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Phylogenetic Aspects and Taxonomy of Calcareous Dinoflagellates

Dissertation

zur Erlangung des Doktorgrades der Naturwissenschaften
Fachbereich Geowissenschaften
Universität Bremen

vorgelegt von
Michael Streng
Bremen, 2003

For my father

Tag des Kolloquiums:
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Gutachter:
1. Prof. Dr. H. Willems
2. Prof. Dr. H. Keupp

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1. Prof. Dr. R. Henrich
2. Prof. Dr. J. Bohrmann



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SUMMARY

Calcareous dinoflagellates are known to constitute a significant member of the fossil marine phytoplankton, however, their phylogeny and development since their first appearance is poorly known. Therefore, phylogenetic trends of calcareous dinoflagellates since the Late Triassic have been reconstructed using morphological features of the cysts and the development of calcareous dinoflagellate associations especially during the Cenozoic has been analyzed. Special emphasis has been placed on the relation of significant changes in the associations and major paleoenvironmental changes. The data used for this study has been obtained by the examination of samples from three cores of the Ocean Drilling Project (ODP) and some supporting samples of different localities. The ODP material originates from the eastern Indian Ocean (Leg 122, Site 761, Wombat Plateau), the southern Indian Ocean (Leg 120, Site 747, Kerguelen Plateau), and the eastern Weddell Sea (Leg 113, Site 689, Maud Rise), whereas the first site represents a low latitude position in contrast to the latter two which are from high latitude regions. In addition to the analyzed samples, an extensive evaluation of the taxonomic and stratigraphic data on calcareous dinoflagellates available from literature has been performed.

The archeopyle represents an important characteristic of dinoflagellates, however it generally has been underestimated within the calcareous dinoflagellates. Therefore, a comprehensive review of all fossil species of calcareous dinoflagellates regarding their archeopyle type has been accomplished to reveal potential phylogenetic lineages within this group. The stratigraphic distribution of the recognized archeopyle types evinced a phylogenetic trend that is characterized by an increase of the number of plates involved in the archeopyle. Seven archeopyle types have been distinguished which are accommodated in three categories, i.e., apical, intercalary, and combination archeopyles. The significance of the different archeopyle types and their use as the major characteristic in taxonomy is emphasized. A new concept for the classification of calcareous dinoflagellates which focuses on the different archeopyle types is discussed.

The distribution patterns of calcareous dinoflagellate taxa obtained from the three studied ODP cores show that major paleoenvironmental changes are a substantial factor affecting changes in calcareous dinoflagellate associations. Significant changes occur during the Cretaceous/Tertiary transition (K/T transition), the middle-late Eocene transition, the early Oligocene, and during the Neogene. In contrast to the assemblage changes at the K/T transition which are related to the drastic modifications in the biosphere following the K/T impact event, all other observed shifts correlate with the major steps of the Cenozoic climatic evolution. Besides the modifications due to major paleoenvironmental changes, spatial distributions of distinct taxa evinced to be related to ecological preferences. E.g., depicts the analysis of the regional distribution of the two species of the new genus *Caracomia* that *Caracomia arctica* is restricted to cold waters of both hemispheres, whereas *Caracomia stella* as yet has only been described from warmer environments. Thus, *C. arctica* can be used as a cold water indicator.

In addition to the distribution patterns of the individual taxa and the variations in the abundance of calcareous dinoflagellates, shifts in the stratigraphic distribution of the different archeopyle types have been analyzed for the two cores from the Indian Ocean. Two major groups of archeopyle types have been distinguished, small and large archeopyles. The obtained ratios between small and large archeopyles turned out to be a potential tool for the reconstruction of the large-scale climatic development in high latitudes.

According to the new insights into the systematics of calcareous dinoflagellates obtained by the analysis of the different archeopyle types, various taxonomical rearrangements and emendations became necessary. Thus, the genera *Echinodinella* Keupp, 1980a, *Fuettererella* Kohring, 1993a, *Orthopithonella* Keupp in Keupp and Mutterlose, 1984, and *Pernambugia* Janofske and Karwath in Karwath, 2000 are emended. The genus *Sphaerodinella* Keupp and Versteegh, 1989 became obsolete. The new genus *Caracomia* is proposed and accommodates *C. arctica* (Gilbert and Clark, 1983) n. gen. n. comb., *Caracomia arctica* forma *spinosa* n. gen. n. form, and *C. stella* n. gen. n. sp. Furthermore, the following taxa have been newly combined: *Cervisiella operculata* (Bramlette and Martini, 1964) n. comb., *Fuettererella deflandrei* (Kamptner, 1956) n. comb., *Fuettererella flora* (Fütterer, 1990) n. comb., *Praecalcionellum sulcatum* (Keupp, 1979a) n. comb., and *Praecalcionellum dolium* (Keupp, 1979b) n. comb. Additionally, several new taxa are described: *Calciodinellum clamosum* n. sp., accommodating two subspecies (*Calciodinellum clamosum clamosum* Autonym and *Calciodinellum clamosum latum* n. sp. n. ssp.), *Calciodinellum kerguelensis* n. sp., *Fuettererella belliata* n. sp., and *Pernambugia? patata* n. sp. The formerly as obsolete regarded species *Orthopithonella?*

minuta Fütterer, 1990 and *Pirumella johnstonei* (Bolli, 1974) Lentini and Williams, 1993 are retained as separate taxa. The systematic position of the problematic species *Thoracosphaera? prolata* Bukry and Bramlette, 1969 and its relation to and potential synonymy with *Calciodinellum elongatum* (Hildebrand-Habel et al., 1999) Meier et al., 2002 is discussed in detail.

ZUSAMMENFASSUNG

Kalkige Dinoflagellatenzysten repräsentieren einen wichtigen Bestandteil des fossilen, marinen Phytoplanktons. Ihre Phylogenie und Entwicklung seit ihrem ersten Auftreten in der späten Trias sind allerdings weitgehend unerforscht. Um diese Lücke zu schließen, wurden einerseits phylogenetische Entwicklungslinien kalkiger Dinoflagellaten mit Hilfe morphologischer Merkmale ihrer Zysten rekonstruiert und andererseits die Entwicklung des Formenspektrums und der Assoziationen genauer betrachtet. Besondere Aufmerksamkeit galt den Veränderungen der Zystenvergesellschaftungen in Abhängigkeit von den einschneidenden Klimaschwankungen des Känozoikums. Die Basis dieser Untersuchungen bilden Daten, die aus der Analyse von drei Kernen des *Ocean Drilling Projects* (ODP) und einigen unterstützenden Proben unterschiedlicher Lokalitäten gewonnen wurden. Die ODP-Kernproben stammen aus dem östlichen Indischen Ozean (Leg 122, Site 761, Wombat Plateau), dem südlichen Indischen Ozean (Leg 120, Site 747, Kerguelen Plateau) und aus dem östlichen Weddell Meer (Leg 113, Site 689, Maud Rise), wobei die Proben vom Wombat Plateau die niederen Breiten und die beiden letztgenannten Lokalitäten die hohen Breiten repräsentieren. Zusätzlich zu den Untersuchungen der einzelnen Proben wurden alle verfügbaren Daten zur stratigraphischen Verbreitung und Morphologie der bekannten Taxa aus der vorhandenen Literatur ausgewertet.

Die Archäopyle von Dinoflagellaten repräsentiert ein wichtiges, allerdings innerhalb der kalkigen Dinoflagellatenzysten bislang weitgehend unterschätztes, morphologisches Merkmal. Um phylogenetische Entwicklungslinien innerhalb der kalkigen Dinoflagellaten aufzudecken wurden deshalb die Archäopylentypen aller bekannten Arten genau untersucht. Die stratigraphische Verbreitung der einzelnen Typen zeigt einen deutlichen, evolutiven Trend, der durch die Zunahme der die Archäopyle bildenden Platten gekennzeichnet ist. Sieben unterschiedliche Archäopylentypen konnten unterschieden werden, die zu drei Großgruppen gehören: apikale, interkalare und kombinierte Archäopylen. Die Relevanz dieser unterschiedlichen Archäopylentypen für die Systematik wird verdeutlicht und ihre Anwendung in der Taxonomie empfohlen. Zusätzlich wird ein neues Klassifikationsschema für kalkige Dinoflagellatenzysten diskutiert, das auf den unterschiedlichen Archäopylentypen basiert.

Die aus den Untersuchungen der drei ODP-Kerne gewonnenen Verbreitungsmuster der unterschiedlichen Arten zeigen, daß die globalen Klimaschwankungen des Känozoikums maßgeblich an den Veränderungen der Vergesellschaftungen kalkiger Dinoflagellatenzysten beteiligt sind. Hauptphasen der Veränderungen konzentrieren sich auf bestimmte stratigraphische Bereiche (die Kreide-Tertiär-Grenze, die Mitteleozän-Obereozän-Grenze, das frühe Oligozän und das Neogen). Neben den Veränderungen durch globale Klimaschwankungen konnten auch regionale, ökologische Abhängigkeiten der Zysten erarbeitet werden. So haben zum Beispiel Untersuchungen zur räumlichen Verbreitung der neuen Gattung *Caracomia* unterschiedliche regionale Präferenzen der beiden zugehörigen Arten aufgezeigt. *Caracomia arctica* kommt ausschließlich in den kühlen Gewässern der hohen Breiten vor, wohingegen *Caracomia stella* gemäßigte Breiten bevorzugt. *Caracomia arctica* kann deshalb als Kaltwasseranzeiger gewertet werden.

Zusätzlich zu den Untersuchungen zur stratigraphischen Verbreitung der einzelnen Arten und zur generellen Häufigkeit kalkiger Zysten, wurden zum ersten Mal auch die Veränderungen in bezug auf den vorherrschenden Archäopylentyp an Hand der zwei Kerne aus dem Indischen Ozean untersucht. Dafür wurden die unterschiedlichen Arten in zwei Großgruppen unterteilt: Arten mit kleiner und Arten mit großer Archäopyle. Das für die hohen Breiten gewonnene Verhältnis dieser Archäopylengruppen spiegelt die globale klimatische Entwicklung des untersuchten Zeitraums wider.

Die aus den Untersuchungen der unterschiedlichen Archäopylontypen gewonnenen Erkenntnisse in bezug auf Systematik und Taxonomie, machten einige taxonomische Neuordnungen und Emendierungen unumgänglich. So wurden die Gattungen *Echinodinella* Keupp, 1980a, *Fuettererella* Kohring, 1993a, *Orthopithonella* Keupp in Keupp & Mutterlose, 1984 und *Pernambugia* Janofske & Karwath in Karwath, 2000 emendiert und die Gattung *Sphaerodinella* Keupp & Versteegh, 1989 wurde hinfällig. Die neue Gattung *Caracomia* wurde aufgestellt und beinhaltet *C. arctica* (Gilbert & Clark, 1983) gen. et comb. nov., *Caracomia arctica* forma *spinosa* gen. et forma nov. und *C. stella* gen. et sp. nov. Folgende Arten wurden neu kombiniert: *Cervisiella operculata* (Bramlette & Martini, 1964) comb. nov., *Fuettererella deflandrei* (Kamptner, 1956) comb. nov., *Fuettererella flora* (Fütterer, 1990 comb. nov., *Praealcalcionellum sulcatum* (Keupp, 1979a) comb. nov. und *Praealcalcionellum dolium* (Keupp, 1979b) comb. nov. Weiterhin wurden nachstehende Arten neu beschrieben: *Calciodinellum clamosum* sp. nov. mit zwei Unterarten (*C. clamosum clamosum* Autonym und *C. clamosum latum* sp. et ssp. nov.), *Calciodinellum kerguelensis* sp. nov., *Fuettererella belliata* sp. nov. und *Pernambugia? patata* sp. nov. Die bereits als redundant betrachteten Arten *Orthopithonella? minuta* Fütterer, 1990 und *Pirumella johnstonei* (Bolli, 1974) Lentin & Williams, 1993 werden wieder als eigenständige Arten angesehen. Die Beziehung der problematischen Art *Thoracosphaera? prolata* Bukry & Bramlette, 1969 zu *Calciodinellum elongatum* (Hildebrand-Habel et al., 1999) Meier et al., 2002 wird eingehend diskutiert.

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1 Introduction

PREFACE

In recent years, the increased scientific interest in dinoflagellates has been stimulated by the importance of these organisms as primary producers in the oceans, the recognition that local population explosions of several species are the cause of paralytic shellfish poisoning or massive fish kills, and the demonstration that their cysts are of high biostratigraphic and paleoecological value. Furthermore, it has become apparent that also the calcareous dinoflagellates are an useful tool for the reconstruction of paleoenvironmental conditions, not only for short-term variations during the Late Quaternary, but also for the long-term climatic variations of the Cenozoic era. However, calcareous dinoflagellates still represent a poorly studied group in many respects: the phylogenetic development since their first appearance is barely known; the taxonomic affiliation of many taxa is still a matter of debate, as the applied taxonomic concept lacks consistency and needs revision; studies on long-term evolutionary trends are still scarce and regionally limited. The aim of this study is to clarify major taxonomic inconsistencies of the group and to provide an elaborated concept for the classification of calcareous dinoflagellates. Additionally, new data on the spatial and stratigraphic distribution and diversity of Cenozoic calcareous dinoflagellates is presented and correlated with the major paleoclimatological changes of the Cenozoic, for which a consistent taxonomic concept is indispensable.

DINOFLAGELLATES IN GENERAL

Dinoflagellates (Division Dinoflagellata (Bütschli, 1885) Fensome et al., 1993) are an eukaryotic, predominantly single-celled aquatic group of organisms. Dinoflagellates (subdivision Dinokaryota) have, apart from a few exceptions, an unique and characteristic type of cell nucleus, termed a dinokaryon, which distinguishes the Dinokaryota from all other eukaryotic organisms. Dinoflagellates typically occur as motile cells with two characteristic flagella, a transverse and a longitudinal flagellum which are in most cases ventrally inserted (= dinokont dinoflagellates). The transverse flagellum is ribbon-like running along the outer edge of the motile cell and is typically located in a transverse groove, called the cingulum (Fig. 1). The longitudinal flagellum projects posteriorly with its proximal end usually in a longitudinal furrow, termed the sulcus (Fig. 1). The synchronous movement of both flagella results in the eponymous spirally swimming behavior (Greek $\delta\acute{\iota}\nu\eta$ = dino, meaning vortex, whirl). The cingulum generally divides the cell in an anterior (= epitheca or episome) and in a posterior part (= hypotheca or hyposome). The ventrally situated sulcus roughly divides the cell into right and left halves (Fig. 1). The motile cell is covered by a complex series of membranes termed the amphiesma which includes a layer of so-called amphiesmal vesicles. In many taxa, these vesicles contain cellulosic plates (= thecal plates) which vary interspecifically in thickness and grade of ornamentation. Species having cellulosic plates are called thecate, in contrast to athecate taxa whose vesicles lack thecal plates. The sum of all cellulosic plates which tightly fit together constitutes the theca and generates a distinct tabulation pattern. Neither athecate nor thecate motile cells are known to fossilize.

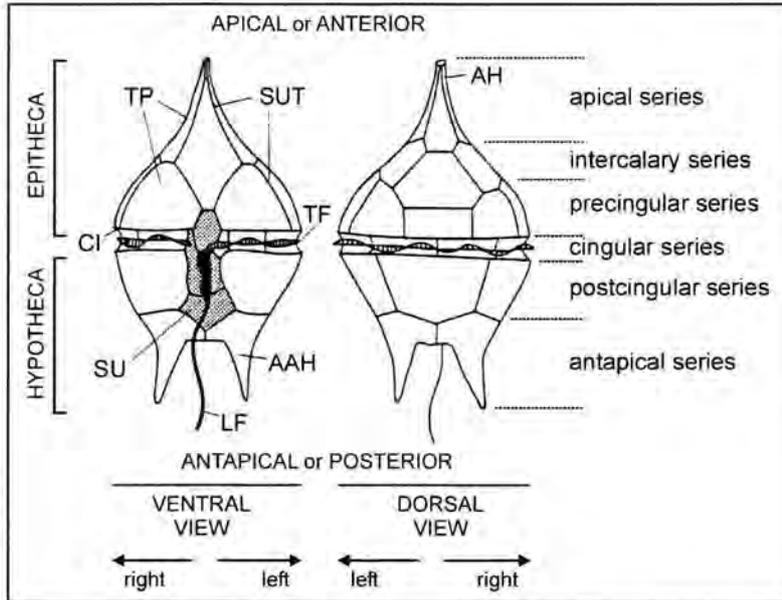


Figure 1. The principal morphologic features of a typical thecate motile cell of a dinokont dinoflagellate (modified after Evitt, 1985). AAH = antapical horn; AH = apical horn; CI = cingulum; LF = longitudinal flagellum; SU = sulcus; SUT = suture between thecal plates; TF = transversal flagellum; TP = thecal plates.

Nutritional strategies of living dinoflagellates are quite diverse, varying from autotrophic/phototrophic (= photosynthetic), heterotrophic/phagotrophic (= ingestion of dissolved or solid organic matter), auxotrophic (autotrophs, unable to synthesize essential nutrients by themselves) to mixotrophic (= heterotrophs bearing chloroplasts). Some dinoflagellates even have more than one strategy (see Gaines and Elbrächter, 1987 for details). Most dinoflagellates live planktonic or benthic, but symbiotic (e.g., as 'zooxanthellae' in reef-building corals) or parasitic forms are also known. Dinoflagellates inhabit most aquatic environments of all climatic regions, ranging from marine to freshwater habitats, and have also been found in snow and interstices of wet sand (see Taylor, 1987). However, most of the taxa are marine and they reach their highest diversity in the shelf areas (Stover et al., 1996). Dinoflagellates constitute a major component of the marine phytoplankton and represent important primary producers in the oceans.

LIFE CYCLE OF DINOFLAGELLATES

The life cycles of living dinoflagellate taxa are evinced to be extremely diverse and multi-faceted ranging from simple to highly complex. The general life cycle normally includes a simple asexual (= vegetative) reproduction of the haploid motile cell through mitosis, meaning the division of one cell into two daughter cells (binary fission). However, more intricate life cycles occur in many free living forms which are characterized by a non-motile phase during which the cell is enclosed in a cyst. (Fig. 2). The cyst walls consist either of an organic polymer called dinosporin (organic-walled dinoflagellate cysts), calcite (calcareous dinoflagellate cysts), silica (siliceous dinoflagellate cysts) or, like the motile cells, of cellulose. With the exception of the latter, all forms are fossilizable since they are relatively resistant to dissolution and/or microbial disintegration. Three major types of cysts are distinguished according to their function: 1) temporary cysts (motile cells that temporarily lose their

flagella and outer wall as a reaction to stressful conditions), 2) vegetative cysts (metabolically and/or reproductively active, non-motile cells covered by a continuous wall), and 3) resting cysts, representing a dormant stage in which most life processes are highly reduced. They are generally formed as part of the sexual reproduction. Since they are the result of sexual fusion, they are diploid and thus zygotic resting cysts, termed hypnozygotes. A motile diploid zygotic cell (planozygote) forms after the fusion of haploid motile cells (gametes) and resembles the former haploid cells. Planozygotes often show paired flagella and typically increase in size before they become non-motile hypnozygotes (= cysts). This process from planozygote to hypnozygote with the formation of membranes to serve as the future cyst wall and the final loss of the thecal plates is called encystment. Resting cysts are generally produced inside the dinoflagellate theca. The cyst shape may resemble that of the motile cell or may comprise a more or less spherical central body which can bear processes or crests. The obligate period of dormancy following the encystment is highly variable in length and may last from 12 hours to several months (Pfiester and Anderson, 1987). Following upon the dormancy period, the hypnozygote emerges through a distinct aperture called archeopyle (excystment) which resulted from the loss of an intraspecifically consistent number of plates (= operculum). The cycle closes with meiotic divisions producing new haploid cells and starting a new phase of vegetative reproduction (Fig. 2).

Most fossil dinoflagellates are believed to represent hypnozygotes (Pfiester and Anderson, 1987; Fensome et al., 1996a). However, since the sexual reproduction of dinoflagellates, which produces fossilizable resting cysts, is known for only 13-16% of all extant species (Head, 1996), the question arises as to how representative and selective the dinoflagellate record is (Evitt, 1985).

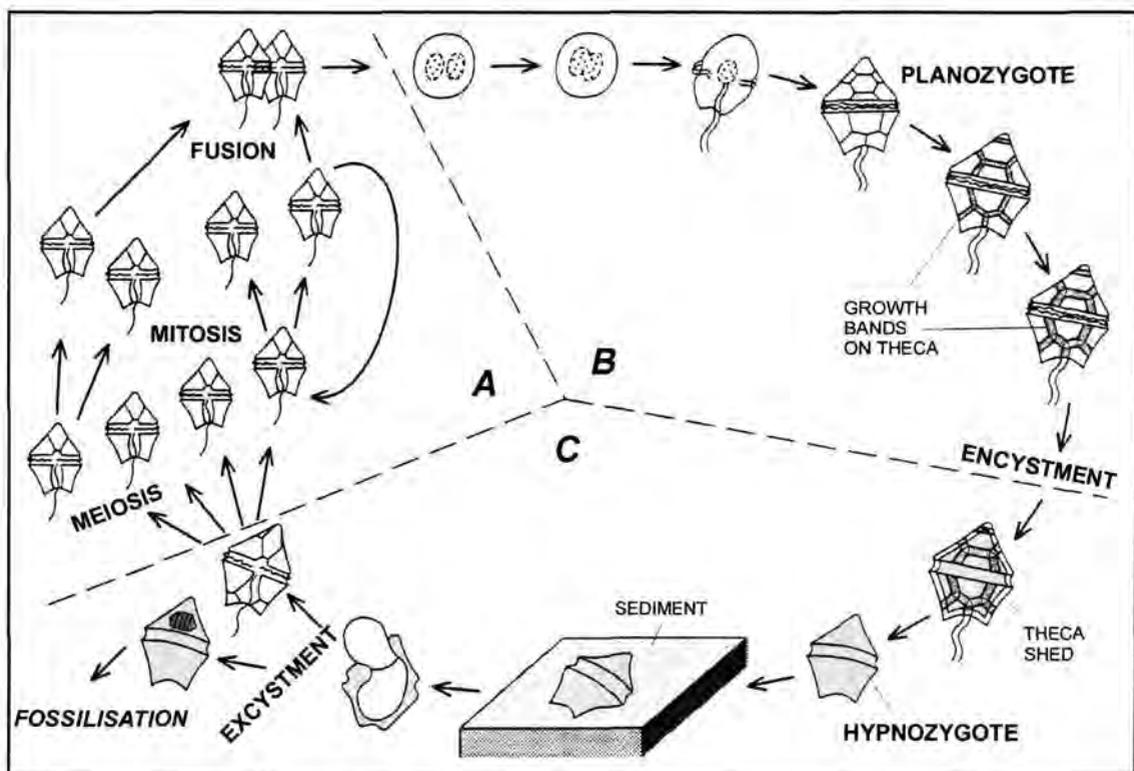


Figure 2. Idealized haplontic life cycle of dinoflagellates involving sexual reproduction and cyst formation. A) Cells in this segment are motile and haploid (= schizonts). B) Cells in this segment are motile and diploid (nucleus dotted) (= planozygotes). C) Cells in this segment are non-motile (except for the excysted cell shown to the left) and diploid (= hypnozygotes). Hatched area in discarded cyst at bottom left represents the archeopyle. (after Fensome et al., 1996a).

DINOFLAGELLATES IN THE FOSSIL RECORD

Biological and biochemical evidence implies that dinoflagellates have been present throughout the Phanerozoic and indicate a Precambrian origin for the dinoflagellate lineage (e.g., Moldowan and Talyzina, 1998). However, with the exception of two questionable taxa from the Silurian and Devonian (Calandra, 1964; Vozzhennikova and Sheshegova, 1989), dinoflagellates have not been documented in the geologic record prior to the Late Triassic. The absence of dinoflagellates in Paleozoic strata may be attributed to two reasons: 1) No remains of dinoflagellates are preserved. As the production of preservable cysts is obviously an exception among modern dinoflagellates, it can be assumed that many fossil dinoflagellate taxa may analogously have existed without leaving fossilizable remains. 2) Dinoflagellates are not recognized as such. The affiliation of modern cysts to dinoflagellates can be tested in culturing experiments, however, the identification of fossil cysts and their potential dinoflagellate affinity has to be based on morphological criteria. The minimum set of characteristics required to justify naming a specimen a dinoflagellate is still a matter of debate. Generally, cysts are regarded as dinoflagellates if they have an appropriate size, the shape and morphological features of a cingulum and sulcus, and/or they exhibit at least traces of a pattern of polygons which is consistent with a thecal tabulation (Evitt, 1985). However, even verified modern dinoflagellate cysts often lack these diagnostic features. Therefore, many taxa described from the Paleozoic as organic-walled microfossils of unknown biological affinity (acritarchs), may in fact be dinoflagellate cysts (Bujak and Williams, 1981; Fensome et al., 1999). Some of those taxa even show an archeopyle-like opening and a consistent polygonal pattern, but do not possess an arrangement of morphological elements that unequivocally permits to identify them as dinoflagellates. However, the lack of the typical dinoflagellate-like arrangement of morphological features, e.g., of the cingulum and the sulcus, is probably due to the fact that these features are linked to a more advanced evolutionary level, which was not reached before the Late Triassic (Bujak and Williams, 1981). The trigger for

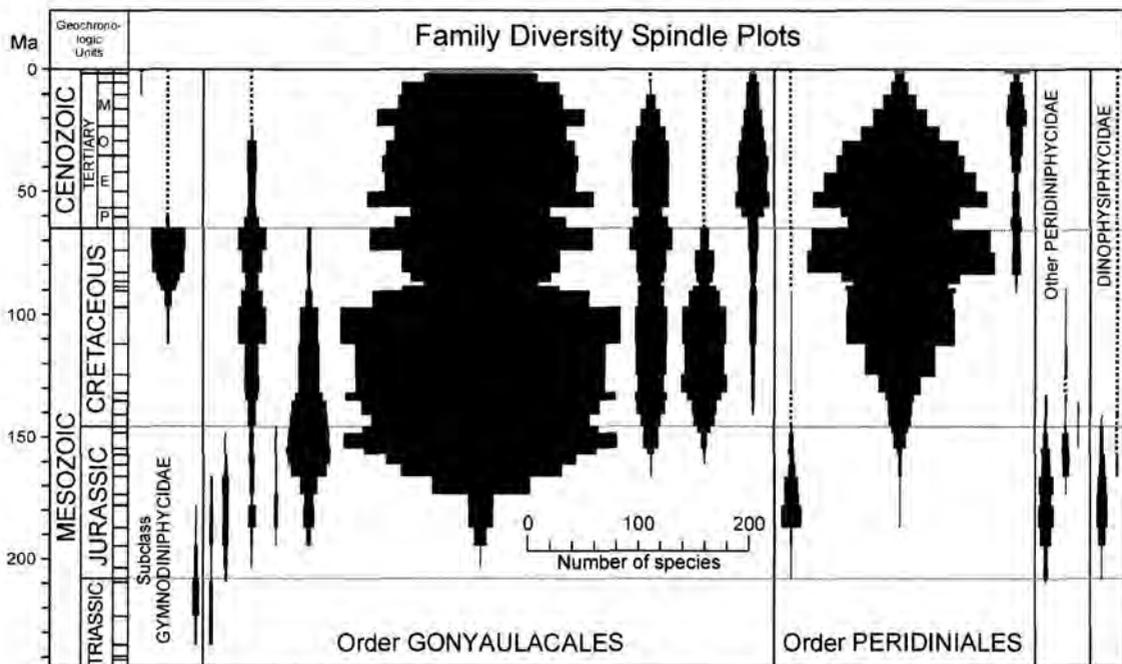


Figure 3. Spindle plots showing the number of species per dinoflagellate family per geologic stage. (from Fensome et al., 1996b)

affect the diversity patterns and the resulting evolutionary lineages, ranging from the sediment type analyzed, the volume of material available, and the preservation of the material to the research interests (Raup, 1976). Moreover, two factors especially influence the diversity pattern of dinoflagellates: the previously discussed selectivity of the geological record (only durable cysts are preserved) and the fact that some species obviously form more than one type of cyst. However, there is no alternative to diversity plots which can be applied for the reconstruction of evolutionary lineages and the current knowledge is perhaps no less complete than the fossil record of other microfossils (see also Fensome et al., 1993). Additionally, the phylogenetic development of at least the peridiniinean group can be traced back from their living descendents to the Early Cretaceous (Bujak and Davies, 1983), indicating a possibly comprehensive and continuous fossil record of this group.

