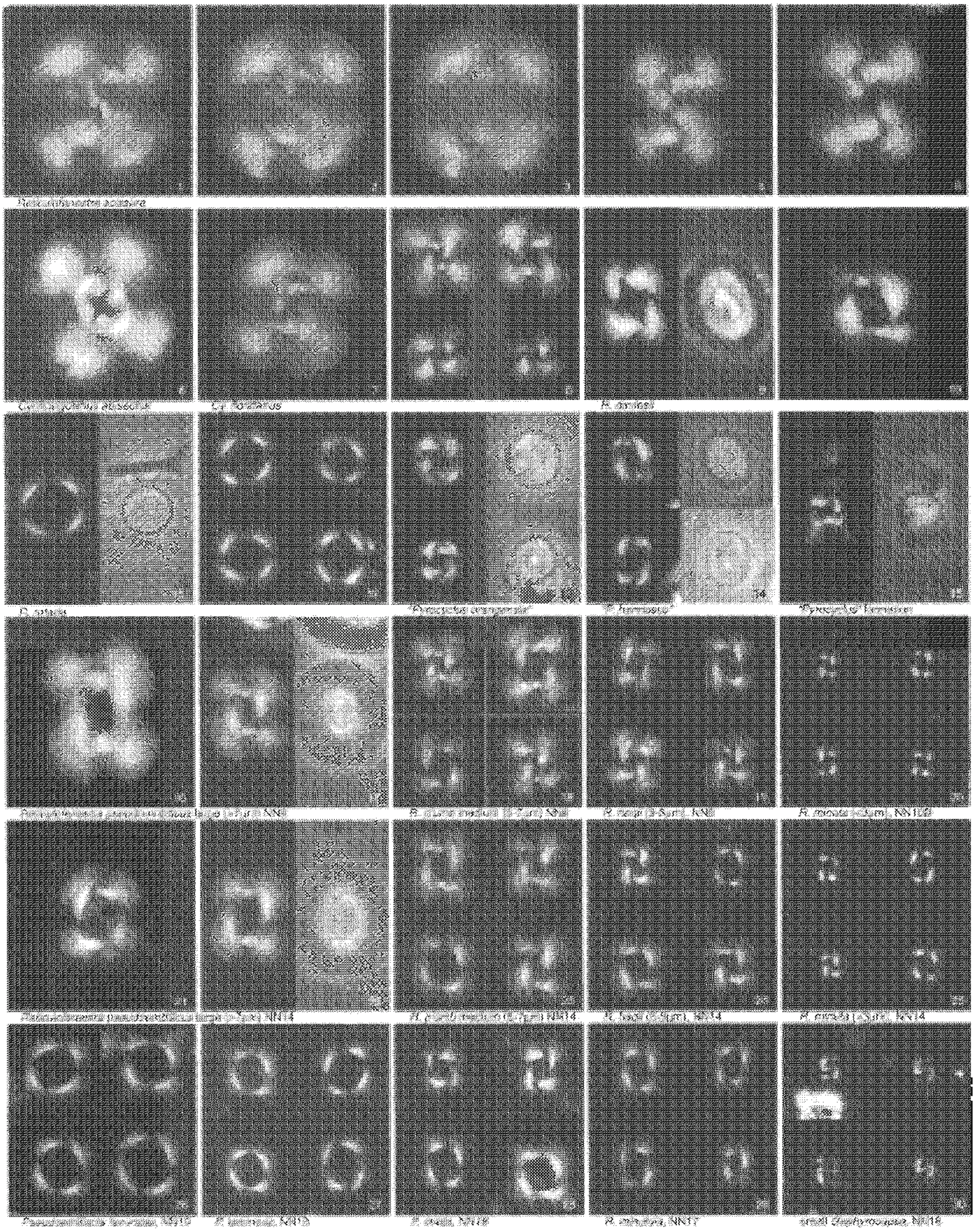
Genus DISCOSPHAERA Haeckel, 1894
Fig. 30. ***Discosphaera tubifera*** (Murray and Blackman, 1898) Ostenfeld, 1900 [*Rhabdosphaera*]. Small trumpet-shaped coccoliths; in fossil material the basal disk is usually missing. RANGE: NN11?–21.

Plate 8.3

Order PRINSIALES Young and Bown, 1997b
Family NOELAERHABDACEAE Jerkovic, 1970 emend. Young and Bown 1997b
Coccoliths are placoliths with rim structure similar to *Emiliania* and *Reticulofenestra*: R-unit forms virtually entire structure, V-unit vestigial. SYNONYM: Gephyrocapsaceae Black, 1971c.

Genus CYCLICARGOLITHUS Bukry, 1971a
Circular to sub-circular with small central-area, included in *Reticulofenestra* by some authors.

Fig. 6. ***Cyclicargolithus abisectus*** (Müller, 1970b) Wise, 1973 [*Coccolithus*?]. Large specimens (>11µm), usually sub-circular, an arbitrary distinction from *C. floridanus* but of some biostratigraphic use (Olafsson, 1992). RANGE: Palaeogene–NN1.



Reticulofenestra scissura

Cyclicargolithus abisectus

Cy. floridanus

R. [illegible]

D. [illegible]

"Pyrocyclus orangensis"

"P. hermosus"

"Pyrocyclus" hermosus

Reticulofenestra pseudoumbilicus large (>7µm) NN9

R. pseudoumbilicus medium (5-7µm) NN9

R. haqii (3-5µm), NN9

R. minuta (<3µm), NN10b

Reticulofenestra pseudoumbilicus large (>7µm) NN14

R. pseudoumbilicus medium (5-7µm) NN14

R. haqii (3-5µm), NN14

R. minuta (<3µm), NN14

Pseudoemiliania lacunosa, NN19

P. lacunosa, NN19

P. ovata, NN19

R. minutula, NN17

small Gephyrocapsa, NN18

10µm

Plate 8.3 cont'd

Figs 7–8. ***Cyclicargolithus floridanus*** (Roth and Hay *in* Hay *et al.*, 1967) Bukry, 1971a [*Coccolithus*]. Common form, <10µm. RANGE: Palaeogene–NN7.

Genus RETICULOFENESTRA Hay *et al.*, 1966
Circular to elliptical, central-area open or closed, no special structures. Subdivision largely arbitrary, see taxonomic notes. SYNONYM: *Dictyococcites* Black, 1967 – like *Reticulofenestra* but with closed central-area.

Figs 1–5. ***Reticulofenestra bisecta*** (Hay *et al.*, 1966) Roth, 1970 [*Syracosphaera*]. Medium to large, central-area closed by plates on distal surface of coccolith. RANGE: Eocene–NN1. SYNONYMS: *Dictyococcites bisectus* (Hay *et al.*, 1966) Bukry and Percival, 1971 – alternative combination; *R. scissura* Hay, Mohler and Wade, 1966 – see Gartner (1971) for discussion. VARIANTS: *R. stavensis* (Levin and Joerger, 1967) Varol, 1989d; *Dictyococcites scrippsae* Bukry and Percival, 1971. N.B. Two different taxonomic subdivisions are in use: (1) specimens <10µm = *D. scrippsae*, >10µm = *D. bisectus*; (2) specimens <10µm = *R. bisecta*, >10µm *R. stavensis*.

Figs 9–10. ***Reticulofenestra daviesii*** (Haq, 1968) Haq, 1971 [*Stradnerius*]. Medium size with plug in central-area formed from proximal grill, surrounded by narrow ring of pores. RANGE: Palaeogene–NN2.

Figs 16–18, 21–23. ***Reticulofenestra pseudoumbilicus*** (Gartner, 1967b) Gartner, 1969c [*Coccolithus*]. >5µm (e.g. Backman, 1980; Young, 1991), but for biostratigraphy it is better to separate the >7µm specimens (e.g. Rio *et al.*, 1990b; Raffi *et al.*, 1995). RANGE: NN4–15. VARIANTS: *R. ampliumbilicus* Theodoridis, 1984 – very wide central-area, ?possibly early growth-phase; *R. antarctica* (Haq, 1976) Driever, 1988 [*Dictyococcites*] – closed central-area; *R. tenuistriata* (Kamptner, 1963) Martini, 1979 [*Coccolithus*] – *sensu* Varol, 1989d = 5–7µm *R. pseudoumbilicus.*

Figs 19, 24. ***Reticulofenestra haqii*** Backman, 1978. 3–5µm, intergrades with *R. pseudoumbilicus*. RANGE: NN2–15.

Figs 20, 25. ***Reticulofenestra minuta*** Roth, 1970. <3µm. Probably includes several different species. RANGE: Palaeogene–NN21.

Figs 11–12. ***Reticulofenestra rotaria*** Theodoridis, 1984. Circular, with wide central-area, 5–7µm, never abundant but distinctive. RANGE: short interval within NN11B.

Fig. 29. ***Reticulofenestra minutula*** (Gartner, 1967b) Haq and Berggren, 1978 [*Coccolithus*]. 3–5µm, Late Pliocene forms intergrade with *P. lacunosa*. RANGE: NN15–18. SYNONYMS: *R. ampla* Sato *et al.*, 1991 – synonym of *R. minutula* and homonym of *R. ampla* (Kamptner, 1955) Jafar, 1975; *R. doronicoides* (Black and Barnes, 1961) Pujos, 1985 [*Coccolithus*] – see section 8.6.

Not figured. *Reticulofenestra asanoi* Sato and Takayama, 1992. >6.5µm sub-circular or broadly elliptical species. Possibly derived from *P. lacunosa*, but without slits. RANGE: Short interval within NN19.

Genus PSEUDOEMILIANIA Gartner, 1969c
Circular to broadly elliptical with variable number of slits in distal shield. RANGE: NN15–19.

Figs 26–27. ***Pseudoemiliania lacunosa*** (Kamptner, 1963) Gartner, 1969 [*Ellipsoplacolithus*]. Circular to sub-circular with >12 slits, >4µm. Abundant in the Late Pliocene, but well-developed, large, circular forms only occur in the Pleistocene. RANGE: NN15–19. SYNONYM: *Emiliania annula* (Cohen, 1964) Bukry, 1971a [*Coccolithus*].

Fig. 28. ***Pseudoemiliania ovata*** (Bukry, 1973b) Young comb. nov. [*Emiliania*]. Basionym: *Emiliania ovata* Bukry, 1973b (*Initial Reports of the DSDP*, **16**, p.678, pl. 2, figs 10–12). Elliptical variety of *P. lacunosa* with <12 slits in the distal shield. See also Young (1990). RANGE: NN14–19.

Plate 8.3 cont'd

Fig. 30. Genus GEPHYROCAPSA Kamptner, 1943
Like *Reticulofenestra* but with bridge formed from inner tube. Only small specimens (<3µm) occur in the Pliocene and it is conventional to record these as 'small *Gephyrocapsa*'. RANGE: NN15–21. SYNONYM: *Crenalithus* Roth, 1973 – the holotype, *C. doronicoides* (Black, 1967), is a proximal view of *G. oceanica.*

Genus EMILIANIA Hay and Mohler in Hay *et al.*, 1967
Not figured. *Emiliania huxleyi* (Lohmann, 1902) Hay and Mohler in Hay *et al.*, 1967 [*Pontosphaera*]. Slits between all elements of distal shield. RANGE: NN21.

Genus NOELAERHABDUS Jerkovic, 1970
Not figured. *Noelaerhabdus bozinovicae* Jerkovic, 1970. Like *Reticulofenestra* but with single, large spine formed from inner tube, endemic to central Paratethys. RANGE: Pannonian, ?equivalent of NN10 or 11. VARIANT: *N. jerkovici* Bona and Gal, 1985 – longer spine. Various other species of *Noelaerhabdus* were described by Jerkovic, but none of these are convincingly distinct.

Genus BEKELITHELLA Bona and Gal, 1985
Not figured. *Bekelithella echinata* Bona and Gal, 1985. Like *Reticulofenestra* but with circlet of small spines formed from inner tube, endemic to central Paratethys. RANGE: Pannonian, ?equivalent of NN10 or 11.

Figs 13–15. [PYROCYCLUS Hay and Towe, 1962]. This 'genus' is based on preservational relics and early growth stages of *Reticulofenestra* and *Cyclicargolithus.* See discussion in section 8.6.

Plate 8.4

Order COCCOSPHAERALES Haeckel, 1894

Family COCCOLITHACEAE Poche, 1913 emend. Young and Bown 1997b
Coccoliths are placoliths with rim structure similar to *Coccolithus*: V-unit forms distal shield and lower cycle of central-area, R-unit forms proximal shield and upper cycle of central-area.

Genus COCCOLITHUS Schwarz, 1894
Figs 1–5, 10. ***Coccolithus pelagicus*** (Wallich, 1877) Schiller, 1930 [*Coccosphaera*]. Default name applied to wide range of morphotypes, size 3–16µm, central-area open or with transverse bar. RANGE: Palaeogene–NN21. VARIANTS: *C. pelagicus* ssp. *floralis* Wei and Wise, 1992 – collar formed from upper cycle of central-area; *C. pliopelagicus* Wise, 1973 – small central-area, no bar; *C. streckeri* Takayama and Sato, 1987 – early growth-stage of large *C. pelagicus* with bar (Fig. 10); C. *tenuiforatus* (Clocchiatti and Jerkovic, 1970) Wise, 1983 – medium to large with cross in narrow central-area, only consistently distinguishable in the SEM. Especially common in Paratethys.

Not figured. *Coccolithus miopelagicus* Bukry, 1971a. Large form, >14µm, usually 15–17µm, no bar. RANGE: NN5?–8.

Not figured. *Cocccolithus neohelis* McIntyre and Bé, 1967. Small with cross in central-area. Often placed in *Cruciplacolithus* but it is probable that it is an unrelated homoeomorph of Palaeogene *Cruciplacolithus.* RANGE: NN?–NN21.

Genus CLAUSICOCCUS Prins, 1979
Central-area filled by perforate plate, structure like *Coccolithus*, i.e. with both proximal shield and upper layer of central-area formed from R-units and so bright in XPL.

Figs 6–8. ***Clausicoccus fenestratus*** (Deflandre and Fert, 1954) Prins, 1979. Typical, medium-sized *Clausicoccus* species. RANGE: Palaeogene–NN1.

Plate 8.4 cont'd

Genus SOLIDOPONS Theodoridis, 1984
Fig. 9. ***Solidopons petrae*** Theodoridis, 1984. Elliptical placolith with narrow rim and wide central-area spanned by disjunct, transverse bridge. RANGE: NN3–9.

Family CALCIDISCACEAE Young and Bown, 1997b
Coccoliths are placoliths with rim structure similar to *Calcidiscus*: V-units form distal shield and central-area/tube, R-units form proximal shield only.

Genus CALCIDISCUS Kamptner, 1950
Circular to sub-circular proximal shield, birefringent. Distal shield non-birefringent with curved sutures. Shields easily separated (Figs 12–13, and see Gartner, 1967a). SYNONYMS: *Cyclococcolithina* Wilcoxon, 1970a; *Cyclococcolithus* Kamptner, 1954; *Cycloplacolithus* Kamptner, 1963. VARIANT: *Cycloperfolithus* Lehotayova and Priewalder, 1978 – with fine grill in central-area, and bicyclic proximal shield.

Figs 11–13. ***Calcidiscus leptoporus*** (Murray and Blackman, 1898) Loeblich and Tappan, 1978 [*Coccosphaera*]. Circular to sub-circular, closed central-area, default name covering a wide range of variation. RANGE: NN2–21. VARIANTS: *C. fuscus* (Backman, 1980) Janin, 1987 – small, broadly elliptical; *C. pataecus* (Gartner, 1967b) de Kaenel and Villa, 1996 – small, broadly elliptical.

Figs 14–15. ***Calcidiscus macintyrei*** (Bukry and Bramlette, 1969a) Loeblich and Tappan, 1978 [*Cyclococolithus*]. >10µm circular form, with central opening. RANGE: NN7–19 but usually only distinguished in the Upper Pliocene and Quaternary.

Figs 16–20. ***Calcidiscus tropicus*** Kamptner, 1956 *sensu* Gartner, 1992. Circular with open central-area, 7–10µm. Often not differentiated from *C. leptoporus*. Miocene forms often have a bicyclic proximal shield (Fig. 18). Pliocene forms may show a coarse grill in central opening (Fig. 19). RANGE: NN4–10?. VARIANTS: *C. leptoporus* ssp. *centrovalis* (Stradner and Fuchs, 1980) Perch-Nielsen, 1984 – similar to *C. tropicus* but sub-circular; *C. carlae* (Lehotayova and Priewalder, 1978) Janin, 1992 [*Cycloperfolithus*] – Paratethyan form, with fine grill in central-area and bicyclic proximal shield.

Figs 21–22. ***Calcidiscus premacintyrei*** Theodoridis, 1984. Elliptical with open, elliptical central-area. RANGE: NN4–6.