SYSTEMATICS OF DINOFLAGELLATES

As previously outlined, dinoflagellates are somewhat special since they produce both fossilizable cysts and thecate stages during different stages of their life cycle. This peculiarity of dinoflagellates caused discrepancies in the systematic concepts used by biologists and paleontologists. When describing new species, biologists have generally concentrated on the motile stage, whereas paleontologists and neontologists are compelled to use differences in cyst morphology for classification. These two opposite approaches led to duplicate descriptions of several taxa under different names, especially of Quaternary and modern species (see, e.g., Head, 1996). Today scientists endeavor to relate cysts with modern thecae and to unveil potential cyst-theca relationships when publishing new taxa, thus striving for an integrated whole-organism nomenclature. However, several peculiar features of dinoflagellates bring up uncertainties and problems by hampering this attempt: 1) cysts may, or may not resemble the corresponding motile cell. In the latter case, cysts-theca relationships can only be proven by culturing experiments; 2) culturing experiments have shown that virtually identical thecate cells hatched from notably different cysts and *vice versa* (e.g., Wall and Dale, 1968). It is not yet clear if this means that a single species produces different cyst morphotypes or if the cysts of two different species might be much more distinct than their corresponding thecae; and 3) cysts generally show a higher morphological complexity than thecae, which induced the description of new, potentially unnecessary taxa. The application of consistent criteria in both fossil and modern dinoflagellate genera will lead to a subdivision of several modern taxa as well as to a merging of fossil genera (see Evitt, 1985).

Nevertheless, an intense investigation, comparing fossil and modern taxa and especially focussing on the cysts' tabulation patterns, resulted in an integrated phylogenetic classification of fossil and living dinoflagellates (Fensome et al., 1993). Tabulation patterns of cysts are generally reflected in ridges delineating individual plates or in miscellaneous forms of processes. To a varying degree, these patterns may reflect the tabulation of the motile cells. Consequently, tabulation patterns provide the primary basis for the classification of dinoflagellates. However, reduced tabulations or smooth, entirely unornamented cysts are also common. In the latter case, only the archeopyle may in some cases reflect the tabulation (= cryptotabulation). The different dinoflagellate tabulation patterns can be grouped into six types, which represent the main orders of the class Dinophyceae:

1) The gymnodinoid tabulation type is characterized by numerous, small, polygonal plates. Fossil cysts of this type are rare and have only been recognized by means of comparison with similar living forms.

or between the postcingular and antapical series, are called anterior and posterior intercalary series, respectively. For each plate, an individual label comprising plate number and symbol of the series, is used. The following symbols are applied to the plate series: apical plates ('), anterior intercalary plates (a), precingular plates ("), cingular plates (c), postcingular plates (""), posterior intercalary plates (p), and antapical plates (""") (compare Fig. 5). Sulcal plates (s) have their own labeling according to their relative position in the sulcal area (Fig. 5). The sum of all labels of a particular taxon can be outlined in a tabulation formula expressing the number of plates in each series, e.g., 4', 3a, 7", 6c, 5"", 2", 4s (a standard peridiniacean tabulation), meaning 4 apical plates, 3 anterior intercalary plates, 7 precingular plates, and so on. The gonyaulacoid-peridinioid tabulation type is realized in two orders: the Gonyaulacales and Peridinales. These two orders are distinguished by the shape of the first apical plate, which is asymmetrical in the Gonyaulacales and symmetrical in the Peridinales, and in the number and arrangement of the fundital plates (= plates posterior to the postcingular series and external to the sulcus) (Fensome et al., 1996a). The Peridinales are of special interest herein, since the calcareous dinoflagellates belong to this order.

CALCAREOUS DINOFLAGELLATES IN PARTICULAR

Calcareous dinoflagellates are a group of dinoflagellates that produce cysts during their life cycle which are characterized by the incorporation of calcite in at least one layer of the cyst wall. Additional organic layers may occur. Wall structures of calcareous cysts range from three massive calcareous layers, to a single organic layer covered with small calcareous *verrucae* or spines. Calcareous dinoflagellates are known only from marine environments, especially of low and middle latitudes, but also high latitude forms are known (e.g., Gilbert and Clark, 1983; Dale and Dale, 1992). Modern dinoflagellates, known to produce calcareous cysts, are exclusively single-celled and have a thecate motile cell. They are believed to be planktonic at least during one phase of their life-cycle and to live photoautotrophic, whereas mixotrophic forms are possible (D. Janofske, pers. comm.).

The life-cycle of modern calcareous dinoflagellates is poorly studied, especially the trigger and modes of cyst formation are barely understood and obviously vary interspecifically. On the one hand, cyst formation as part of the sexual life cycle is reported (e.g., Olli and Anderson, 2002), and on the other, also asexual cyst formation is obviously possible (Janofske and Karwath, 2000). Therefore, calcareous cysts, especially fossil ones, cannot generally be regarded as resting cysts, as commonly believed (Evitt, 1985; Fensome et al., 1996a).

Calcareous dinoflagellates are conventionally placed in the single subfamily Calciodinelloideae (Order Peridinales), which is characterized by a peridiniinean tabulation type, a bipesoid (plates 4", 2a and 3' are symmetrically and middorsally aligned) epithecal tabulation and a six-sided second anterior intercalary plate (2a). The cyst wall includes at least one calcareous layer and bears an apically located archeopyle (see Fensome et al., 1993). Cysts of the Calciodinelloideae may reflect in varying degree the tabulation of the parental theca, however, tabulation of calcareous cysts typically is reduced and holotabulated cysts, i.e., all plates of the theca are reflected, are an exception (e.g., *Calciodinellum operosum*; Fig. 6.1). Likewise, intratabulate species, in which tabulation is solely reflected by processes representing individual plates, are exceptional (e.g., *Alasphaera tuberculata*; Fig. 6.2). More often cingulotabulate taxa occur, which are characterized by a tabulation which is reduced to the indication of the cingulum (e.g., *Carinasphaera cimbra*; *Carinellum* spp., Fig. 6.4). However, cryptotabulate species represent the most common type of tabulation with more than 50 percent of all

known calcareous dinoflagellates (Streng, unpublished data). In cryptotabulate taxa, tabulation patterns are reflected by the shape and position of the archeopyle, only (Fig. 6.6). A tabulation type characterized by a distinct but variably reduced tabulation represents the second most common type within the calcareous cyst. Those cysts are characterized by the fusion of distinct plates or even plate series culminating in extreme forms that show only three or four faces (e.g., *Calcicarpinum* spp.; Figs. 6.3, 6.5). Additionally, a variety of ornamentation occurs in calcareous cysts, which may resemble reduced tabulation, but cannot unambiguously be related to tabulation (e.g., *Orthotabulata obscura*). Likewise, reduced tabulation may resemble ornamentation, or potential tabulation might be obscured by additional ornamentation (e.g., *Bicarinellum pulchrum*) aggravating the distinction between tabulation and ornamentation. Another peculiarity of calcareous cysts is, that externally cryptotabulate species may have either an internal holotabulated periphragm (*Pirumella multistrata* forma *patriciagreeleyae*; see also Keupp 1981)), or an reduced tabulation represented by calcareous ridges connecting a distal and a proximal calcareous layer (*Tetramerosphaera lacrimula*; see Willems, 1985).

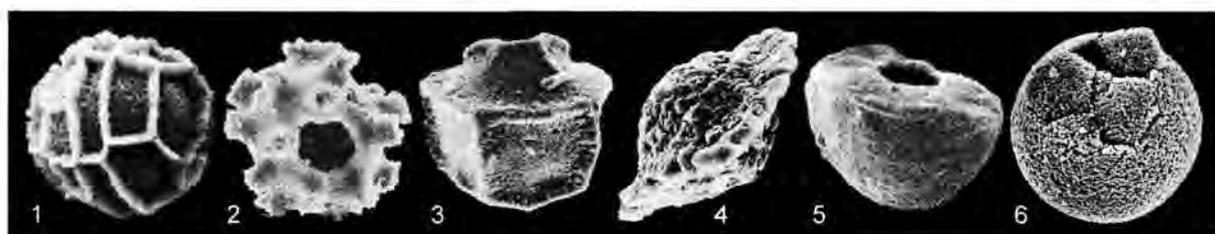


Figure 6. Miscellaneous examples of the different tabulation types of calcareous dinoflagellate cysts: 1) holotabulated cysts of *Calciodinellum operosum* (from D'Onofrio et al., 1999, fig. 15); 2) intratabulate cysts of *Alasphaera tuberculata* (from Monnet, 1993, pl. 10, fig. 5); 3) cyst of *Calcigonellum?* *ansatum* showing reduced tabulation pattern (from Hildebrand-Habel and Willems, 1999, pl. 1, fig. 10); 4) cingulotabulate cyst of *Carinellum lenticulare* (from Keupp, 1987, pl. 12, fig. 1); 5) *Calcicarpinum bivalvum* with extremely reduced tabulation (from Versteegh, 1993, pl. 3, fig. 3); 6) cryptotabulate cyst of *Orthophithonella gustafsonii* (from Keupp, 1980b, pl. 31, fig. 1). All not to scale.

In earth history calcareous dinoflagellates appear more or less synchronously with the organic-walled dinoflagellates in the Late Triassic (Janofske, 1992). However, analogous to the organic walled cysts questionable calcareous cysts are already known from the Paleozoic. In many Paleozoic carbonate sediments, especially in the Devonian (e.g., Whalen et al., 2002), calcareous hollow spheres are frequently observed in thin sections. Those spheres, conventionally denoted as 'calcispheres', resemble spherical calcareous cysts in shape and size. Recently, calcispheres have even been observed in Silurian sediments (Munnecke, 1997) showing multi-layered walls and tabulation-like segmentation of the inner wall. However, in none of these calcispheres an archeopyle could be observed which would support their dinoflagellate affinity. In fact, calcispheres are generally related to reproductive cysts (aplanospores) of certain green algae.

The Triassic and Jurassic record of calcareous dinoflagellates is very scarce (e.g., Janofske, 1992; Bolli, 1974) and generally comprises simple spherical cysts without any tabulation pattern besides a simple cryptotabulation. The first distinctly tabulated species occur in the Oxfordian. *Bicarinellum jurassicum* (Deflandre, 1948) clearly shows a reduced tabulation comprising two ridges and/or several hunches on the epi- and hypocyst. The two ridges represent the cingulum, whereas the total of hunches corresponds to the number of pre- and postcingular plates of the standard peridinialean tabulation

(Keupp, 1984). *Heptasphaera paulaworstelliae* from the Oxfordian/Kimmeridgian interval (Bolli, 1978b) is the first cyst showing a tabulation pattern that reflects distinct plate series by ridges. During the Early Cretaceous tabulation patterns get more diverse (see e.g., Keupp, 1979b, 1981, 1987) and concomitantly calcareous dinoflagellates become widely distributed evolving to a great diversity. Since then, they may constitute a major to even dominant component of many carbonate sediments (e.g., Willems, 1996).

In the early Cretaceous a group of calcareous microfossils appeared, i.e., the pithonelloids, which resemble cryptotabulate calcareous cysts in size and shape. Because of this general resemblance, they conventionally have been regarded as calcareous dinoflagellates (Bujak and Davies, 1983; Keupp, 1987). Though the cyst-like tests of pithonelloids show an aperture, no opercula have been observed in any pithonelloid species. Additionally, these apertures appear to be too small to represent archeopyles. Furthermore, the ultrastructure of the test walls is completely different to those of calcareous cysts, as it is composed of uniformly obliquely oriented crystallites, typically generating a characteristic parquet-like pattern on the outer surface of the test. Moreover, hollow tube-like crystallites occur which are unknown from other calcareous cysts, implying a primarily different mineralization processes. The pithonelloids probably present an independent group of planktonic microorganisms, which were typical for Cretaceous outer shelf environments (e.g., Villain, 1981; Zügel, 1994). They became extinct at the Cretaceous/Tertiary boundary in the Tethyan Realm, but succeed to survive into the Danian in the Boreal Realm (Kienel, 1994).

About 200 species of calcareous dinoflagellates have been described from the sediment record, with the pithonelloid species not considered (Streng, unpublished data). Additionally, about 10 species have only been reported from modern surface waters, mainly representing poorly calcified cysts which easily disintegrate after sedimentation. Calcareous dinoflagellates are generally long-living taxa and are of minor biostratigraphic value, a characteristic which makes them suitable for long-range paleoenvironmental reconstruction though. Variations in the abundance and shifts in associations of calcareous dinoflagellates have successfully been applied to reconstruct long-term environmental and paleoecological changes, especially in the Cenozoic (Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000). Furthermore, for the Quaternary, calcareous cysts have been found to be useful for the reconstruction of paleoceanographic conditions, e.g., paleoproductivity, and rapid climatic changes (e.g., Esper et al., 2000; Vink et al., 2001). Therefore, calcareous dinoflagellates are believed to have a high potential as indicator for changes in paleoclimatology and paleoceanography.

THORACOSPHAERA HEIMII

A single dinoflagellate species is known to produce calcareous cysts asexually during its life cycle (vegetative cysts), i.e., *Thoracosphaera heimii* (see Tangen et al., 1982). In contrast to the calcareous dinoflagellates (Subfamily Calciodinelloideae) the cyst phase of *T. heimii* represents the principal stage of its life cycle. Additionally, the motile cell of *T. heimii* is athecate and the small circular to subcircular aperture of the cyst through which the motile cell emerges is not believed to represent a distinct thecal plate (Tangen et al., 1982; Inouye and Pienaar, 1993). Consequently, no tabulation type of *T. heimii* is known aggravating its assignment to a distinct order within the Dinoflagellata. Therefore, the order Thoracosphaerales was established to accommodate only *T. heimii* (Tangen et al., 1982). Because of the general resemblance of the vegetative cysts of *T. heimii* to the calcareous cysts of the Calciodinelloideae, the Thoracosphaerales probably have a close affinity to the

Calciodinelloideae. However, the athecate motile cell contradicts this affiliation. Therefore, the Thoracosphaerales are treated as a dinophycean order of uncertain subclass assignment (Fensome et al., 1993). Cysts of *Thoracosphaera heimii* are known since the Paleocene (Keupp, 1991b) and are extremely abundant in modern sediments (e.g., Vink et al., 2000).

MOTIVATION AND MAIN OBJECTIVES

Calcareous dinoflagellates are known since the Late Triassic and represent a significant component of the marine calcareous phytoplankton at least since the Early Cretaceous. However, only very few studies focused on the phylogeny and evolution of this particular group. Consequently, little is known of the factors and influences controlling their phylogenetic development. Recently, major shifts in calcareous dinoflagellate associations of the late Cretaceous to Paleogene period have been applied successfully to reconstruct major paleoenvironmental changes (Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000). However, as these studies concentrated on mid-latitude assemblages of the South Atlantic Ocean only, additional studies from spatially and latitudinally different localities are needed to verify the present results and to improve the knowledge of calcareous dinoflagellate distribution and diversity. Modern associations for example, which are generally low in diversity and comprise only a few distinct species, are quite different in species composition to fossil assemblages. Although during the Neogene, the development to the typical modern associations must have taken place, assemblages of calcareous dinoflagellates from this period are widely neglected. Therefore, the objective of this study encompasses two distinct, but interdependent aspects:

1. Phylogeny and taxonomy of calcareous dinoflagellates

(Chapter 2.1 and Chapter 2.2)

As the phylogeny of a distinct group of organisms should be reflected in its taxonomy, the present taxonomic system has to be critically examined on its accordance with potential phylogenetic lineages. A former classification of the calcareous dinoflagellates regarded the ultrastructure of the calcareous wall as the major taxonomic criterion (Keupp, 1987; Kohring, 1993a; Janofske, 1996). According to the different types recognized, four subfamilies have been established. However, Fensome et al. (1993) refused this system as they consider wall structure to be of unproven value for the identification of phylogenetic groupings. Consequently, they accommodated all calcareous dinoflagellates in the single subfamily Calciodinelloideae without distinguishing lower taxonomic levels.

In order to unveil phylogenetic lineages within the Calciodinelloideae, other characters besides the wall structure have to be investigated and evaluated. The different archeopyle types of calcareous cysts appear to have a high potential to obtain supplementary evidence for the phylogenetic development of this particular group. As phylogenetic trends may be biased by incorrect stratigraphic ranges of taxa through erroneous species determinations and inaccurate or generalized definitions of genera and species, the established definitions of distinct taxa must be verified and where necessary revised. A variety of taxa has to be reexamined using available data from literature and new sample material. The final aim of this study is to present a comprehensive and consistent taxonomic concept which will help to unveil intraspecific discrepancies by the involvement of additional, previously neglected or underestimated morphological features. As a consequence, the stratigraphic range of at

least some taxa is expected to decrease significantly. The sum of all obtained taxonomic results serves as a basis for the second part of this dissertation.

2. New data on the distribution of Cenozoic calcareous dinoflagellates

(Chapter 2.3 and Chapter 2.4)

To achieve new data on the spatial and stratigraphic distribution as well as diversity of calcareous dinoflagellates, the Indian Ocean was chosen as an appropriate region, as calcareous dinoflagellates of the Indian Ocean are poorly studied so far. Previous studies from Bolli (1974) and Keupp (1992a) described calcareous cyst assemblages from the eastern Indian Ocean. However, both studies dealt with Jurassic and/or Cretaceous material. Reports of Cenozoic taxa from the Indian Ocean are extremely limited and generally comprise only a few taxa (Bukry and Bramlette, 1969; Wei and Pospichal, 1991; Siesser and Bralower, 1992). Additionally, high latitude assemblages of calcareous dinoflagellates are barely known, solely Fütterer (1990) described associations from the Cretaceous/Tertiary interval of the eastern Weddell Sea.

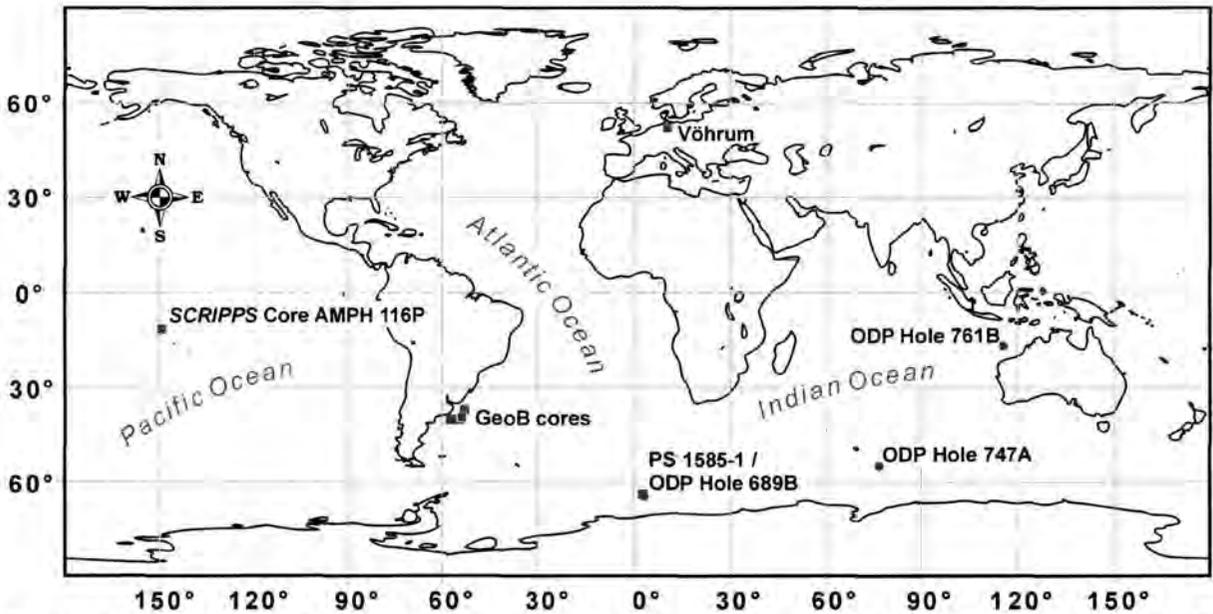


Figure 7. Location of the three studied cores of the Ocean Drilling Project (ODP) (circles). In addition to the ODP cores some samples from additional locations have been analyzed to achieve supplementary data (squares).

Sample material of three cores of the Ocean Drilling Project (ODP) has been selected (Fig. 7). One core originates from the low-latitude eastern Indian Ocean, one from the of the high-latitude southeastern Indian Ocean, which cover both late Cretaceous to Pleistocene sediments. Additionally, another high latitude core from the eastern Weddell Sea ranging from the late Cretaceous to early Miocene has been considered. The main objective is to analyze species-environment relation by correlating shifts in the obtained distribution patterns with the major changes in the Cenozoic climatic evolution. Special interest will be given to times of major environmental and climatic changes, like the Cretaceous/Tertiary, Paleocene/Eocene, Eocene/Oligocene and Miocene/Pliocene boundaries. The Neogene is of special interest, as during this period the change from typical fossil assemblages to those known from modern environments must have taken place. Additionally, variations in the

abundance and diversity of calcareous dinoflagellates have to be evaluated. The already attained detailed taxonomic results provide a useful supplement and permit a more explicit description of the stratigraphic distribution patterns. The obtained results from the three localities are compared with published data of isochronous localities to provide new insights in calcareous dinoflagellate evolution, their diversity and abundance distribution through time, and the factors controlling their distribution

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Revision of the genera *Sphaerodinella* Keupp and Versteegh, 1989 and
Orthopithonella Keupp in Keupp and Mutterlose, 1984
(Calciodinelloideae, calcareous dinoflagellate cysts)

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ABSTRACT.—The genus *Sphaerodinella* Keupp and Versteegh, 1989 became obsolete by the assignment of its type *S. albatrosiana* (Kamptner, 1963) to the genus *Calciodinellum* Deflandre, 1947. For the single remaining species of *Sphaerodinella*, which does not fit into the genus *Calciodinellum*, the new genus *Caracomia* is proposed, whose type is *C. arctica* (Gilbert and Clark, 1983) new genus, new combination. Additionally, a new species of *Caracomia* is described: *Caracomia stella* new genus and species. The regional distribution of the two species of *Caracomia* shows distinct regional preferences: *Caracomia arctica* is restricted to cold waters of both hemispheres, whereas *Caracomia stella* as yet has only been described from warmer environments. Thus, *C. arctica* can be used as a cold water indicator. Comparison of *Caracomia* with other genera has shown a close relationship to the type of *Orthopithonella* and exposed a common misinterpretation of this genus. Therefore, the genus *Orthopithonella* Keupp in Keupp and Mutterlose, 1984, is emended to unquestionably accommodate only the type *O. gustafsonii*.

INTRODUCTION

Increasing knowledge of the diversity of fossil calcareous dinoflagellate cysts over the past two decades has given rise to a taxonomic concept that regards the crystallographic orientation of the c-axis of the wall-forming crystals as being the most significant attribute for the classification of calcareous dinoflagellate cysts (e.g., Keupp and Mutterlose, 1984; Keupp, 1987; Kohring, 1993a). Detailed light optical analyses of calcareous dinoflagellate cysts have shown that four different ultrastructure types exist: the oblique, the radial, the tangential and the pithonelloid wall type (Young et al., 1997). However, subsequent studies have shown that the morphological long-axis of a crystal does not necessarily correspond to the crystallographic c-axis (e.g., Janofske, 1996; Hildebrand-Habel et al., 1999). Thus, misinterpretations in classifying calcareous dinoflagellates using SEM studies exclusively are widespread in the literature. Furthermore, Fensome et al. (1993) rejected this taxonomic concept and regarded the wall structure of calcareous dinoflagellate cysts to be of unproven value for phylogenetic considerations. We agree with this point of view. Another problem that has become increasingly evident is that both the shape of the archeopyle and the type of the operculum were widely neglected as important taxonomic features. As a consequence, archeopyle characteristics are often missing in diagnoses of genera, which thereby permitted species lacking distinct features to be lumped together leading to an immense number of species within a single genus. The aim of this study is to clarify and to correct at least two of these problematic genera: *Sphaerodinella* Keupp and Versteegh, 1989, and *Orthopithonella* Keupp in Keupp and Mutterlose, 1984.

The genus *Sphaerodinella* was established by Keupp and Versteegh (1989) to unite calcareous dinoflagellate cysts with a radial crystallographic orientation of the wall crystals and a large operculum that includes all apical and intercalary plates. Subsequent examinations of the ultrastructure of the three included species (*S. albatrosiana*, *S. arctica*, and *S. tuberosa*) have revealed a tangential orientation of the crystallographic c-axes for *S. albatrosiana*, an oblique orientation for *S. tuberosa*, and a radial orientation for *S. arctica* (Janofske, 1996 and unpublished observations). This led Janofske and Karwath (2000) to revise *S. albatrosiana* and *S. tuberosa*. Because of its tangential ultrastructure and the large archeopyle, they regarded *S. albatrosiana* as a species of *Calciodinellum* Deflandre, 1947. To accommodate the unique characteristics of *S. tuberosa*, namely an oblique ultrastructure combined with a large archeopyle, and to include details of the motile stage, they established the new genus *Pernambugia* Janofske and Karwath, 2000. As *S. albatrosiana* is the type of *Sphaerodinella*, *Sphaerodinella* consequently became a taxonomic junior synonym of *Calciodinellum*, and *S. arctica* took its former name *Thoracosphaera arctica*. However, the genus *Thoracosphaera* Kamptner is regarded (e.g., Karwath, 2000) as a monospecific genus, because of the unique life cycle of its type species *T. heimii* (see Tangen et al., 1982). Therefore, the new genus *Caracomia* is proposed to include *T. arctica*, as no genus exists that coincides with the characteristics of *T. arctica*. Additionally, a new species of *Caracomia* is described: *Caracomia stella* n. gen. and sp., a species that has been mistaken in the past for *C. arctica* but bears clear differences in morphology as well as regional distribution.

Comparison of *Caracomia* n. gen. with other genera has evinced a close relationship to the type of *Orthopithonella* Keupp in Keupp and Mutterlose, 1984: *O. gustafsonii* (Bolli, 1974). A subsequent study of the published data on *O. gustafsonii* has revealed a frequent misinterpretation of this species. As a consequence, the genus *Orthopithonella* is emended and the species *O. gustafsonii* redefined.

METHODS

The specimens described herein originate mainly from samples of the Ocean Drilling Program (ODP): Leg 120, Hole 747A (Kerguelen Plateau), and Leg 122, Hole 761B (Wombat Plateau). Additional material was obtained during research cruises of the R. V. Polarstern (ANT-VI/3, Maud Rise, Fütterer, 1988) and the R. V. Meteor (M 46/2 and M 46/3, offshore Argentina). The samples consist of cream-colored foraminifer diatom oozes (Hole 747A, sections 1H-5, 2H-4, 3H-3, 4H-1 and 4H-3; PS 1585-1), white nannofossil oozes (Hole 747A, sections 4H-3 and 6H-1; Hole 761B, sections 4H-1, 5H-5, 7H-4), gray to olive muddy diatom oozes (M 6308-1, M 6330-1), and olive-gray muddy foraminifer nannofossil oozes (M 6317-2). Lithologic information on sample M 6231-1 obtained by the R. V. Meteor is not available.

The individual samples were suspended in a weak solution of water and ammonia and repeatedly frozen and thawed to achieve complete disintegration. Afterwards, the material was washed through a 125 μm and 20 μm sieve. The residue was dried and the fraction between 20 and 125 μm was used to pick the specimens under a binocular microscope. The selected specimens were mounted on aluminum stubs, sputter-coated with gold, and photographed under a scanning electron microscope (SEM) at the University of Bremen (CamScan-44).

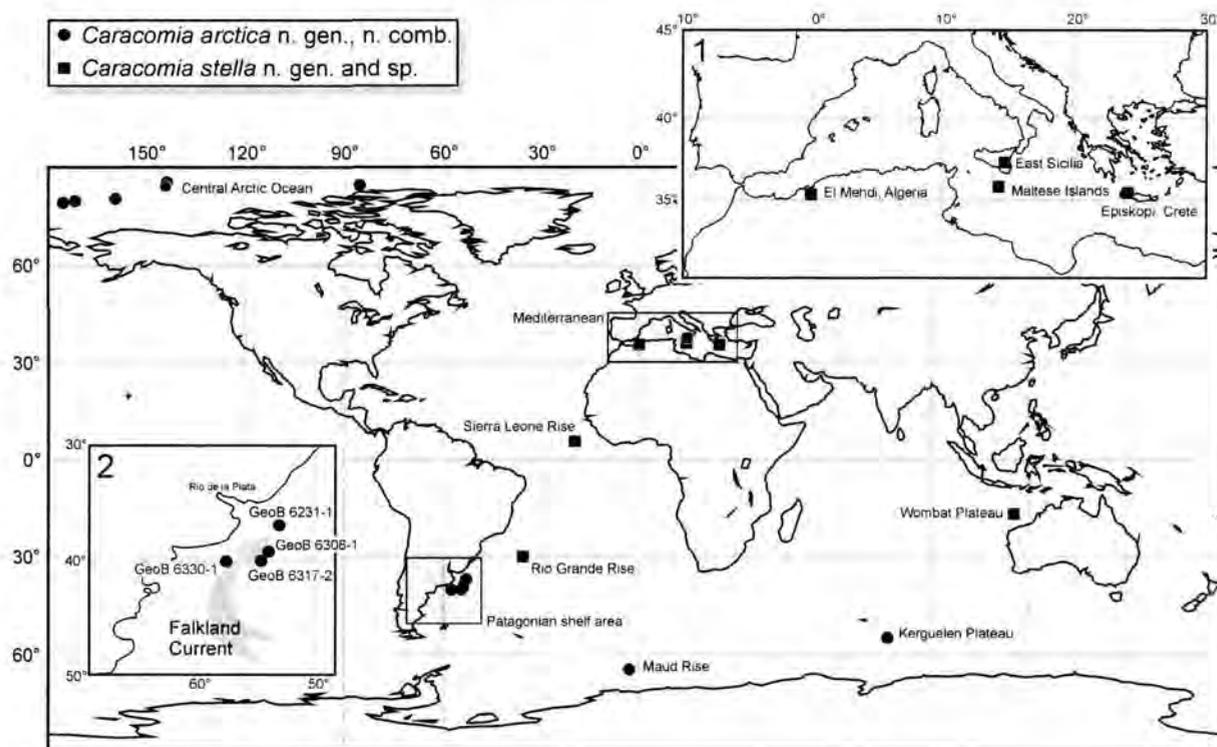


Figure 1. Spatial distribution of *Caracomia arctica* n. gen., n. comb. and *Caracomia stella* n. gen. and sp. according to literature data and own observations. Note the preference of *C. arctica* for cold waters (samples offshore Argentina are influenced by the cold Falkland Current). 1 and 2, detailed maps of the Mediterranean and the Patagonian shelf area, respectively.

SYSTEMATIC PALEONTOLOGY

The suprageneric classification of calcareous dinoflagellates is in accordance with Fensome et al. (1993). The description of morphologic features of the archeopyle and the operculum, respectively, follows the overview given by Fensome et al. (1996). Tabulation patterns are described using the Kofoid tabulation system (see Fensome et al., 1996). The nanoplankton zonation is according to Martini (1971). The studied material is deposited in the collection of the Division of Historical Geology and Paleontology, University of Bremen, Germany.

Division DINOFLAGELLATA (Bütschli, 1885) Fensome et al., 1993

Subdivision DINOKARYOTA Fensome et al., 1993

Class DINOPHYCEAE Pascher, 1914

Subclass PERIDINIPHYCIDAE Fensome et al., 1993

Order PERIDINIALES Haeckel, 1894

Suborder PERIDINIINEAE Autonym

Family PERIDINIACEAE Ehrenberg, 1831

Subfamily CALCIODINELLOIDAE Fensome et al., 1993

Genus *Caracomia* new genus

Type of genus.—The holotype of *Caracomia arctica* (Gilbert and Clark, 1983) n. gen., n. comb., early Pleistocene.

Included species.—*Caracomia arctica* (Gilbert and Clark, 1983) n. gen., n. comb., and *Caracomia stella* n. gen. and sp.

Diagnosis.—Spherical to ovoid cysts with single-layered calcareous wall; wall-forming crystals radially arranged; morphological long-axes of crystals correspond to crystallographic *c*-axes; combination archeopyle polygonal in outline; simple operculum includes apical (2'-4') and intercalary plates (1a-3a); tabulation typically restricted to operculum.

Etymology.—Named after the Greek *charakōma* (= palisade), in allusion to the palisade-like arrangement of wall-forming crystals in cross-section.

Occurrence.—Worldwide except for Pacific Ocean; known from the lower Oligocene to Holocene (see occurrence of the species for details and Fig. 1).

Discussion.—*Caracomia* n. gen. is distinguished from other genera of calcareous dinoflagellates by its combination of morphological characters: radial ultrastructure, large polygonal archeopyle and absence of tabulation as reflected by crests or processes. *Pernambugia* Janofske and Karwath, 2000 and *Calciodinellum* Deflandre, 1947 bear the same type of archeopyle, but have different ultrastructures. *Orthopithonella* Keupp in Keupp and Mutterlose, 1984 is in many aspects similar to *Caracomia*: 1) radial ultrastructure; 2) polygonal archeopyle; and 3) also no ornamentation. However, *Orthopithonella* is distinguished from *Caracomia* by its unique opercular structure with a variable archeopyle and several disarticulated opercular pieces (see Description of *Orthopithonella gustafsonii*). Furthermore, a significant stratigraphic gap in the occurrence of these two genera supports the distinction: *Orthopithonella* is apparently restricted to the middle Cretaceous (Aptian to Cenomanian) whereas *Caracomia* does not appear earlier than the Oligocene. Badly preserved specimens of *Caracomia* and undehisced specimens without a delineated archeopyle may superficially resemble several other species in pattern and arrangement of crystals on the outer surface (e.g., *Orthopithonella? globosa* (Fütterer, 1984) and *Orthopithonella? multipora* Kienel, 1994). In these cases more detailed examination of specimens is necessary (e.g., by breaking the cyst wall to determine number of layers and arrangement of crystals).

***Caracomia arctica* (Gilbert and Clark, 1983) new genus, new combination**

Figures 4, 8.1-8.7

Thoracosphaera arctica GILBERT AND CLARK, 1983, p. 400, pl. 1, figs. 1-15.

Not *Sphaerodina arctica* (Gilbert and Clark, 1983). KEUPP AND VERSTEEGH, 1989, pl. 1, fig. 14; KOHRING, 1993a, p. 52-53, pl. 38, figs. a-c, 1993b, p. 16, pl. 1, figs. 6-7, 1997, p. 160, figs. 4e-4f; KEUPP AND KOHRING, 1993, p. 29, pl. 2, figs. 1-8, 1999, p. 37-38, pl. 1, figs. f-i; HILDEBRAND-HABEL AND WILLEMS, 2000, fig. 6b.

Basionym.—*Thoracosphaera arctica* Gilbert and Clark, 1983, p. 385-401, pl. 1, figs. 1-15; holotype: pl. 1, fig. 1.

Diagnosis.—Species of *Caracomia* with wall built of elongated, rod-shaped crystals; wall-forming crystals generally increase in thickness towards distal and proximal ends; operculum polygonal in outline comprising apical and intercalary plate homologs.

Description.—Calcareous cysts are spherical to ovoid in shape, minimum diameter 26 to 55 μm (mean = 38 μm , $n = 85$), maximum diameter 31 to 59 μm (mean = 44 μm , $n = 21$). Minimum and maximum

diameters of measured specimens show a positive linear relationship. Apical combination archeopyle polygonal in outline, measuring about 70 to 75 percent of the minimum cyst diameter. Simple polyplacoid operculum comprises plates 2'-4' and 1a-3a (archeopyle formula: (3AtI); Fig. 3). Cyst wall 1.4 to 4.3 μm thick and consists of densely packed rod- to bone-shaped crystals, which typically increase in thickness towards proximal and distal ends. Crystals divided into distal and proximal part by a faint suture (Figs. 3.2, 4.4, 4.10) situated in middle of crystals in relatively thick walls, and more proximally in thinner walls. Inner and outer surfaces of cysts are characterized by dense pattern of trigonal ends of the wall forming crystals, giving cyst surfaces a smooth appearance in general. Relatively well-preserved, diagenetically unaffected specimens show a more loose arrangement of crystals, resulting in a pattern of interfingering, polylobate-triradiate crystal tops on outer surface of cyst (Fig. 4.5, 4.6, 4.12). Furthermore, several cysts show a presumably secondary growth of individual distal ends of crystals in length as well as in thickness, giving the outer surface a somewhat spinose and a less organized appearance (Figs. 4.8, 4.11, 8.2, 8.6; also compare with Type II to IV of Gilbert and Clark, 1983). No pores observed in any of the cysts. Generally preserved rough inner organic layer, about 0.2 μm thick (Figs. 4.7, 8.3).

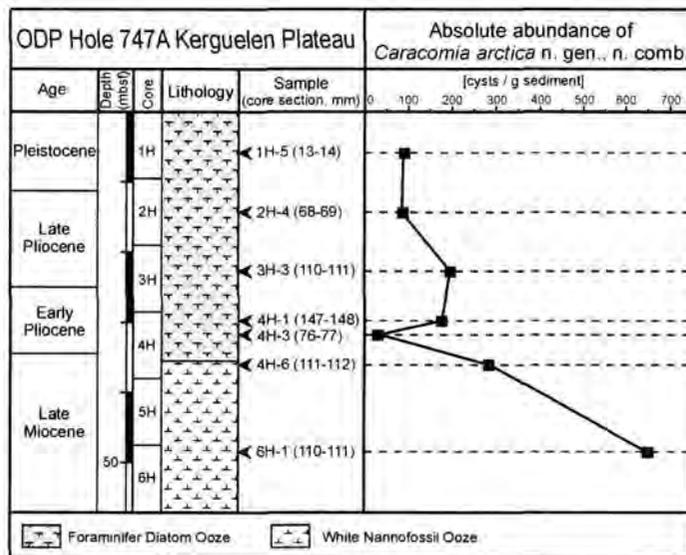


Figure 2. Absolute abundance of *Caracomia arctica* n. gen., n. comb. and stratigraphy at ODP Site 747A, Kerguelen Plateau.

Material examined.—About 150 cysts from the Kerguelen Plateau (ODP Leg 120, Hole 747A, samples 1H-5 (13-14 cm), 2H-4 (68-69 cm), 3H-3 (110-111 cm), 4H-1 (147-148 cm), 4H-3 (76-77 cm), 4H-6 (111-112 cm), 6H-1 (110-111 cm), see also Fig. 2), 6 cysts from the Maud Rise (surface sample PS 1585-1) and about 15 cysts from surface sediments offshore Argentina (samples M 6231-1, M 6308-1, M 6317-2, M 6330-1). Figured specimens are 120-1H-5/I5, 120-1H-5/IX8, 120-3H-3/V6, 120-3H-3/VII2, 120-3H-3/X9, 120-4H-1/II9, 120-4H-1/XIII7, 120-6H-1/IV11, 120-6H-1/V25, 120-6H-1/VII1, 120-6H-1/IX24, 120-6H-1/X13, 120-6H-1/X4, M6317-2/II, PS1585-1/V5.

Occurrence.—*Caracomia arctica* is restricted to polar and cold oceans, respectively: late Miocene to Holocene of Central Arctic Ocean (Gilbert and Clark, 1983), ?modern southern South Atlantic Ocean (Patagonian shelf and Maud Rise), and late Miocene (*G. scitula* biozone) to Pleistocene of the southern Indian Ocean (Kerguelen Plateau) (see also Fig. 1). *Caracomia arctica* is thought to be extant, as several cysts have been found in surface samples of the South Atlantic Ocean. However,

these cysts have not yet been observed in the water column and the corresponding motile thecae are not known.

Discussion.—See discussion of *Caracomia stella* n. gen. and sp.

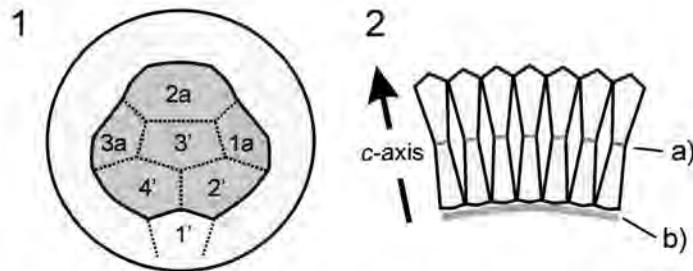


Figure 3. Schematic drawings of *Caracomia arctica* n. gen., n. comb. 1, Archeopyle and involved plates; 2, cross section of wall showing crystal arrangement with faint median suture (a) and inner organic layer (b).

Caracomia stella new species

Figures 7, 8.8-8.10

Thoracosphaera sp. 2 FÜTTERER, 1977, p. 717, pl. 7, figs. 1, 4, 6, not figs. 2, 3, 5.

Sphaerodiniella arctica (auct. non Gilbert and Clark, 1983). KEUPP AND VERSTEEGH, 1989, pl. 1, fig. 14; KOHRING, 1993a, p. 52-53; pl. 38, figs. a-c, 1993b, p. 16, pl. 1, figs. 6-7, 1997, p. 160, figs. 4e-4f; KEUPP AND KOHRING, 1993, p. 29, pl. 2, figs. 1-8, 1999, p. 37-38, pl. 1, figs. f-i; HILDEBRAND-HABEL AND WILLEMS, 2000, fig. 6b.

Diagnosis.—Species of *Caracomia* with a relatively thick wall typically penetrated by numerous true pores; wall-forming crystals rod-like; each single crystal is constructed of a sequence of several tiny crystallites; operculum simple, polygonal in outline, comprising plates 2'-4' and 1a-3a.

Description.—Spherical cysts variable in size, with a diameter ranging from 27 to 44 μm ($n = 14$). Massive, single-layered calcareous wall 3.1 to 5.9 μm thick. Wall-forming crystals thin and densely packed, stem-like in shape and consist of a linear succession of tiny rhombohedrons that obviously have grown on each other (epitaxially). Wall pierced by numerous, equally distributed pores with diameters of 0.2 to 0.3 μm . Outer surface is characterized by a pattern of slightly elongated triradiate crystal tops, which show no distinct arrangement around pores. The combination archeopyle is polygonal in outline, involving plates 2'-4' and 1a-3a (archeopyle formula: (3AtI); Fig. 6). The polyplacoid operculum is simple.

Etymology.—Named after the Latin *stella* = star, as the polygonal operculum resembles a star.

Types.—Holotype: cyst 122-4H-1/VI3 (Figs. 7.1, 8.10); type locality and stratum: Wombat Plateau, eastern Indian Ocean, ODP Leg 122, Hole 761B - Late Pliocene, nannoplankton zone NN16, sample 122-761B-4H-1 (122-123 cm); paratypes: cysts 122-4H-1/XIII7, 122-5H-5/XIV10, 120-7H-4/X16, 120-7H-4/X20.

Other material examined.—Twelve additional cysts from the Wombat Plateau, ODP Leg 122, Hole 761B, samples 4H-1 (122-123 cm), 5H-5 (62-63 cm) and 7H-4 (50-51 cm), early Miocene, NN1 to

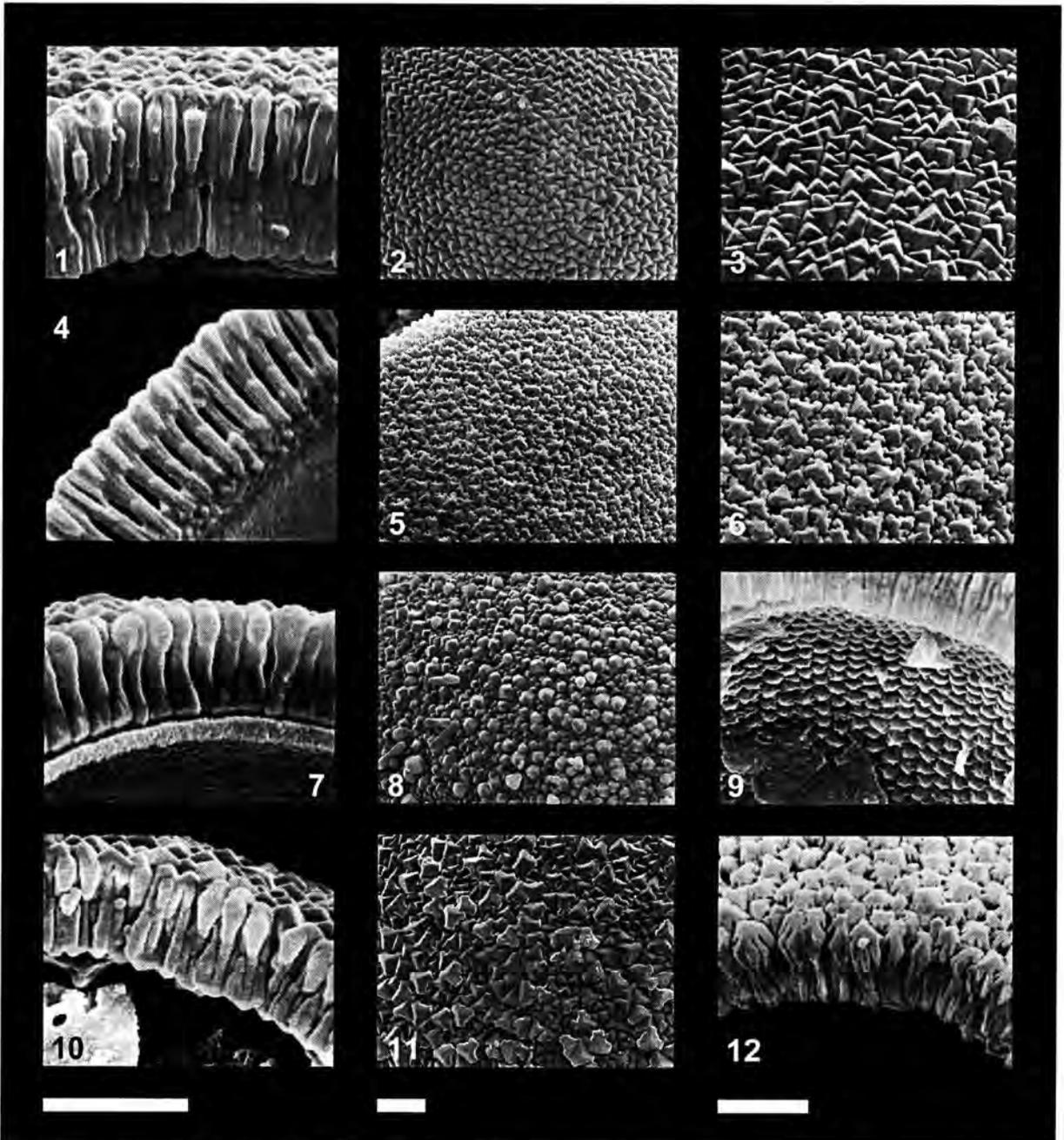


Figure 4. *Caracomia arctica* n. gen., n. comb. 1, 4, 7, 10, various cross-sections of walls showing different states of crystallization; 2, 5, 8, 11, different crystal patterns of outer cyst surface depending on grade of diagenesis and preservation; 3, 6, close-ups of outer cyst surface; 9, inner cyst surface; 12, oblique view of cyst wall and surface with skeletal-like crystal growth. 1, 120-3H-3/X9; 2, 120-6H-1/VI11; 3, 7, 120-4H-1/II9; 4, 120-1H-5/IX8; 5, 6, 120-3H-3/V6; 8, 120-6H-1/IV11; 9, 120-3H-3/X9; 10, 120-3H-3/VI12; 11, 120-4H-1/XIII7; 12, PS1585-1/V5. Scale bars equal 3 μm and refer to the corresponding column.

late Pliocene, NN16 (see also Fig. 5): 120-4H-1/IV15, 120-5H-5/XIII10, 120-5H-5/XIII17, 120-5H-5/V7-2, 120-5H-5/VI9-2, 120-7H-4/IV19, 120-7H-4/VII3, 120-7H-4/X13, 120-7H-4/XIII21, 120-7H-4/XIV9, 120-7H-4/XIV11, 120-7H-4/XIV18.

Discussion.—*Caracomia arctica* and *C. stella* are distinguished by several details: 1) Habit of wall forming crystals, which are a succession of several tiny crystallites in *C. stella*, in contrast to the bone-to-hour-glass-shaped crystals of *C. arctica*; 2) *C. stella* generally has pores, *C. arctica* does not; 3)

trigonal crystal tops on the outer surface are equilateral in *C. arctica* and broad isosceles in *C. stella* (compare Figs. 4.2 and 7.2); 4) *C. arctica* is spherical to commonly ovoid in shape; only spherical cysts are known for *C. stella*.

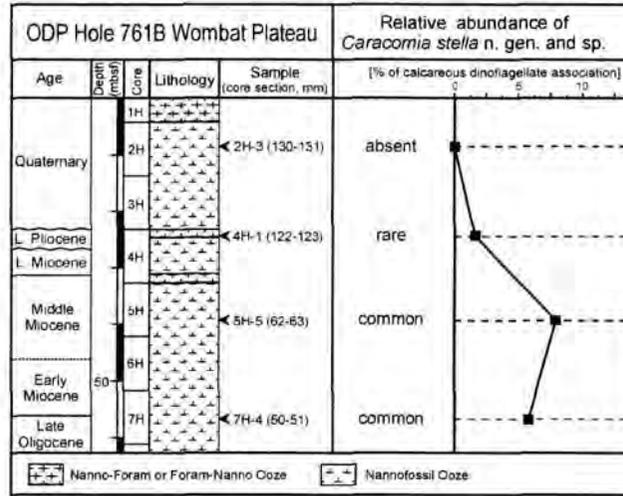


Figure 5. Relative abundance of *Caracomia stella* n. gen. and sp. and stratigraphy at ODP Site 761B, Wombat Plateau.

Caracomia stella resembles *Orthopithonella? multipora* Kienel, 1994, regarding crystal pattern on outer and inner surfaces and in the presence of pores, but differs in the habit of the individual crystals in cross-section. *Orthopithonella? multipora* is described by Kienel (1994) as a spherical, single-layered cyst with radially arranged crystals and a wall penetrated by numerous, regularly arranged pores. Although no archeopyle was observed in the type material by Kienel (1994), she assumed a small circular archeopyle, as she placed *Orthopithonella* sp. 2 of Kohring (1993b) and parts of the material of Dale (1992b, pl. 2.1, figs. 13-16), described as *Thoracosphaera granifera* Fütterer, 1977 [now: *Leonella granifera* (Fütterer, 1977) Janofske and Karwath, 2000], in synonymy. For both synonyms a small circular archeopyle is described and depicted. However, we regard the original designation of Dale (1992b) as being correct and the only depicted specimen with a circular archeopyle of *Orthopithonella* sp. 2 by Kohring (1993b; pl. 9, fig. d) is obviously a different species, as it has a distinct coarser crystal arrangement. Therefore, the true nature of the archeopyle of *O.? multipora* remains undetermined and consequently so does the generic position of this species. Further investigations are necessary to reveal the precise characteristics of the archeopyle, in order to determine whether *O.? multipora* is a species of *Caracomia* n. sp. or that of a different genus.

Occurrence.—*Caracomia stella* is known from the late Miocene and early Pliocene of the Mediterranean area (Keupp and Versteegh, 1989; Kohring, 1993a, 1993b, 1997; Keupp and Kohring, 1999), the middle and late Miocene of the North Atlantic Ocean, Sierra Leone Rise (Fütterer, 1977), the early Oligocene, NP23 and early Miocene, NN1 of the South Atlantic Ocean, Rio Grande Rise (Hildebrand-Habel and Willems, 2000) and the early Miocene, NN1 to late Pliocene, NN16 of the eastern Indian Ocean, Wombat Plateau (this paper) (see also Fig. 1).

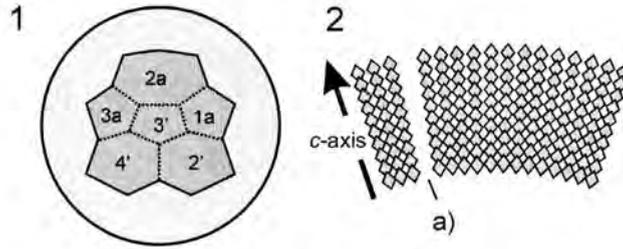


Figure 6. Schematic drawings of *Caracomia stella* n. gen. and sp. 1. 1, Archeopyle and involved plates; 2, cross section of wall showing crystal arrangement and pore (a).

***Orthopithonella* Keupp in Keupp and Mutterlose, 1984 emend.**

Type of genus.—The holotype of *Orthopithonella gustafsonii* (Bolli, 1974) Lentin and Williams, 1985.

Included species.—*Orthopithonella gustafsonii* (Bolli, 1974) Lentin and Williams, 1985.

Original diagnosis.—Cysts with predominantly single-layered calcareous walls, built of blocky to rod-like, radially arranged crystallites (c-axis perpendicular to surface). Generally no paratabulation. (Translated from Keupp in Keupp and Mutterlose, 1984, p. 158).

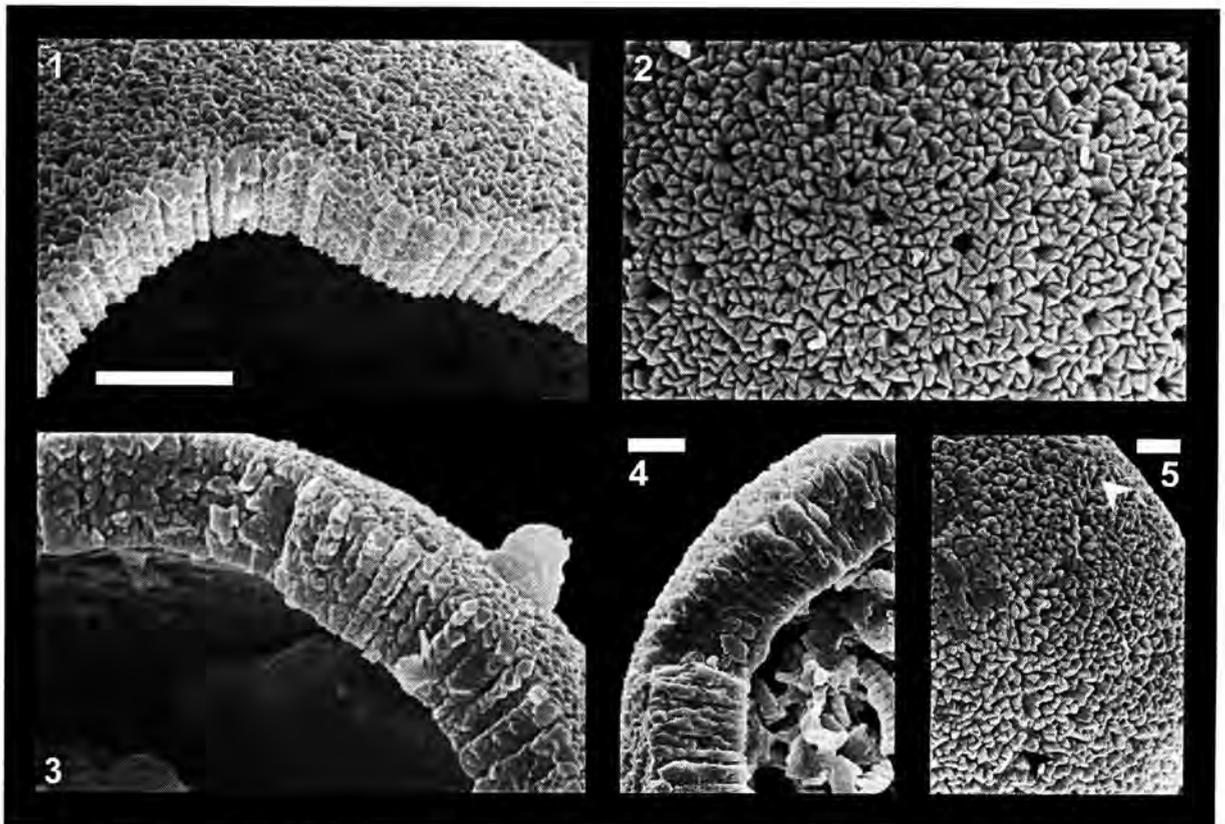


Figure 7. *Caracomia stella* n. gen. and sp. 1, oblique view of cyst surface and wall with epitaxially grown wall-forming crystals; 2, outer cyst surface with regularly arranged pores; 3, 4, cross sections of walls, revealing different diagenetic overprints; 5, outer cyst surface with faint archeopyle suture (arrows). 1, 122-4H-1/VI3, holotype; 2, 3, 122-4H-1/XIII7; 4, 122-7H-4/X20; 5, 120-7H-4/X16. Scale bars equal 3 μ m; 1-3 same scale.

Emended diagnosis.—Single-layered calcareous dinoflagellate cyst with radially oriented crystallographic c-axes of wall forming crystals; compound operculum disarticulates in several opercular pieces; polygonal archeopyle reflects tabulation and involves apical and intercalary plates.

Occurrence.—*Orthopithonella* Keupp in Keupp and Mutterlose, 1984, has been reported from the following localities: Albian of the eastern Indian Ocean (Bolli, 1974; Keupp, 1992a), middle Aptian to late Albian of Lower Saxony, Germany (e.g., Keupp, 1980b, 1992b, 1995b), and early Cenomanian of northern France (Zügel, 1994).