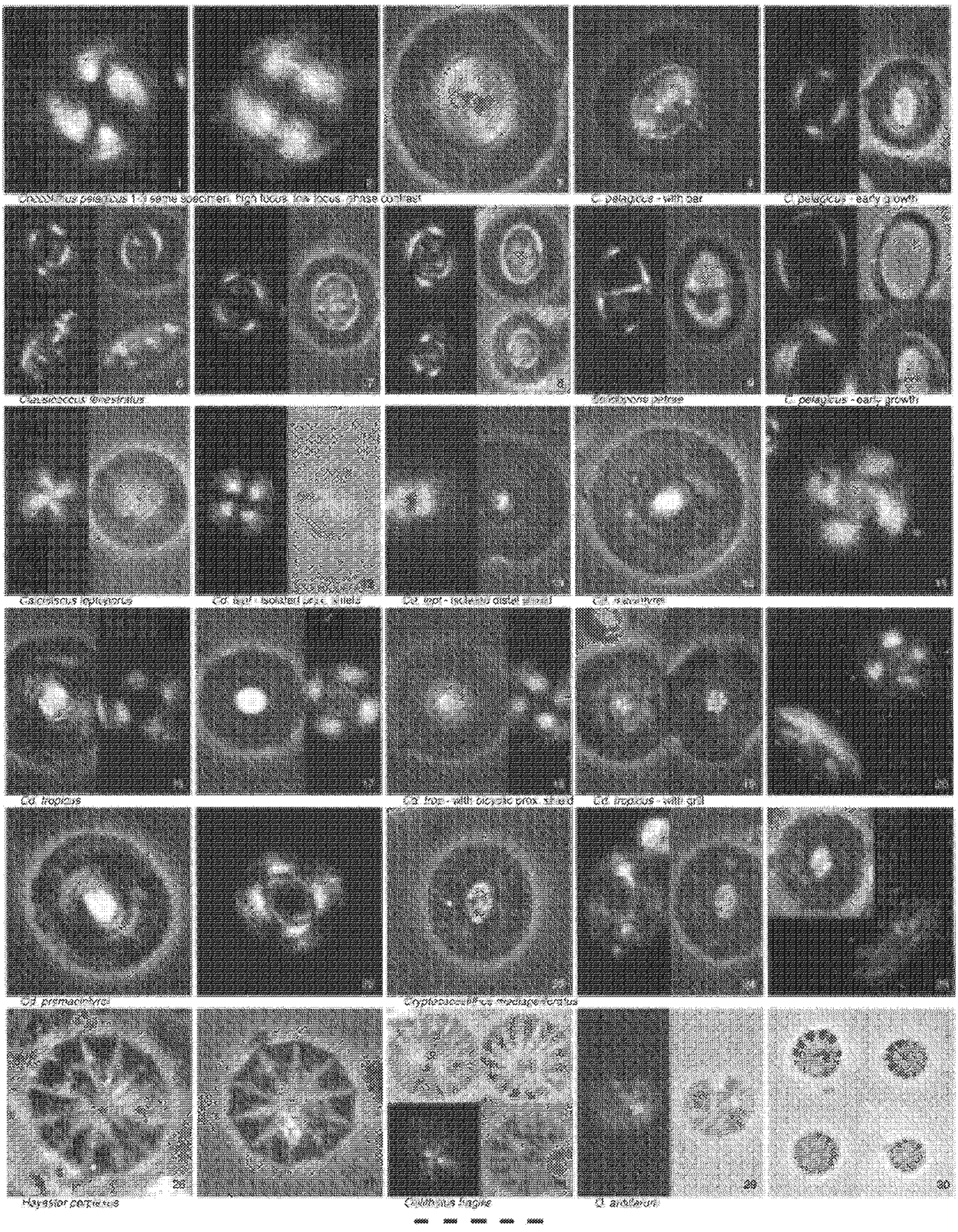
Genus CRYPTOCOCCOLITHUS Gartner, 1992
Figs 23–25. ***Cryptococcolithus mediaperforatus*** (Varol, 1991) de Kaenel and Villa, 1996 [*Birkelundia*]. Elliptical, medium-sized placolith. Central-area with coarse grill clearly visible in LM. Proximal shield is birefringent but thin and often detached, so coccolith is characteristically dark in XPL. RANGE: NN3–11. SYNONYM: *C. takayamae* Gartner, 1992.

Genus HAYASTER Bukry, 1973c
Figs 26–27. ***Hayaster perplexus*** (Bramlette and Riedel, 1954) Bukry, 1973 [*Discoaster*]. Distal shield consists of only 10–14 rays, proximal shield diminutive. Often disintegrates into separate elements. RANGE: Palaeogene–NN21.

Genus OOLITHOTUS Reinhardt *in* Cohen and Reinhardt, 1968
Similar to *Calcidiscus* but asymmetric (shields wider one side), central-area closed, proximal shield small, monocyclic.

Fig. 28. ***Oolithotus fragilis*** (Lohmann, 1912) Martini and Müller, 1972 [*Coccolithophora*]. RANGE: NN15?–21.

Figs 29–30. ***Oolithotus antillarum*** (Cohen, 1964) Reinhardt *in* Cohen and Reinhardt, 1968 [*Discolithus*]. Small form, coccoliths <5µm. RANGE NN19?–21. SYNONYM: *O. fragilis* var. *cavum* (Okada and McIntyre, 1977) Jordan and Young, 1990 [*O. fragilis* ssp. *cavum*] – see Kleijne (1991) for discussion.



Coccolithus pelagicus 1-3 same specimen, high focus, low focus, phase contrast

C. pelagicus - with bar

C. pelagicus - early growth

Clausicoccus fenestratus

[illegible] petrae

C. pelagicus - early growth

Calcidiscus leptoporus

Cd. lept - isolated prox. shields

Cd. lept - isolated distal shield

Cd. macintyrei

Cd. tropicus

Cd. trop - with bicyclic prox. shield

Cd. tropicus - with grill

Cd. premacintyrei

Cryptococcolithus mediaperforatus

Hayaster perplexus

Oolithotus fragilis

O. antillarum

Plate 8.5

Genus UMBILICOSPHAERA Lohmann, 1902
Distal shield sutures complex. V-units do not form significant cycle on proximal side. Proximal shield may be mono- or bicyclic, sometimes broader than the distal shield. SYNONYM: *Geminilithella* Backman, 1980; see section 8.6.

Figs 1–2. ***Umbilicosphaera sibogae*** var. ***sibogae*** (Weber-van Bosse, 1901) Gaarder, 1970 [*Coccosphaera*]. Central opening wide. Proximal shield monocyclic, wider than distal shield. RANGE: NN16?–21. SYNONYM: *U. mirabilis* Lohmann, 1902. N.B. The type specimen is a typical *U. sibogae sibogae* but many authors have applied the name to *U. sibogae foliosa.*

Figs 3–4. ***Umbilicosphaera sibogae*** var. ***foliosa*** (Kamptner, 1963) Okada and McIntyre, 1977 [*Cycloplacolithus*]. Central opening narrow. Proximal shield bicylic. RANGE: NN16?–21.

Fig. 5. ***Umbilicosphaera hulburtiana*** Gaarder, 1970. Elliptical, otherwise similar to *U. sibogae* var. *foliosa*; rare. RANGE: NN19?–21.

Figs 6–7. ***Umbilicosphaera jafari*** Müller, 1974b. Small form with narrow central-area. Shields often separated (Fig. 7); common. RANGE: NN2–19. VARIANT: *Geminilithella petaliformis* (Varol, 1982) Varol, 1989d [*Umbilicosphaera*] – similar but with bicylic proximal shield.

Figs 8–10. ***Umbilicosphaera rotula*** (Kamptner, 1956) Varol, 1982 [*Cyclococcolithus*]. Wide central-area, narrow rim. Often placed in *Geminilithella.* RANGE: NN2–16. VARIANT: *Umbilicosphaera lordii* Varol, 1982 – like *U. rotula* but showing no obvious birefringence, probably a preservational relic.

Not figured. '*Cyclolithus*' *annulus* Lecal, 1967. Broadly elliptical with open central-area. Probably should be included in *Umbilicosphaera.* RANGE: NN19?–21. SYNONYMS: *Geminilithella subtilis* (Müller, 1975) Varol, 1989d [*Cyclococcolithus*]; *U. calvata* Steinmetz, 1991; *U. scituloma* Steinmetz, 1991.

COCCOLITHS *INCERTAE SEDIS*

Genus CORONOCYCLUS Hay *et al.*, 1966
Figs 11–15. ***Coronocyclus nitescens*** (Kamptner, 1963) Bramlette and Wilcoxon, 1967a [*Umbilicosphaera*]. Ring-shaped coccoliths with open central-area. No clear shield development, spines on distal side. Strongly birefringent. RANGE: Palaeogene–NN6. SYNONYM: *Coronocyclus serratus* Hay *et al.*, 1966. VARIANT: Elliptical forms with narrow rims occur in NN5–6 (Figs 14–15).

Genus HAYELLA Gartner, 1969a
Figs 16–17. ***Hayella challengeri*** (Müller, 1974a) Theodoridis, 1984 [*Nannocorbis*]. Tubular murolith with proximal and distal flanges, medium-sized (size cited as 3.5–4µm in original description but holotype is 7µm across). Superficially similar to *U. rotula* but easily distinguished by through-focusing. N.B. Assignment to *Hayella* is uncertain since structure of the Eocene type species *H. situliformis* is unclear. *H. challengeri* appears structurally similar to *Ochrosphaera neapolitana.* RANGE: NN1?–?12, common in NN4–6. SYNONYM: *Hayella aperta* Theodoridis, 1984 – supposedly larger, but the holotype is only 8.5µm *vs.* 7µm for *H. challengeri.*

Genus HUGHESIUS Varol, 1989d
Non-birefringent with 2–4 plates filling central-area. There appears to be a lineage extending from *Clausicoccus fenestratus* via *H. tasminiae* to *H. gizoensis*, involving size decrease and reduction of the R-units.

Figs 18–20. ***Hughesius gizoensis*** Varol, 1989d. <4µm, 2 plates in central-area, very common. RANGE: NN2–11.

Figs 22–24. ***Hughesius tasmaniae*** (Edwards and Perch-Nielsen, 1975) de Kaenel and Villa, 1996 [*Ericsonia*]. 3–5µm, 4 plates in central-area. RANGE: Palaeogene–NN9, rare above NN3. SYNONYM: recorded as *Hughesius* sp. by Varol (1989d).

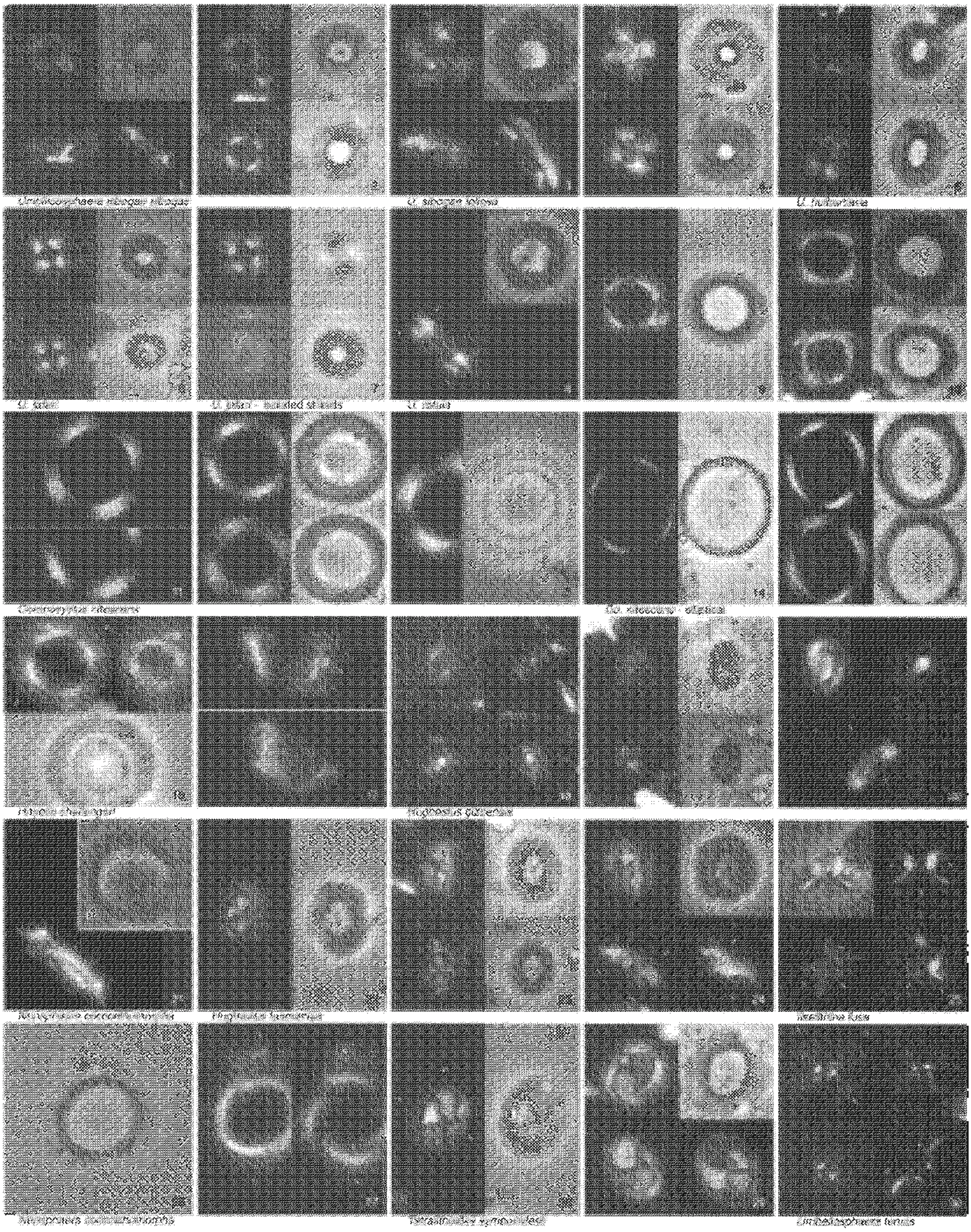

Umbilicosphaera sibogae sibogae
U. sibogae foliosa
U. hulburtiana
U. jafari
U. jafari - banded shields
U. rotula
Hughesius gizoensis
Tetralithoides symeonidesii
Umbellosphaera tenuis
10μm

Plate 8.5 cont'd

Genus ILSELITHINA Stradner *in* Stradner and Adamiker, 1966
Fig. 25. ***Ilselithina fusa*** Roth, 1970. Placolith-like coccolith but with distal shield reduced to a ring of spines; usually seen in cross-section. RANGE: Palaeogene–NN2.

Genus NEOSPHAERA Lecal-Schlauder, 1950
Figs 21, 26–27. ***Neosphaera coccolithomorpha*** Lecal-Schlauder, 1950. Circular, ring-shaped coccoliths with open central-area. Single shield and tube, no distal shield. Superficially similar in LM to *Umbilicosphaera rotula* but shield paler in PC and distinctive pseudoextinction cross seen in XPL at high focus. RANGE: NN19?–21. SYNONYMS: *Craspedolithus vidalii* Bukry, 1975; *C. declivus* Kamptner, 1963; *C. ragulus* Kamptner, 1967.

Genus TETRALITHOIDES Theodoridis, 1984 emend. Jordan *et al.*, 1993
Figs 28–29. ***Tetralithoides symeonidesii*** Theodoridis, 1984. Elliptical with moderately narrow rim surrounding central-area filled by four plates. RANGE: NN2?–12? N.B. The extant and Quaternary form, *T. quadrilaminata* (Okada and McIntyre, 1977) Jordan *et al.*, 1993, is significantly smaller and has a much narrower rim so *T. symeonidesii* should probably be retained as a discrete species.

Genus UMBELLOSPHAERA Paasche *in* Markali and Paasche, 1955
Trumpet-shaped. Main part is R-unit with narrow V-unit round base but only the tube is thick enough to give strong birefringence. SYNONYM: *Ellipsodiscoaster* Boudreaux and Hay, 1969.

Not figured. *Umbellosphaera irregularis* Paasche *in* Markali and Paasche, 1955. Without ridges on the distal surface. N.B. The epithet refers to irregular shape in side view. RANGE: NN15?–21. SYNONYM: *Ellipsodiscoaster lidzii* Boudreaux and Hay, 1969.

Fig. 30. ***Umbellosphaera tenuis*** (Kamptner, 1937) Paasche *in* Markali and Paasche, 1955 [*Coccolithus*]. With ridges on the distal surface. RANGE: NN15?–21.

Plate 8.6

Family CALYPTROSPHAERACEAE Boudreaux and Hay, 1969
Holococcoliths are virtually absent in Neogene nannofloras. By contrast, modern nannofloras include >50 holococcolithophore species (Kleijne, 1991; Jordan and Kleijne, 1994) but most species produce very small coccoliths (often <2µm) with low preservation potential. RANGE: Lower Jurassic–NN21.

Genus HOLODISCOLITHUS Roth, 1970
Fig. 26. ***Holodiscolithus macroporus*** (Deflandre *in* Deflandre and Fert, 1954) Roth, 1970 [*Discolithus*]. Sub-elliptical holococcolith with one or two prominent cycles of pores. Dark in PC and XPL. RANGE: Palaeogene–NN18.

Genus ZYGRHABLITHUS Deflandre *in* Deflandre and Fert, 1959
Fig. 27. ***Zygrhablithus bijugatus*** (Deflandre, 1954) Deflandre, 1959 [*Zygolithus*]. Rod-shaped holococcolith with small basal disk. RANGE: Palaeogene–NN1, rarely NN2 (de Kaenel and Villa, 1996).

NANNOLITHS

Genus FLORISPHAERA Okada and Honjo, 1973
Figs 20, 25. ***Florisphaera profunda*** Okada and Honjo, 1973. *Florisphaera* is abundant in modern, deep-photic communities and is believed to be an haptophyte but its precise affinities are uncertain. The coccospheres are artichoke-like with individual liths formed of single calcite crystals. Very abundant in well-preserved Neogene open-ocean sediments, but easily overlooked and so rarely recorded. Monospecific. RANGE: NN5?–21. VARIANT: *Florisphaera profunda* var. *elongata* Okada and McIntyre, 1980 – more elongate, not consistently differentiable.