Discussion.—The genus *Orthopithonella* was established by Keupp in Keupp and Mutterlose (1984) to include calcareous dinoflagellates with predominantly one layer, generally without visible tabulation and a radial crystallographic orientation of the wall-forming rhombohedrons. No details of the archeopyle were given. As the type, *Pithonella gustafsonii* Bolli, 1974 was favored. The emendation of the genus by Keupp and Versteegh (1989) slightly modified the original diagnosis by excluding single-layered cysts with a radial ultrastructure and a large tabulate operculum (i.e., apical and intercalary plates). As a result, all spherical to ovoid cysts with a presumably radial ultrastructure, a small apical archeopyle and no other distinct features except the habit and arrangement of the crystallites, were integrated into *Orthopithonella*. This led to the assignment of numerous species with different types of archeopyle and different ultrastructures to the genus *Orthopithonella*. However, as with organic-walled dinoflagellate cysts, we regard the archeopyle of calcareous dinoflagellate cysts as being a major taxonomic feature for the differentiation of genera. Consequently, we consider the distinct and unequivocal features of *O. gustafsonii* described below as possibly unique within the calcareous dinoflagellate cysts. Thus, all other species previously assigned to *Orthopithonella* are accepted only questionably, pending their more detailed restudy. The potential assignment of several species to, e.g., the genus *Leonella* Janofske and Karwath, 2000, a genus which is characterized by a radial ultrastructure and a small circular archeopyle, remains to be proven individually in further investigations. The revision of two other species, i.e., *Orthopithonella flora* Fütterer, 1990 and *Orthopithonella deflandrei* (Kamptner, 1956), is currently in progress (Hildebrand-Habel, personal commun., 2001). However, a general reallocation of the remaining species of *Orthopithonella* based on the current morphological data as available from the literature is impossible. As long as no additional information is available, all these species should be retained questionably in *Orthopithonella*.

Orthopithonella Keupp in Keupp and Mutterlose, 1984 is in many details similar to *Echinodinella* Keupp, 1980a: radial ultrastructure, an obviously tabulate (polygonal) and variable archeopyle, as well as the general spherical shape of the cysts. However, in contrast to *Orthopithonella*, the species of *Echinodinella* (*E. erinacea* Keupp, 1980a and *E. levata* Keupp, 1981) are characterized by long and spiny wall-forming crystallites and may show external tabulation, especially in the zone of the cingulum. Furthermore, no reliable assignment of plates within the operculum of *Echinodinella* is possible. Generally, a distinct similarity between these two genera is evident (see also Keupp, 1992b) because of the morphological characteristics mentioned above, and because both genera overlap stratigraphically. *Echinodinella* is principally known from the late Hauterivian (e.g., Keupp, 1981) to the middle Cenomanian (Zügel, 1994); however, sparse findings from the Danian (Kienel, 1994) and Oligocene (Hildebrand-Habel and Willems, 2000) have also been reported. In contrast, *Orthopithonella*, as newly defined, is known only from the middle Aptian (Keupp, 1992b) to early Cenomanian (Zügel, 1994).

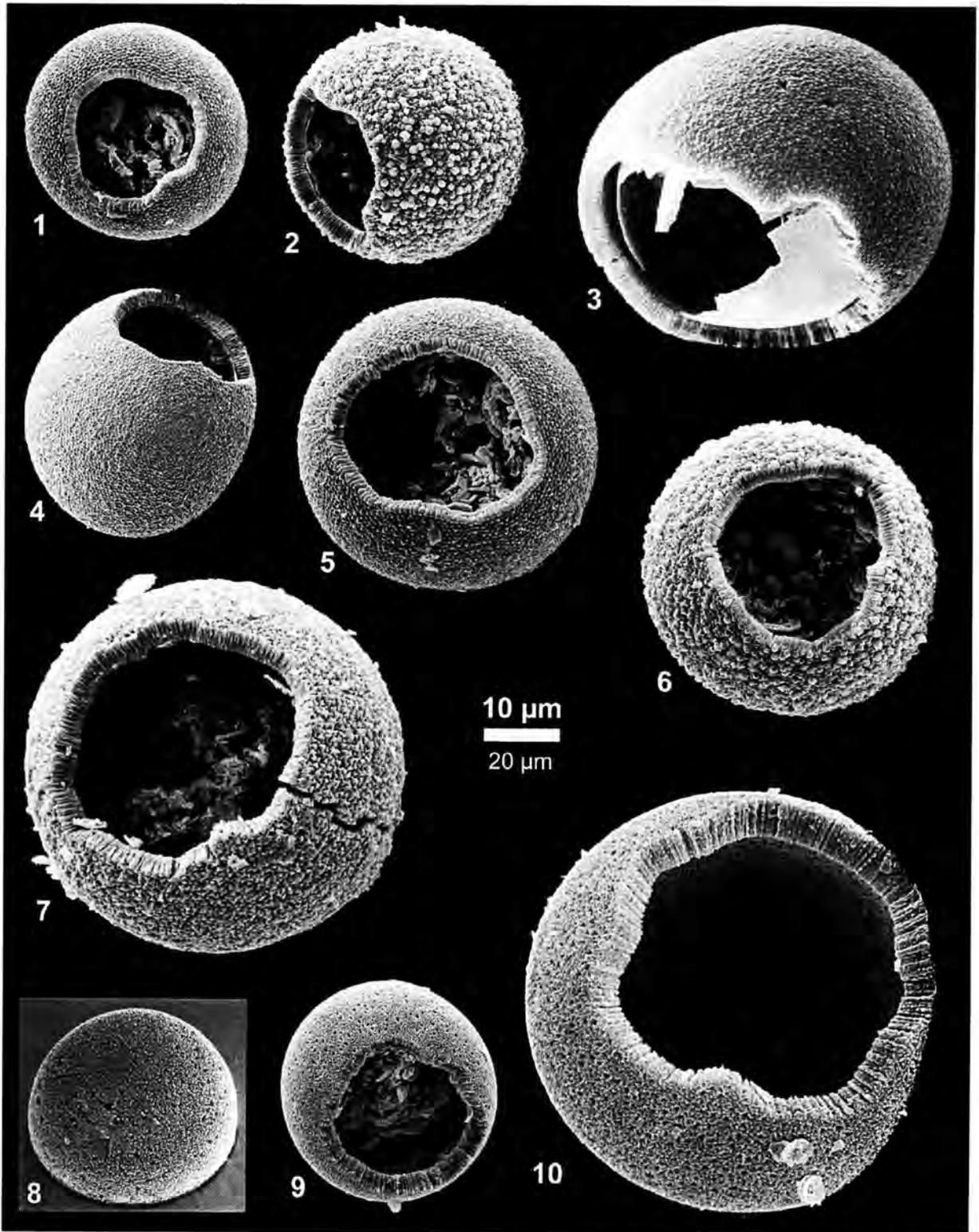


Figure 8. 1-7, *Caracomia arctica* n. gen., n. comb.; 1, relatively small cyst with delineated archeopyle; 2, 6, spherical cysts with secondary growth of wall-forming crystals resulting in a less organized appearance of outer surface; 3, large damaged ovoid cyst revealing preserved inner organic layer; 4, small ovoid cyst with smooth outer surface; 5, cyst with relatively broad archeopyle; 7, large spherical cyst. 8-10, *Caracomia stella* n. gen. and sp.; 8, cyst with star-like delineated archeopyle suture; 9, cyst with damaged archeopyle; 10, cyst with preserved tabulated archeopyle. 1, 120-6H-1/IX24; 2, 120-6H-1/V25; 3, 120-1H-5/IX8; 4, 120-1H-5/I5; 5, 120-6H-1/X13; 6, 120-6H-1/X4; 7, M6317-2/I1; 8, 122-5H-5/XIV10; 9, 122-4H-1/XIII7; 10, 122-4H-1/VI3, holotype. Scale bar equals 10 μm , except 10 (20 μm).

***Orthopithonella gustafsonii* (Bolli, 1974) Lentini and Williams, 1985 emend.**

Pithonella gustafsoni [sic] BOLLI, 1974, p. 854, pl. 3, figs. 9-12, pl. 12, figs. 7-12, pl. 13, figs. 1-2, pl. 22, fig. 3; KEUPP, 1981, pl. 9, figs. 1-7, pl. 10, fig. 3. Not: KEUPP, 1977, p. 62, pl. 21, figs. 1-4, pl. 22, figs. 1, 3, 1978, p. 89, figs. 3-5; BOLLI, 1980, p. 527, pl. 2, figs. 3-6. ?KEUPP, 1981, pl. 9 figs. 8-12, pl. 10, figs. 1-2, 4-9.

Pithonella paratabulata KEUPP, 1980b, p. 242-243, pls. 30-31, 1982, p. 315-316, pl. 6.2-2, figs. 7-11; BUJAK AND DAVIES, 1983, pl. 12, figs. 1-4.

Orthopithonella gustafsoni [sic] (Bolli, 1974) LENTINI AND WILLIAMS, 1985, p.384; BANDEL AND KEUPP, 1985, fig. 4.3; KEUPP AND VERSTEEGH, 1989, pl. 2, figs. 13-14. Not: KEUPP in KEUPP AND MUTTERLOSE, 1984, p. 158-159, pl. 20, figs. 1-11; WILLEMS, 1988, p. 437-445, pl. 1, figs. 1-6, pl. 2, figs. 7-9; KEUPP AND ILG, 1989, p. 168, pl. 1, figs. 1-3; FÜTTERER, 1990, p. 538-539, pl. 4, figs. 4-5, 8-10; BANTEL, SCHWEIGERT, NOSE, AND SCHULZ, 1999, pl. 4, figs. 2-3. ?KEUPP, 1987, p. 43, pl. 7, figs. 7-9.

Orthopithonella gustafsonii (Bolli, 1974). KEUPP, 1991b, fig. 7, 1992a, p. 499, pl. 1, figs. 1-5, 1992b, p. 130, pl. 4, figs. 2-9, 1995a, figs. 2.1-2.2; KEUPP, MONNET, AND KOHRING, 1991, pl. 1, fig. 10; MONNET, 1993, p. 22-24, pl. 4, figs. 1-3. Not: IVANOVA AND KEUPP, 1999, p. 9-10, pl. 1, figs. 3-5, pl. 2, figs. 3-4; NEUMANN, 1999, p. 22, pl. 1, fig. 7. ?KEUPP, 1995b, p. 163, pl. 8, fig. 12.

Orthopithonella aff. *gustafsonii* (Bolli, 1974). ZÜGEL, 1994, pl. 19, figs. 10-11, not pl. 19, figs. 1-9.

Not *Orthopithonella* aff. *gustafsonii* (Bolli, 1974). KEUPP, 1991, p. 129, pl. 1, figs. 1-4; KOHRING, 1993a, p. 31-32, pl. 8, figs. h-m.

Not *Orthopithonella* sp. aff. *gustafsonii* (Bolli, 1974). WILLEMS, 1996, p. 223, pl. 1, fig. 1; HILDEBRAND-HABEL, WILLEMS, AND VERSTEEGH, 1999, pl. 2, figs. 18-19; HILDEBRAND-HABEL AND WILLEMS, 2000, fig. 5i.

Not *Orthopithonella* cf. *gustafsonii* (Bolli, 1974). KEUPP, 1992b, p. 130-131, pl. 3, fig. 12, pl. 4, fig. 1; KEUPP AND KOWALSKI, 1992, p. 217-218, pl. 1, figs. 12-13; KEUPP AND MUTTERLOSE, 1994, p. 748, fig. 8.5; KIENEL, 1994, p. 34; HILDEBRAND-HABEL AND WILLEMS, 1997, p. 184, pl. 2, figs. 11-13.

? *Orthopithonella* aff. *gustafsonii* (Bolli, 1974). KEUPP, MONNET, AND KOHRING, 1991, pl. 1, fig. 9.

Basionym.—*Pithonella gustafsonii* Bolli, 1974 p. 843-907, pl. 3, figs. 9-12, pl. 12, figs. 7-12, pl. 13, figs. 1-2, pl. 22, fig. 3.

Holotype.—Bolli, 1974, pl. 3 figs. 9, pl. 12, fig. 9, pl. 22, fig. 3; middle Albian.

Original diagnosis.—Test spherical, formed by one layer of about 4 μm thickness. Outer surface consists of subrounded to angular fairly regular in size calcite crystals of 1-2 μm , arranged in tight, cobblestone-like pattern. Crystals elongate in cross-section, slightly conical with long axis in radial position. Wall thickness equals length of crystals. Inner surface similar to outer, but crystal ends more angular, slightly smaller and with faces better developed. Circular aperture fairly small, regular. Plate 12, Figures 7, 8, and 12 shows specimens where apertures are enlarged because part of rim is broken out. (Original description from Bolli, 1974, p. 854, which served as a diagnosis).

Emended diagnosis.—Species of *Orthopithonella* with radially arranged wall-forming crystals. Cysts spherical to ovoid in shape; inner surface similar to outer surface; tabulation delineated by faint sutures; opercular pieces monoplacoid.

Description.—Spherical to slightly ovoid calcareous dinoflagellate cysts with single-layered walls. Diameter of cysts ranges from 30 to 60 μm , thickness of wall from 1.5 to 4 μm . Wall consists of radially oriented and elongated, generally triradiate calcite rhombohedrons. Distal crystal growth often leads to development of skeletal-like or dendritic crystal ends. An inner organic layer occasionally preserved. Epicyst reflects standard peridinialean tabulation delineated by faint sutures. Number and visibility of reflected plates varies depending on the state of preservation of the sample material. Operculum is variable, simple monoplacoid or compound polyplacoid, comprised of one to six plates. Opercular pieces all monoplacoid, separated by accessory archeopyle sutures. Resulting potential archeopyle formulas are: A_2 (respectively A_4 , see Discussion), A_3 , $2A_{2-3}$, $2A_{2-4}$, $3A_{2-4}$ (apical

archeopyles, Fig. 9.2-9.6), $3A_{2-4}I_{1a}$, and $3A_{2-4}tI$ (combination archeopyles, Fig. 9.7-9.8). However, the presumed principal archeopyle suture surrounds apical and intercalary plates. Accordingly, the archeopyle formula is $3A_{2-4}tI$. (Based on the descriptions and illustrations of Bolli, 1974; Keupp, 1980b, 1982, 1992b; and Monnet, 1993).

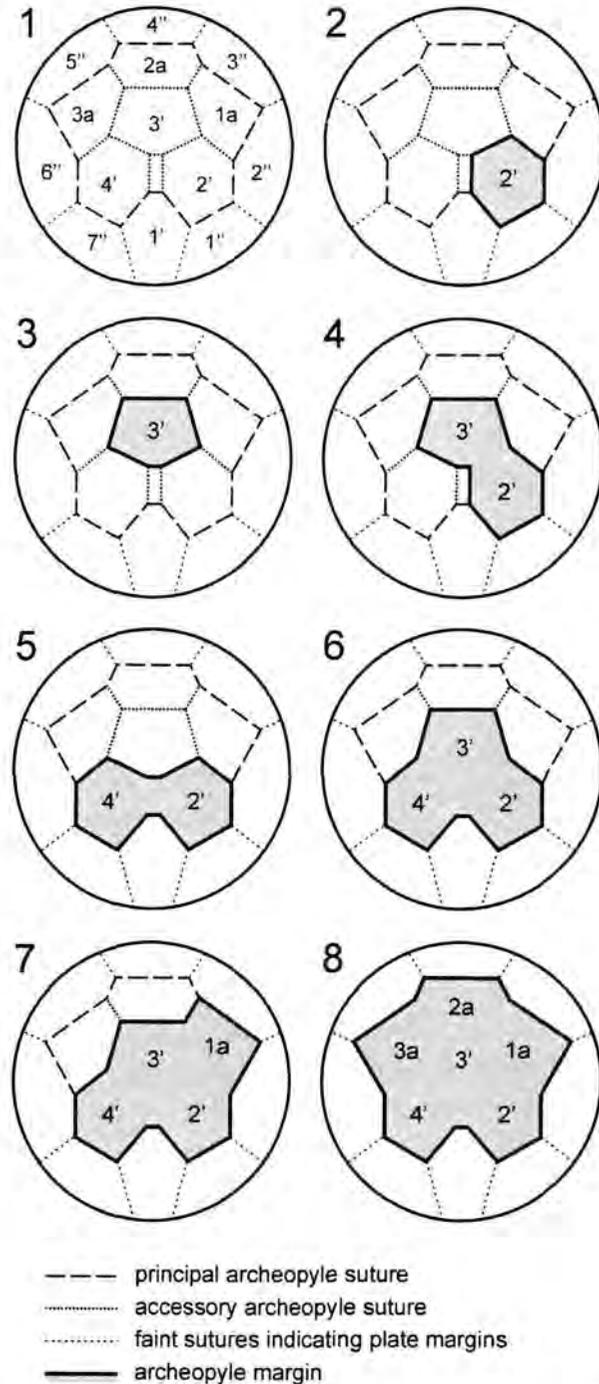


Figure 9. Schematic drawings of epicyst of *Orthopithonella gustafsonii* (Bolli, 1974) in apical view. 1, Epicystal peridinial tabulation pattern of *O. gustafsonii* (modified after Keupp, 1981, fig. 5); 2-8, potential archeopyle types and involved corresponding plates (see text and Table 1 for details).

Occurrence.—As for genus.

Discussion.—Within the species *O. gustafsonii*, two different morphotypes were previously recognized (e.g., Keupp, 1981 and Willems, 1988): *O. gustafsonii* (Bolli, 1974) *sensu stricto* with a polygonal archeopyle, and a morphotype with an equivalent wall structure but circular archeopyle. The reason for this unification was the misinterpretation of the holotype in the original description of Bolli (1974) and by subsequent authors (e.g., Keupp, 1981 and Fütterer, 1990). Bolli (1974) described *O. gustafsonii* as having a circular aperture and depicted a specimen with a small archeopyle that superficially appears circular but is in fact polygonal and results from the absence of one of the apical plates. This assumption is confirmed by the illustrated paratypes of Bolli (1974, e.g., pl. 12, fig. 7) which precisely show the absence of all three apical plates. Bolli, for his part, interpreted these archeopyles as secondarily enlarged. Keupp (1981) recognized the tabulation in Bolli's paratypes, but still considered the archeopyle of the holotype as being circular. He described two variants, a tabulate and a non-tabulate morphotype, both of which he included in *Orthopithonella gustafsonii*. Fütterer (1990) was the first to point out that the archeopyle of calcareous dinoflagellate cysts is an important systematic feature. Accordingly, he rejected the concept of Keupp (1981), but failed to recognize the polygonal nature of the archeopyle of the holotype of *O. gustafsonii* and furthermore excluded the tabulate morphotype from the species itself. Finally, Keupp (1991a, 1992a) accepted the polygonal character of the archeopyle in the type material of Bolli (1974) and suggested separation of cysts with circular archeopyles from *O. gustafsonii*. Subsequent authors generally followed this suggestion and described these cysts as *Orthopithonella* aff. *gustafsonii* and *O. cf. gustafsonii*, respectively. However, no formal names for these cysts have ever been established. Willems (1988) and Ivanova and Keupp (1999) synonymized several taxa with *O. gustafsonii*, which were only known from cross sections and thin sections, respectively. However, as an archeopyle is not visible in any of these species, this synonymy is rejected. Further investigations are necessary to clarify their true generic and specific position.

Table 1. Depicted archeopyle types of *Orthopithonella gustafsonii* (Bolli, 1974) in literature.

archeopyle formula	references
A_2 / A_4	Bolli, 1974, pl. 3, fig. 9, pl. 12, fig. 9, pl. 22, fig. 3; Keupp, 1980b, pl. 31, fig. 6; ?Keupp, Monnet, and Kohring, 1991, pl. 1, fig. 9.
A_3	Keupp, 1982, pl. 6.2-2, fig. 11, 1992b, pl. 4, figs. 3-4, 1995a, fig. 2.1; Keupp and Versteegh, 1989, pl. 2, fig. 14.
$2A_{2-3}$	Keupp, 1980b, pl. 31, fig. 4.
$2A_{2+4}$	Keupp, 1992a, pl. 1 fig. 2.
$3A_{2-4}$	Bolli, 1974, pl. 12, figs. 7, 12; Keupp, 1974, pl. 31, fig. 3; Keupp, 1981, pl. 9, fig. 2, Keupp, 1982, pl. 6.2-2, fig. 10; Bujak and Davies, 1983, pl. 12, figs. 3-4; Keupp and Versteegh, 1989, pl. 2, fig. 13; Keupp, 1991b, fig. 7; Keupp, 1992a, pl. 1, fig. 1; Keupp, 1995a, fig. 2.2.
$3A_{2-4}I_{1a}$	Zügel, 1994, pl. 19, fig. 10.
$3A_{2-4}tI$	Keupp, 1981, pl. 9, fig. 3.

The archeopyle formula A_2 and A_4 , respectively, as given in the description of *O. gustafsonii*, is somewhat hypothetical, as it is derived from illustrations of Bolli (1974, pl. 12, fig. 9) and Keupp (1980b, pl. 31, fig. 6), both of whom depicted specimens of *O. gustafsonii* with a clearly equilateral, six-sided archeopyle involving a single plate. Keupp (1980b) interpreted the archeopyle as resulting from the loss of apical plate 3'. The shape of these archeopyles, however, looks quite different from the typical 3' apical plates of *O. gustafsonii* (e.g., Keupp, 1992b, pl. 4, fig. 3). The shape of plate 3' resembles a pentagon, as its antapically directed margin to the platelet between plate 2' and 4' (see Fig. 9.1) is distinctly narrower than all other margins of this plate, in contrast to the hexagonal, approximately equilateral plates 2' and 4'. Therefore, the archeopyles depicted in Bolli (1974) and Keupp (1980b) more likely correspond to plates 2' or 4', respectively. According to Fensome et al. (1993), however, the third apical plate is always involved in archeopyle formation in the Calciodinelloideae. It is therefore assumed that when fully developed the archeopyle of *O. gustafsonii* comprises apical and intercalary plates (archeopyle formula $3A_{2-4}tI$). All other observed archeopyles appear to represent incomplete loss of plates (Tab. 1).

CONCLUSIONS

When Janofske and Karwath (2000) assigned the type of the genus *Sphaerodinella* Keupp and Versteegh, 1989, i.e., *S. albatrosiana* (Kamptner, 1963), to the genus *Calciodinellum* Deflandre, 1947, they made the erection of a new genus for the remaining species *S. arctica* (Gilbert and Clark, 1983) inevitable. The new genus *Caracomia* is introduced to include the former *S. arctica*, now newly combined as *Caracomia arctica*, and an additional new species *Caracomia stella*. The two species of *Caracomia* have evidently contrasting regional distributions. *Caracomia arctica* is restricted to the cold oceans of both hemispheres in contrast to *C. stella* which prefers tropical to temperate environments. The genus *Caracomia* is closely related to the type of *Orthopithonella* Keupp in Keupp and Mutterlose, 1984, *O. gustafsonii* (Bolli, 1974). Inconsistencies in the literature concerning this species have necessitated an emendation of both the species and the genus. *Orthopithonella* is redefined and only *O. gustafsonii* is included with certainty. Other presently accepted species of *Orthopithonella* should probably be excluded from this genus. However, as no reliable data of these species is available, especially concerning the crystallographic wall structure, a reallocation is not yet possible. Accordingly we retain these species questionably in *Orthopithonella*, pending their future restudy.

Inconsistencies within the generic affiliations of calcareous dinoflagellate cysts are a widespread phenomenon that may be partly due to a taxonomic concept introduced by Keupp and Mutterlose (1984) and Keupp (1987). This concept regards the wall ultrastructure of fossil calcareous dinoflagellate cysts as the most significant feature for its classification. Subsequent authors who applied this concept therefore often neglected tabulation and cryptotabulation patterns. We assume that tabulation, especially of the archeopyle, is of major taxonomic relevance for calcareous dinoflagellate cyst classification (see also Fütterer, 1990). To avoid future discrepancies, we propose a more detailed and elaborate taxonomic concept for classifying fossil calcareous dinoflagellate cyst genera, which includes the following attributes: 1) type of tabulation; 2) number of wall layers (and whether number is constant); and 3) ultrastructure of the individual layers. Differentiation at the species level should take into account crystal habit and arrangement, shape of the cyst, and other morphological details, such as number and size of pores, and the proportions of plate homologues. The

extent to which nontabular ornamentation (e.g., spines) is diagnostic of specific or generic level must be assessed and tested in each case.

It must be emphasized, however, that this concept is a parataxonomy, to be used alongside taxonomy developed for the motile stage, bearing in mind that the detailed biological identity of these cysts remains unknown. However, this concept appears to be the most useful and practicable for classifying fossil calcareous dinoflagellate cysts at the moment. Further investigations, especially those based on molecular data of extant species, will probably unveil and clarify the complete taxonomic identities of the individual calcareous cysts. Studies dealing with this subject are currently in progress (D'Onofrio et al., 1999; Montresor, personal commun., 2000). Whether there is a potential applicability of such studies to fossil species, however, still remains to be seen.

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Archeopyles of fossil calcareous dinoflagellate cysts (Calciodinelloideae)

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ABSTRACT.—An extensive review of all fossil species of calcareous dinoflagellate cysts regarding their archeopyle type is given. After evaluating the phylogenetic significance of archeopyles in calcareous dinoflagellate cysts, we developed a concept for classification which focuses on the different archeopyle types. As a mutual basis for this concept, the different known excystment strategies and archeopyle types are described. Until now, three categories of archeopyles have been recognized within the calcareous dinoflagellate cysts, i.e., apical, intercalary, and combination archeopyles, which can be subdivided into seven archeopyle types and several variations. Archeopyles that cannot be assigned to a distinct type and those with outlines that do not allow an accurate accommodation, respectively, are summarized under miscellaneous archeopyles. The stratigraphic distribution of the different archeopyle types reveals a phylogenetic trend that is characterized by an increase of the number of plates involved in the archeopyle. The potential use of archeopyle types for taxonomy is discussed. Two new terms are proposed to describe archeopyles of calcareous dinoflagellate cysts, i.e., mesoepicystal archeopyle and archeopyle area. Additionally, the following taxa are newly described and combined, respectively: *Calciodinellum clamosum* n. sp., accommodating two subspecies: *Calciodinellum clamosum clamosum* Autonym, and *Calciodinellum clamosum latum* n. sp. and ssp.; *Calciodinellum kerguelensis* n. sp.; *Fuettererella belliata* n. sp.; *Pernambugia? patata* n. sp.; *Cervisiella operculata* (Bramlette and Martini, 1964) n. comb.; *Praecalzigonellum sulcatum* (Keupp, 1979a) n. comb.; *Praecalzigonellum dolium* (Keupp, 1979b) n. comb. The genera *Echinodinella* Keupp, 1980a, *Fuettererella* Kohring, 1993a, and *Pernambugia* Janofske and Karwath in Karwath, 2000 are emended. The species *Orthopithonella? minuta* Fütterer, 1990 and *Pirumella johnstonei* (Bolli, 1974) Lentini and Williams, 1993 are retained as separate taxa. A list of all fossil calcareous dinoflagellate species is given comprising the corresponding archeopyle type of each species.

INTRODUCTION

Classification of fossil calcareous dinoflagellate cysts has been based for a long time mainly on the ultrastructure of the calcareous wall. Four wall types have been distinguished: (radial, tangential, oblique, and pithonelloid) according to the orientation of the crystallographic c-axes of the wall-forming crystallites (summarized in Young et al., 1998). Many authors assumed these wall types to be the most significant feature for classification (e.g., Keupp, 1987; Kohring, 1993a; Janofske, 1996) and therefore insufficiently described other taxonomically important characteristics of the cyst, e.g., the archeopyle, which is often the only feature that reflects tabulation (cryptotabulate cysts). As a consequence, cysts with different archeopyle characteristics (i.e., different cryptotabulation) were unified within the same genus (see Streng et al., 2002 [Chapter 2.1], and Appendix I herein). Moreover, Fensome et al. (1993) regarded the wall structure of calcareous dinoflagellate cysts to be of unproven value for phylogenetic considerations. Streng et al. (2002) followed this view and proposed

a more elaborate concept to describe fossil calcareous dinoflagellate cysts: In addition to the wall structure, it takes especially the characteristics of the archeopyle into account, such as outline, number and pattern of plates involved and features of the operculum. As those features have been overlooked by many authors in earlier studies, no distinct archeopyle types, like in the organic-walled cysts (e.g., Evitt, 1967), have been defined. Furthermore, the specific terminology for the description of archeopyles is entirely based on organic dinoflagellate cysts. This terminology is in many aspects appropriate for the description of calcareous cysts, but not all characteristics of the archeopyle and the operculum of organic cysts are comparable to those of the calcareous cysts. The aim of this study is to review and to describe in detail the presently known archeopyle characteristics and types of calcareous dinoflagellate cysts, thus creating a common descriptive terminology for future studies.

The term archeopyle was introduced by Evitt (1961) to describe openings in fossil dinoflagellate cysts resulting from the release of plates (operculum) along predetermined lines. This definition has been improved and generalized by subsequent authors (e.g., Evitt, 1967; Lentin and Williams, 1976) by including any kind of aperture of a dinoflagellate cyst that serves for excystment (see also Fensome et al., 1996 for details). In the calcareous dinoflagellate cysts, different types of excystment strategies as well as various archeopyle types exist that are in many aspects similar to those of organic walled dinoflagellate cysts, but often show differences. Terms for the description of archeopyles used herein are summarized in Williams et al. (1978, 2000), and Fensome et al. (1996). Additionally, we propose new terms for some particular characteristics of calcareous cysts.

EXCYSTMENT TYPES OF CALCAREOUS DINOFLAGELLATE CYSTS

Excystment of calcareous dinoflagellate cysts typically occurs by the loss of an operculum. Opercula of calcareous cysts are generally simple and free, mono- or polyplacoid, and are delineated by a principal archeopyle suture. This suture may or may not be visible in undehisced cysts. However, several exceptions to this general way of excystment occur:

- 1) The Cretaceous species *Orthopithonella gustafsonii* (Bolli, 1974) and probably *Echinodinella erinacea* Keupp, 1980a emend. have a compound operculum involving several accessory archeopyle sutures (see Streng et al., 2002 [Chapter 2.1] and description of *E. erinacea* herein).
- 2) *Pernambugia? patata* n. sp. has a principal archeopyle suture that does not completely surround the operculum. For excystment, a secondary unpredetermined archeopyle suture is generated, that makes the release of the operculum possible. The resulting archeopyle is principally similar to slit-like archeopyles of the organic-walled cysts, however, in contrast to the pliable organic cysts, the calcareous walls of *P.? patata* are rigid and consequently, the operculum and sometimes cyst parts, that would have stayed attached in the organic walled dinoflagellates, break off to enable hatching (see also chapter Epicystal Archeopyles and Description of *P.? patata* n. sp.).
- 3) *Calcicarpinum bivalvum* (Fig. 1.6), *Calciperidinium asymmetricum* (Fig. 1.13), and *Follisdinellum splendidum*, described from the Pliocene of the Mediterranean Sea by Versteegh (1993), obviously have an unique type of excystment. They have an apically located area indicating the location of excystment which is visible on the outer cyst surface. This area, which will be called archeopyle area in the following, is generally discernible in closed cysts by its specific crystal pattern, different to that of the adjacent cyst surface. Dehisced cysts of this type typically show a partial, barely a complete loss of this area, resulting in archeopyles with variable outlines (see Versteegh, 1993, pls. 2, 3, 5). As a result, no operculum in the common sense is released, but parts of this area either break off or are

dissolved for excystment. Tabulation is generally reflected by the archeopyle area rather than by the archeopyle itself which is typically smaller and randomly shaped. Only if the archeopyle matches the archeopyle area, it reflects the tabulation. However, the interpretation of plate numbers involved in an archeopyle area is complex, especially in *F. splendidum*, as the archeopyle area is often transitional to the adjacent cyst surface and no clear outline is visible.

In all excystment strategies described above excystment along predetermined intraspecifically consistent sutures is presumed. However, from many species, especially from the Triassic and Cretaceous, the way of excystment is dubious and unknown, respectively, for the following reasons: 1) Many species have been described only from undehisced cysts without any observed sutures or openings (see Appendix I). Furthermore, 2) a lot of species show irregularly shaped archeopyles with no obvious relation to tabulation (e.g., many species of the genus *Pirumella* Bolli, 1980). The irregular shape of the archeopyles may either be the result of inappropriate preservation, breakage, or due to a coarse crystal structure of the cyst wall that does not allow the reflection of plates. Nevertheless, a potential plate-unrelated excystment for those species cannot be excluded, as they are generally bare of any kind of tabulation pattern. Furthermore, the dinoflagellate nature of certain species, especially of those without any kind of visible aperture, is still questionable. Their accommodation within the calcareous dinoflagellates is based on the comparison of the wall structure with unequivocal and approved representatives of the Calciodinelloideae (see also Fensome et al., 1993).

ARCHEOPYLE TYPES OF CALCAREOUS DINOFLAGELLATE CYSTS

Fossil calcareous dinoflagellate cysts exhibit many different archeopyle types, which can be grouped into four of the five categories of Evitt (1967): apical, intercalary, and combination archeopyles as well as miscellaneous archeopyles. Precingular archeopyles, Evitt's fifth category, typical for certain non-peridinioid cysts, have not been observed in the Calciodinelloideae. All archeopyles of calcareous dinoflagellate cysts seem to be restricted to the epicyst, because there is always an apical excystment opening in those cysts that allow orientation based on the tabulation. In cysts that possess a clear tabulation, the archeopyle outline is symmetrical

For each archeopyle type, the type formula developed by Evitt (1967, 1985) is given. Species with a pithonelloid wall are treated as a separate group as their affiliation to the dinoflagellates is still under discussion. For explanation of different type formulas see Appendix III.

Category 1: Apical archeopyles

Apical archeopyles (Evitt, 1961) are archeopyles that only involve plates from the apical series. Within the calcareous dinoflagellates currently three types of apical archeopyles have been recognized, accommodated in two groups, i.e., apical archeopyles with monoplacoid operculum (Type A) and apical archeopyles with polyplacoid operculum (Type 3A) and Type 3A).

Apical archeopyles with monoplacoid operculum

Figures 1.1-1.12, 10.2, 10.5, 10.8

In the calcareous dinoflagellates relatively small, circular to slightly angular archeopyles are interpreted as apical archeopyles including the single plate 3' (e.g., Keupp and Versteegh, 1989; Fensome et al., 1993), representing the Type A *sensu* Evitt (1985). The apical position of these

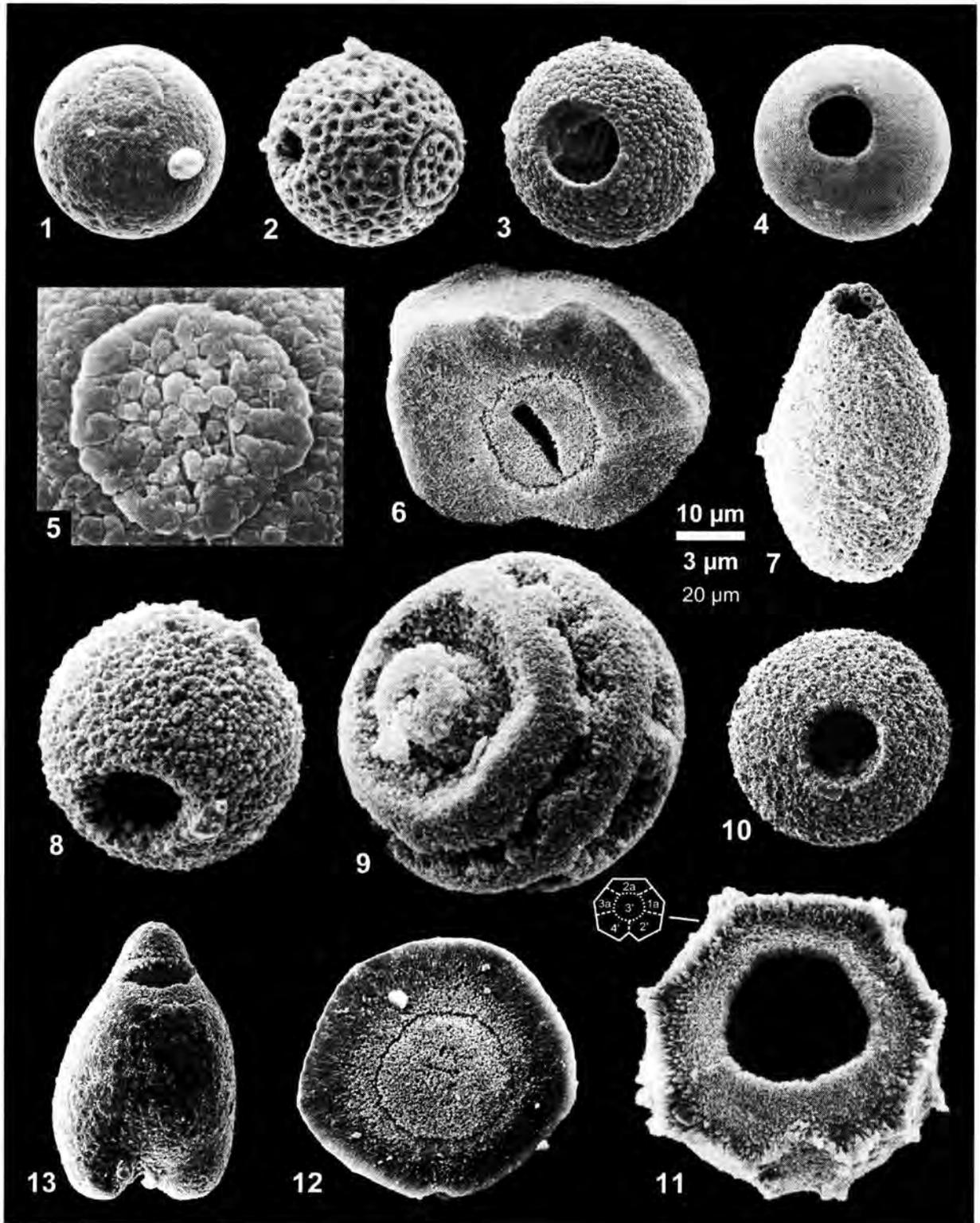


Figure 1. 1-11, Various examples of calcareous dinoflagellate cysts with an apical archeopyle that includes the single apical plate 3', Type A. 12, Species with a presumed apical archeopyle. 13, Species with a potential intercalary archeopyle. Localities: 1-5, 7 = Wombat Plateau, ODP Site 761; 8, 10 = Kerguelen Plateau, ODP Site 747; 6, 9, 13 = Southern continental margin of Crete; 11 = Vöhrum clay pit, Lower Saxony, Germany; 12 = Calabria, south Italy. 1, Cyst of *Cervisiella saxea* (Stradner, 1961) Hildebrand-Habel et al., 1999 bearing a distinct operculum; early Miocene. 2, Cyst of *Cervisiella operculata* (Bramlette and Martini, 1964) n. comb.

archeopyles has been assumed based on comparison with orientated taxa, like ovoid or tabulated species (e.g., *Fuetererella belliata* n. sp. (Figs. 10), *Bicarinellum tricarinelloides* Versteegh, 1993 (Fig. 1.9)). The generally small size of the archeopyle, typically about 30 percent of the cyst diameter, suggests the involvement of only a single plate, assumed to be the apically situated plate 3'. Additionally, several tabulated species confirm this type of archeopyle, e.g., *Keuppisphaera radiata* (Keupp, 1987) and *Heptasphaera michaelii* (Keupp, 1979b). However, relatively large circular archeopyles, with a cyst-archeopyle diameter ratio of up to 0.5, have also been interpreted as representing the single plate 3' (e.g., *Praecalcionellum polymorphum* (Keupp, 1980a); see Fig. 1.11). In those cases, unequivocal tabulation patterns are required for accurate interpretations.

The monoplacoid apical archeopyle type is most common within the calcareous dinoflagellate cysts and four variations can be distinguished:

- A) The archeopyle is created by the loss of an operculum that is distinguished from the adjacent cyst surface by a distinct groove. Therefore, the operculum is always visible in undehisced specimens. The crystal pattern on the outer surfaces of cyst and operculum are more or less identical. The opercula may be strengthened by a distinct rim (Fig. 1.5). Examples of this variation are: *Leonella granifera* (Fütterer, 1977) Janofske and Karwath in Karwath, 2000 (Fig. 1.4); *Cervisiella saxea* (Stradner, 1961) Hildebrand-Habel et al., 1999 (Figs. 1.1, 1.5).
- B) The operculum is indiscernible in closed cysts. The archeopyle is relatively small and circular or slightly angular in outline. The crystal pattern on the outer surfaces of cyst and operculum are identical (e.g., *Fuetererella belliata* n. sp. (Fig. 10); *Pirumella edgarii* (Bolli, 1974) Lentin and Williams, 1993).
- C) The archeopyle area is distinguished from the surrounding cyst surface by a different crystallographic pattern. There is no release of an operculum, but a part of the archeopyle area is opened for excystment (*Calcicarpinum bivalvum* Versteegh, 1993, Fig. 1.6).
- D) The operculum is superimposed and morphologically distinguished from the adjacent cyst surface (e.g., *Calcicarpinum perfectum* Versteegh, 1993; *Bicarinellum tricarinelloides* Versteegh, 1993, Fig. 1.9)

with distinct operculum; late Paleocene. 3, Dehisced cyst of *Fuetererella deflandrei* (Kamptner, 1956) Hildebrand-Habel and Streng (in review) revealing circular archeopyle; middle Miocene. 4, Cyst of *Leonella granifera* (Fütterer, 1977) Janofske and Karwath in Karwath, 2000; late Pliocene. 5, Operculum of *Cervisiella saxea*; middle Miocene. 6, Apical view of *Calcicarpinum bivalvum* Versteegh, 1993 showing archeopyle area and partly lost operculum; late Pleistocene. 7, Single layered *Pirumella* cf. *amplicrystallina* (Pflaumann and Krashennikov, 1978) Lentin and Williams, 1993; late Maastrichtian. 8, Dehisced cyst of *Pirumella edgarii* (Bolli, 1974) Lentin and Williams, 1993; early Paleocene. 9, *Bicarinellum tricarinelloides* Versteegh, 1993; late Pleistocene. 10, *Fuetererella flora* (Fütterer, 1990) Hildebrand-Habel and Streng (in review); early Eocene. 11, *Praecalcionellum polymorphum polymorphum* Autonym with relatively large archeopyle; Aptian-Albian boundary interval. 12, *Praecalcionellum schizosaeptum* Versteegh, 1993; late Pliocene. 13, Dorsal view of *Calciperidinium asymmetricum* Versteegh, 1993 showing partly removed archeopyle area; late Pleistocene.

1, 122-7H-4/IV16; 2, 122-16X-2/IX3-2; 3, 122-5H-5/X9; 4, 122-4H-1/XIII6; 5, 122-5H-5/VI2; 6, T20-S1/80-81/70. 7, 122-22X-3/19-2; 8, 120-20X-1/VIII20; 9, T20-S1/80-81/74; 10, 120-19X-2-11/IX37; 11, Voe6-62; 12, 9453/52; 13, T20-S1/80-81/106. Scale bar equals 10 µm for whole cysts (1-4, 6, 8, 9, 11-13) and 3 µm for close-up (5); except 7 and 10 (20 µm).

Apical archeopyles with polyplacoid operculum

Figures 2.2-2.6, 2.10

Apical archeopyles that involve more than one plate are extremely rare within the calcareous dinoflagellates and have been proven for a single species only, i.e., *Bitorus turbiformis* Keupp, 1992a from the Valanginian of the eastern Indian Ocean. According to Keupp (1992a), the operculum of *B. turbiformis* includes the apical plates 2'-4'. For the two Cenozoic representatives of this genus, *B. bulbjergensis* Kienel, 1994 and *B. truncus* Hildebrand-Habel and Willems, 1999, the same archeopyle type is assumed although it is not perceivable. The Cretaceous genus *Echinodinella* Keupp, 1980a, emended herein (see also Systematic Paleontology), is obviously another genus that possesses the same archeopyle type as *B. turbiformis*, though with some minor differences. Therefore, two types of polyplacoid apical archeopyles can be distinguished:

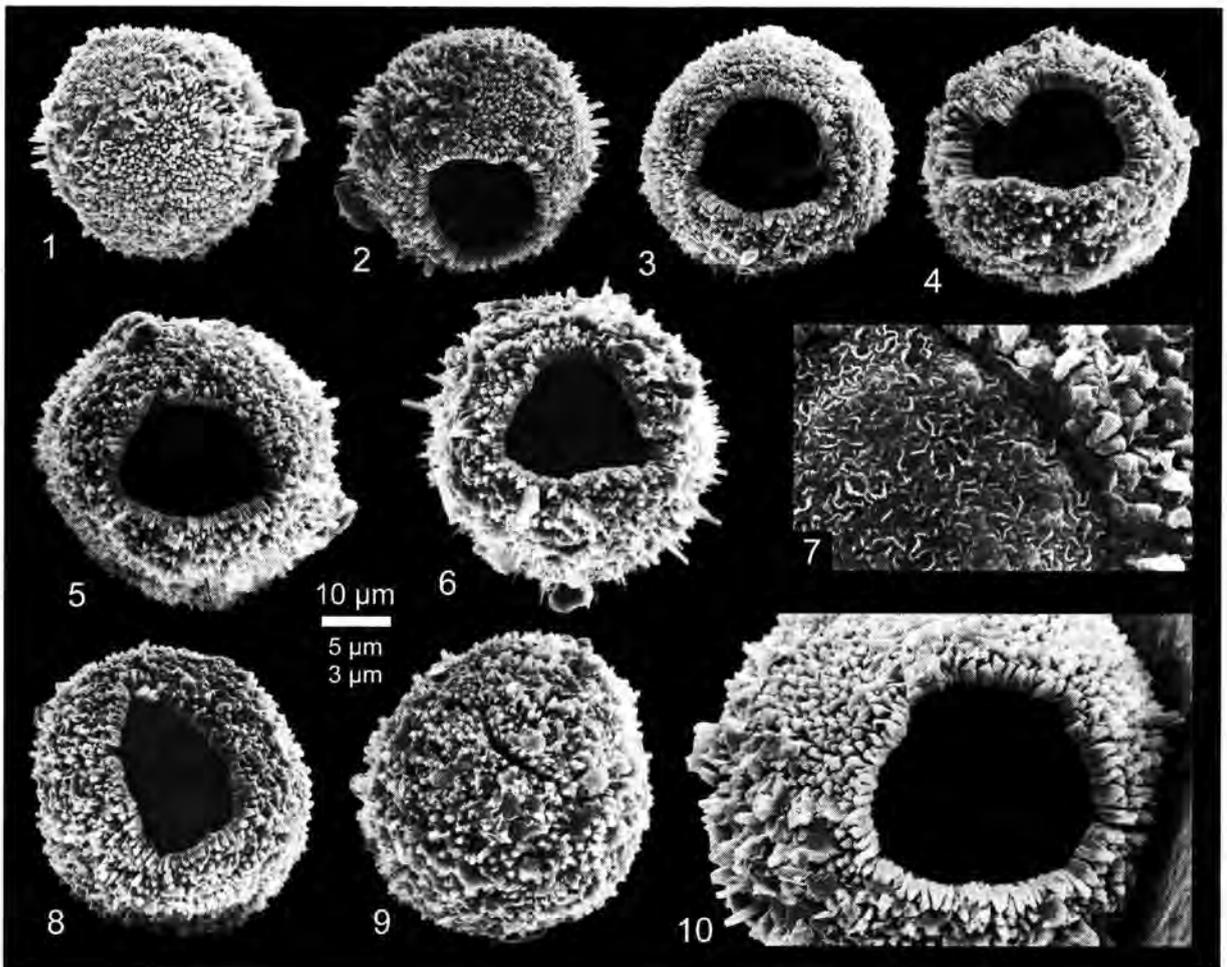


Figure 2. *Echinodinella erinacea* Keupp, 1980a emend. from the Aptian-Albian boundary interval of the Vöhrum clay pit, Lower Saxony (Germany) showing a Type 3A archeopyle. 1, Lateral view of cyst with cingulum reflected by elongated crystals. 2, Same specimen as in 1, showing tabulated archeopyle and reflected cingulum. 3, 5, Cysts with rounded archeopyle outline. 4, 6, Cysts showing lateral enlarging of archeopyle. 7, Outer surface of inner organic layer showing residues of the solvable matrix delineating triradiate crystal bases. 8, Cyst with irregularly shaped aperture of unknown origin. 9, Undehisced cyst showing rarely observable archeopyle suture. 10, Perfectly preserved tabulated archeopyle; same specimen as in 1 and 2.

1, 2, 10, Voe8-23; 3, Voe6-64; 4, Voe6-25; 5, Voe6-86, 6, Voe6-29; 7, Voe6-48; 8, Voe6-5; 9, Voe6-72.

Type (3A).—The archeopyle is created by the loss of a simple operculum. The archeopyle suture is predictable through the external tabulation of the cyst. (e.g., *Bitorus turbiformis* Keupp, 1992a)

Type 3A.—The archeopyle is created by the loss of a presumed compound operculum. Archeopyle sutures are generally indistinct in undehisced cysts. (e.g., *Echinodinella erinacea* Keupp, 1980a; Fig. 2)

A species with an enigmatic archeopyle was described by Hultberg (1985) as *Pithonella organica* from the early Paleocene of Sweden. It is characterized by two layers, a probably oblique outer calcareous wall with a rugulate surface and an inner tabulated organic layer. In contrast to the calcareous layer that obviously has a circular archeopyle, a 3A archeopyle was described for the inner organic layer, involving plates 2'-4'. As these features are unique within the calcareous dinoflagellate cysts, the species needs reallocation and reexamination to find an appropriate genus that coincides with these particular characteristics. Therefore, this species is cited as *Pithonella? organica* Hultberg, 1985 in Appendix I.

Category 2: Intercalary archeopyles

Figure 1.13

Intercalary archeopyles (Evitt, 1961) are quite common within the organic-walled Peridinales (Evitt, 1985). However, only a single tentative description of an intercalary archeopyle for a calcareous cyst has been given, i.e., *Calciperidinium asymmetricum* Versteegh, 1993 (Fig. 1.13). *Calciperidinium* is a monospecific genus, known from late Pleistocene and Recent sediments of the Mediterranean area, and was described as having a typical peridinioid shape with one apical and two antapical horns. The dorsal position of the archeopyle, beneath the apex, suggests, in analogy with organic-walled cysts, an intercalary archeopyle. Number and label of plates involved are not mentioned. However, as cysts of *Calciperidinium* are dorsally and ventrally flattened and the archeopyle is located centrally on the dorsal face, it presumably includes at least plate 2a, therefore, representing Type I of Evitt (1967).

Category 3: Combination archeopyles

A combination archeopyle (Evitt, 1967) includes plates from two or more series. Within the calcareous dinoflagellate cysts, two groups of combination archeopyles can be distinguished, mesoepicystal and epicystal archeopyles, accommodating three types.

Mesoepicystal archeopyles

Figures 3, 8.1, 8.2, 8.4

The most common and important combination archeopyles within the calcareous dinoflagellate cysts is an archeopyle that involves three apical and all intercalary plates, e.g., *Caracomia* spp., *Calciodinellum* spp. To distinguish this type from other combination archeopyles, like epicystal (Lentin and Williams, 1976) or hemiepicystal archeopyles (Bujak and Davies, 1983), the new term mesoepicystal archeopyle is proposed, as it is characterized by the loss of the central part of the epicyst. Mesoepicystal archeopyles are divided into two archeopyle types and show many variations.

Type (3AtI).—The typical and most common archeopyle variation of this type is an archeopyle that results from the loss of a simple unornamented operculum. This variation is realized in several species, in which the archeopyle suture may or may not be visible in undehisced cysts, such as *C.*

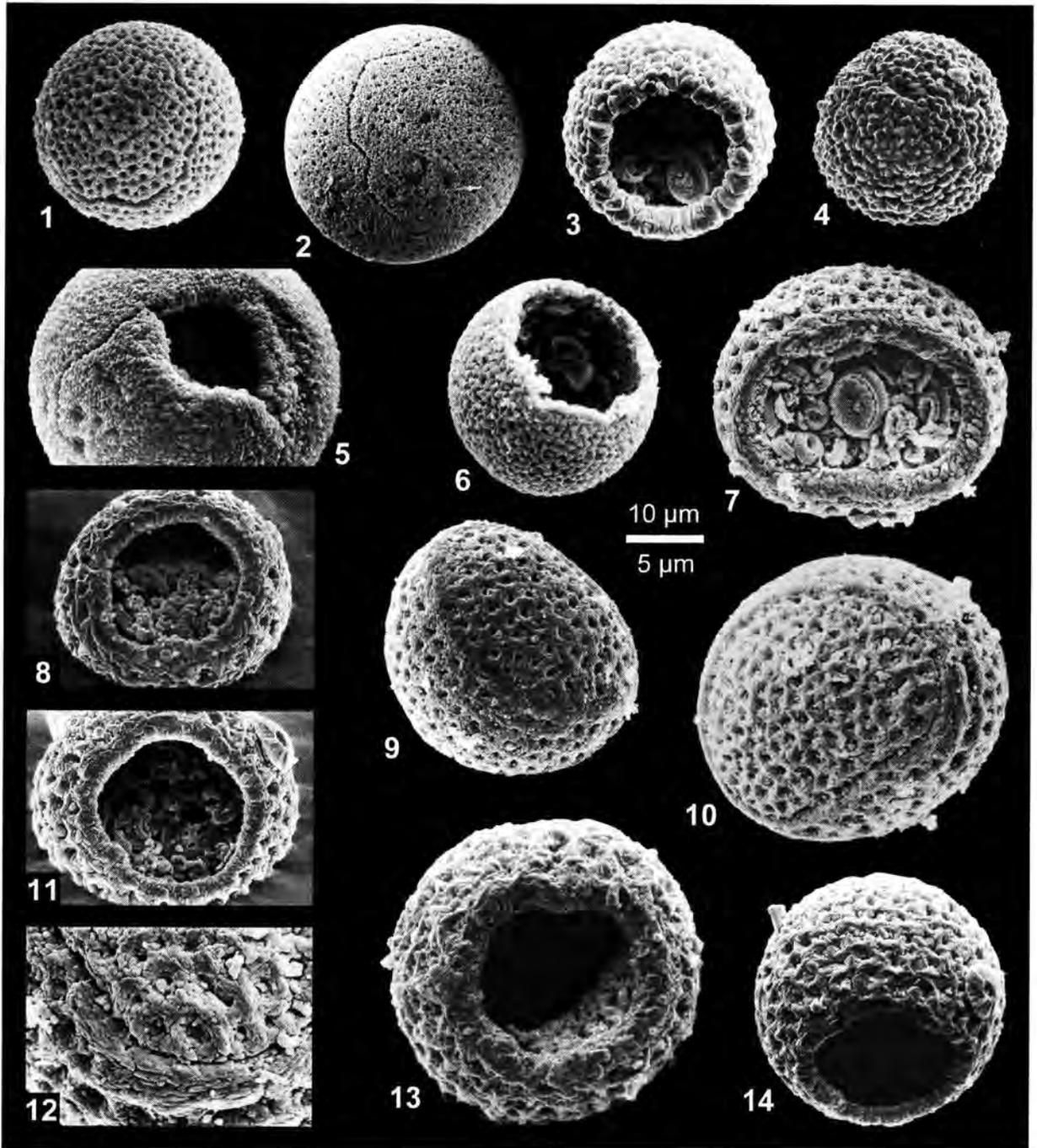


Figure 3. Various examples of species having a combination archeopyle that involves three apical and all intercalary plates = mesoepicystal archeopyle, Type (3AtI). Localities: 3, 4, 5, 8, 11, 13, 14 = Kerguelen Plateau, ODP Site 747; 1, 2, 6, 7, 9, 10, 12 = Wombat Plateau, ODP Site 761. 1, Oblique apical view of *Calciadinellum albatrosianum* (Kamptner, 1963) Janofske and Karwath in Karwath, 2000; late Pliocene. 2, Cyst of *Caracomia stella* Streng et al., 2002 with distinct archeopyle suture; plate 2' is faintly delineated by pores; middle Miocene. 3, 4, *Orthopithonella?* cf. *minuta* Fütterer, 1990. 3, Apical view showing ?combination archeopyle; early Miocene. 4, Lateral view of undehisced cyst with discernible operculum; early Eocene. 5, Apical view of *Caracomia arctica* with archeopyle suture and operculum partly broken off; early Miocene. 6, Cyst of *Calciadinellum levantinum* Meier et al., 2002 in oblique dorsal view; Pleistocene. 7-14, Cysts of *Calciadinellum clamosum* n. sp. 7, 9, 10, 12, *Calciadinellum clamosum latum* n. sp. and ssp.; late Paleocene. 8, 11, 13, 14, *Calciadinellum clamosum clamosum* Autonym; early and late Paleocene. →

albatrosianum (Kamptner, 1963) Janofske and Karwath in Karwath, 2000 (Fig. 3.1), *C. kerguelensis* n. sp. (Fig. 8), *C. levantinum* Meier et al., 2002 (Fig. 3.6), and *Caracomia arctica* (Gilbert and Clark, 1983) Streng et al., 2002 (Fig. 3.5). Opercula with ridges reflecting the tabulation belong to distinctly tabulated species, such as *Calciodinellum operosum* Deflandre, 1947 or *Calcigonellum? granulatum* Kohring, 1993a. Occasionally, tabulation is partly reflected by faint lines of pores as in the operculum of *Caracomia stella* Streng et al., 2002 (Fig. 3.2) [Chapter 2.1]. The archeopyle of *Calciodinellum clamosum* n. sp. (Fig. 3.12) is characterized by a distinct rim with a crystal arrangement that differs from that of the remaining cyst surface.