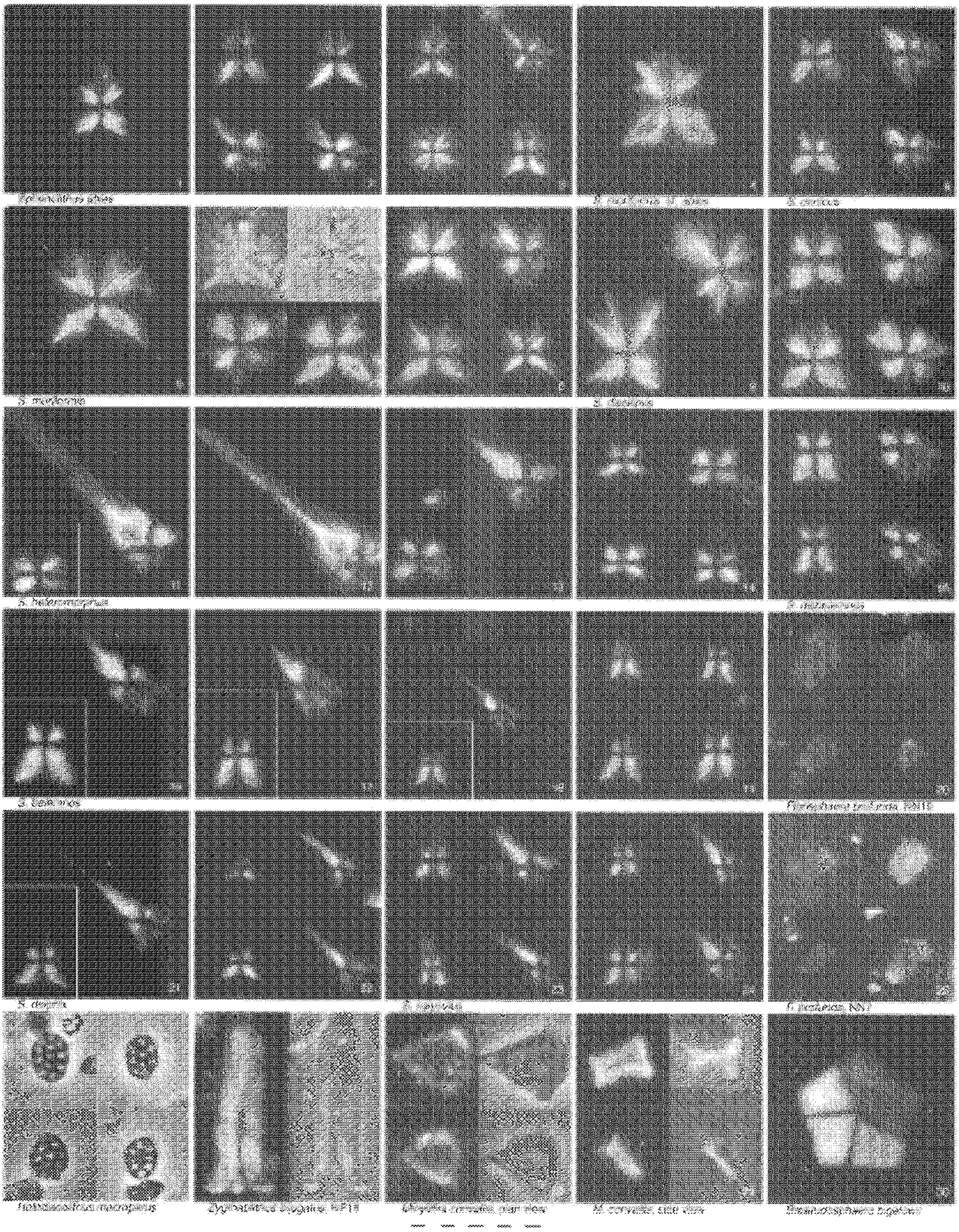

1
2
3
4
5
Sphenolithus abies
S. neoabies, S. abies
S. grandis
6
7
8
9
10
S. moriformis
S. distentus
11
12
13
14
15
S. heteromorphus
S. ciperoensis
16
17
18
19
20
S. belemnos
Fasciculithus tympaniformis, NN15
21
22
23
24
25
S. delphix
S. capricornutus
S. predistentus, NN1
26
27
28
29
30
Holodiscolithus macroporus
Zygrhablithus bijugatus, NP18
Minylitha convallis, plan view
M. convallis, side view
Braarudosphaera bigelowii
10μm

Plate 8.6 cont'd

Genus MINYLITHA Bukry, 1973b
Figs 28–29. ***Minylitha convallis*** Bukry, 1973b. Rhomb-shaped nannoliths with elevated rim. Monospecific. RANGE: NN9–11A.

Family BRAARUDOSPHAERACEAE Deflandre, 1947a
Genus BRAARUDOSPHAERA Deflandre, 1947a
Fig. 30. ***Braarudosphaera bigelowii*** (Gran and Braarud, 1935) Deflandre, 1947a [*Pontosphaera*]. Coccosphere dodecahedral, formed of 12 pentaliths, each with 5 crystal-units showing tangential c-axis orientation. RANGE: Cretaceous (Aptian)–NN21.

Not figured. Genus MICRANTHOLITHUS Deflandre *in* Deflandre and Fert, 1954
Similar to *Braarudosphaera* but sutures emerge through corners of pentalith and edges often indented. Most of the common Eocene species have been recorded in the Miocene but only sporadically and not in open-ocean deposits. RANGE: Lower Cretaceous–?NN9.

Family SPHENOLITHACEAE Deflandre, 1952
Genus SPHENOLITHUS Deflandre *in* Grassé, 1952
SYNONYMS: *Furcatolithus* Martini, 1965; *Sphenaster* Wilcoxon, 1970b.

A. SPECIES WITHOUT PROMINENT APICAL SPINES.
Figs 1–3. ***Sphenolithus abies*** Deflandre *in* Deflandre and Fert, 1954. Similar to *S. moriformis* but more elevated and with cuspate outline. RANGE: NN7?–15. VARIANTS: *S. grandis* Haq and Berggren, 1978 – large form; *S. neoabies* Bukry and Bramlette, 1969 – small form; *S. verensis* Backman, 1978 – slight elongations of elements; *S. quadrispinatus* Perch-Nielsen, 1980, with 4 elements elongated into spines; rare.

Figs 4, 6–8. ***Sphenolithus moriformis*** (Brönnimann and Stradner, 1960) Bramlette and Wilcoxon, 1967a [*Nannoturbella*]. Generalized form. No spine, upper and lower parts of similar size. Typical forms are shown in Figs 1–3; more elevated Lower Miocene forms similar to *S. abies* in Fig. 4. RANGE: Lower Eocene–NN10. SYNONYM: *S. pacificus* Martini, 1965. VARIANT: *S. compactus* Backman, 1980 – small form.

Fig. 5. ***Sphenolithus conicus*** Bukry, 1971a. Apical spine diminutive, base similar to *S. moriformis*. RANGE: Oligocene–NN3.

Figs 9–10. ***Sphenolithus dissimilis*** Bukry and Percival, 1971. Similar to *S. moriformis* but with apical cycle of elements extended to form circlet of spines. RANGE: Oligocene–NN3.

Fig. 15. ***Sphenolithus disbelemnos*** Fornaciari and Rio, 1996. Similar to *S. belemnos* but apical spine diminutive. RANGE: NN2–3. SYNONYMS: *S. aubryae* de Kaenel and Villa, 1996. *Sphenolithus dissimilis-belemnos* intergrade Rio *et al.* (1990a).

B. SPECIES WITH PROMINENT, MONOCRYSTALLINE APICAL SPINES.
Figs 11–14. ***Sphenolithus heteromorphus*** Deflandre, 1953. Apical spine very well-developed. Lateral elements nearly as large as proximal elements. RANGE: NN4–5.

Figs 16–19. ***Sphenolithus belemnos*** Bramlette and Wilcoxon, 1967a. Dart-shaped, apical spine well-developed. Lateral elements much smaller than proximal elements. RANGE: NN3.

Figs 21–22. ***Sphenolithus delphix*** Bukry, 1973b. Small with single apical spine and flaring proximal cycle. RANGE: NN1.

Figs 23–24. ***Sphenolithus calyculus*** Bukry, 1985. Small with long apical spine and compact base. RANGE: Palaeogene–NN1. SYNONYM: *S. elongatus* Martini, 1986.

Not figured. *Sphenolithus capricornutus* Bukry and Percival, 1971. Small with two diverging apical spines. RANGE: Palaeogene–NN1.

Plate 8.7

Family DISCOASTERACEAE Tan, 1927b
Genus DISCOASTER Tan, 1927b
A. 6-RAYED DISCOASTERS WITH BIFURCATIONS

This is the predominant group of Neogene discoasters. N.B. Asymmetric 5-rayed specimens of all these species occasionally occur.

Figs 1–3. ***Discoaster deflandrei*** Bramlette and Riedel, 1954. Central-area wide and rather featureless, rays with short, wide bifurcations. Asymmetric 5- and 7-rayed forms occur. RANGE: Palaeogene–NN7. VARIANTS: *D. moorei* Bukry, 1971b – asymmetric 5-rayed form (Fig. 3); *D. aulakos* Gartner, 1967b – smaller central-area and weaker bifurcations, arguably an intermediate form between *D. deflandrei* and *D. exilis*. N.B. Hay *et al.*, 1967 described many other variants of *D. deflandrei*.

Not figured. *Discoaster druggii* Bramlette and Wilcoxon, 1967a. Like *D. deflandrei* but larger, >15µm, and with small bifurcations. RANGE: NN2–3.

Figs 4–5. ***Discoaster kugleri*** Martini and Bramlette, 1963. Central-area wide and flat, free rays short with notched ends rather than true bifurcations. RANGE: NN7.

Figs 6–8. ***Discoaster exilis*** Martini and Bramlette, 1963. Central-area small, usually with weak distal and proximal bosses. Bifurcations acutely angled in plan view and wedge-shaped in cross-section. RANGE: NN4–9. VARIANTS: *Eu-discoaster protoexilis* Theodoridis, 1984 – intermediate to *D. deflandrei*, large bifurcations, medium central-area. N.B. If this morphotype was distinguished then other names, e.g. *D. aulakos* Gartner, 1967b, would have priority; *D. signus* Bukry, 1971b – form with well-developed bifurcations; *D. subsurculus* Gartner, 1967b – with trifurcate tip, due to bifid proximal extensions in centre of bifurcations.

Figs 9–10, 15. ***Discoaster petaliformis*** Moshkovitz and Ehrlich, 1980. Similar to *D. exilis* but with large distal boss and very large, mushroom-shaped proximal boss. Central-area narrow. RANGE: NN4–5. SYNONYMS: *D. signus* Bukry, 1971b emend. Theodoridis, 1984; *D. tuberi* Filewicz, 1985.

Not figured. *Discoaster musicus* Stradner, 1959a. Similar to *D. exilis* but with large, wide distal boss with projections extending between the rays. RANGE: NN5. SYNONYM: *D. sanmiguelensis* Bukry, 1981a.

Figs 11–12. ***Discoaster challengeri*** Bramlette and Riedel, 1954. Central-area narrow and with only weak bosses. Bifurcations well developed. Rather a generalized form, but distinguishing it gives stratigraphic value to *D. exilis* and *D. variabilis*. RANGE: NN5–10. VARIANTS: *D. perclarus* Hay *in* Hay *et al.*, 1967 – longer bifurcations and more delicate form; *D. pseudovariabilis* Martini and Worsley, 1971 – with bifid proximal extensions between the bifurcations and so weakly trifurcate.

Figs 13–14. ***Discoaster bollii*** Martini and Bramlette, 1963. Similar to *D. exilis* but with large distal boss, wide central-area, and usually smaller (<10µm). RANGE: NN8–9.

Figs 16–19. ***Discoaster variabilis*** Martini and Bramlette, 1963. Central-area with proximal and distal ridges but weak bosses. Bifurcations well developed. RANGE: NN9–16. VARIANTS: *D. decorus* (Bukry, 1971b) Bukry, 1973b [*D. variabilis decorus*] – small bifurcations (Fig. 19); *D. icarus* Stradner, 1973 – bifurcations broad and space between often partly filled by thin 'webbing'; *D. mirabilis* Duan, 1985 – asymmetric 5-rayed variety; *D. pansus* (Bukry and Percival, 1971) Bukry, 1973b [*D. variabilis pansus*] – large, wide bifurcations (Fig. 18).

Fig. 20. ***Discoaster loeblichii*** Bukry, 1971a. Like *D. variabilis* but bifurcations asymmetric. RANGE: NN10–11.

Figs 21–22. ***Discoaster surculus*** Martini and Bramlette, 1963. Similar to *D. variabilis* but with proximal ray-tip extensions giving trifurcate appearance to ray-tips. N.B. Through-focusing is often needed to see the ray-tip extensions. RANGE: NN10–16.

Plate 8.7 cont'd

B. *D. BROUWERI* GROUP
6-rayed discoasters without bifurcations and forms closely related to *D. brouweri* with fewer rays.

Figs 23–25. ***Discoaster calcaris*** Gartner, 1967b. Rays with clockwise-deflected (in distal view) proximal extensions. RANGE: NN9–11. VARIANT: *D. neohamatus* Bukry and Bramlette, 1969a – with more obviously asymmetric tips.

Fig. 26. ***Discoaster braarudii*** Bukry, 1971b. Similar to *D. brouweri* but ray-tips simple, without proximal extensions. N.B. Discoasters with this general morphology also often occur through dissolution or poor development of other species, e.g. *D. exilis, D. brouweri.* RANGE: NN7–11.

Not figured. *Discoaster neorectus* Bukry, 1971a. Very large (>20μm), flat, simple ray-tips. RANGE: NN10B–11A.

Figs 27–29. ***Discoaster brouweri*** Tan, 1927b emend. Bramlette and Riedel, 1954. Ray-tips non-bifurcate and with marked proximal extensions. RANGE: NN9–18. VARIANTS: *Eu-discoaster brouweri* ssp. *streptus* Theodoridis, 1984 – with proximal boss; *D. blackstockae* Bukry, 1973c – 4-rayed form with inter-ray angles of 60° and 120°; *Eu-discoaster giganteus* Theodoridis, 1984 – very large, ray-tips blunt but with long proximal extensions. If used should be recombined into *Discoaster*.

Fig. 30. ***Discoaster asymmetricus*** Gartner, 1969c. Asymmetric 5-rayed variety of *D. brouweri.* RANGE: common NN15–16, occasional specimens NN9–21.

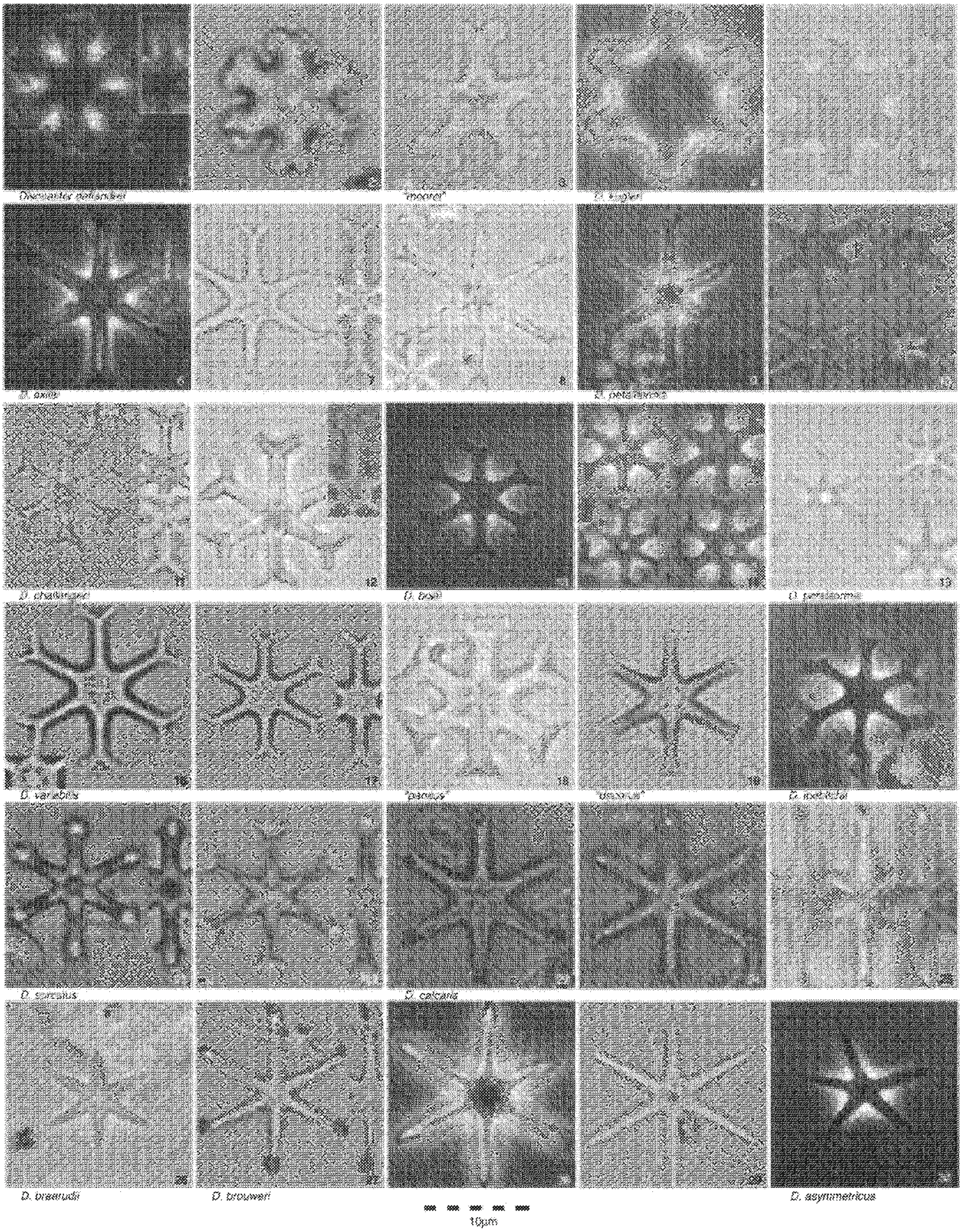

1
2
3
4
5
Discoaster deflandrei
"moorei"
D. kugleri
6
7
8
9
10
D. exilis
D. petaliformis
11
12
13
14
15
D. challengeri
D. bollii
D. pentaradiatus
16
17
18
19
D. variabilis
"pansus"
"[illegible]"
D. [illegible]
D. surculus
D. calcaris
26
27
29
D. braarudii
D. brouweri
D. asymmetricus
10µm

Plate 8.8

Fig. 1. ***Discoaster asymmetricus*** Gartner, 1969c. See Plate 8, Fig. 30.

Fig. 2. ***Discoaster tamalis*** Kamptner, 1967. Symmetric 4-rayed variety of *D. brouweri*. RANGE: NN14–16.

Fig. 3. ***Discoaster triradiatus*** Tan, 1927b. Symmetric 3-rayed variety of *D. brouweri*. RANGE: common in upper part of NN18, occasional specimens NN9–21.

Figs 4–5. ***Discoaster altus*** Müller, 1974a. Central-area broad with prominent, wide proximal and narrow distal knobs. Ray-tips simple. RANGE: NN14–15. SYNONYM: *D. tristellifer* Bukry, 1976 – see taxonomic notes.

C. SYMMETRIC 5-RAYED DISCOASTERS

Figs 6–7. ***Discoaster bellus*** Bukry and Percival, 1971. Symmetric 5-rayed species with simple ray-tips. Intergrades with *D. hamatus*. RANGE: NN8–11.

Figs 8–10. ***Discoaster hamatus*** Martini and Bramlette, 1963. 5-rayed. Rays with clockwise-deflected (in distal view) proximal extensions. RANGE: NN9.

Not figured. *Discoaster bergenii* Knuttel *et al.*, 1989. Like *D. quinqueramus* but central-area very wide (>2x free ray length). RANGE: NN11A.

Figs 11–12. ***Discoaster berggrenii*** Bukry, 1971b. Like *D. quinqueramus* but central-area wide (1–2x free ray length). RANGE: NN11A.

Figs 13–15. ***Discoaster quinqueramus*** Gartner, 1969c. 5-rayed. Central-area, with prominent distal sutural ridges and large proximal boss. Rays concavo-convex. RANGE: NN11A–11B. SYNONYM: *D. quintatus* Bukry and Bramlette, 1969a.

Figs 16–18, 21. ***Discoaster pentaradiatus*** Tan, 1927b. 5-rayed. Acute bifurcations. Strongly concavo-convex and birefringent (each ray is a separate crystal-unit, with c-axes inclined slightly from vertical toward radial). RANGE: NN10B–17. SYNONYMS: *D. anconitanus* Borsetti and Cati, 1972 – etched form lacking bifurcations; *D. misconceptus* (Theodoridis, 1984) Muza and Wise *in* Muza *et al.*, 1987 [*Eu-discoaster*]; *D. tridenus* Kamptner, 1967 etched form, lacking bifurcations. VARIANTS: *D. ono* Styzen, 1994 – very short, non-bifurcate rays, probably a preservational artefact (Fig. 21); *D. quadramus* Bukry, 1973c – 4-rayed form with inter-ray angles of 60° and 120° (Fig. 18). Less birefringent than normal *D. pentaradiatus*.

Figs 19–20. ***Discoaster prepentaradiatus*** Bukry and Percival, 1971. 5-rayed. Broad bifurcations. Planar and non-birefringent. RANGE: NN9–10.

D. PRESERVATIONAL FORMS

Figs 22–23. **Unidentifiable discoasters** (Fig. 22) are common, and for biostratigraphic precision it is best to record them as such (see section 8.6). In addition, isolated rays and pairs of rays are common (Fig. 23); care is sometimes needed to avoid misidentifying these as, e.g., *Amaurolithus*.

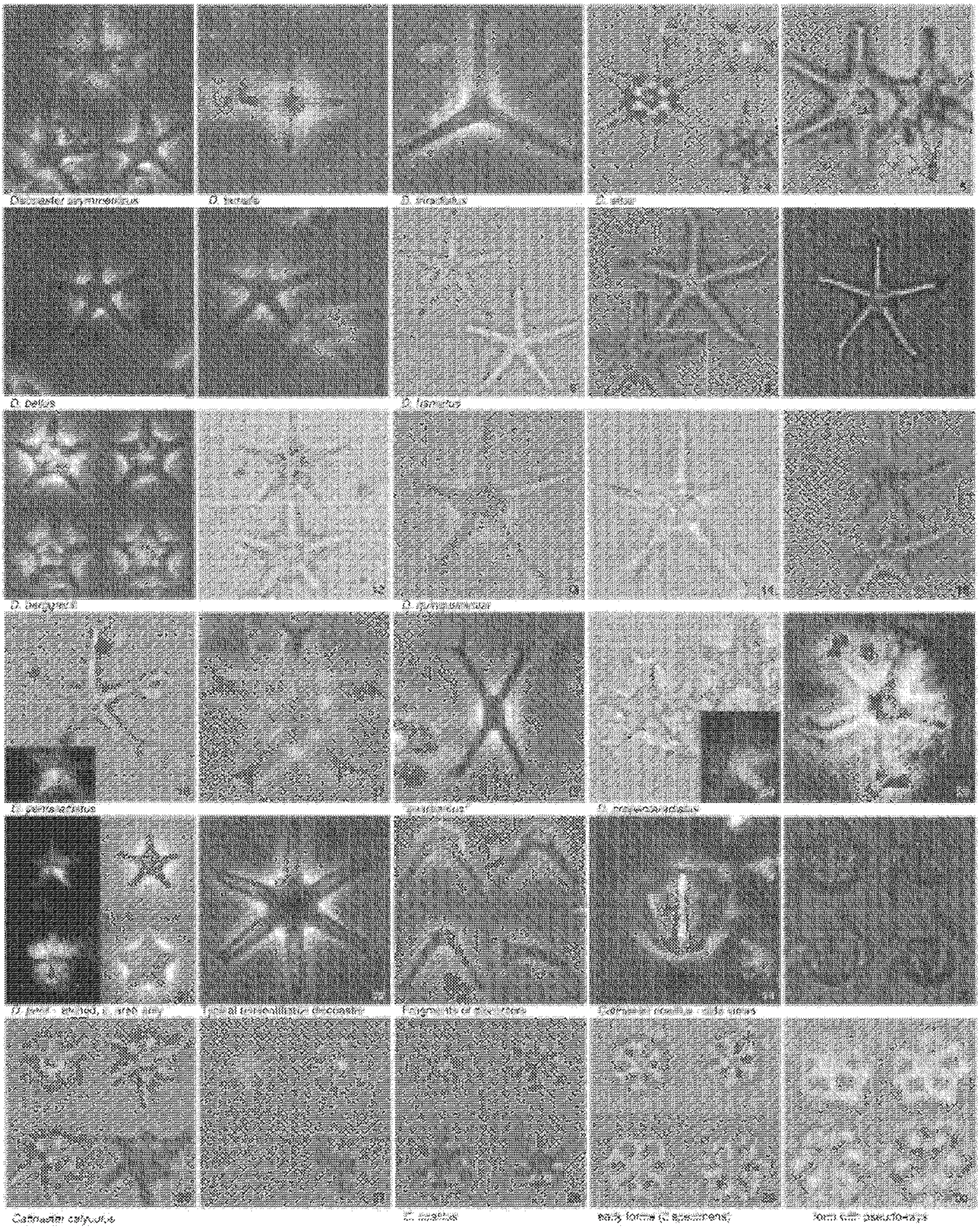
E. GENUS *CATINASTER* MARTINI AND BRAMLETTE, 1963

Basket-shaped nannolith formed by fusion of the bifurcations of a small discoaster (see also Peleo-Alampay *et al.*, in press). RANGE: NN8–10.

Figs 24–25, 28–30. ***Catinaster coalitus*** Martini and Bramlette, 1963. Rays confined to basket (N.B. short pseudo-rays are often formed where the tips of bifurcations meet – Fig. 30). RANGE: NN8–10.

Figs 26–27. ***Catinaster calyculus*** Martini and Bramlette, 1963. Curved rays extend beyond basket. (N.B. Peleo-Alampay and Wei (1995) and Peleo-Alampay *et al.* (in press) use basket shape as an alternative criterion for defining *C. calyculus*, but without markedly better biostratigraphic discrimination). RANGE: NN9–10.

Not figured. [*Catinaster mexicanus* Bukry, 1971b]. These do not have the open morphology of *Catinaster* specimens, and their detailed geometry is different. They are probably isolated central-areas of discoasters.



Discoaster asymmetricus

D. tamalis

D. triradiatus

D. [illegible]

D. bellus

D. hamatus

D. berggrenii

D. quinqueramus

D. pentaradiatus

'[illegible]'

D. prepentaradiatus

D. [illegible] - etched, [illegible]

Typical [illegible] discoaster

Fragments of discoasters

Catinaster coalitus - side views

Catinaster calyculus

C. mexicanus

early forms (2 specimens)

form with pseudo-rays

10μm

N.B. Figs. 25-28 and 30 each consist of four views of a single specimen, at different focal depths

Plate 8.9

Family TRIQUETRORHABDULACEAE Lipps, 1969
Genus TRIQUETRORHABDULUS Martini, 1965
Elongate nannoliths formed of three blades. Entire nannolith formed of a single calcite crystal, but with variable c-axis orientation (see section 8.6).

A – SPECIES WITH C-AXIS PARALLEL TO LENGTH OF NANNOLITH
Figs 1–2, 6–8. ***Triquetrorhabdulus carinatus*** Martini, 1965. Elongate (up to 50µm), all three blades identical, without ridges. RANGE: Palaeogene–NN2.

Figs 3–5, 9–10. ***Triquetrorhabdulus challengeri*** Perch-Nielsen, 1977. Two blades wider and with one or more subsidiary ridges. RANGE: NN1–2.

Figs 14–15. ***Triquetrorhabdulus milowii*** Bukry, 1971a. Short (8–15µm), broad (5–8µm) with curved sides. All blades similar. RANGE: NN1–6. VARIANT: *T. auritusus* Stradner and Allram, 1982 – more wedge-shaped, occasionally with ridges at blunt end. RANGE: NN5–6.

B – SPECIES WITH C-AXIS PERPENDICULAR TO LENGTH OF NANNOLITH
Figs 17–20. ***Triquetrorhabdulus rioi*** Olafsson, 1989. Narrow, straight forms. Superficially similar to *T. carinatus* but with c-axis perpendicular to length of nannolith. Often lie in an orientation in which they show birefringence. N.B. *rioi* is a corrected form of the name *rioensis*. RANGE: NN6–7.

Figs 21–25. ***Triquetrorhabdulus rugosus*** Bramlette and Wilcoxon, 1967a. Default name, rather variable, straight or slightly curved, one lateral blade often slightly wider than the other. RANGE: NN6–12. VARIANT: *Ceratolithus farnsworthii* (Gartner, 1967b) Perch-Nielsen, 1984 – more asymmetric (cf. Figs 24–25).

Figs 26–29. ***Triquetrorhabdulus striatus*** Müller, 1974a. With subsidiary ridges on one lateral blade. RANGE: NN10–12.

Fig 30. ***Triquetrorhabdulus extensus*** Theodoridis, 1984. One lateral blade very wide, with weak ridges. RANGE: NN11B–12.

Not figured. *Triquetrorhabdulus finifer* Theodoridis, 1984. Horseshoe-shaped with short median blade and elongate, curved lateral blades. RANGE: NN11B–12.

Genus ORTHORHABDUS Bramlette and Wilcoxon, 1967a
Figs 11–13, 16. ***Orthorhabdus serratus*** Bramlette and Wilcoxon, 1967a. Optical orientation similar to *T. rugosus* but triangular-shaped and median blade broader than lateral blades. Typical forms are symmetric (Figs 11–12) but specimens with a spine developed from one blade occur in upper part of range (Fig. 13). RANGE: NN2–6. SYNONYM: *Triquetrorhabdulus martinii* Gartner, 1967b.

Plate 8.10

Family CERATOLITHACEAE Norris, 1965
Horseshoe-shaped nannoliths formed of a single calcite crystal.

Genus AMAUROLITHUS Gartner and Bukry, 1975
Non-birefringent, or only weakly birefringent, c-axis perpendicular to plane of horseshoe.

Figs 1–2. ***Amaurolithus primus*** (Bukry and Percival, 1971) Gartner and Bukry, 1975 [*Ceratolithus*]. Simple form with short arms, broad arch and weakly developed keels. RANGE: NN11B–12.

Figs 3–5. ***Amaurolithus amplificus*** (Bukry and Percival, 1971) Gartner and Bukry, 1975 [*Ceratolithus*]. Like *A. primus* but angular; right arm with rodded keel and longer than left. RANGE: restricted to short interval within NN11B. SYNONYM: *C. dentatus* Bukry, 1973b.

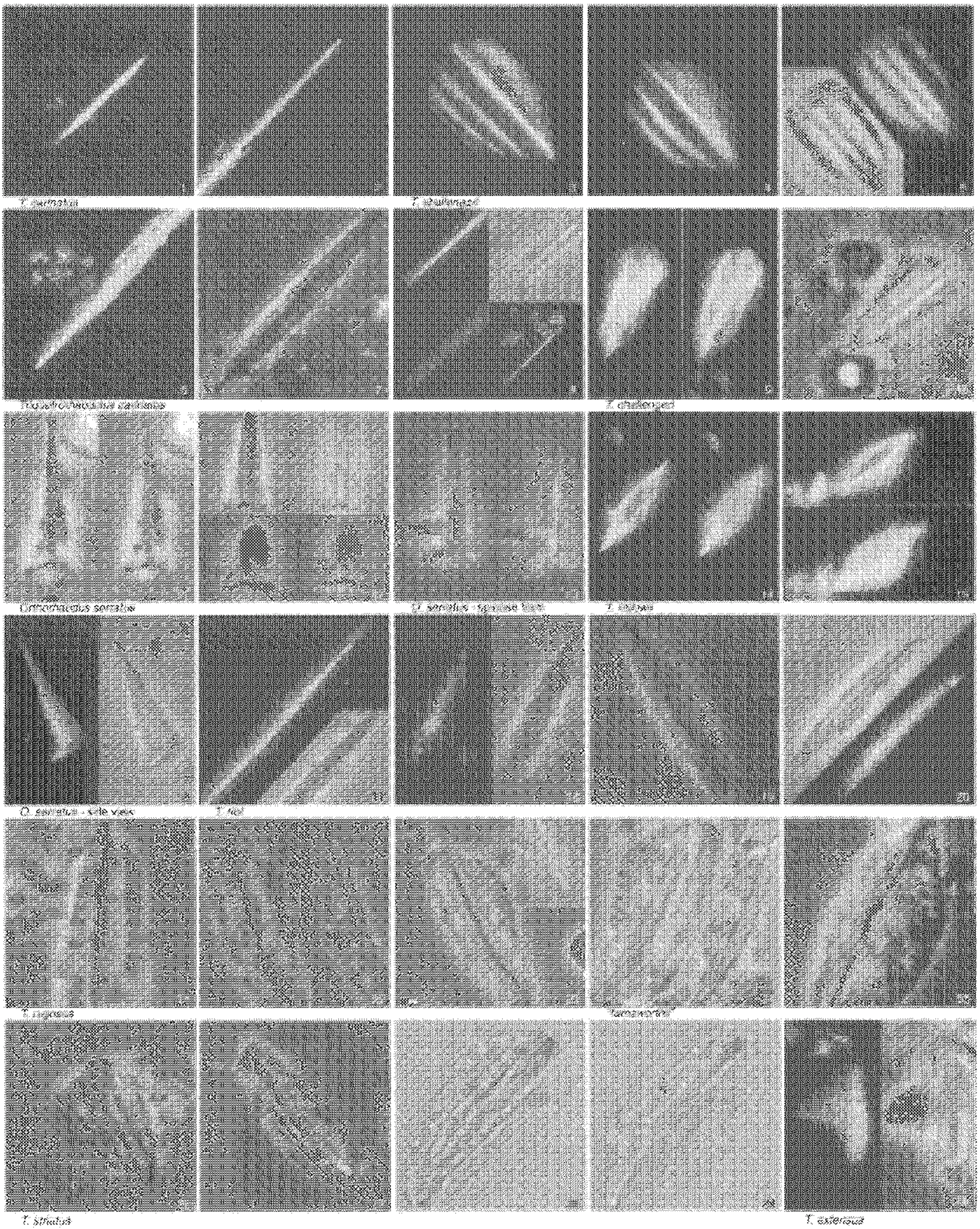

T. palmatus
T. challengeri
T. challengeri
Onthomaculus serratus
O. serratus - spinose tips
O. serratus - side view
T. rugosus
T. striatus
T. asterius
10µm

Plate 8.10 cont'd

Figs 6–8. ***Amaurolithus delicatus*** Gartner and Bukry, 1975. Simple, horseshoe-shaped amauroliths. Grades into other morphotypes, especially *A. primus* (Fig. 6) and *A. tricorniculatus*. RANGE: NN11B–14. VARIANT: *A. ninae* Perch-Nielsen, 1977 – like *A. delicatus* but with well-developed apical region.

Figs 9–12. ***Amaurolithus tricorniculatus*** (Gartner, 1967b) Gartner and Bukry, 1975 [*Ceratolithus*]. Right arm extended into apical spur. RANGE: NN11B–14. VARIANT: *A. bizarrus* (Bukry, 1973b) Gartner and Bukry, 1975 [*Ceratolithus*] – ornate *A. tricorniculatus* with additional spines (Figs 11–12).

Genus CERATOLITHUS Kamptner, 1950
Strongly birefringent, c-axis lies in plane of horseshoe, perpendicular to length.

Figs 13–15. ***Ceratolithus armatus*** Müller, 1974a. Left arm extends into apical spur producing a triangular apical area. Right arm longer than left. RANGE: NN12. VARIANT: *C. acutus* Gartner and Bukry, 1974 – described simultaneously to *C. armatus* for the same taxon, but often used for less-ornate forms (Fig. 15).

Figs 16–19. ***Ceratolithus cristatus*** Kamptner, 1950. Horseshoe-shaped ceratolith. Variable in size and degree of ornamentation. RANGE: NN13–21. SYNONYM: *C. rugosus* Bukry and Bramlette, 1968 – overgrown *C. cristatus*, mostly recorded from Pliocene but, as argued by Bergen (1984), this is simply a function of preservation (Fig. 16). VARIANTS: *C. simplex* Bukry, 1979 – small, smooth form, occurs throughout range of *C. cristatus*; *C. separatus* Bukry, 1979 – both arms slightly extended beyond the arch, may be biostratigraphically useful.

Fig 20. ***Ceratolithus cristatus*** var. ***telesmus*** (Norris, 1965) Jordan and Young, 1990 [*C. telesmus*]. Variety with long sinuous arms. RANGE: NN16–21.