Type 3Atl.—The only species known having a compound mesoepicystal archeopyle is *Orthopithonella gustafsonii* (Bolli, 1974) Lentini and Williams, 1985 emend. Streng et al., 2002. The operculum of *O. gustafsonii* disarticulates in an inconstant number of monoplacoid opercular pieces. See Streng et al. (2002) [Chapter 2.1] for further details on the archeopyle of *O. gustafsonii*.

Epicystal archeopyles

Figures 4.1-4.7, 11.1, 11.2, 11.4, 11.5, 11.7

For the following reasons an epicystal archeopyle has not been recognized until recently among the calcareous cysts. Descriptions of epicystal archeopyles are very limited, and only Keupp (1984) supposed an epicystal archeopyle for *Calcigonellum infula* Deflandre, 1948 (Fig. 4.7). This archeopyle was subsequently interpreted as a combination archeopyle of all apical and intercalary plates by Keupp and Versteegh, 1989, though. Several authors depicted specimens with an epicystal archeopyle without recognizing the true nature of the archeopyle (e.g., Fütterer, 1977: pl. 8, figs. 3, 8; Kohring, 1997: figs. 4o, 4p). As a consequence, an epicystal archeopyle type remained unknown within the calcareous dinoflagellate cysts, until Meier et al. (2002) proved the true epicystal nature of the archeopyle of *Lebessphaera urania*. Therefore, we retain the interpretation of Keupp (1984) as it appears to be the most plausible interpretation of the archeopyle of *C. infula*. Additionally, an epicystal archeopyle is proposed for *Pernambugia tuberosa* (Kamptner, 1963) Janofske and Karwath in Karwath, 2000 (see also discussion of the genus *Pernambugia* herein; Figs. 4.4-4.5). Currently, three variations of epicystal archeopyles can be distinguished, accommodated in a single type:

Type (tAtlP).—This type is characterized by the loss of a simple polyplacoid operculum that comprises the entire epicyst. The archeopyle suture marks the border between the epicyst and the cingulum. Three variations can be distinguished:

- A) Epicystal archeopyle with plain rim: The archeopyle margin is characterized by a planar cingular displacement (e.g., *Pernambugia tuberosa* (Kamptner, 1963) Janofske and Karwath in Karwath, 2000 (Figs. 4.4-4.5); *Calcigonellum infula* Deflandre, 1948 (Fig. 4.7)).
- B) Epicystal archeopyle with stepped rim: The archeopyle margin is characterized by a descending (levorotatory) cingular displacement (Figs. 4.1, 4.2, ?4.6). Cysts bearing an ascending (dextrorotatory) cingular displacement have not been found within the Calciodinelloideae as yet.
- C) Epicystal archeopyle with incomplete archeopyle suture: This archeopyle type is unique within the calcareous dinoflagellate cysts. It is realized in a single species, i.e., *Pernambugia? patata* n. sp. (Fig. 11). It is characterized by an incomplete archeopyle suture that only embraces about half of

the cyst. Hence, for excystment, an auxiliary suture develops in the unsutured half of the cyst and two more-or-less equally sized hemicysts are produced. The incomplete archeopyle suture is interpreted as a transverse split in the dorsal part of the cyst running parallel to the equatorial plane between the precingular and the cingular plates. Consequently, the two hemicysts roughly represent epi- and hypocyst. The commissural plane between both hemicysts is divided in a dorsal (primarily sutured) and a ventral (primarily unsutured) half, of which the latter is characterized by a distinct dorsally descending slope. Therefore, the epicyst is generally slightly smaller than the hypocyst. For further details see also description and discussion of *Pernambugia? patata* n. sp. and the chapter on Excystment types.

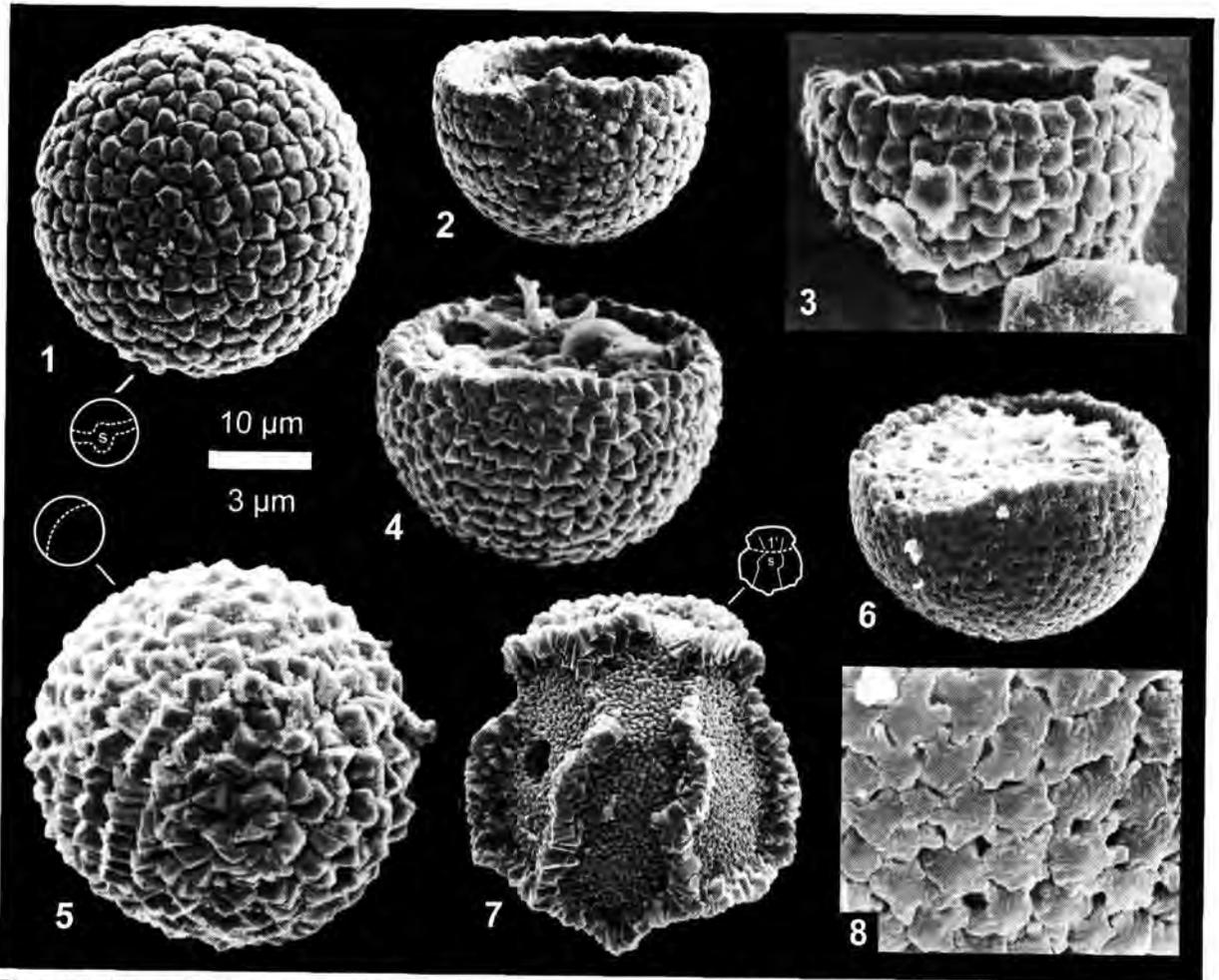


Figure 4. Examples of species with an epicystal archeopyle, Type (3AtItP). Localities: 1 = Kerguelen Plateau, ODP Site 747; 2, 4-6, 8 = Wombat Plateau, ODP Site 761; 3 = central Pacific; 7 = southern continental margin of Crete. 1, 2, *Lebessphaera urania* Meier et al., 2002. 1, Ventral view of undehisced cyst faintly showing cingulum and sulcus. Cingulum is reflected by parallelly organized rows of crystals and sulcal area by distinctly smaller crystals; early Miocene. 2, Dehisced specimen clearly showing descending cingular displacement; middle Miocene. 3, Dehisced specimen of *Lebessphaera?* sp. B.; middle Eocene. 4, 5, *Pernambugia tuberosa* (Kamptner, 1963) Janofske and Karwath in Karwath, 2000. 4, Epi- or hypocyst divulging planar cingular displacement; middle Miocene. 5, Cyst with equatorial archeopyle suture; early Miocene. 6, 8, *Lebessphaera?* sp. A. 6, Dehisced specimen; late Pliocene. 8, Crystal pattern of outer cyst surface; detail of 6. 7, Cyst of *Calcigonellum infula* Deflandre, 1949 emend. Montresor in D'Onofrio et al., 1999, ventral view; late Pleistocene. 1, 120-14H-2/V14; 2, 122-5H-5/1B9; 3, 116P/VIII10-2; 4, 122-5H-5/X14; 5, 122-7H-4/X8; 6, 8, 122-4H-1/IV8; 7, T20-S1/80-81/58. Scale bar equals 10 µm for cysts (1-7) and 3 µm for close-up (8).

For the organic-walled dinoflagellate cysts, two principal archeopyles groups have been proposed: theropylic archeopyles which are characterized by an incomplete archeopyle suture and an operculum that stays attached after excystment (= adnate), and saphopylic archeopyles which result from the loss of an operculum (Matsuoka, 1988). However, *Pernambugia? patata* n. sp. fits in none of the two groups as it has an incomplete archeopyle suture and nonetheless releases an operculum. Therefore, the archeopyle of *P.? patata* would be best described as "pseudosaphopylic".

Category 4: Miscellaneous archeopyles

Many species exhibit an archeopyle that cannot be assigned to one of the types described above. Those openings are characterized by an irregular circular outline that cannot be related to any kind of tabulation with certainty. As already mentioned (see chapter Excystment types), the irregular outline is probably in most cases due to inappropriate preservation and may in many cases represent secondarily enlarged simple, monoplacoid apical archeopyles (A_3). However, as long as no reliable information on the archeopyles of these species is available, no archeopyle type can be designated. Another reason for an irregular archeopyle outline might be a potential plate-unrelated origin, a case that cannot be excluded with certainty. Matsuoka (1985) introduced the term tremic archeopyle for more or less circular, plate-unrelated openings in gymnodinioid cysts. In analogy, this term is suggested to be appropriate for several calcareous cysts.

All species belonging to one of these categories are listed in Appendix I as species with unidentified archeopyle type.

Apertures of pithonelloid species

Calcareous, single or double layered cyst-like microfossils with a pithonelloid wall structure, which means that the wall forming crystals are uniformly oblique orientated, are conventionally regarded as calcareous dinoflagellate cysts, although their dinoflagellate nature is still under debate (Fensome et al., 1993). Tabulated species with a presumed pithonelloid wall, like *Amphora coronata* Willems, 1994, have probably an oblique wall structure, or, like *Tetratropis* spp. (Willems, 1990), already turned out to have in fact an oblique wall structure (Hildebrand-Habel and Willems, 1997). Additionally, the observed apertures of true pithonelloid species, located apically or in the center of the presumed apical face, generally appear to be too small to represent an archeopyle. Furthermore, no distinct opercula have been detected in any species with pithonelloid wall structure, although plug-like structures were described for *Pithonella ovalis* (Kaufmann in Heer, 1865) Lorenz, 1902 by Masters and Scott (1978), which are probably an artifact, though. Therefore, we accommodate pithonelloid species only tentatively within the Calciodinelloideae and handle them regarding the aperture as a separate group (see also Fensome et al., 1993, and Keupp, 1987).

SYSTEMATIC PALEONTOLOGY

Methods.—The specimens described herein originate mainly from core material recovered during Ocean Drilling Program (ODP) Leg 120 at Site 747, Kerguelen Plateau, south eastern Indian Ocean and Leg 122 at Site 761, Wombat Plateau, eastern Indian Ocean. A single sample from the central Pacific Ocean was put at disposal from the Scripps Institute of Oceanography (AMPH 116P) (Fig. 5.1). The samples consist of cream-colored foraminifer diatom oozes (sections 1H-5, 2H-4, 3H-3, 4H-

1 and 4H-3), white nannofossil oozes (sections 4H-6, 6H-1, 7H-4, 9H-5, 12H-2, 14H-2 and 14H-5), white to pale brown nannofossil chalks (sections 1R-4, 19X-2, 20X-1 and 21X-1), and brown calcareous nannofossil ooze (AMPH 116P). Additional material originates from a clay pit about 1.6 km SW of Vöhrum (Lower Saxony, Germany; Fig. 5.2). Pictures of *Bicarinellum tricarinelloides*, *Calcicarpinum bivalvum*, *Calcigonellum infula*, and *Calciperidinium asymmetricum* are courtesy of G. Versteegh. For sample locations and preparation of these species see Keupp and Versteegh (1989) and Versteegh (1993).

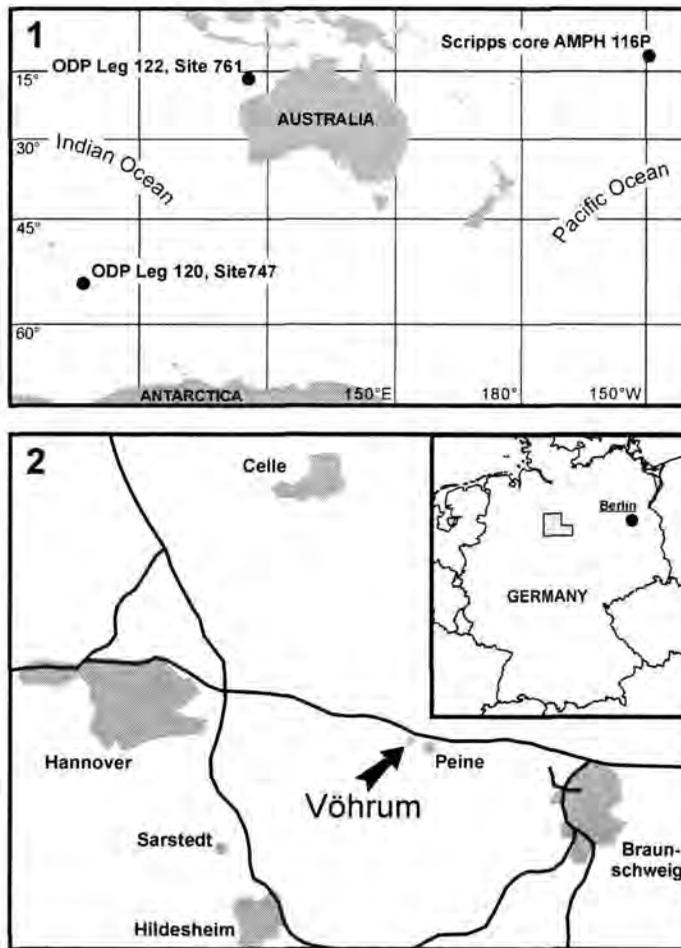


Figure 5. Sample locations of 1) the core material from ODP Sites in the Indian and Pacific Ocean, and 2) the clay pit near Vöhrum, Germany.

The individual samples were suspended in a weak solution of water and ammonia and repeatedly frozen and thawed to achieve complete disintegration. Afterwards, the material was washed through a 125 μm and 20 μm sieve. The residues were dried and the fraction between 20 and 125 μm was used to pick the specimens under a binocular microscope. The selected specimens were mounted on aluminum stubs, sputter-coated with gold, and photographed under a scanning electron microscope (SEM) at the University of Bremen (CamScan-44).

Determination of the crystallographic orientation of the c-axes of the wall forming crystals follows the technique developed by Janofske (1996): selected specimens were examined under the SEM, afterwards embedded in resin and cut into 3 μm thin sections using a rotation microtome (Leica 2055).

Finally, these thin sections were examined under polarized light to obtain the optic sign using a Zeiss Axioplan light microscope.

The suprageneric classification of calcareous dinoflagellates is in accordance with Fensome et al. (1993). The description of morphological features of the archeopyle and the operculum, respectively, follows the overview given by Fensome et al. (1996). Additional terms for the description of archeopyles of calcareous dinoflagellate cysts are proposed. Tabulation patterns are described using the Kofoid tabulation system (see Fensome et al., 1996). The nannoplankton zonation is in accordance with Martini (1971).

The studied material is deposited in the collection of the Division of Historical Geology/Paleontology, University of Bremen, Germany.

Division DINOFLAGELLATA (Bütschli, 1885) Fensome et al., 1993

Subdivision DINOKARYOTA Fensome et al., 1993

Class DINOPHYCEAE Pascher, 1914

Subclass PERIDINIPHYCIDAE Fensome et al., 1993

Order PERIDINIALES Haeckel, 1894

Suborder PERIDINIINEAE Autonym

Family PERIDINIACEAE Ehrenberg, 1831

Subfamily CALCIODINELLOIDEAE Fensome et al., 1993

Genus *Calciodinellum* Deflandre, 1947 emend. Janofske and Karwath in Karwath, 2000

Type.—*Calciodinellum operosum* Deflandre, 1947 emend. Montresor et al., 1997.

Included species.—*C. operosum* Deflandre, 1947 emend. Montresor et al., 1997; *C. limbatum* (Deflandre, 1948) Kohring, 1993a; *C. albatrosianum* (Kamptner, 1963) Janofske and Karwath in Karwath, 2000; *C. levantinum* Meier et al., 2002; *C. kerguelensis* n. sp., *C. clamosum* n. sp.

Diagnosis of cyst.—Cysts bear one calcareous layer; crystallographic axes (c-axes) of wall forming crystals tangentially orientated with respect to the cyst surface; tabulation patterns always present; combination archeopyle involves apical plates (2'-4') and all intercalary plates (1a-3a) (after Janofske and Karwath in Karwath, 2000).

Occurrence.—The genus *Calciodinellum* is known from the late Maastrichtian (Hildebrand-Habel and Willems, 2000) to Recent (e.g., Dale, 1992a).

Discussion.—One of the characteristics of the genus *Calciodinellum* Deflandre, 1947 according to the emendation of Janofske and Karwath in Karwath (2000) is the presence of tabulation patterns in all species within this genus. *Calciodinellum albatrosianum* (Kamptner, 1963) a cryptotabulate species has been accommodated within the genus *Calciodinellum* by Janofske and Karwath in Karwath (2000), therefore, presence of tabulation means at least the presence of cryptotabulation.

Calciodinellum clamosum new species

Diagnosis.—Species of *Calciodinellum* with a pattern of pore-like structures on the outer cyst surface; slat-like crystallite terminations tangentially arranged around pores; rounded archeopyle margin pointed by a distinct rim.

Description.—Cysts are single-layered, spherical or broad-ovoid in shape with a maximum diameter of 29.0 to 45.8 µm; calcareous wall about 2 to 3 µm thick, generally thicker near margin of archeopyle

because of massive rim that encompasses archeopyle; archeopyle large, rounded to slightly angular in outline, involving apical plates 2'-4' and all intercalary plates. Wall composed of numerous crystallites whose arrangement appears irregular in cross section; outer surface of cyst characterized by a pattern of 1 to 2 μm wide pore-like structures around which crystallites are arranged tangentially or nearly so; inner surface similar to outer.

Etymology.—Named after the Latin *clamosus* (= shouting loud) in allusion to the large archeopyle that resembles an open mouth.

Types.—Holotype: cyst 120-19X-2-139/XIII32 (Figs. 3.11, 3.14); type locality and stratum: Kerguelen Plateau, south eastern Indian Ocean, ODP Leg 120, Hole 747A - late Paleocene, nannoplankton zone interval NP11-NP13, sample 120-747A-19X-2 (139-141 cm); paratypes: cysts 120-20X-1/V10 and 120-20X-1/VIII3.

Occurrence.—*C. clamosum* n. sp. is known from the Danian and the early and late Paleocene (see Occurrence of subspecies for details).

Discussion.—Within *Calciodinellum clamosum* n. sp., two morphotypes have been observed which are clearly separated by the shape of their cysts. This justifies a separation of this species into two distinct subspecies. *Calciodinellum clamosum clamosum* Autonym is characterized by its spherical shape in contrast to *Calciodinellum clamosum latum* n. spp. which is clearly distinguished from the first-mentioned by its oval equatorial outline and apically flattened epicyst (see Description of both subspecies for details).

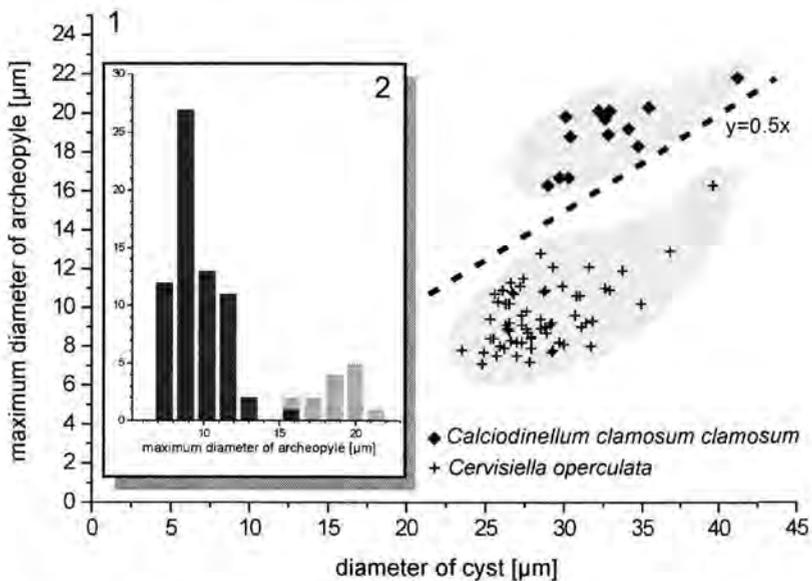


Figure 6. 1, Bivariate scattergram of measurements on the maximum archeopyle diameter and the corresponding cyst diameter of the two similar species *Cervisiella operculata* n. comb. (N = 66) and *Calciodinellum clamosum clamosum* Autonym (N = 13). Both species show a wide variation concerning the diameter of the archeopyle but are still clearly distinguishable. 2, Corresponding frequency distribution of archeopyle measurements (dark gray = *Cervisiella operculata* n. comb.; light gray = *Calciodinellum clamosum clamosum* Autonym).

Calciodinellum clamosum clamosum Autonym

Figures 3.8, 3.11, 3.13, 3.14

? *Thoracosphaera operculata* Bramlette and Martini, 1964. JAFAR, 1979, pl.1, fig. 7.

Obliquipithonella operculata (Bramlette and Martini, 1964). KIENEL, 1994, pl. 9, figs. 1-2.

Diagnosis.—Spherical subspecies of *Calciodinellum clamosum* n. sp.; archeopyle outline characterized by a ventral concavity.

Description.—Cysts are spherical in shape with a diameter of 29.0 to 41.2 μm (mean = 32.3, n = 15); archeopyle slightly angular in outline; distinct small concavity in archeopyle outline reflects apically directed tip of plate 1' (Figs. 3.8, 3.11, 3.13). Transversal archeopyle diameter ranges from 16.7 to 21.8 μm (mean = 19.0, n = 13), roughly positively correlated to cyst diameter (Fig. 6.1); archeopyle diameter about 53 to 65 percent of cyst diameter; operculum unknown as all observed specimens are dehisced.

Types.—As for nominate species.

Other material examined.—12 specimens from ODP Leg 120, Hole 747A (Kerguelen Plateau), samples 120-747A-19X-2 (139-141 cm), late Paleocene, and 120-747A-20X-1 (138-139 cm), early Paleocene (NP2).

Occurrence.—*C. clamosum clamosum* Autonym is known from the Danian of Nennhausen, Lower Saxony (Germany) (Kienel, 1994) and the early and late Paleocene of the Kerguelen Plateau.

Discussion.—See discussion of *Calciodinellum clamosum latum* n. sp. and ssp.

Calciodinellum clamosum latum new species and subspecies

Figures 3.7, 3.9, 3.10, 3.12

Operculodinella operculata (Bramlette and Martini, 1964). HILDEBRAND-HABEL et al., 1999, pl. 6, fig. 8.

Diagnosis.—Apically flattened subspecies of *Calciodinellum clamosum* n. sp. bearing an oval equatorial outline.

Description.—Calcareous cysts are single-layered with an apically flattened epicyst and an oval equatorial outline; width greater than thickness and height, for thickness roughly equals height. Width of cysts ranges from 30.0 to 45.8 μm (mean = 36.4, n = 12), thickness and height about 85 percent of width. Operculum simple, polyplacoid, slightly exceeding diameter of archeopyle, kidney-shaped in outline with a straight ventral side. Archeopyle bordered by a 2 to 3 μm broad, distinct rim of typically tangentially aligned crystallites; wall penetrated by numerous equally distributed, about 1 μm wide pores; regular lines of pores parallel to the equatorial plane occur especially directly posterior to the archeopyle.

Etymology.—Latin, *latus*, broad, denoting the width of cyst and operculum.

Types.—Holotype: cyst 122-18X-2/IV13 (Figs. 3.10, 3.12); type locality and stratum: Wombat Plateau, eastern Indian Ocean, ODP Leg 122, Hole 761B – late Paleocene, nannoplankton zone NP5, sample 122-761B-18X-2 (130-131 cm); paratypes: cysts 122-18X-2/VIII1 and 122-18X-2/X25 (Figs. 3.7, 3.9).

Other material examined.—91 additional specimens from sample 122-747A-18X-2 (130-131 cm) (late Paleocene, NP5) and 2 specimens from sample 122-747A-16X-2 (90-91 cm) (late Paleocene, NP9), both ODP Leg 122, Hole 747A (Wombat Plateau).

Occurrence.—*C. clamosum latum* n. sp. and ssp. is known from the late Paleocene (NP6) of the South Atlantic Ocean (Hildebrand-Habel et al., 1999) and the late Paleocene (NP5 and NP9) of the Wombat Plateau, eastern Indian Ocean.

Discussion.—*Calciodinellum clamosum* n. sp. and *Cervisiella operculata* n. comb. have been formerly united within a single species, i.e., *Operculodinella operculata* (Bramlette and Martini, 1964). This is due to the following reasons: 1) the more-or-less identical stratigraphic occurrence, 2) analogous appearance because of the equivalent wall structure, and 3) great variability of the archeopyle diameter. However, measurements of the archeopyle diameter of *Calciodinellum clamosum clamosum* and *Cervisiella operculata* display an evident discrimination of both taxa (Fig. 6). Additionally, the undulating archeopyle outline of *Calciodinellum clamosum clamosum* is clearly different to the typically circular archeopyle of *Cervisiella operculata* (compare Fig. 7). As size and outline of the archeopyle are obviously unambiguous expressions of different tabulation patterns and of the number of plates involved in the operculum, respectively, a separation on genus level is therefore justified. Clearly, a visible archeopyle is needed to distinguish between the two species. *C. clamosum latum* n. sp. and ssp. differs from these two taxa by its unmistakably broad shape and the wide kidney-shaped archeopyle. Future investigations might reveal different stratigraphic distributions as well as divergent ecological preferences of the three taxa.

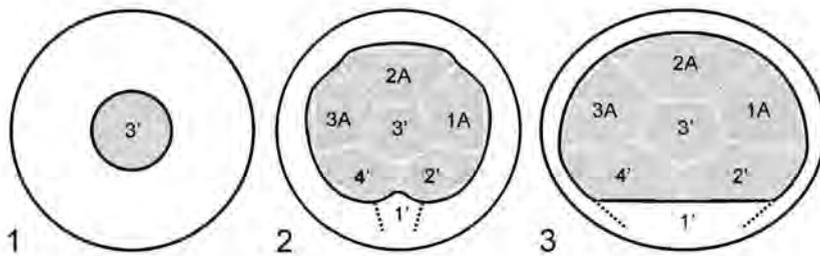


Figure 7. Schematic diagrams in apical view of the former single species *Operculodinella operculata* (Bramlette and Martini, 1964) that is now regarded as belonging to two different species comprising three morphotypes. Interpretations of the different archeopyles and involved plates are shown. 1, *Cervisiella operculata* (Bramlette and Martini, 1964) n. comb. with a simple circular apical archeopyle involving plate 3'. 2, *Calciodinellum clamosum clamosum* Autonym bearing a rounded combination archeopyle (mesoepicystal archeopyle). 3, *Calciodinellum clamosum latum* n. sp. and ssp. characterized by a broad rounded mesoepicystal archeopyle. All not to scale.

Calciodinellum kerguelensis new species

Figure 8

Diagnosis.—Species of *Calciodinellum*; spherical to slightly ovoid shape; wall penetrated by numerous pores; crystals show no distinct arrangement on outer surface.