Figs 21–22. ***Ceratolithus? atlanticus*** Perch-Nielsen, 1977. Ornate form, very rare. Described from NN12 but the illustrated specimens are from NN9 and similar specimens, also from NN9, have been illustrated by Raffi and Flores (1995), as *Ceratolithus*? RANGE: NN9?–?12.

NON-HAPTOPHYTE CALCAREOUS NANNOFOSSILS

Genus ANGULOLITHINA Bukry, 1973b
Fig. 26. ***Angulolithina arca*** Bukry, 1973b. Arrowhead-shaped dibrachiate nannofossil with c-axis parallel to length. Almost certainly unrelated to true ceratoliths, and possibly fragments of a larger microfossil. Monospecific, occurrence sporadic. RANGE: NN5?–?19

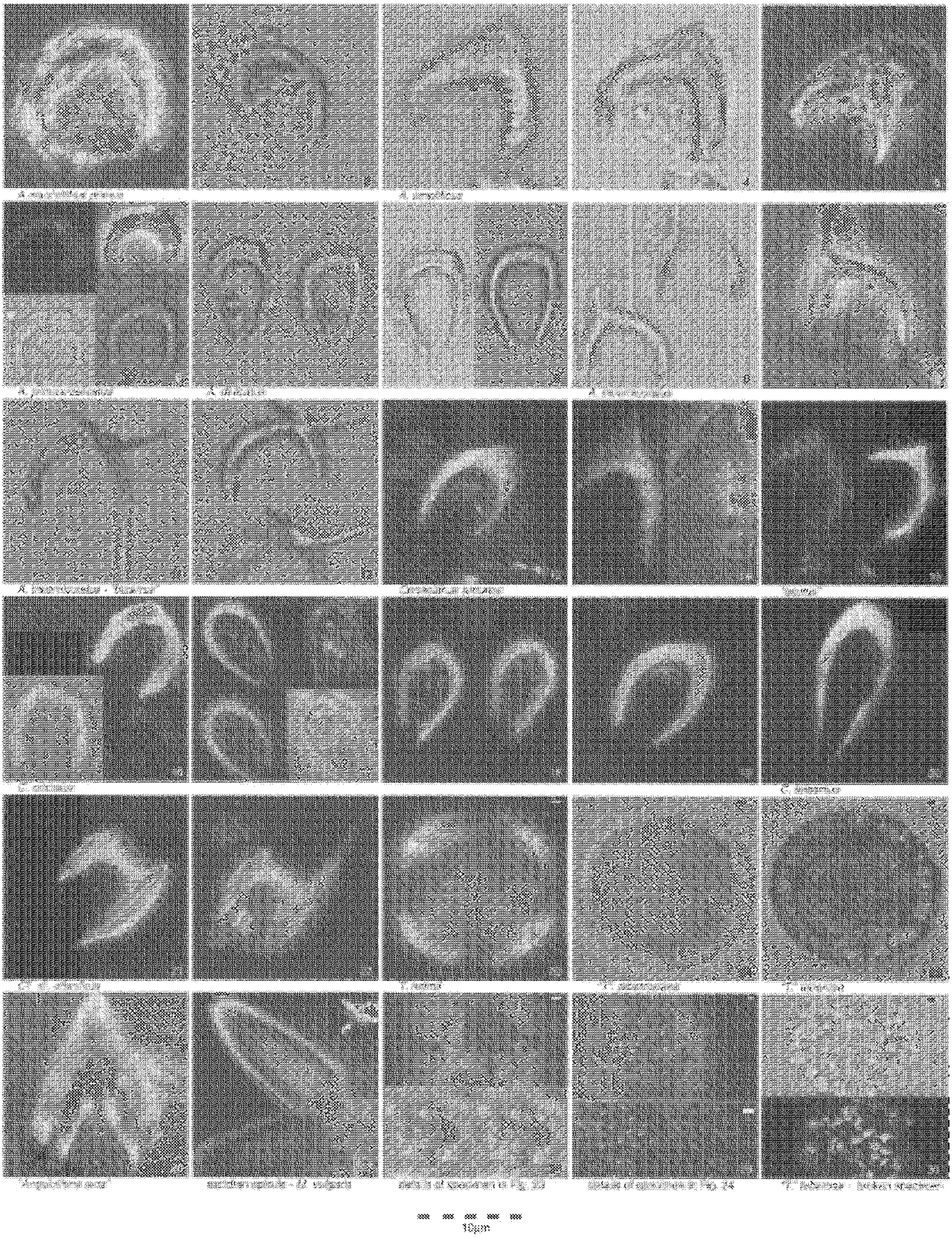
Phylum CHORDATA, Class ASCIDIACEAE (ascidians)
Genus MICRASCIDITES Deflandre and Deflandre-Rigaud, 1956
Fig. 27. ***Micrascidites vulgaris*** Deflandre and Deflandre-Rigaud, 1956. Ascidian spicules are found quite commonly in shelf sediments and sporadically in deep-sea deposits. They are formed of aragonite with the c-axis parallel to the spicule length. *M. vulgaris* is the most common species and the only one routinely cited. See Varol and Houghton (1996) for a review of literature and other species.

Division DINOFLAGELLATA Butschli, 1885
Family THORACOSPHAERACEAE Schiller, 1930
Genus THORACOSPHAERA Kamptner, 1927
N.B. Modern calcisphere taxonomy excludes all species from *Thoracosphaera* except *T. heimii* but the generic assignments of the other species have been highly volatile and are in the process of further revision due to reinterpretation of wall-structure (Janofske, 1996).

Figs 23, 28. ***Thoracosphaera heimii*** (Lohmann, 1919) Kamptner, 1941 [*Syracosphaera*]. Wall formed of large plates with holes when well preserved. C-axes tangential to surface but otherwise randomly distributed. RANGE Palaeogene–NN21.

Figs 24, 29. **'*Thoracosphaera*' *albatrosiana*** Kamptner, 1963. Wall formed of small crystallites surrounding perforations. C-axes tangential to surface and parallel to sides of perforations. With gypsum plate, wall has a reticulate appearance. RANGE: Palaeogene–NN21.

Figs 25, 30. **'*Thoracosphaera*' *tuberosa*** Kamptner, 1963. Wall crystallites large and irregular (1–2μm). C-axes oblique to surface (Janofske, 1996). RANGE: Palaeogene–NN21.



A. [illegible]

A. [illegible]

A. [illegible]

A. [illegible]

A. [illegible]

A. [illegible] - "[illegible]"

[illegible]

"[illegible]"

C. [illegible]

C. [illegible]

C. cf. [illegible]

T. [illegible]

"C." [illegible]

"T." [illegible]

"[illegible]"

[illegible] - M. vulgaris

details of specimen in Fig. 23

details of specimen in Fig. 24

"T." [illegible] - broken specimen

9

Quaternary

N. Hine and P.P.E. Weaver

9.1 INTRODUCTION

The Quaternary Sub-era provides an excellent opportunity for studying marine fossil sequences, due to the ready accessibility of sediments from marine sampling. The most continuous sections of Quaternary sediments have been cored by the DSDP and ODP, although considerable numbers of piston cores also exist, usually containing only late Quaternary sequences. The less-complete shelf sequences and outcrop sections are often best interpreted by comparison with the more complete open-ocean data.

One of the highest-resolution stratigraphies for this interval is provided by oxygen isotopes. Fluctuations in the ∂O^{18} record have been large through the last 2.4myr due to ice volume and temperature changes. Within the Quaternary, a total of 63 oxygen isotope stages have been defined (Ruddiman *et al.*, 1986), with an average duration of 26 000 years for each stage. This level of resolution is not commonly attained elsewhere in the geological column and thus the Quaternary is set apart as a time when geological processes can be examined in most detail. It can, however, often be difficult to identify specific glacials and interglacials from each other in the ∂O^{18} record, especially if there has been reworking or sediment removal. Calcareous nannofossils provide a high-resolution stratigraphy for the Quaternary which, in combination with isotope data, is a powerful stratigraphic tool. Once substantiated in a number of locations the nannofossil stratigraphy can be used independently of the oxygen isotope record to identify short time intervals throughout the Quaternary and, in many cases, individual isotope stages can be recognized.

The availability of complete Quaternary sequences, which can be dated and subdivided into short time units by oxygen isotope and geomagnetic polarity data, provides an excellent background for investigating the timing and duration of nannofossil datum events. It has been possible to identify diachronism across a range of latitudes, and also between oceans as exemplified in the work of Thierstein *et al.* (1977) and Wei (1993). The resultant stratigraphic scheme is, therefore, not only of high resolution, due to the large number of identifiable events, but its accuracy is also known within relatively small limits.

9.2 IMPORTANT REFERENCES

Quaternary nannofloras are dominated by members of the family Noelaerhabdaceae, in particular, *Reticulofenestra*, *Pseudoemiliania*, *Gephyrocapsa* and *Emiliania*. The taxonomy of these genera are discussed in Gartner (1977), Pujos-Lamy (1977a, b), Bréhéret (1978), Samtleben (1978, 1980), Backman (1980), Backman and Shackleton (1983), Perch-Nielsen (1985b), Pujos (1987), Gallagher (1989), Matsuoka and Okada (1990), Young (1990), Sato and Takayama (1992) and Bollman (1997).

The stratigraphic potential of Quaternary calcareous nannofossils was first noted by Bramlette and Riedel (1954). Subsequently, Boudreaux and Hay (*in* Hay *et al.*, 1967) proposed the first zonation scheme for the Cenozoic. The subsequent schemes of Martini (1971), Gartner (1977) and Okada and Bukry (1980) provide the basic nannofossil biostratigraphy for the Quaternary. This has been supplemented by the recognition of acme intervals of individual species, as used in the zonation schemes of, e.g., Gartner (1977), Pujos-Lamy (1977b), Bréhéret (1978), Weaver (1983), Verbeek (1990) and Pujos and Giraudeau (1993).

Calcareous nannoplankton have been relatively little used for Pleistocene palaeoclimatic and palaeoceanographic reconstruction by comparison with other fossil groups. This is primarily due to their high rate of evolutionary divergence, compounded by a succession of assemblages being dominated by single, relatively cosmopolitan species. These factors prove problematic in transfer function analysis. Some of the more significant papers include McIntyre *et al.* (1970, 1972), Ruddiman and McIntyre (1976), Molfino and McIntyre (1987), Gard (1988, 1989), Gard and Backman (1990), Giraudeau and Pujos (1990) and Baumann and Matthiessen (1992). Much of this work has been carried out within multidisciplinary studies, such as CLIMAP (1976, 1981). Nannofossils are responsible for producing the long-chain ketones which have been used successfully in determining palaeotemperatures in the Upper Quaternary. A limited number of species (including particularly *Emiliania huxleyi* and some or all of the *Gephyrocapsa* species) produce different unsaturated ratios of ketones (U^{k}_{37} index) in different water temperatures. Measurement of these ratios in sediment samples gives a direct indication of surface-water temperature (Brassell *et al.*, 1986). More recently, attempts have been made to assess the coccolith flora against alkenone results (Jordan *et al.*, 1996) so as to determine the consequences of the changing coccolith species acmes on alkenone ratios.

9.3 QUATERNARY NANNOFOSSIL SUCCESSION

Nannofossils have a rapid turnover through the Quaternary, providing useful first and last occurrance datum levels (Fig. 9.1). These easily recognized events enable the Quaternary Sub-era to be divided into units of time averaging less than 0.2myr. This resolution can be further enhanced by the semi-quantitative analysis of nannofossil assemblages and the recognition of acme intervals.

Quaternary nannofossil assemblages are characterized by the family Noelaerhabdaceae which includes the genera *Reticulofenestra*, *Pseudoemiliania*, *Gephyrocapsa* and *Emiliania*. The Noelaerhabdaceae are responsible for a number of acme intervals throughout the Quaternary, where a particular species dominates the assemblage over an interval of time, often constituting over 90% of the total nannoflora. Some of these acme intervals, such as the acme of *Emiliania huxleyi*, have been known for many years and used successfully in global stratigraphic correlation. The recognition of this succession of Quaternary acme intervals is only just being determined using DSDP and ODP continuously-cored sequences. Apart from the Noelaerhabdaceae, more than 30 accessory taxa are regularly recorded in standard smear slides. Figure 9.2 provides a range chart of biostratigraphically useful taxa together with some of the longer ranging taxa commonly recorded in Quaternary samples.

9.4 BIOSTRATIGRAPHY

An overview of the standard biostratigraphic schemes of various authors is detailed below. This acts as a framework into which a series of acme events can be interpolated. These acme events are based on original research by Hine (1990), and result in a high-resolution biostratigraphic scheme.

The Cenozoic magnetobiochronology of Cande and Kent (1992) has significantly improved upon that of Berggren *et al.* (1985) and now provides the standard means for translating biostratigraphic information into numerical ages. Wei and Peleo-Alampay (1993) converted the magnetobiochronological ages of Berggren to the new time-scale of Cande and Kent for the entire Cenozoic, and recorded recalculated ages differing by up to 2.9myr. The Quaternary Sub-era is not so greatly affected. The recalculated age for the oldest datum event (LO *Discoaster brouweri*) differs by 100kyr, and the youngest event (FO *Emiliania huxleyi*) by 19kyr.

9.4.1 Standard Quaternary biostratigraphy

The zonation schemes of Martini (1971), Gartner (1969c, 1977) and Okada and Bukry (1980) are

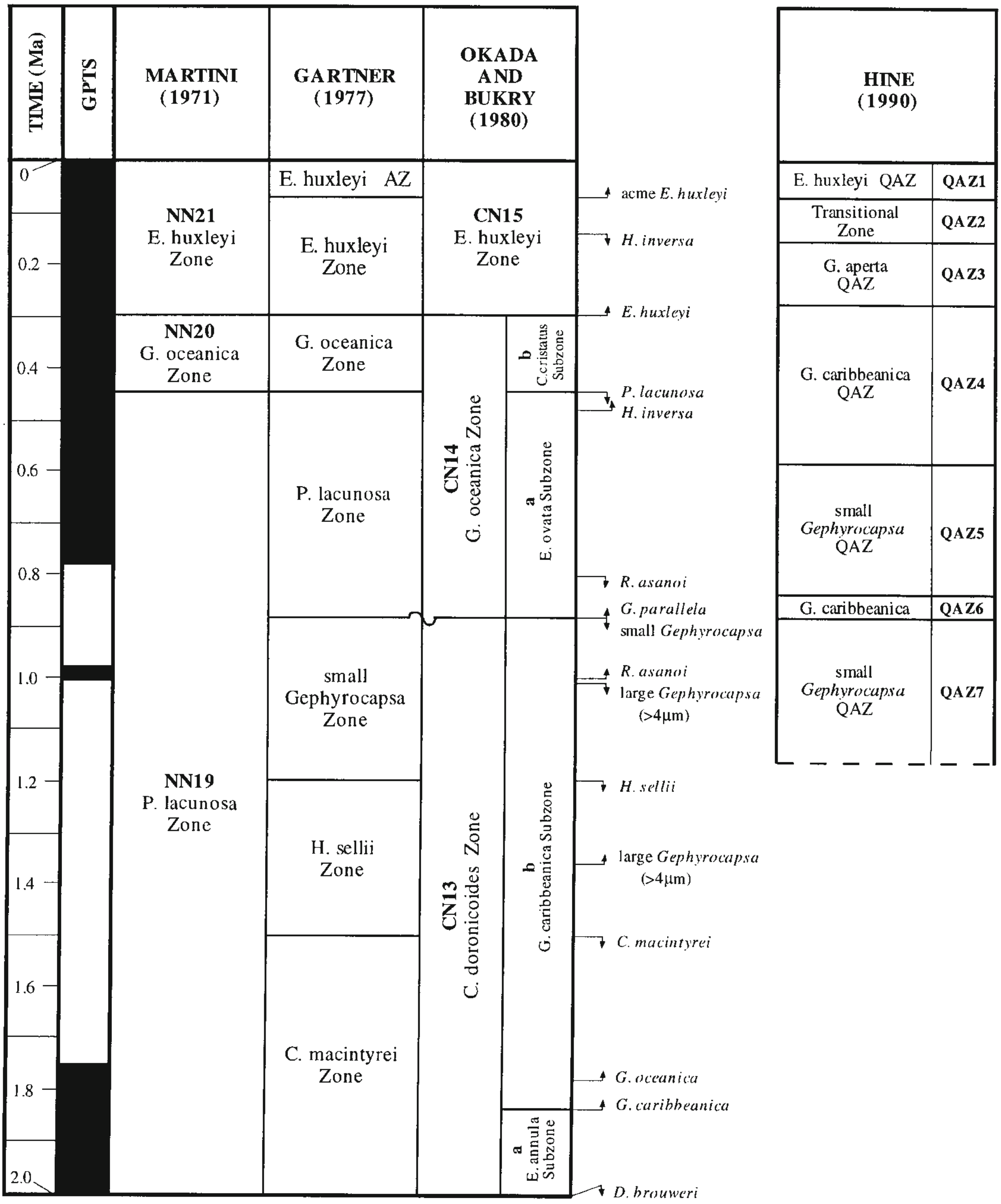


Fig. 9.1 Comparison of selected Quaternary nannofossil zonation schemes. GPTS = Geomagnetic Polarity Time-scale (after Cande and Kent, 1992), QAZ = Quaternary Acme Zone.

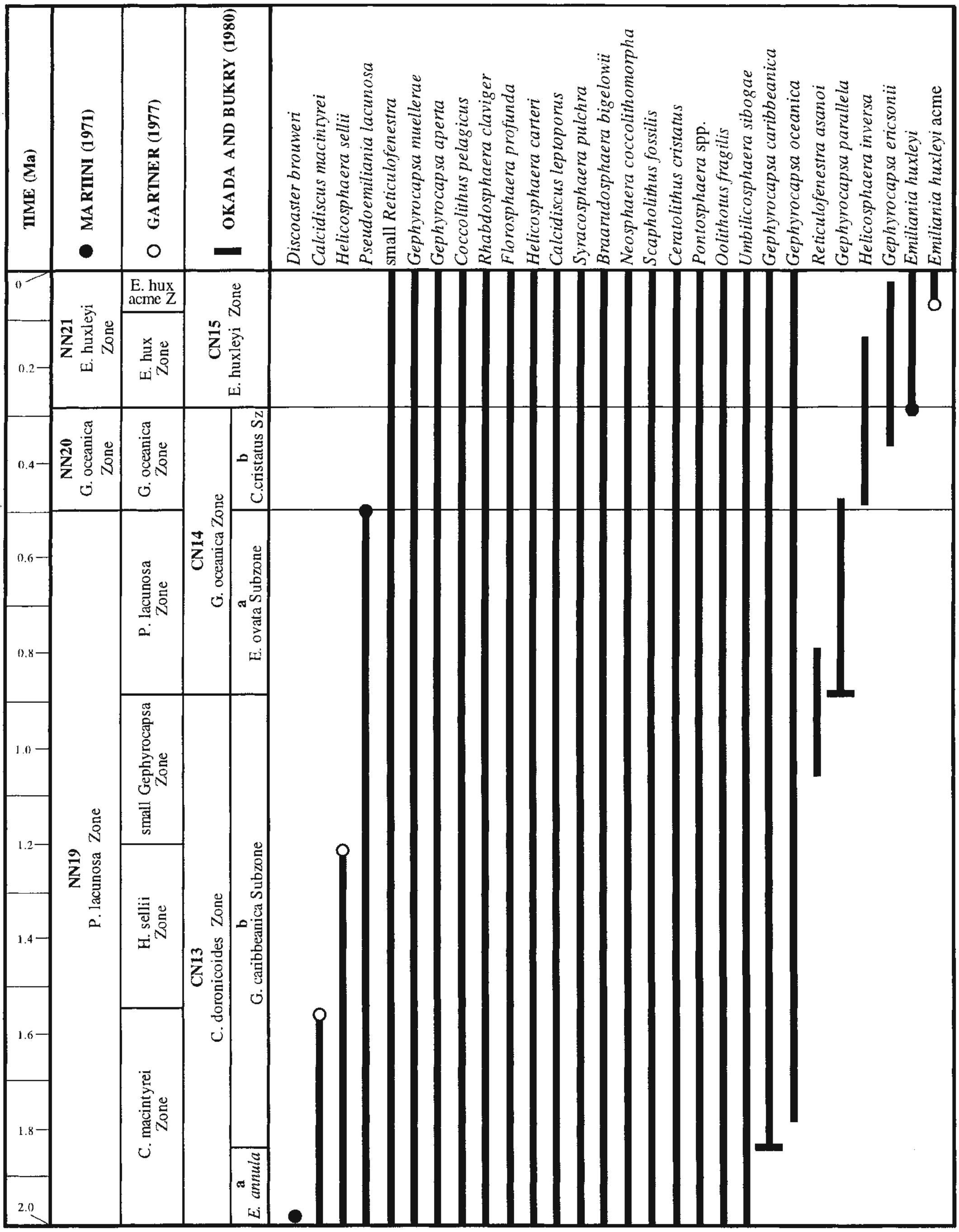


Fig. 9.2 Stratigraphic distribution of selected Quaternary calcareous nannofossils.

illustrated in Fig. 9.1. These can be combined to form a basic stratigraphy spanning the last 2myr These well established zones are described below in stratigraphic order (oldest to youngest).

NN19 Pseudoemiliania lacunosa Zone

Author. Gartner (1969c).
Definition. LO of *Discoaster brouweri* to the LO of *Pseudoemiliania lacunosa*.
Range. Lower Pleistocene.
Remarks. This zone can be subdivided into four subzones as follows:

Calcidiscus macintyrei Subzone

Author. Bukry (1973a).
Definition. LO of *Discoaster brouweri* to the LO of *Calcidiscus macintyrei*.
Range. Lower Pleistocene.
Remarks. The LO of *D. brouweri* occurs at 2Ma and the LO of *C. macintyrei* occurs at 1.54Ma (Wei and Peleo-Alampay, 1993). The former event consistently occurs above the Olduvai normal magnetic event.

Helicosphaera sellii Subzone

Author. Gartner, 1977.
Definition. LO of *Calcidiscus macintyrei* to the LO of *Helicosphaera sellii*.
Range. Lower Pleistocene.
Remarks. The LO of *H. sellii* was investigated by Backman and Shackleton (1983) who reported this datum to be slightly diachronous (1.37Ma near the equator and 1.22Ma at higher latitudes). Wei and Peleo-Alampay (1993) recalculated the age of this event as 1.46Ma.

Small Gephyrocapsa Subzone

Author. Gartner, 1977.
Definition. LO of *Helicosphaera sellii* to the LO of dominantly small *Gephyrocapsa*.
Range. Lower Pleistocene.
Remarks. *Reticulofenestra asanoi* is restricted to the *P. lacunosa* Zone. Takayama and Sato (1987) and Sato and Takayama (1992) record its FO at 1.06Ma, although reported values for the FO span 15kyr (Wei, 1993). The LO of *R. asanoi* is consistently recorded at 0.8Ma, in oxygen isotope stage 22 (Takayama and Sato, 1987; Matsuoka and Okada, 1989; Hine, 1990; Sato and Takayama, 1992; Wei, 1993).

Pseudoemiliania lacunosa Subzone

Author. Gartner, 1977.
Definition. LO of dominantly small *Gephyrocapsa* to the LO of *Pseudoemiliania lacunosa.*
Range. Lower Pleistocene.
Remarks. According to Takayama and Sato (1987) the FO of *Helicosphaera inversa* occurs at 0.48Ma. This is supported by Hine (1990) who records this event in oxygen isotope stages 12 and 13. The absence of *H. inversa* from sites above 45°N in the Atlantic was attributed to the temperature sensitive nature of this species (Takayama and Sato, 1987).

NN20 Gephyrocapsa oceanica Zone

Author. (Boudreaux and Hay, 1967) Gartner (1969c).
Definition. LO of *Pseudoemiliania lacunosa* to the FO of *Emiliania huxleyi*.
Range. Upper Pleistocene.
Remarks. The LO of *P. lacunosa* was considered a synchronous event by Berggren *et al.* (1980), consistently occurring in oxygen isotope stage 12, at 0.47Ma. According to Hine (1990), this event occurs at 0.443Ma in the NE Atlantic, using the time-scale of Berggren *et al.* (1985), which equates to mid-oxygen isotope stage 12. Wei and Peleo-Alampay (1993) recalculated the age of this event as 0.506Ma.

NN21 Emiliania huxleyi Zone

Author. Boudreaux and Hay (1967).
Definition. Interval above the FO of *Emiliania huxleyi.*
Range. Upper Pleistocene–Holocene.
Remarks. Thierstein *et al.* (1977) concluded that the FO of *E. huxleyi* was a synchronous event, occurring at 0.268Ma, in oxygen isotope stage 8, based on data from a global array of cores. Hine (1990) recorded the FO of *E. huxleyi* in upper oxygen-isotope stage 8. It is a slightly time-transgressive event occurring in progressively younger sediments from north to south in the NE Atlantic, but with an average age of 0.291Ma. The event duration is seen to span 30kyr, or the equivalent of half of isotope stage 8. Wei and Peleo-Alampay (1993) recalculated the age of this event as 0.294Ma.

Helicosphaera inversa became extinct in the middle of the *E. huxleyi* Zone. According to Takayama and Sato (1987) this event occurs at

150ka. Hine (1990) suggested this event to be slightly time transgressive (over 47kyr) with an average age of 140ka, occurring within oxygen isotope stages 5 and 6.

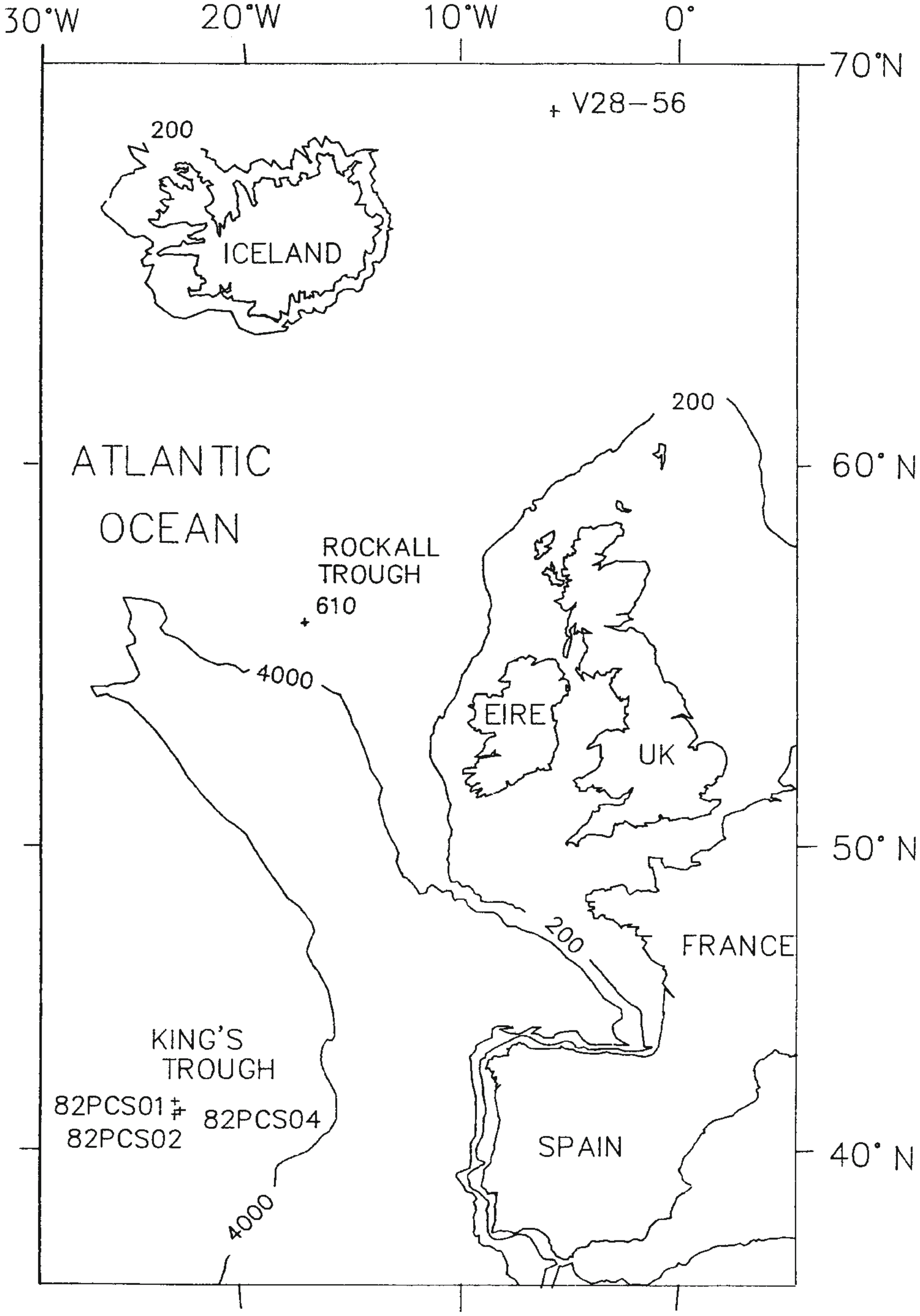
Emiliania huxleyi Acme Zone
Author. Gartner and Emiliani (1976).
Definition. Interval above the dominance reversal to *Emiliania huxleyi* from large *Gephyrocapsa*.
Range. Upper Pleistocene–Holocene.
Remarks. This zone is equivalent to the upper part of NN21. Thierstein *et al.* (1977) showed this event to be diachronous between 85ka in low latitudes, and 73ka in transitional waters, restricting this event to oxygen isotope stage 5. Hine (1990) recorded this event at dates as young as 62ka in the N Atlantic (49°N), extending this event into oxygen isotope stage 4. Gard (1986, 1989) dated this dominance reversal at 61ka in the high latitude N Atlantic. The Acme Zone of *E. huxleyi* continues to the present day.

9.4.2 Acme intervals

The acme of *E. huxleyi* is preceded by several acme events of the Noelaerhabdaceae. Case histories of two N Atlantic sites are outlined below in order to highlight this sequence of events, firstly from the Rockall Trough and secondly from the Kings Trough.

(a) Rockall Trough
Site 610, drilled by the DSDP during Leg 94 (Ruddiman, Kidd *et al.*, 1987), is one of the closest drill sites to the UK which shows a complete Quaternary sequence with abundant calcareous nannofossils. The site was drilled on the western side of the Rockall Trough (53°13.30'N; 18°53.21'W) below the present day boundary of the subpolar and subtropical gyres (Fig. 9.3). The sediments consist of calcareous oozes which have a characteristic banding due to variation in carbonate content developed in response to glacial-interglacial cycles (Ruddiman, Kidd *et al.*, 1987). Some short-duration, barren intervals are present at this site, particularly in the upper part of the sequence, representing advances in the polar front and deposition of ice-rafted detritus. Figure 9.4 shows the succession of acme intervals from Hole 610B (Hine, 1990). Within zone NN21 (oxygen isotope stages 1–8), three intervals are recognized: the acme of *E. huxleyi,* a transitional interval, and the acme of *Gephyrocapsa aperta*. At high to mid latitudes, the transitional interval is dominated by *Gephyrocapsa muellerae*. The acme of *G. aperta* is preceded by an acme of *Gephyrocapsa caribbeanica*. This interval is equivalent to zone NN20 and the top of NN19 and spans oxygen isotope stages 8 to 15. Below this is an interval dominated by small *Gephyrocapsa* (*G. aperta*, small forms of *G. caribbeanica* and other small *Gephyrocapsa* spp.). This interval is equivalent to part of NN19 and spans oxygen isotope stages 15 to 25.

(b) Kings Trough
The area to the south of Kings Trough, at 42°N in the N Atlantic (Fig. 9.3), has remained south of the polar front throughout the Quaternary, and consequently sediment cores show no coccolith-barren intervals. The flora from the last 0.4myr was described by Weaver (1983) and Weaver *in* Kidd *et al.* (1983) and shows essentially the same sequence of acme intervals as Site 610 (Fig. 9.5). Kidd *et al.* (1983) used data from eight gravity and three piston cores, all of which consisted of calcareous oozes and marls, representing alternations between glacial and interglacial conditions. Individual glacials and interglacials have been identified from core 82PCS01 by oxygen isotope stratigraphy, and this has been used to provide an independently dated, high-resolution stratigraphic framework for the cores. Within zone NN21 the acmes of *E. huxleyi* and *G. aperta* are easily recognized and are separated by an interval with abundant *G. muellerae* and *G. aperta* (Fig. 9.5). In this interval, from isotope stage 4 to the upper half of stage 5, and in mid-stage 6, *G. muellerae* is the dominant species. The lower half of stage 5 and the upper half of stage 6 are dominated by *G. aperta*. The acme of *G. aperta* extends through the lower part of stage 6, through stage 7 and into the top of stage 8, below which *G. caribbeanica* becomes dominant. Zone NN20 is dominated by *G. caribbeanica*. This sequence is the same in each core and Fig. 9.5 shows the excellent correlation which can be obtained by using acme intervals. It should be noted on this figure that the acmes cross oxygen isotope stage boundaries suggesting that these floral successions were little


30°W
20°W
10°W
0°
70°N
60° N
50° N
40° N
V28–56
200
ICELAND
200
ATLANTIC
OCEAN
ROCKALL
TROUGH
610
4000
EIRE
UK
200
FRANCE
KING'S
TROUGH
82PCS01
82PCS02
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4000
SPAIN

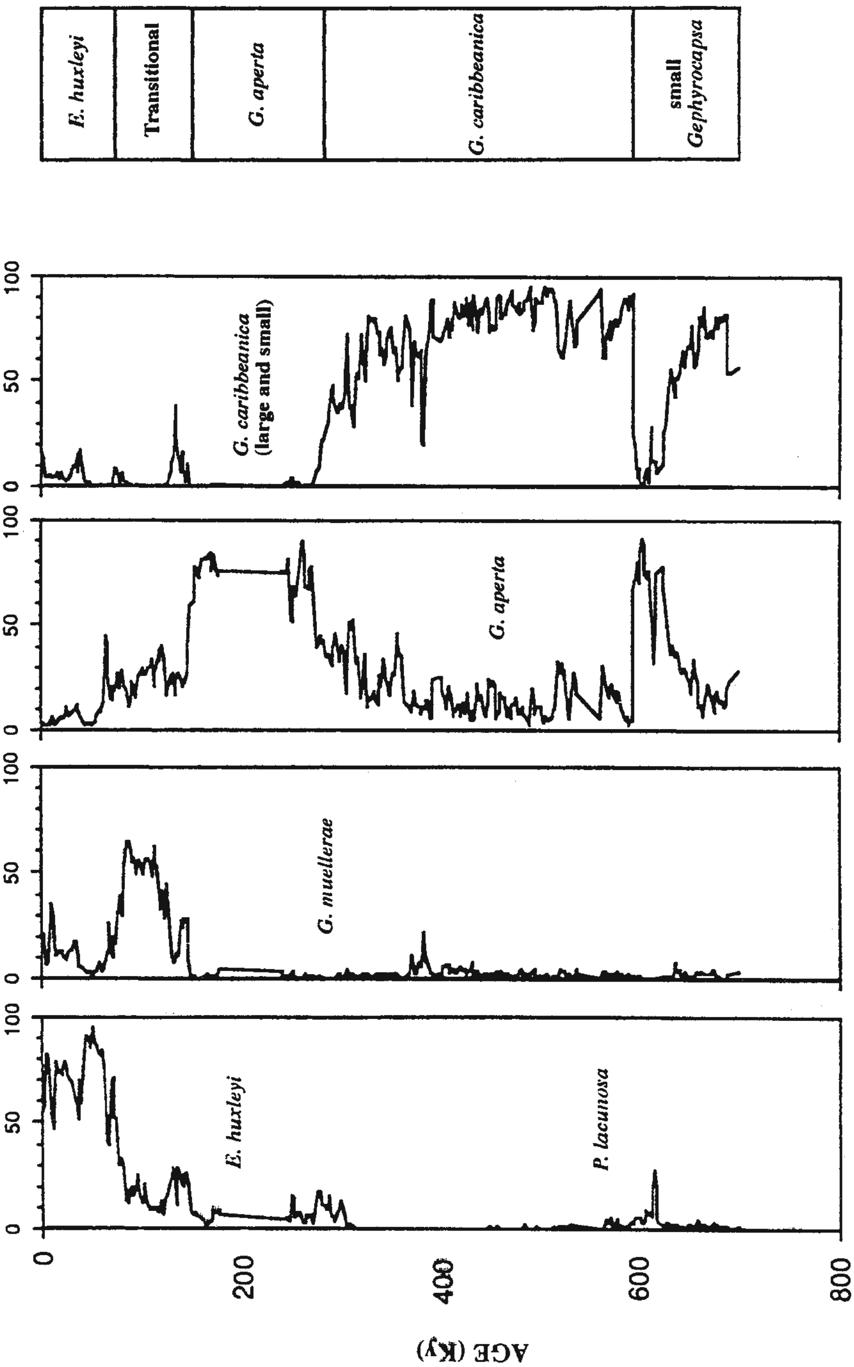


Fig. 9.4 Acme intervals determined from DSDP Site 610 (Hole 610B). Graphs refer to percentage relative abundance of nannoplankton species. The time-scale is derived from linear interpolation of sample ages between the core top and the Brunhes/Matuyama boundary at 0.73Ma (Berggren *et al.*, 1985).