Description.—Calcareous cysts are generally spherical in shape; slightly ovoid cysts are infrequently observed (elongated antapical-apical); cyst diameters range from 24.7 to 40.2 μm (mean = 30.9, n = 99), walls are 2 to 4.1 μm thick, thickness of wall roughly positively correlated to cyst diameter; wall consists of numerous short and sturdy, radially arranged rounded crystallites; crystallographic optic axis of each crystallite tangentially oriented to cyst surface; inner and outer cyst surfaces characterized by an irregular pattern of rounded tips of wall forming crystals; wall penetrated by numerous, typically equally distributed pores; crystallites around pores show no distinct arrangement; pores about 1 μm in diameter, obviously the result of a single missing crystallite; operculum polyplacoid and simple,

subangular in outline, involving plates 2'-4' and 1a-3a; faint principal archeopyle suture typically visible in closed cysts; archeopyle diameter about 60 to 65 percent of cyst diameter.

Etymology.—After the type locality, the Kerguelen Plateau.

Types.—Holotype: cyst 120-6H-1/X17 (Fig. 8.1); type locality and stratum: Kerguelen Plateau, south eastern Indian Ocean, ODP Leg 120, Hole 747A – late Miocene, *G. scitula* biozone, sample 120-747A-6H-1 (110-111 cm); paratypes: cysts 120-6H-1/VI24, 120-6H-1/VI10, 120-6H-1/VI12, 120-4H-6/V9, 120-6H-1/VII3.

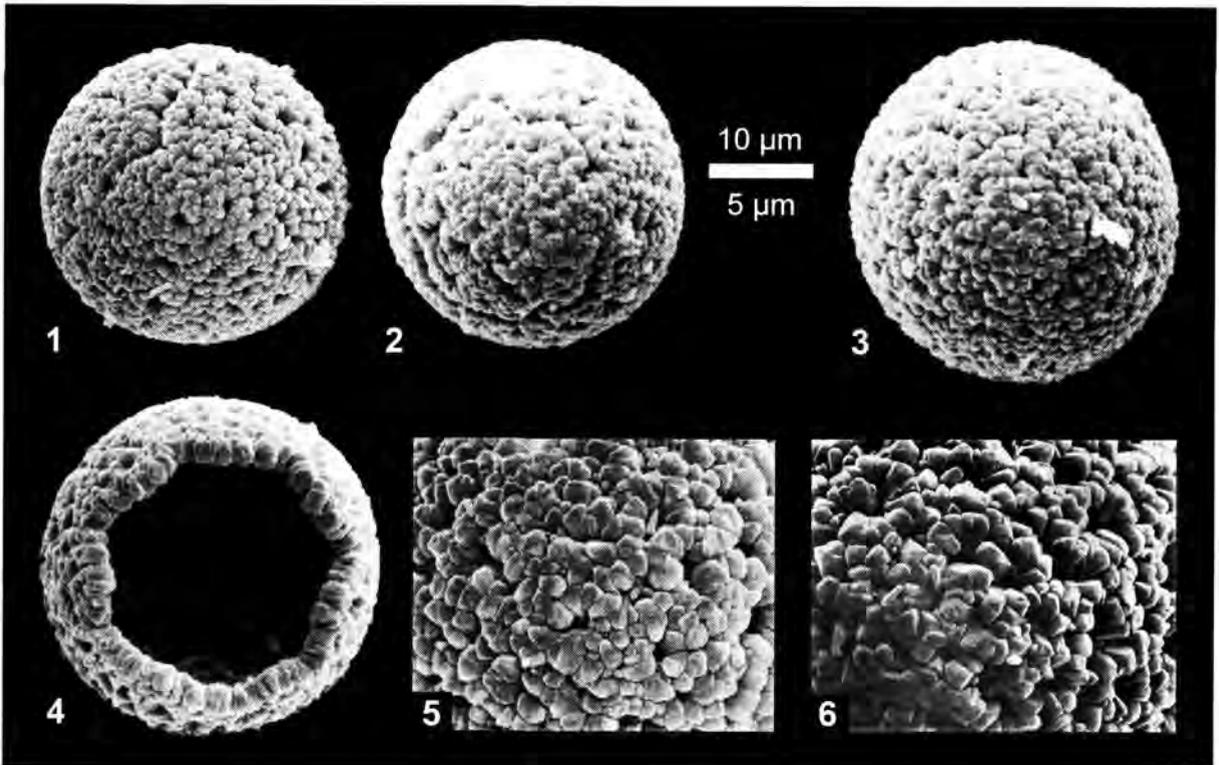


Figure 8. *Calciadinellum kerguelensis* n. sp. from the late Miocene and early Pliocene (Kerguelen Plateau, ODP Site 747). 1, Lateral view of holotype with archeopyle suture. 2, Apical view of paratype showing archeopyle suture and angular operculum. 3, Undehisced cyst lacking visible archeopyle suture. 4, Apical view of dehisced cyst revealing angular combination archeopyle. 5, 6, Surface pattern of two different cysts showing pores and crystallite arrangement.

1, 120-6H-1/X17 (holotype); 2, 120-6H-1/VI24; 3, 120-6H-1/VI10; 4, 120-6H-1/VI12; 5, 120-4H-6/V9; 6, 120-6H-1/VII3. Scale bar equals 10 μm for cysts (1-4) and 5 μm for surface patterns (5, 6).

Other material examined.—107 additional cysts from four samples of ODP Leg 120, Hole 747A (Kerguelen Plateau): 12 specimens of sample 120-747A-4H-1 (147-148 cm) (early Pliocene), 2 specimens of sample 120-747A-4H-3 (76-77 cm) (early Pliocene), 20 specimens of sample 120-747A-4H-6 (111-112 cm) (late Miocene), and 73 specimens of sample 120-747A-6H-1 (110-111 cm) (late Miocene).

Occurrence.—*C. kerguelensis* n. sp. is known from late Miocene to early Pliocene of the Kerguelen Plateau.

Discussion.—*C. kerguelensis* n. sp. is very similar to *C. albatrosianum* regarding size and general appearance. However, both species are clearly separated by 1) the arrangement of crystallites around the pores, which appears unorganized in *C. kerguelensis* compared to the rosette-like patterns in *C. albatrosianum*; 2) the number of pores, which are distinctly lower in *C. kerguelensis*; and 3) size and habit of crystallites, which appear more massive in *C. kerguelensis*.

Genus *Cervisiella* Hildebrand-Habel, Willems, and Versteegh., 1999

Type of genus.—*Cervisiella saxea* (Stradner, 1961) Hildebrand-Habel et al., 1999.

Included species.—*C. saxea* (Stradner, 1961) Hildebrand-Habel et al., 1999; *C. operculata* (Bramlette and Martini, 1964) n. comb.

Diagnosis.—Spherical to ovoid single-layered calcareous dinoflagellate cysts with a circular to slightly subangular archeopyle formed by the loss of the single plate 3'. The wall consists of apparently obliquely arranged crystallites, however, thin sections of cysts reveal a positive optic sign, indicative for a tangential ultrastructure (modified after Hildebrand-Habel et al., 1999).

Discussion.—*Cervisiella* matches *Fuettererella* in many aspects, such as a tangential ultrastructure and a relatively small archeopyle, interpreted for both species to be the result of the loss of the single apical plate 3'. Based on these two major features, it would be reasonable to regard *Cervisiella* as a junior synonym of *Fuettererella*. The two genera are distinguished by the arrangement of the wall-forming crystals only, which appear obliquely oriented in *Cervisiella* and radially in *Fuettererella*. Another potential characteristic to distinguish between the two genera is the lid-like operculum that is developed in both, *C. saxea*, and *C. operculata* and is visible in undehisced cysts. In contrast to *Fuettererella* where attached opercula never have been observed. As long as no further information is available on the taxonomic relevance of 1) the development of the operculum and 2) the detailed crystal arrangement, we retain both genera.

Cervisiella operculata (Bramlette and Martini, 1964) new combination

Figure 1.2

Thoracosphaera operculata BRAMLETTE AND MARTINI, 1964, p. 305-306, pl. 5, figs. 3-7.

Obliquipithonella operculata (Bramlette and Martini, 1964). FÜTTERER, 1990, p. 540-541, pl. 2, figs. 1-6.

Pirumella operculata (Bramlette and Martini, 1964). WILLIAMS et al., 1998, p. 490.

Operculodinella operculata (Bramlette and Martini, 1964). HILDEBRAND-HABEL et al., 1999, p. 79-80, pl. 6, figs. 4-7, 9-13, not fig. 8.

(selected synonymy)

Basionym.—*Thoracosphaera operculata* Bramlette and Martini, 1964, p. 305-306, pl. 5, figs. 3-7; holotype: pl. 5, figs. 4, 5.

Diagnosis.—Spherical species of *Cervisiella* with archeopyle circular, oval or slightly subangular in outline; archeopyle diameter less than 50 percent of cyst diameter; archeopyle bordered by distinct rim; outer wall surface ornamented by several pore-like structures.

Description.—Calcareous single-layered cysts spherical in shape and characterized by a homogenous pattern of pore-like structures on the inner and outer surface; diameter of cysts varies from 20.1 to 39.6 μm (mean = 28.1 μm , n = 139); wall about 2 μm thick, built of numerous irregularly arranged crystallites, however, thin sections of cysts reveal a positive optic sign indicating a tangential orientation of the c-axes of wall forming crystals; apical archeopyle circular to slightly oval or angular

in outline, variable in size, ranges from 7.1 to 16.3 μm in diameter; archeopyle diameter positively correlated to cyst diameter (Fig. 6.1); archeopyle framed by a distinct rim of tangentially arranged crystallites; crystal pattern of circular operculum corresponds to that of the cyst.

Material examined.—157 cysts from the Wombat Plateau (ODP Leg 122, Hole 761B), samples 122-761B-16X-2 (90-91 cm), late Paleocene (NP9), sample 122-761B-20X-2 (9-11 cm), early Paleocene (NP3-NP4), and sample 122-761B-21X-2 (50-52 cm), early Paleocene; 218 cysts from the Kerguelen Plateau (ODP Leg 120, Hole 747A), sample 120-747A-19X-2 (139-141 cm), latest Paleocene and sample 120-747A-20X-1 (138-139 cm), early Paleocene (NP2).

Occurrence.—*Cervisiella operculata* n. comb. is known from the early Maastrichtian to early Eocene (e.g., Hildebrand-Habel et al., 1999). Cysts reported for the Oligocene (Kohring, 1993a; Keupp and Kohring, 1994) represent most probably reworked specimens.

Discussion.—Hildebrand-Habel et al. (1999) accommodated *C. operculata* in the genus *Operculodinella* Kienel, 1994 based on the analogous wall structure of *C. operculata* and the species of *Operculodinella*, i.e., *O. costata* Kienel, 1994, *O. reticulata* Kienel, 1994, and *O. hydria* Kienel, 1994. However, the archeopyles of these three species resemble a combination archeopyle, including apical and intercalary plates. The monoplacoid apical archeopyle clearly distinguishes *C. operculata* n. comb. from the species of *Operculodinella*. Furthermore, these species clearly exhibit, besides the archeopyle, various expressions of a reduced external tabulation. Therefore, a reallocation of *C. operculata* is inevitable. See also discussion of genus *Cervisiella* Hildebrand-Habel et al., 1999 and *Calciadinellum clamosum latum* n. sp. and ssp.

Genus *Echinodinella* Keupp, 1980a emend.

Type of genus.—The holotype of *Echinodinella erinacea* Keupp, 1980a.

Included species.—*Echinodinella erinacea* Keupp, 1980a, and *E. levata* Keupp, 1981.

Original diagnosis.—Calcareous dinoflagellate cysts without a distinct paratabulation of the surface. The calcareous wall consists of one layer of radially arranged trigonal calcite crystals. The surface becomes prickly due to a tapering of the distal ends of the calviform crystals. The outline of the archeopyle is variable. The more or less spheric organic capsula is constructed by two primary membranes, which are partly intergrown. In some cases the interspace between the endo- and periphragm is filled with a spongy tissue. (Keupp, 1980a, p. 132-133)

Emended diagnosis.—Single layered calcareous dinoflagellate cysts with radially arranged crystals; crystallographic c-axes correspond to morphological long-axes of crystals; trapezium-shaped apical archeopyle includes plates 2'-4' (archeopyle formula $3A_{2'-4'}$); occasionally tabulation pattern reflected by single ridges or dents on outer surface.

Occurrence.—The genus is definitely known from the late Hauterivian (Keupp, 1980a) to the middle Cenomanian (Zügel, 1994) of northern Germany and south-east England. Specimens from the Danian are questionable (Kienel, 1994).

Discussion.—See Discussion of *Echinodinella erinacea* Keupp, 1980a.

Echinodinella erinacea Keupp, 1980a emend.

Figure 2

? *Thoracosphaera spinosa* KEUPP, 1979b, p. 17-18, pl. 1, fig. 7, not fig.6.

Echinodinella erinacea KEUPP, 1980a, p. 133-134, pl. 16, figs. 7-15, pl. 17, figs. 1-9; Keupp, 1981, p. 17-18, pl. 5, figs. 11-12, pl. 6, figs. 1-9, pl. 7, figs. 1-15; Keupp, 1982, p. 313, pl. 6.2-1, figs. 7-12; Monnet, 1990, p. 53, pl. 1, figs. 1-15; Keupp, Monnet, and Kohring, 1991, pl. 1, figs. 12-15, not fig. 11; Monnet, 1993, p. 17-19, pl. 1, figs. 1-12, pl. 12, figs. 1-2; Keupp and Neumann, 1996, pl. 1, fig. 3; Neumann, 1999, p. 20-21, pl. 1, figs. 12-15. Not: Hildebrand-Habel and Willems, 2000, fig. 5d.

Not *Echinodinella* cf. *erinacea* Keupp, 1980a. Keupp, 1982, p. 313-314, pl. 6.2-2, figs. 1-3.

“*Echinodinella*” *erinacea* Keupp, 1980a. Keupp, 1992b, p. 129, pl. 3, figs. 8-10; Keupp, 1993, p. 27, pl. 1, fig. 4; ?Kienel, 1994, p. 37; Keupp and Mutterlose, 1994, p. 752, fig. 8.8; Zügel, 1994, p. 85-86, pl. 20, figs. 6-7.

Basionym.—*Echinodinella erinacea* Keupp, 1980a, p. 133-134, pl. 16, figs. 7-15, pl. 17, figs. 1-9; holotype: pl. 16, fig. 7.

Original diagnosis.—Calcareous dinoflagellate cysts with a spherical shape. In single cases a rudimentary paratabulation of the surface is visible. The archeopyle is triangular, pentagonal, round, or composed by two plates. The single-layered thick calcareous wall consists of claviform calcite crystals without a strong distal growth-limitation. Their basic pattern is triangular. The organic capsula is primarily constructed by two phragms. The interspace between these membranes is partly filled with a spongy tissue. (Keupp, 1980a, p. 134)

Emended diagnosis.—Species of *Echinodinella*, spherical to slightly ovoid in shape; wall consists of long spiny crystals with triradiate bases; crystals taper distally and may reflect reduced tabulation patterns; inner organic layer typically preserved.

Description.—Calcareous cysts are spherical to slightly ovoid in outline; maximum diameter ranges from 31.7 μm to 48.3 μm (mean = 38.8 μm , n = 41); single-layered wall consists of spiny radially arranged about 3 μm long crystals with characteristic triradiate bases; crystals may locally reach lengths of up to 9 μm and may then reflect reduced tabulation patterns especially in the zone of the cingulum; apical archeopyle trapezoid in outline involving plates 2'-4' (archeopyle formula $3A_{2'-4'}$); incomplete archeopyles involving only plate 2' and 4' occur; consequently, operculum may be compound. However, no further details of the operculum are known as archeopyle sutures are generally indistinct in undehisced cysts; height (ventral-dorsal diameter) of archeopyle is about 40 percent of corresponding cyst diameter; archeopyle often secondarily enlarged in direction of plates 2'' and 6''; inner organic layer typically preserved and shows linings of triradiate bases of crystals on its outer surface. For further detailed descriptions see Keupp (1980a, 1981, 1982, 1992b) and Monnet (1993).

Material examined.—81 specimens from 6 different samples (Voe5, Voe6, Voe7, Voe8, Voe11, Voe12) from a clay pit near Vöhrum, Lower Saxony (Germany; Fig. 5.2), Aptian-Albian boundary interval.

Occurrence.—As for genus.

Discussion.—The archeopyle of *Echinodinella erinacea* has been enigmatic for a long time. Keupp (1980a) and subsequent authors already suggested a tabulated archeopyle that involves several plates, due to the rectangular outline. However, none of the authors gave any relation to definitely involved plates. Three circumstances aggravate the plate interpretation: 1) The original rectangular outline of the archeopyle often appears rounded due to inappropriate preservation (Figs. 2.3, 9.3), 2) an incomplete loss of the plates produces an uncharacteristic archeopyle outline (Fig. 9.2), and 3) irregularly shaped apertures that are not clearly related to tabulation may occur (Fig. 2.8). However,

examination of new material near the type locality and detailed study of the published illustrations suggest an apical archeopyle involving three apical plates for *E. erinacea* (Figs. 2.10, 9.1). This suggestion is confirmed by a specimen of *E. erinacea* depicted in Keupp (1980a, pl. 16, fig. 14) showing an untypical rectangular archeopyle involving only two plates (2' and 4', see Fig. 9.2) leaving plate 3' attached. Therefore, opercula of *E. erinacea* are obviously compound, similar to *Orthopithonella gustafsonii* (Bolli, 1974) emend. Streng et al., 2002.

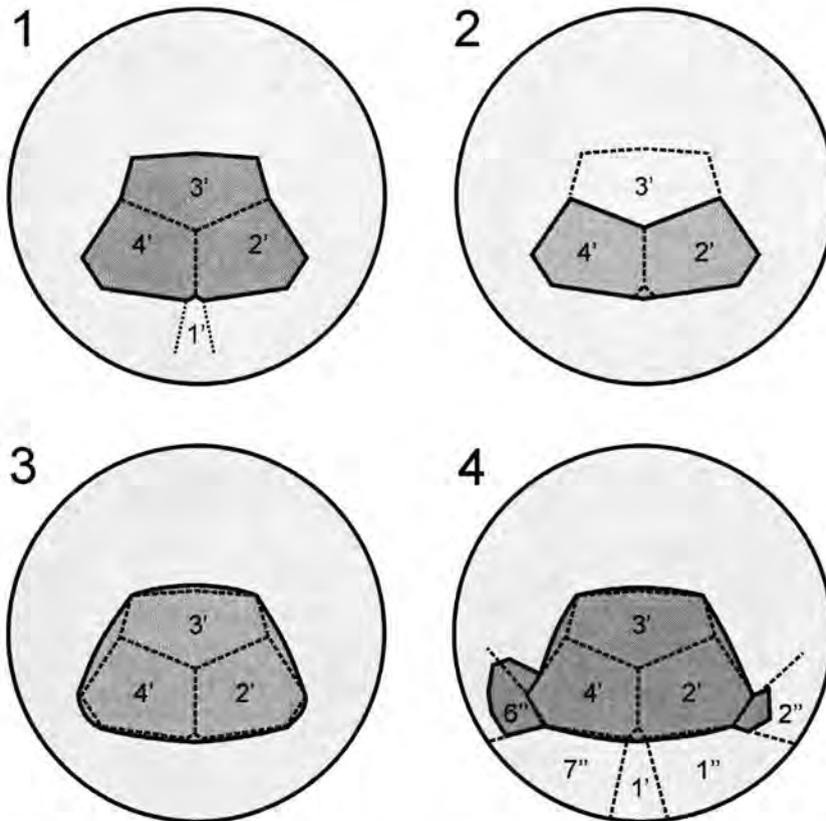


Figure 9. Schematic drawings of epicyst of *Echinodinella erinacea* Keupp, 1980a in apical view illustrating different potential archeopyle outlines. 1, Archeopyle outline and involved plates (compare with Fig. 2.10). 2, Incomplete archeopyle, indicative of a compound operculum (depicted in Keupp, 1980a, p. 145, pl. 16, fig. 14 and Keupp, 1982, p. 347, pl. 6.2-1, fig. 11). 3, Secondarily enlarged archeopyle with a rounded outline (compare with Fig. 2.3). 4, Secondarily laterally enlarged archeopyle (compare with Figs. 2.4 and 2.6).

Rounded archeopyles of *E. erinacea* superficially resemble those of *Caracomia arctica* (Gilbert and Clark, 1983) and those of species with a relatively large apical archeopyle of the type $A_{3'}$ (e.g., *Praecalcionellum polymorphum* (Keupp, 1980a) Lentini and Williams, 1993). However, as intercalary plates are involved in the archeopyle of *C. arctica*, the height of its archeopyle is about 50 percent of the corresponding cyst diameter, in contrast 40 percent in *E. erinacea*. To distinguish between rounded $3A_{2',4'}$ and large $A_{3'}$ archeopyles well preserved specimens or external tabulation patterns are required.

Genus *Fuettererella* Kohring, 1993a emend.

Type of genus.—*Fuettererella conforma* Kohring, 1993a.

Included species.—*Fuettererella deflandrei* (Kamptner, 1956) Hildebrand-Habel and Streng (in review) [Chapter 2.3]; *Fuettererella tesserula* (Fütterer, 1977) Kohring, 1993a; *Fuettererella flora* (Fütterer, 1990) Hildebrand-Habel and Streng (in review) [Chapter 2.3]; *Fuettererella conforma* Kohring, 1993a; *Fuettererella elliptica* Kohring, 1993a; *Fuettererella fungiforma* Hildebrand-Habel and Willems, 1999; *Fuettererella belliata* n. sp.

Original diagnosis.—Calcareous dinoflagellate cyst with a pseudoorthopithonelloid outer wall, however, wall crystals with the c-axis parallel to cyst's surface (Kohring, 1993a, p. 88).

Emended diagnosis.—Spherical to ovoid calcareous dinoflagellate cyst; wall single-layered with tangentially oriented crystallographic c-axes of wall-forming crystals; inner and outer surface of cyst without tabulation; archeopyle situated apically to subapically, relatively small, circular to irregular circular in outline involving single apical plate 3'.

Discussion.—In the original diagnosis of Kohring (1993a), *Fuettererella* was defined by the tangential orientation of the wall forming crystals only. Here we refine the diagnosis of the genus by including further relevant features, such as the archeopyle. The small apically situated archeopyles of *Fuettererella* are interpreted as the equivalent of the single apical plate 3'.

Fuettererella belliata new species

Figure 10

Diagnosis.—Ovoid species of *Fuettererella* with elongated, radially arranged slit-like wall-forming crystals; terminations of crystals organized in a rosette-like pattern on inner and outer surface of cyst.

Description.—Calcareous cysts with single-layered massive walls, always ovoid in shape; minimum cyst diameter ranges from 27.5 to 51.1 μm , maximum diameter from 32.9 to 59.3 μm ; wall built of sturdy stem-like to wedge-shaped crystallites with their morphological long-axes radially arranged; individual crystals are 5.5 to 9.1 μm long, slightly tapering to the center of cyst; length of crystals equals thickness of wall; proximal crystal terminations on inner surface square to polygonal in outline, about 0.7 to 0.8 μm in diameter, arranged in regular patterns around pores; distal crystal terminations on outer surface rectangular in outline, 1 to 2 μm long and about 0.8 μm wide, also typically arranged in a regular pattern around pores; due to different crystal terminations, inner surface distinct from outer; typical pattern of outer surface often obscured by secondary overgrowth, giving the surface a less organized appearance (Figs. 10.4, 10.5, 10.10); cyst wall surrounding archeopyle often appears "pseudo-double-layered" (Fig. 10.8); archeopyle irregularly circular to slightly polygonal in outline, measuring 11 to 13.8 μm in diameter.

Etymology.—Named after the Latin *belliatus* = beautiful.

Types.—Holotype: cyst 120-19X-2-11/IV2 (Fig. 10.1); type locality and stratum: Kerguelen Plateau, ODP Leg 120, Hole 747A - early Eocene, nannoplankton zone interval NP11-NP13, sample 120-747A-19X-2 (11-12 cm); paratypes: cysts 120-19X-2-11/IV1, 120-19X-2-11/VII8, 120-19X-2-11/VII6, 120-19X-2-11/X1, 120-19X-2-11/X50, 120-19X-2-11/VII16, 120-19X-2-11/VII4.

Other material examined.—117 cysts from the Kerguelen Plateau (ODP Leg 120, Hole 747A), sample 120-747A-19X-2 (11-12 cm), early Eocene (NP11-NP13).

Occurrence.—Only known from the early Eocene of the Kerguelen Plateau.

Discussion.—*Fuettererella belliata* n. sp. resembles *Fuettererella conforma* Kohring, 1993a regarding

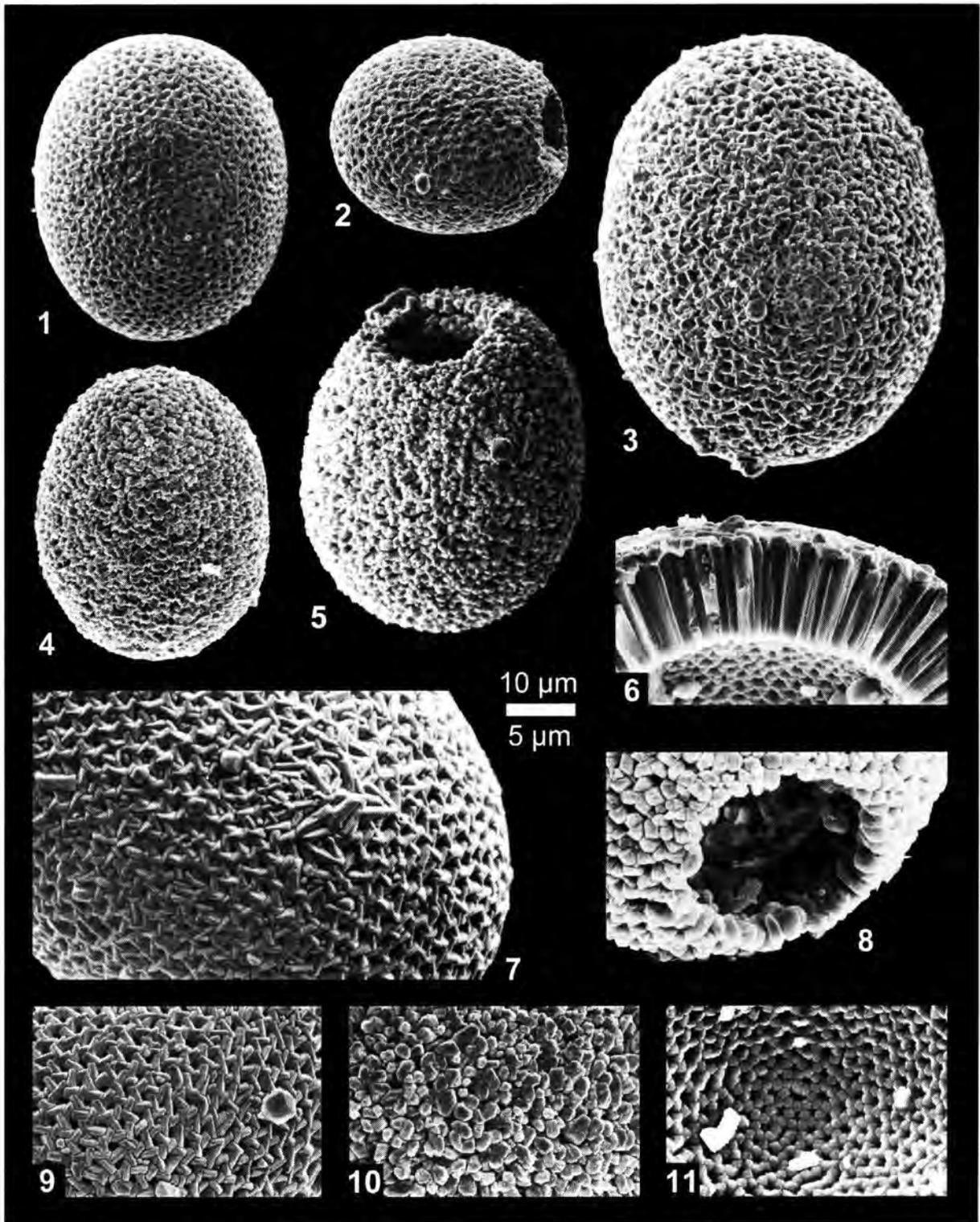


Figure 10. *Fuettererella belliata* n. sp. from the early Eocene (Kerguelen Plateau, ODP Site 747). 1, Undehisced cyst, holotype. 2, Relatively small dehisced cyst. 3, Relatively large cyst. 4, Cyst with secondary growth of wall forming crystals. 5, Medium sized dehisced cyst. 6, Cross section of single layered wall. 7, Crystal pattern on outer cyst surface showing irregular growth of some crystals. 8, Oblique view of archeopyle with "pseudo-double-layered" wall. 9, Regular arrangement of crystals on outer cysts surface. 10, Outer surface of cyst; secondary growth of crystals obscures their typical regular pattern. 11, Crystal pattern of inner cyst surface. 1, 120-19X-2-11/IV2 (holotype); 2, 120-19X-2-11/ IV1; 3, 120-19X-2-11/VIII8; 4, 10, 120-19X-2-11/VII16; 5, 120-19X-2-11/VII24; 6, 11, 120-19X-2-11/X1; 7, 120-19X-2-11/X50; 8, 120-19X-2-11/VII16; 9, 120-19X-2-11/VII4. Scale bar equals 10 μm for whole cysts (1-5) and 5 μm for close-ups (6-11).

habit of crystals and their arrangement visible in cross-section, but clearly differs in having an ovoid shape and a regular rosette-like pattern on the inner and outer cyst surface. The latter also distinguishes *F. belliata* from all other species of *Fuettererella*.