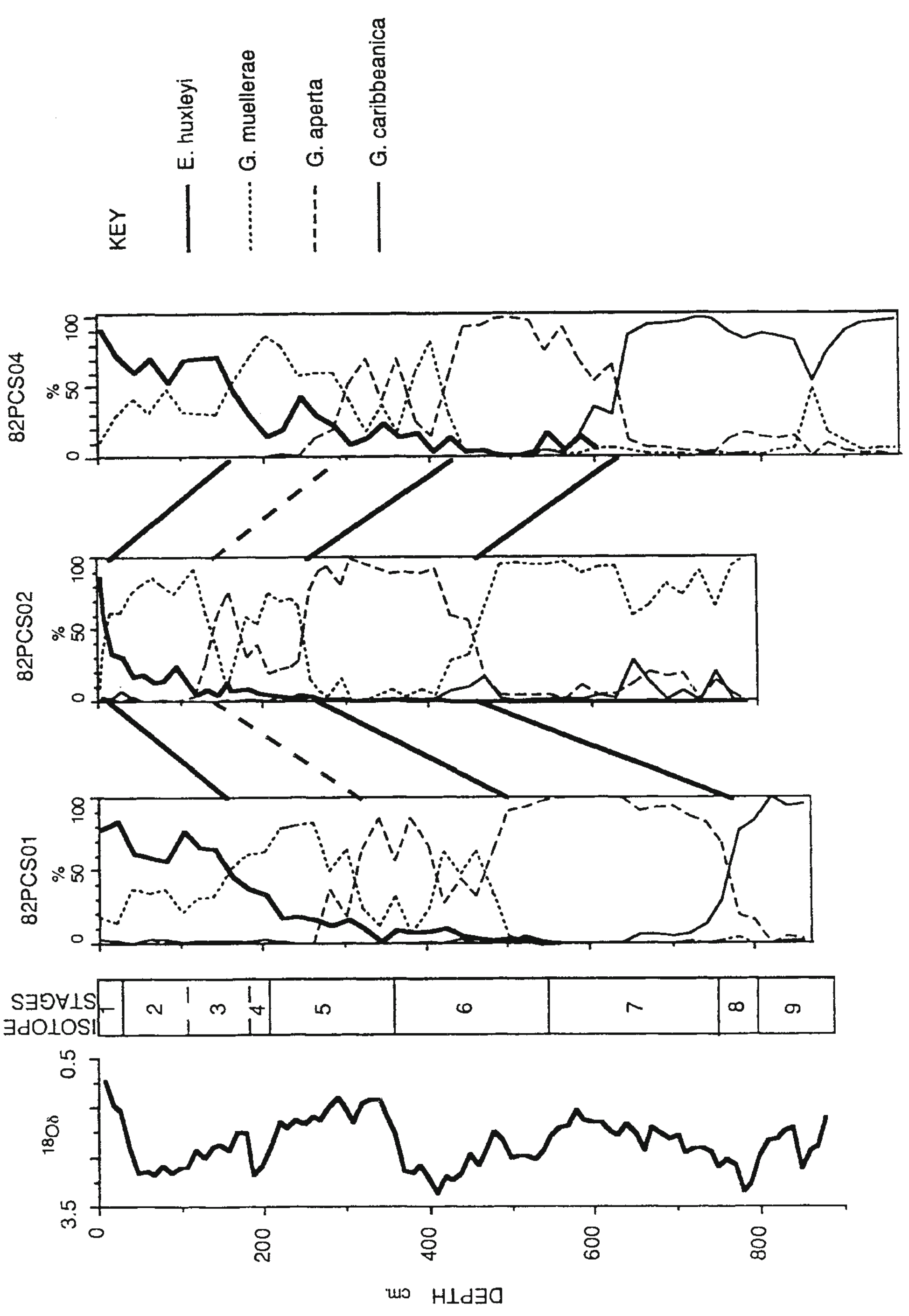


Fig. 9.5 Comparison of acme intervals in three piston cores from the King's Trough flank. The oxygen isotope curve is derived from measurements of the planktonic foraminifera *Globigerinoides bulloides* in Core 82PĆSO1.

affected by temperature; e.g. the *E. huxleyi* acme, here developed in isotope stage 4, lasted to the present day through both the last ice age and the Holocene.

9.4.3 Summary of acme intervals

Common elements from these studies, together with those of Pujos-Lamy (1977b) and Bréhéret (1978), can be combined, resulting in the seven acme intervals described below. They are described in stratigraphic order with reference to the isotope stratigraphy of Imbrie *et al.* (1984).

QAZ7 Small Gephyrocapsa Acme Zone
An acme interval dominated by small *Gephyrocapsa*. This interval is equivalent, at least in part, to the Small *Gephyrocapsa* Zone of Gartner (1977). The base of this acme zone was not encountered by Hine (1990) although she recorded it through oxygen isotope stages 41 to lower stage 28. The Jaramillo magnetic event is recorded in this interval. The top of the acme zone is marked by the reversal in dominance from small *Gephyrocapsa* to *Gephyrocapsa caribbeanica*.

QAZ6 Gephyrocapsa caribbeanica Acme Zone
An acme interval dominated by *G. caribbeanica*. This interval spans the upper part of isotope stage 28 to the lower part of isotope stage 25. The top of the acme zone is marked by the reversal in dominance from *G. caribbeanica* to small *Gephyrocapsa*. The base of Chron C1n (Brunhes) is recorded in this interval.

QAZ5 Small Gephyrocapsa Acme Zone
An acme interval dominated by small *Gephyrocapsa*, mainly *Gephyrocapsa aperta* and small specimens of *G. caribbeanica*. The top of the acme zone is marked by the reversal in dominance from small *Gephyrocapsa* back to *G. caribbeanica*. This interval includes the upper part of oxygen isotope stage 25 to the lower part of oxygen isotope stage 15.

QAZ4 Gephyrocapsa caribbeanica Acme Zone
An acme interval dominated by *G. caribbeanica*. The top of this acme zone is marked by the reversal in dominance from *G. caribbeanica* to *G. aperta*. The zone spans the upper part of oxygen isotope stage 15 to the lower part of oxygen isotope stage 8 (Hine, 1990). This interval can be distinguished from the older interval QAZ6, which was similarly dominated by *G. caribbeanica*, by the absence of *Reticulofenestra asanoi* which has its LO in the lower part of QAZ5.

Pujos and Giraudeau (1993) similarly record the acme of 'closed' *Gephyrocapsa* in oxygen isotope stages 13, 11, 9 and event 8.5. In low latitudes, *G. oceanica* and *G. margerelii* may increase in abundance at the expense of *G. caribbeanica* (Matsuoka and Okada, 1989, 1990; Su Xin, 1995).

QAZ3 Gephyrocapsa aperta Acme Zone
An interval dominated by *G. aperta*. The top of this acme zone is defined by the reduction in abundance of *G. aperta* to less than 90% of the *Gephyrocapsa*s. The zone spans the top of oxygen isotope stage 8, all of stage 7 and the lower part of oxygen isotope stage 6. This interval can be distinguished from the older interval QAZ5, also dominated by small *Gephyrocapsa*, by the absence of *P. lacunosa* which has its LO in QAZ4.

Verbeek (1990) similarly records an acme interval of small *Gephyrocapsa* (NAN3a) starting in isotope stage 8. He uses the FO of *E. huxleyi* to mark the upper boundary of this interval. Pujos and Giraudeau (1993) record the acme of 'small' *Gephyrocapsa* in oxygen isotope stage 7 and event 6.5.

QAZ2 Transitional Zone
An acme interval dominated primarily by *Gephyrocapsa muellerae*. At high latitudes *G. muellerae* tends to dominate the nannoflora, but at lower latitudes other noelaerhabdaceans (including *G. oceanica* and *G. margerelii*) make up a significant percentage of the total nannoflora (Hine, 1990). Consequently this zone is referred to as a 'transitional' interval between the *G. aperta* interval (QAZ3) and the *E. huxleyi* acme interval (QAZ1). The top of the interval is marked by the increase in *E. huxleyi* and decrease in abundance of all other placoliths, in particular *G. muellerae*. This acme interval occupies the upper part of oxygen isotope stage 6, all of stage 5 and the lower part of isotope stage 4.

Pujos and Giraudeau (1993) record the acme of 'open' *Gephyrocapsa* in oxygen isotope stages 6.5 and 5.

QAZ1 Emiliania huxleyi Acme Zone
An acme interval dominated by *E. huxleyi*. This acme interval began in the upper part of oxygen isotope stage 4 and continues to the present day.

Pujos and Giraudeau (1993) recorded the acme of 'open' *Gephyrocapsa* together with *E. huxleyi* in oxygen isotope stage 3.

In the high latitude Atlantic and Norwegian Sea, Lower Holocene assemblages are characterized by an abundance peak of *Coccolithus pelagicus*. This abundance peak begins at 10ka, and often accounts for more than 60% of the nannoflora (Gard, 1989; Baumann and Matthiessen 1992).

There is, therefore, an almost continuous succession of acme-intervals of the Noelaerhabdaceae through the last 1.2myr, with each acme lasting an average of 170kyr, although some of these, e.g. QAZ3, can be much shorter. These acmes are easily recognizable and, in combination with FO and LO information, can be clearly distinguished from each other. By comparison with oxygen isotope data they have been shown to be synchronous in terms of a single isotope stage (Hine, 1990), giving reliable correlation throughout the NE Atlantic.

The zones and acme intervals outlined above can be found in open ocean settings which have remained south of the polar front in the N Atlantic Ocean throughout the Quaternary. More extensive global application has been demonstrated by Pujos and Giraudeau (1993) who recorded a similar sequence of acme events over the last 0.5Ma from a variety of climatic zones from the Atlantic and Pacific Oceans. Matsuoka and Okada (1989, 1990) recorded six assemblages (A to F) from the tropical Indian Ocean. These divisions do not correlate with the acme intervals outlined above, however, re-examination of their data enables the identification of the acme intervals outlined above. The main difference is the predominance of *G. oceanica* and *Gephyrocapsa omega* in QAZ4 and QAZ6 in the tropical Indian Ocean and subtropical NW Pacific Ocean, as opposed to *G. caribbeanica* in other regions. However, the same general pattern of small and large *Gephyrocapsa* acme zones appears to be consistent.

Most calcareous nannoplankton do not thrive in very cold or fresh water and thus advances in the polar front during glacial episodes results in horizons barren of calcareous nannoplankton (CLIMAP, 1976, 1981). Gard (1986, 1988) investigated sites from the Norwegian and Arctic Seas, a summary of which is presented below.

9.4.4 Norwegian and Arctic Seas

Calcareous nannofossils from the high latitude N Atlantic Ocean, Norwegian and Arctic Seas have been investigated by Gard (1986, 1988) (Fig. 9.3). In these areas, barren intervals and intervals with reduced numbers of coccoliths are common. The flora is also less diverse: *E. huxleyi* and *Gephyrocapsa* spp. are present, as are *Calcidiscus leptoporus* and *Coccolithus pelagicus*. Other, rarer species include *Helicosphaera carteri* and *Syracosphaera pulchra*. Gard (1988) suggested that the sub-Arctic specimens of *Gephyrocapsa* often represent extreme morphovariants making identification difficult at species level.

Gard (1988) used abundance data of the total coccolith flora, as well as the abundance of individual species, and FO and LO data to produce a zonation scheme for the last 524ka (isotope stages 1–13), incorporating 11 zones (Fig. 9.6). These zones show some correlation to the N Atlantic zonations outlined previously but there are significant differences: *G. aperta* is common in isotope stages 8 and 9 at these high latitudes as opposed to lower isotope stage 6 to upper 8 in the open Atlantic; *G. caribbeanica* declines in abundance at the top of stage 13 as opposed to during stage 8 in the open Atlantic; and there is a peak abundance of *G. muellerae* in isotope stage 11 which is not seen in the open Atlantic. These differences presumably reflect the reaction of the flora to much cooler temperatures, the influences of fresh water and of nutrient supply. The isotope curve for core V28-56 used by Gard (1988) for dating these events was however atypical between isotope stages 6 to 9, and so the dating of these events is open to question, and indeed Gard herself suggested the age determinations of events older than 119ka were tentative. However, the stratigraphy of Gard, characterized by numerous barren horizons, appears useful for sequences north of 65°N. South of the Norwegian Sea the open ocean stratigraphy outlined in Fig. 9.1 should be more applicable.

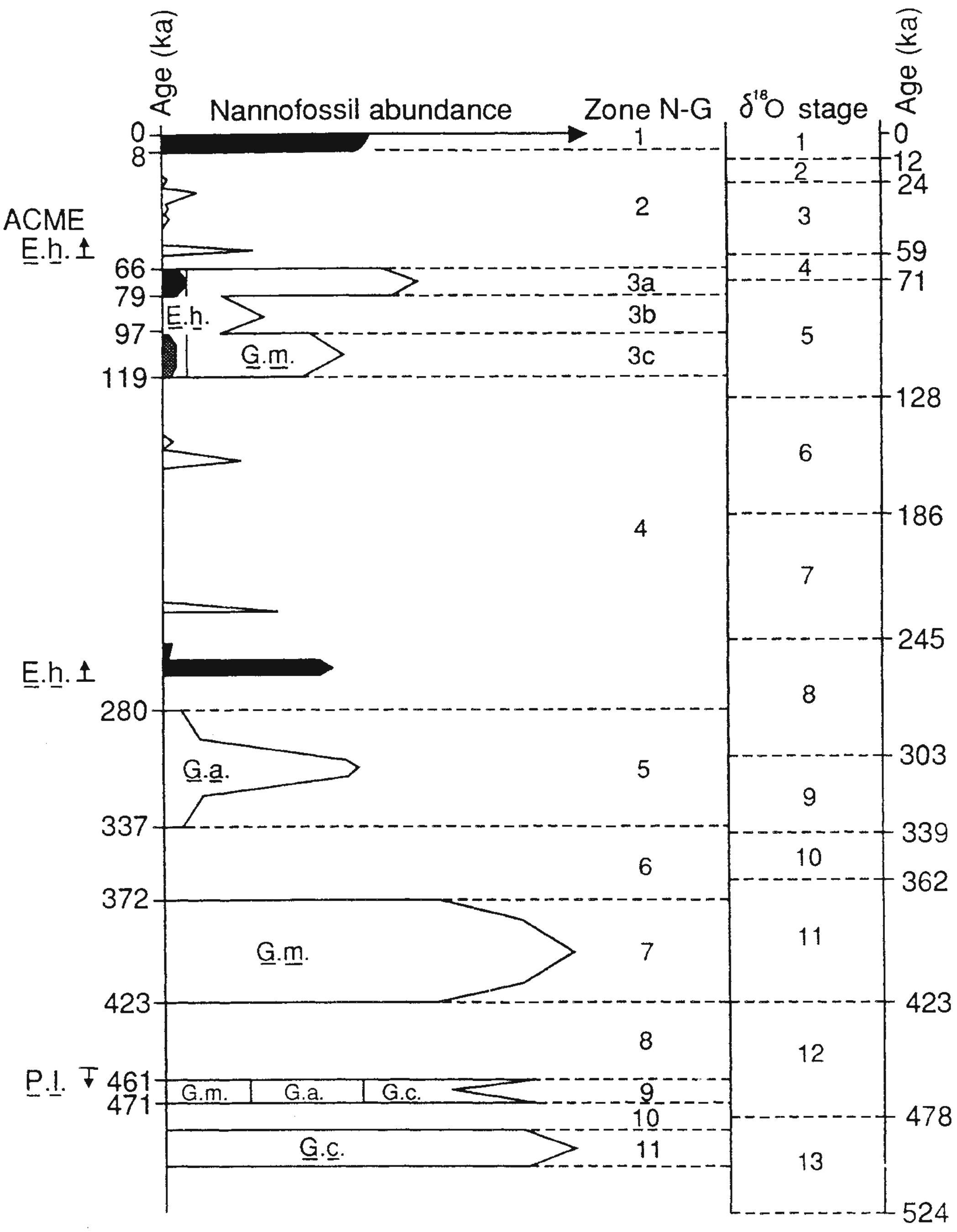


Fig. 9.6 Nannofossil zonation for high latitudes (after Gard, 1988). Black areas represent *Coccolithus pelagicus* and *Emiliania huxleyi* (E. h) together at 0–8 and 66–79 and *C. pelagicus* alone at 260ka; white areas represent placoliths >5μm (*E. huxleyi* and/or *Gephyrocapsa muellerae* (G.m) and/or *Gephyrocapsa aperta* (G.a) and/or *Gephyrocapsa carribeanica* (G.c)) and stippled areas *Calcidiscus leptoporus*; P.l = *Pseudoemiliania lacunosa*. N-G = Norwegian and Greenland Seas.

9.5 CONCLUSIONS

Calcareous nannofossils provide a high-resolution stratigraphy for the Quaternary based on a series of FOs, LOs and acme zones. Many of the datum events have been investigated by reference to oxygen isotope stratigraphy enabling the timing and duration of these events to be established. The resulting calcareous nannoplankton stratigraphy provides resolutions in the order of a few tens of thousands of years for latitudes below 65°N. When the calcareous nannoplankton stratigraphy is used in conjunction with oxygen isotope data then the degree of resolution can be refined still further. The acme zones represent intervals during which a single species dominated the nannoflora and appear independent of Quaternary climate change as demonstrated by their persistence throughout both warm and cold intervals. However, north of about 65°N the stratigraphic sequence of events is interrupted by numerous barren intervals reflecting periods of ice cover or suppressed productivity during deglaciation.

9.6 ATLAS OF SPECIES

Selected Quaternary calcareous nannofossils are listed and illustrated in Plates 9.1 and 9.2. Taxonomic notes are included for species of the Noelaerhabdaceae.

ACKNOWLEDGEMENTS

NH wishes to thank Conoco (UK) Ltd for their support. PPEW was supported by the European Commission on Marine Science and Technology (MAST II) programme, 'Sediment Transport on European Atlantic Margins (STEAM)', grant MAS2-CT94-0083.

Plate 9.1

Light micrographs. All images were taken in XPL and are enlarged equally (scale bar = 10µm). All samples from DSDP Leg 94, Sites 607 (NE Atlantic Ocean, 41°00.07'N;32°57.44'W); 610B (NE Atlantic Ocean, 53°13.30'N; 18°53.21'W); 658B (NE Atlantic Ocean, 20°44.95'N;18°4.85'W); 659C (NE Atlantic Ocean, 18°04.63'N; 21°01.57'W); 663B (Equatorial Atlantic Ocean, 01°11.87'S;11°52.71'W).

Fig. 1. ***Emiliania huxleyi*** (Lohmann, 1902) Hay and Mohler *in* Hay *et al.*, 1967. 658B-4-5, 34–36cm. Range: NN21.

Figs 2–3. ***Gephyrocapsa ericsonii*** McIntyre and Bé, 1967. 658B-3-6, 90–92cm.

Fig. 4. ***Gephyrocapsa aperta*** Kamptner, 1963. 659C-2-4, 120–121cm.

Fig. 5. ***Gephyrocapsa sinuosa*** Hay and Beaudry, 1973. 663B-3-4, 30–32 cm. Small (1.4–3.0µm) elliptical placolith with a distally serrated outer rim. The open central-area is spanned by a broad bridge at 43–58° to the long axis, which is responsible for the distinctive S-shaped interference figure. Range: NN15–NN21.

Figs 6–7. ***Gephyrocapsa muellerae*** Bréhéret, 1978. 6, 658B-4-5, 34–36cm; 7, 659C-2-4, 120–121cm.

Figs 8–9. ***Gephyrocapsa caribbeanica*** Boudreaux and Hay, 1967. 8, 663B-3-4, 30–32cm; 9, 663B-3-3, 30–32cm.

Figs 10, 15. ***Reticulofenestra productella*** (Bukry, 1975) Gallagher, 1989. 663B-3-3, 30–32 cm. Elliptical placolith (3.5–4.5µm) with a serrated outer edge. The central-area is closed and marked distally by a longitudinal slit producing a distinctive swastika-shaped interference figure. Range: NN10–NN21.

Figs 11–12. ***Gephyrocapsa parallela*** Hay and Beaudry, 1973. 11, 663B-3-3, 30–32cm; 12, 659C-1-1, 50–51cm.

Figs 13–14. ***Gephyrocapsa oceanica*** Kamptner, 1943. 13, 663B-3-4, 30–32cm; 14, 658B-4-5, 34–36 cm.

Fig. 16. ***Coccolithus pelagicus*** (Wallich, 1877) Schiller, 1930. 658B-4-5, 34–36cm.

Figs 17–18. ***Pseudoemiliania lacunosa*** (Kamptner, 1963) Gartner, 1969. 17, 610B-5-3, 21–22cm; 18, 663B-3-3, 30–32cm.

Figs 19–20. ***Reticulofenestra asanoi*** Sato and Takayama, 1992. 19, 607-5-2, 119–120cm; 20, 659C-3-7, 40–41cm.

Fig. 21, 26. ***Calcidiscus leptoporus*** (Murray and Blackman, 1898) Loeblich and Tappan, 1978. 21, 610B-5-3, 21–22cm; 26, 663B-3-4, 30–32cm.

Fig. 22. ***Helicosphaera inversa*** (Gartner, 1980) Theodoridis, 1984. 663B-2-2, 90–91cm.

Fig. 23. ***Helicosphaera carteri* var. *wallichii*** (Lohmann, 1902) Theodoridis, 1984. 659C-1- 5, 10–11cm.

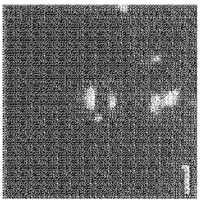
Fig. 24. ***Helicosphaera carteri*** (Wallich, 1877) Kamptner, 1954. 663B-3-4, 30–32cm.

Fig. 25. ***Ceratolithus telesmus*** Norris, 1965. 663B-3-4, 30–32cm.

Fig. 27. ***Umbilicosphaera sibogae*** var. ***foliosa*** (Kamptner, 1963) Okada and McIntyre, 1977. 663B-3-4, 30–32cm.

Fig. 28. ***Syracosphaera histrica*** Kamptner, 1941. 659C-1-1, 50–51cm.

Fig. 29. ***Rhabdosphaera clavigeri*** Murray and Blackman, 1898. 658B-4-5, 34–36cm.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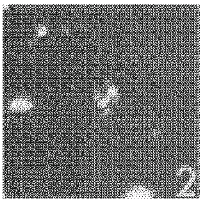
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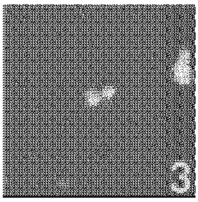
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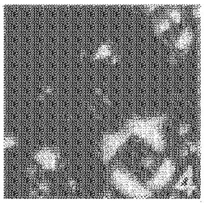
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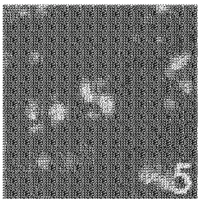
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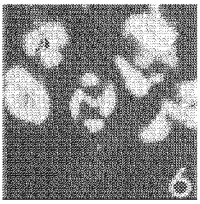
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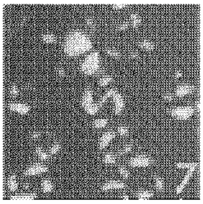
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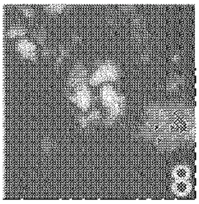
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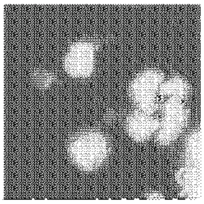
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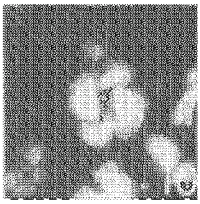
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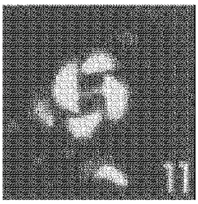
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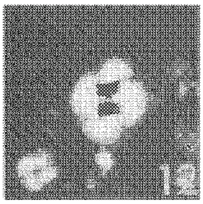
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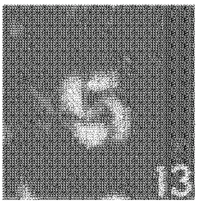
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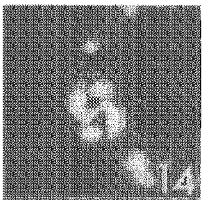
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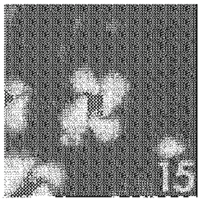
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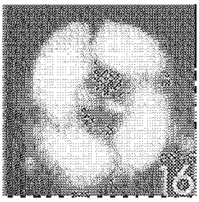
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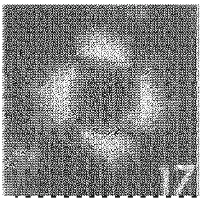
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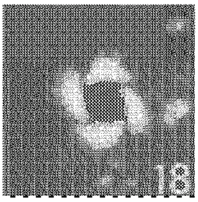
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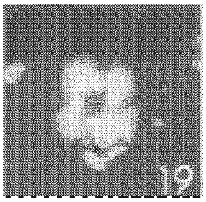
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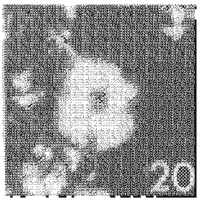
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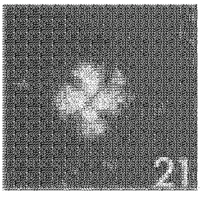
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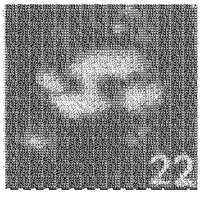
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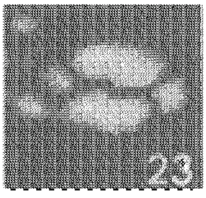
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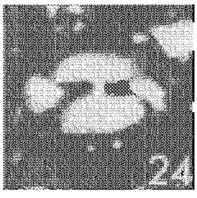
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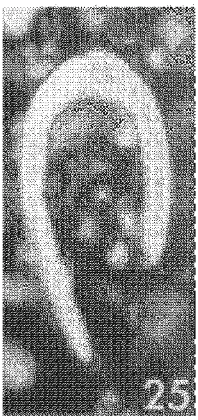
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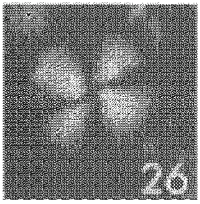
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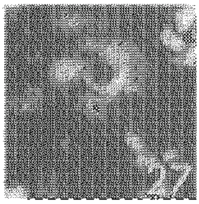
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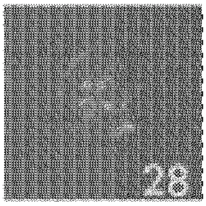
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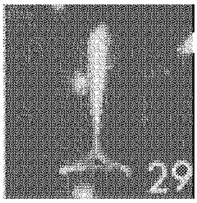
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Plate 9.2

SEM micrographs. All samples from DSDP Leg 94, Sites 609 (NE Atlantic Ocean, 49°52.67'N; 24°14.29'W) and 659C (NE Atlantic Ocean, 18°04.63'N;21°01.57'W). Magnification x20 000 unless otherwise indicated by scale bar which equals 1 µm.

Order PRINSIALES Young and Bown, 1997b
Family NOELAERHABDACEAE Jerkovic, 1970 emend. Young and Bown, 1997b
Fig. 1. ***Emiliania huxleyi*** (Lohmann, 1902) Hay and Mohler *in* Hay *et al*., 1967. Distal view, 609-1-2, 46–47cm. Distal shield elements separated by slits resulting in I-shaped elements. Range: NN21.

Fig. 2. ***Gephyrocapsa ericsonii*** McIntyre and Bé, 1967. Distal view, 609-5-3, 31–32cm. Small (1.4–2.8µm), elliptical placolith, open central-area spanned by a broad, strongly birefringent bridge aligned at 10–45° to the long axis. Range: NN20–NN21.

Fig. 3. ***Gephyrocapsa aperta*** Kamptner, 1963. Distal view, 609-5-3, 31–32cm. Small (1.1–2.6µm), elliptical placolith, open central-area spanned by a narrow bridge aligned at 20–50° to the long axis. Range: NN15–NN21.

Fig. 4. ***Gephyrocapsa parallela*** Hay and Beaudry, 1973. Distal view, 609-6-4, 31–32cm. Large (4.0–6.4µm), circular to sub-circular placolith, open central-area spanned by a bridge aligned at 60–90° to the long axis. Range: NN19–NN21.

Fig. 5. ***Gephyrocapsa oceanica*** Kamptner, 1943. Distal view, 659C-1-7, 0–1cm. Large (2.4–6.0µm), circular to sub-circular placolith, open central-area spanned by a bridge aligned at 43–70° to the long axis. Range: NN19–NN21.

Fig. 6. ***Gephyrocapsa muellerae*** Bréhéret, 1978. Distal view, 609-1-2, 96–97cm. Medium-sized (2.7–5.0µm), elliptical placolith, open central-area spanned by a narrow bridge aligned at 5–45° to the long axis. Range: NN19–NN21.

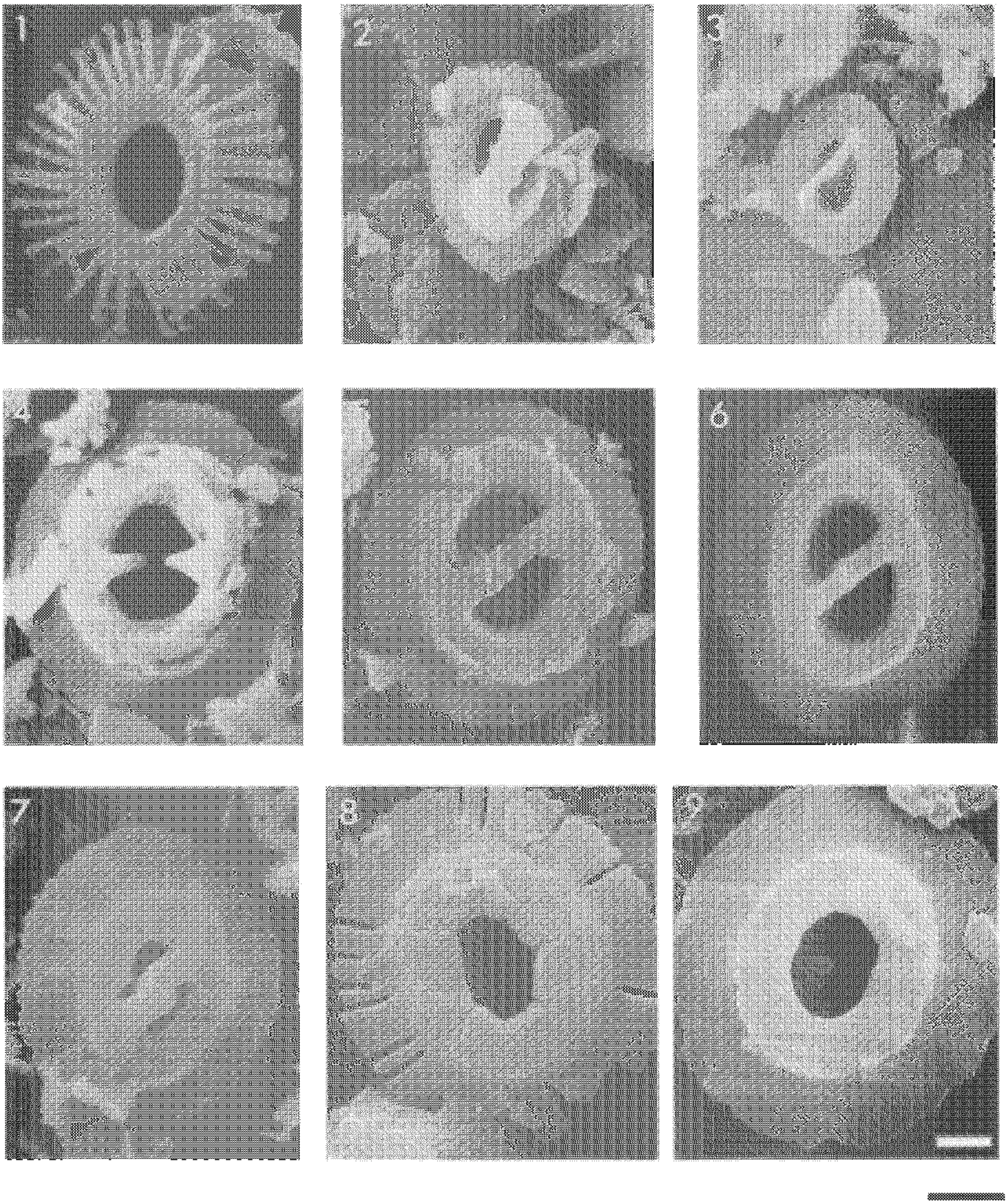
Fig. 7. ***Gephyrocapsa caribbeanica*** Boudreaux and Hay, 1967. Distal view, 609-2-5, 1–2cm. Circular to sub-circular placolith with a bridge partially or completely blocking the central-area so that the placolith produces the characteristic interference figure of a curved swastika. Length ranges from 1.8–6.0µm but may be divided arbitrarily at 2.6µm into small and large forms which have biostratigraphic significance. Range: NN19–NN21.

Not figured. *Gephyrocapsa margerelii* Bréhéret, 1978. Medium-sized (2.7–4.8µm), elliptical placolith with a large, open central-area spanned by a narrow bridge aligned at 35–55° to the long axis. Range: ?NN19–NN20.

Not figured. *Gephyrocapsa ornata* Heimdal, 1973. Small (1.4–3.1µm), elliptical placolith with an open central-area spanned by two highly-arched, plate-like elements aligned at 0–20° to the long axis. The central collar has a crown of distally protruding, tooth-like elements. Range: NN21.

Fig. 8. ***Pseudoemiliania lacunosa*** (Kamptner, 1963) Gartner, 1969. Distal view, 609-5-6, 96–97cm. Circular to elliptical placoliths with radial slits developed between some of the distal shield elements. Range: NN15–NN19.

Fig. 9. ***Reticulofenestra asanoi*** Sato and Takayama, 1992. Distal view, 659C-3-6, 100–101cm. Circular to sub-circular placolith (6.5–8µm) with a protruding collar. The central opening is approximately 1/3 the diameter of the placolith and is often spanned proximally by a reticulate net. Range: NN19.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Taxonomic index

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Subject index

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