Genus *Lebessphaera* Meier et al., 2002

Type of genus.—*Lebessphaera urania* Meier, Janofske, and Willems, 2002.

Diagnosis.—Calciodinelloid dinoflagellate cysts built by a single calcareous layer. Crystals of the calcareous cyst wall layer are oriented with their crystallographic c-axis tangential to the cyst surface. Paratabulation patterns are present. The operculum includes apical, intercalary and precingular paraplates. Epicystal archeopyle (Meier et al., 2002).

Occurrence.—*Lebessphaera* is known from the modern Mediterranean Sea (Meier et al., 2002) and the early and middle Miocene of the Indian Ocean (this paper). Some specimens from the late Pliocene of the eastern Indian Ocean (*Lebessphaera?* sp. A) and from the middle Eocene of the central Pacific Ocean (*Lebessphaera?* sp. B) are tentatively assigned to *Lebessphaera* herein.

Lebessphaera urania Meier et al., 2002

Figures 4.1, 4.2

cf. "*Sphaerodinella*" *tuberosa* (Kamptner, 1963). KEUPP AND KOHRING, 1999, p. 38-39, pl. 3, figs. b-e. Incertae sedis. KOHRING, 1997, p. 161, figs. 4 o-p.

Lebessphaera urania MEIER, JANOSFKE, AND WILLEMS, 2002, p. 610-612, fig. 7.

Material examined.—14 cysts from the Wombat Plateau (ODP Leg 122, Hole 761B), samples 122-761B-5H-5 (62-63 cm), middle Miocene (NN6), and sample 122-761B-7H-4 (50-51 cm), early Miocene (NN1); 24 cysts from the Kerguelen Plateau (ODP Leg 120, Hole 747A), sample 120-747A-14H-2 (50-52 cm), early Miocene (NN1-NN2).

Description.—Calcareous cysts are single-layered and spherical in shape, measuring 26.9 to 42.8 μm in diameter (mean = 32.0, n = 29). Crystals are organized as a dense cobble-stone pattern on outer cyst surface; crystals generally are 2 to 3 μm wide, but may be smaller in the sulcal area (Figs. 4.1, 4.2); proximal crystal tips are plane and angular in outline inducing a smooth inner surface; epicystal archeopyle includes apical, intercalary, and precingular plates; archeopyle suture characterized by a levorotatory (descending) cingular displacement, which is generally preserved in dehisced cysts and may occasionally be observed in closed cysts (Fig. 4.1). Cingular area distinguished from epi- and hypocyst by two or three more-or-less parallel rows of crystals.

Discussion.—*Lebessphaera urania* has been described from surface sediments of the Ionian Sea by Meier et al. (2002) as a potentially extant species. In contrast to the specimens of Meier et al. (2002), the fossil representatives described herein exhibit clearer crystal faces, the crystal tips on the inner surface are less interlocked, and the cyst diameter is distinctly larger; for the Mediterranean Sea specimens diameters ranging from 21.9 to 31.2 μm have been reported (Meier et al., 2002).

Lebessphaera? sp. A

Figures 4.6, 4.8

Material examined.—Two specimens from the late Pliocene (NN16), sample 122-761B-4H-1 (122-123 cm), ODP Leg 122, Hole 761B, Wombat Plateau.

Description.—Single layered cysts are spherical, 29.0 and 38.6 μm in diameter; calcareous cyst wall about 2 μm thick and consists of irregularly shaped interfingering crystals. Planar crystal terminations on outer cyst surfaces about 2 μm in diameter, resembling a pattern of polylobate jigsaw pieces. Archeopyle obviously epicystal, revealing a descending cingular displacement.

Discussion.—See Discussion of *Lebessphaera?* sp. B.

Lebessphaera? sp. B

Figure 4.3

Material examined.—Three specimens from the middle Eocene, sample AMPH-116P (488–489 cm), central Pacific Ocean and two specimens from the late Oligocene, sample 120-747A-14H-5 (120–121 cm), ODP Leg 120, Hole 747A, Kerguelen Plateau, southern Indian Ocean.

Description.—Single-layered calcareous cysts measure 27.4, 31.0, 36.7, 39.8, and 42.9 μm in diameter, spherical in shape; wall of smallest cyst 3.1 μm thick; archeopyle interpreted as epicystal, as cingular displacement is visible in some of the cysts; crystal terminations on outer surface polygonal to irregularly angular in outline, measuring 2 to 3 μm in diameter.

Discussion.—*Lebessphaera?* sp. A and sp. B are questionably assigned to *Lebessphaera* as the crystallographic ultrastructure of both species has not been confirmed by thin sections. *Lebessphaera?* sp. B resembles *L. urania*, however cingular displacement is more indistinct in *L.?* sp. B. Furthermore, the observed irregularly angular outline of many crystals on the outer surface is untypical for *L. urania*, although it was described for the inner surface of the type material of *L. urania* (Meier et al., 2002). More specimens are necessary to confirm the true nature of both species and their relationship to *L. urania*.

Genus *Orthopithonella* Keupp in Keupp and Mutterlose, 1984 emend. Streng et al., 2002

Discussion.—*Orthopithonella* Keupp in Keupp and Mutterlose, 1984 has been emended by Streng et al. (2002), because various taxa bearing different archeopyles types had previously been united within this genus. As a result, *Orthopithonella* is now regarded as a monospecific genus, because of the unique archeopyle characteristics of its type, i.e., *Orthopithonella gustafsonii* (Bolli, 1974) Lentin and Williams, 1985. All species formerly accommodated in *Orthopithonella* are only questionably assigned to this genus pending their reallocation (see Streng et al. (2002) [Chapter 2.1] for details).

Orthopithonella? cf. *minuta* Fütterer, 1990

Figures 3.3, 3.4

Material examined.—12 specimens from the early Eocene and late Paleocene, samples 120-747A-19X-2 (11–12 cm) and 120-747A-19X-2 (138–139 cm) and one specimen from the early Miocene, sample 120-747A-12H-2 (76–77 cm), all ODP Leg 120, Hole 747A, Kerguelen Plateau.

Description.—Single-layered cysts with spherical shape; diameter of cyst 25.5 to 32.6 μm (mean = 27.9, $n = 12$); wall about 2.5 μm thick, composed of radially oriented, about 1 μm wide rhombohedrons; crystal length equals thickness of wall; distal and proximal crystal tips three-sided and pointed. Archeopyle irregular in outline, probably involving more than one plate, no archeopyle type can be designated, though; diameter of archeopyle about 50 to 60 percent of cyst diameter. A circular operculum is visible occasionally, obviously overlapping archeopyle (Fig. 3.4). Orientation of

c-axes of wall-forming crystals unknown, presumably tangential analogous to similar crystals of species with a tangential ultrastructure.

Discussion.—Kohring (1993a, p. 30) regarded *Orthopithonella minuta* Fütterer, 1990 as a junior synonym of *Orthopithonella deflandrei* (Kamptner, 1956) (now *Fuettererella deflandrei*, see Hildebrand-Habel and Streng, in review [Chapter 2.3]) because of similarities of the holotype of Fütterer (1990, pl. 1, figs. 4-5) to depicted specimens of *F. deflandrei*, especially considering the wall-forming crystals. However, we retain *Orthopithonella minuta* because of the following reasons:

Fütterer (1990) described two slightly different morphotypes as *Orthopithonella minuta* distinguished by the habitus of the wall-forming crystals. The first morphotype, the holotype, is characterized by a cobblestone-like pattern of polygonal crystal with rounded terminations on the outer surface. In contrast, the second morphotype which comprises all depicted paratypes, bears an outer cyst surface with trigonal pointed crystal tips. Furthermore, the diameter of the crystals of the holotype is about twice as wide as that of the paratypes, giving the holotype a more robust appearance. The archeopyle of both morphotypes is irregularly round to slightly angular and cannot be assigned to a distinct archeopyle type. We found similar morphotypes in our samples, which reveal additional features. Some undehisced cysts which resemble the second morphotype show a relatively large more-or-less circular operculum measuring about 70 percent of the cyst diameter (Fig. 3.3). Specimens that resemble the holotype of Fütterer (1990), regarding the robust appearance, exhibit a symmetrical and also relatively large archeopyle that may resemble a mesoepicystal archeopyle, albeit the distal crystal tips are also three-sided. In contrast to the even proximal crystal tips of the type material, the specimens described above show distally and proximally pointed crystal terminations. However, as crystal size and habitus may be affected by diagenetic overprint, we accommodate our specimens and the two morphotypes of Fütterer (1990) within the same species. However, as the archeopyle of both morphotypes is clearly distinguished from that of *F. deflandrei* (Kamptner, 1956) (compare Fig. 1.3), we refuse the suggestion of Kohring (1993a) that *O. minuta* is a junior synonym of *F. deflandrei*. As long as the archeopyle characteristics as well as the ultrastructure of *O. minuta* are unknown, an unequivocal accommodation in an appropriate genus is not possible. Therefore, it should be cited as *O.? minuta* Fütterer, 1990.

Additionally, we retain *Pirumella johnstonei* (Bolli, 1974) as a separate species, which has been regarded likewise to *O.? minuta* as a junior synonym of *F. deflandrei* by Kohring (1993a, p. 30). However, *P. johnstonei* is clearly separated from *F. deflandrei* by the crosswise arrangement of the wall forming crystals in cross section (see Bolli, 1974, p. 856).

Genus *Pernambugia* Janofske and Karwath in Karwath, 2000 emend.

Original diagnosis of cyst.—Non-motile stages (cysts) have a single calcareous wall layer. Crystals of the calcareous cyst wall layer are oriented with their crystallographic optic axis (c-axis) irregularly oblique to the cyst surface. The operculum includes apical and intercalary plates (Karwath and Janofske in Karwath, 2000, p. 114).

Emended diagnosis of cyst.—Cysts with a single-layered calcareous wall; crystals of wall layer oriented with their crystallographic axis (c-axis) irregularly oblique to the cysts surface; operculum includes all apical, intercalary, and precingular plates, archeopyle epicystal.

Type.—*Pernambugia tuberosa* Janofske and Karwath in Karwath, 2000.

Discussion.—The genus *Pernambugia* has been established by Janofske and Karwath in Karwath (2000) to include the single species *P. tuberosa* (Figs. 4.4, 4.5), characterized by a relatively large

circular archeopyle and an oblique orientation of the wall-forming crystals. *P. tuberosa* was first described as *Thoracosphaera tuberosa* from middle Pleistocene sediments of the equatorial Pacific Ocean (Kamptner, 1963) and has been misinterpreted by several subsequent authors. They described specimens with a similar wall structure, a presumed radial orientation of the c-axis and an angular archeopyle as *Thoracosphaera tuberosa* and *Sphaerodinnella tuberosa*, respectively (see Janofske and Karwath in Karwath (2000) for details). Those specimens belong to a previously undescribed species of *Calciodinellum*, i.e., *Calciodinellum levantinum* Meier et al., 2002.

According to Janofske and Karwath in Karwath (2000), no tabulation patterns are recognizable in the cysts of *Pernambugia*, as the surface is bare of any ridges or ornamentation and the archeopyle has a circular outline. However, we interpret the archeopyle, analogous to *Lebessphaera*, as an epicystal archeopyle including all apical, intercalary and precingular plates, although the cingulum shows no distinct displacement (compare description of *Lebessphaera urania*). Consequently, tabulation is reflected by the archeopyle suture as the transition of the cingulum to the epicyst.

Pernambugia? patata new species

Figure 11

Diagnosis.—Species of *Pernambugia* with an irregular spherical shape of the cyst. Archeopyle suture incomplete.

Description.—Spherical to irregularly spherical single layered cysts with diameters ranging from 27.3 to 50.3 μm (mean = 37.0 μm , n = 61). Medial situated archeopyle suture incomplete, embracing about half of the cyst, obviously separating epi- and hypocyst. Archeopyle margin circular to irregularly circular, typically characterized by two opposite deflections; deflections define end of principal archeopyle suture; archeopyle is interpreted as a combination archeopyle, including approximately the whole epicyst (epicystal archeopyle; see Discussion); cyst wall about 3 μm thick consisting of relatively large interfering blocky crystals. Inner cyst surface characterized by jigsaw-like pattern of interlocking crystal bases.

Etymology.—After the Spanish *patata* = potato, in allusion to the irregular shape of the cysts.

Types.—Holotype: cyst 120-1R-4/IV15-2 (Fig. 11.1); type locality and stratum: Kerguelen Plateau, southern Indian Ocean, ODP Leg 120, Hole 747C - early Oligocene, nannoplankton zone interval NP23-NP25, sample 120-747C-1R-4 (11-12 cm); paratypes: cysts 120-14H-2/VI17-2, 120-1R-4/V15-2, 120-1R-4/X11-2, 120-1R-4/XIV14-2, 120-1R-4/V18-3, 120-1R-4/VI24, 120-1R-4/V30-2, 120-1R-4/III3-2.

Other material examined.—99 cysts from the early Oligocene, sample 120-747C-1R-4 (66-67 cm), and 32 cysts from the early Miocene, sample 120-747A-14H-2 (50-52 cm), both ODP Leg 120, Holes 747A and 747C, Kerguelen Plateau.

Occurrence.—Early Oligocene and early Miocene of the Kerguelen Plateau.

Discussion.—The archeopyle of *P.? patata* n. sp. with an incomplete principal archeopyle suture (suture does not completely surround operculum) is unique within the calcareous dinoflagellate cysts. Within the organic-walled dinoflagellate cysts such archeopyles are quite common and are characterized by an attached operculum (adnate operculum). In contrast to the organic-walled cysts, an excystment leaving the operculum attached is not possible within the calcareous dinoflagellates. As a consequence, the calcareous operculum of *P.? patata* is obviously broken off, resulting in two more or less hemispherical parts, which roughly represent epi- and hypocyst. Analogous to the organic-walled

cysts we interpret the side of the cysts bearing the suture as the dorsal one, and the unsutured side as ventral.

As the archeopyle of *P.?* *patata* is exceptional within the calcareous dinoflagellate cysts, the taxonomic rank of this feature is hard to predict. Furthermore, as *Pernambugia* is an extant genus, the cyst-theca relationship is part of the definition of the genus. *P.?* *patata*, however, is a fossil species and therefore, the motile stage remains unknown. Hence, *P.?* *patata* is only tentatively assigned to *Pernambugia*. Nevertheless, *Pernambugia* seems to be the only appropriate genus to accommodate this new species, as the broad definition of the cyst, i.e., single layered, oblique ultrastructure, and archeopyle including apical and intercalary plates, leaves the possibility for a wide interpretation. Despite this existing definition, we propose an epicystal archeopyle for both, the type species *P. tuberosa* and the new species *P.?* *patata*, implying a more uncompromising definition of this genus.

The appearance of *P.?* *patata* is characterized by its blocky wall-forming crystals whose appearance is evidently partly due to diagenetic effects. Impressions of coccoliths and the fitting

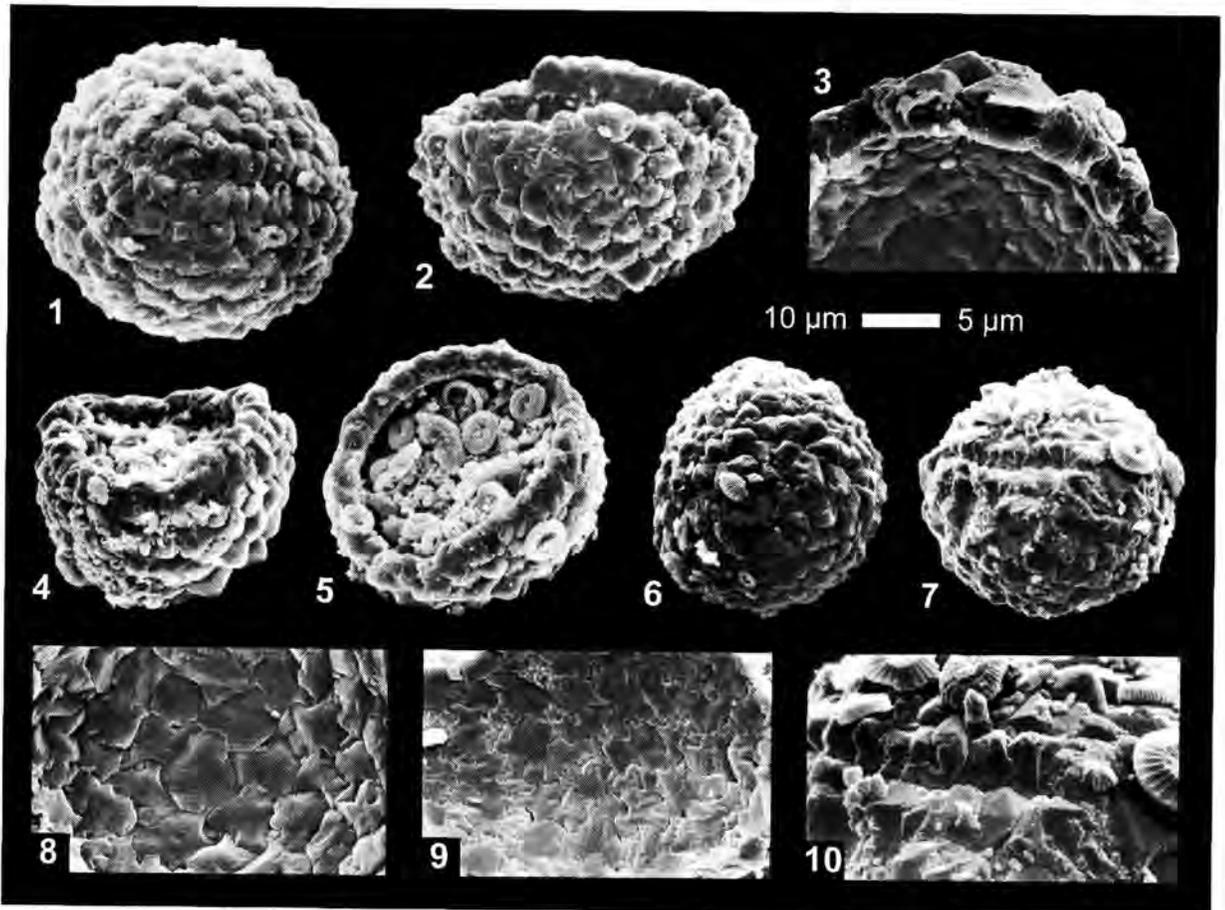


Figure 11. *Pernambugia?* *patata* n. sp. from the early Oligocene and early Miocene (Kerguelen Plateau, ODP Site 747). 1, Holotype in left lateral view showing the incomplete archeopyle suture. 2, Lateral view of epicyst? showing opposite deflections. 3, Cross-section of single-layered calcareous wall. 4, 5, Two hypocysts? in lateral and oblique lateral view. 6, Irregular shaped cyst without archeopyle suture. 7, Cyst in lateral view with archeopyle suture. 8, 9, Inner surface of two different cysts, showing interlocking crystals. 10, Detail of 7, close-up of archeopyle suture.

1, 120-1R-4/IV15-2 (holotype); 2, 120-14H-2/VI17-2; 3, 120-1R-4/V15-2; 4, 120-1R-4/X11-2; 5, 120-1R-4/XIV14-2; 6, 120-1R-4/V18-3; 7, 10, 120-1R-4/VI24; 8, 120-1R-4/V30-2; 9, 120-1R-4/II13-2. Scale bar equals 10 μm for cysts (1, 2, 4-7) and 5 μm for close-ups (3, 8-10).

structure of the crystal bases indicate secondary growth of the wall-forming crystals in vertical and lateral directions. Therefore, the original appearance of the cyst of *P.?* *patata* remains unknown, obscured by a diagenetic overprint. The unequivocal features of the archeopyle, however, are definitely unaffected by diagenesis and thereby the erection of a new species is justified.

P.? *patata* is similar to *Orthopithonella* sp. 1 depicted by Fütterer (1990) in its general appearance characterized by the solid wall-forming crystals as a result of secondary overgrowth. However, *Orthopithonella* sp. 1 is described as a strictly spherical cyst with a circular archeopyle measuring about 56 percent of the cyst diameter. This is in contrast to the generally irregularly shaped cysts of *P.?* *patata* with an epicystal archeopyle whose diameter equals the cyst diameter.

Genus *Praecalcionellum* Keupp and Versteegh, 1989

Type of genus.—The holotype of *Praecalcionellum polymorphum* (Keupp, 1980a) Lentin and Williams, 1993.

Diagnosis.—Dinoflagellate cyst with single-layered, radial-fibrous calcareous walls. The outside parasutural paratabulation is characterized by large prismatic areas constructed by fused pre- and postcingular homologues. The small archeopyle is apical and corresponds to thecal plate 3'. (Keupp and Versteegh, 1989, p. 211)

Included species.—*P. dolium* (Keupp, 1979b) n. comb.; *P. duopylum* Willems, 1995; *P. mutterlosei* (Keupp, 1979b) Lentin and Williams, 1993; *P. polymorphum* (Keupp, 1980a) Lentin and Williams, 1993; *P. schizosaeptum* Versteegh, 1993; *P. sulcatum* (Keupp, 1979a) n. comb.; *P. triangulare* (Keupp, 1980a) Keupp, 1992b.

Occurrence.—The genus is known from the early Hauterivian (Keupp, 1979a) to the late Albian (Keupp, 1995b). Single occurrences are recognized from the early Maastrichtian (Kienel, 1994) and early Danian (Willems, 1996) as well as from the late Pliocene to Recent (see Montresor et al., 1994).

Discussion.—The stratigraphic distribution of *Praecalcionellum* Keupp and Versteegh, 1989 covers three different time intervals: 1) Early Cretaceous, 2) Maastrichtian to Danian, and 3) late Pliocene to Recent. These three time intervals are characterized by two divergent types of cysts. The Early Cretaceous species, i.e., *P. dolium*, *P. mutterlosei*, *P. polymorphum*, *P. sulcatum*, and *P. triangulare*, have a specific barrel-shaped appearance with an apical and an antapical face. This is in contrast to the two remaining species, *P. duopylum* (Maastrichtian to Danian) and *P. schizosaeptum* (late Pliocene to Recent), which are wedge-shaped and characterized by a flattened apical face, tapering antapically. Probably two different genera that differ stratigraphically as well as morphologically, are unified in one genus.

Praecalcionellum polymorphum (Keupp, 1980a) Lentin and Williams, 1993

Discussion.—*Praecalcionellum polymorphum* (Keupp, 1980a) is divided into three subspecies, i.e., *P. polymorphum dentatum* (Keupp, 1980a) Lentin and Williams, 1993, *P. polymorphum polymorphum* Autonym, and *P. polymorphum tenue* (Keupp, 1980a) Lentin and Williams, 1993, which are distinguished by their individually different development of ridges on the outer surface that define tabulation (Keupp, 1980a).

Praecalcionellum polymorphum polymorphum Autonym

Figure 1.11

Calcigonellum polymorphum KEUPP, 1980a, p. 128-131, pl. 15, figs. 7-12; 1981, p. 16-17, pl. 3, figs. 7-12, pl. 4, figs. 1-3, 6; 1982, p. 311-312, pl. 6.2-1, figs. 1-2; Bujak and Davies, 1983, pl. 12, fig. 5.

Praecalcionellum polymorphum (Keupp, 1980a) [nom. illeg.]. Keupp and Versteegh, 1989, p. 211, pl. 2, fig. 10; Monnet, 1990, p. 54, pl. 2, figs. 1-15; Keupp, Monnet, and Kohring, 1991, pl. 1, fig. 7; Keupp, 1992b, p. 128, pl. 1, fig. 9; Monnet, 1992, p. 22-26, pl. 9, figs. 1-6; 1993, p. 21-22, pl. 3, figs. 1-12.

Praecalcionellum cf. *polymorphum* (Keupp, 1980a) [nom. illeg.]. Keupp, 1992b, p. 128, pl. 1, figs. 6-8.

Praecalcionellum polymorphum (Keupp, 1980a) [nom. legit.]. Lentin and Williams, 1993, p. 538;

? *Praecalcionellum* cf. *polymorphum* (Keupp, 1980a). Keupp, 1995a, fig. 2.7.

Material examined.—Two cysts from the Vöhrum clay pit, Voe6-21 and Voe6-62, Aptian-Albian boundary interval.

Occurrence.—Middle Aptian to early Albian of Lower Saxony, Germany (Keupp, 1981, 1995a)

Discussion.—*P. polymorphum polymorphum* bears a slightly convex apical face bearing a relatively large central archeopyle which represents the single apical plate 3'. It is distinguished from *P. polymorphum dentatum* (Keupp, 1980a) Lentin and Williams, 1993 and *P. polymorphum tenue* (Keupp, 1980a) Lentin and Williams, 1993 by a stronger and a more inconspicuous development of tabulation reflecting ridges, respectively.

Praecalcionellum sulcatum (Keupp, 1979a) new combination

Basionym.—*Calcigonellum sulcatum* Keupp, 1979a, p. 658, pl. 6, figs. 16-21.

Discussion.—The combination *Praecalcionellum sulcatum* was not validly published by Keupp and Versteegh (1989, p. 211) as these authors did not fully reference the basionym.

Praecalcionellum dolium (Keupp, 1979b) new combination

Basionym.—*Calcigonellum dolium* Keupp, 1979b, p. 39-40, pl. 9, figs. 7-9.

Discussion.—The combination *Praecalcionellum dolium* was not validly published by Keupp and Versteegh (1989, p. 211) as these authors did not reference the basionym.

DISCUSSION

Since Fensome et al. (1993) all calcareous dinoflagellate cysts have been placed in the single subfamily Calciodinelloideae belonging to the family Peridiniaceae Ehrenberg, 1831. Fensome et al. (1993) rejected the prior subfamily concept of Keupp (1987) which was established solely on the different crystallographic ultrastructure types of the cyst wall. In their opinion, the wall structure should only be applied supplementary to tabulation patterns when pondering phylogenetic relationships. Accordingly, the Calciodinelloideae are defined as Peridiniaceans with bipesoid episomal tabulation, a hexa second anterior intercalary plate (2A), a cyst walls including one or more calcareous layers, and an apically located archeopyle (Fensome et al., 1993).

Judging from the various observed archeopyle types described herein, a subdivision of the Calciodinelloideae based on the major archeopyle categories or types would be conceivable as their stratigraphic distribution obviously reflects a clear phylogenetic trend (Fig. 12). However, some uncertainties and inconsistencies should be solved first:

1) The archeopyles of many species have not been identified yet (compare Appendix I), especially of stratigraphically earlier species whose classification would be essential for phylogenetic considerations. Furthermore, an insufficient number of species has an intercalary or a polyplacoid apical archeopyle to legitimate a separate superordinate taxon.

2) Too little is known regarding the species diversity as well as the regional and stratigraphic distribution during several time periods, especially during the Jurassic, that would prove or manifest the presumed trend.

3) Another uncertainty arises from external tabulation patterns of certain species that question the affiliation of these species at least to the Peridiniaceans. Those tabulation patterns cannot be homologized with any kind of known tabulation types, although their archeopyles may resemble a monoplacoid apical archeopyle. Examples are: 1) *Bicarinellum? pulchrum* Keupp and Kowalski, 1992 from the Albian of S-England and N-Germany. It bears a tabulation pattern that suggests an untypically high number of plates, of which none can be labeled with certainty. 2) *Orthotabulata obscura* Kienel, 1994 described from the Danian of Germany. The holotype of *O. obscura* shows, similar to *B.? pulchrum*, an abnormal tabulation pattern including less plates, though. No archeopyle has been found. 3) *Centosphaera barbata* Wind and Wise in Wise and Wind, 1977 from the Maastrichtian and Danian of the high latitudinal Southern Hemisphere. This species typically has two parallel keels that may reflect the cingulum and a small circular archeopyle that is located between the keels. Therefore, the keels represent either a new type of tabulation or an enigmatic type of ornamentation, as intracingular archeopyles are hardly imaginable.

4) Another reason that gets in the way of a new subdivision of the Calciodinelloideae is the already mentioned inadequate description of cryptotabulate attributes accompanied by inaccurate and broad definitions of many genera and species. These deficiencies caused accommodations of separate taxa in a single taxon (e.g., *Orthopithonella*; see Streng et al., 2002 [Chapter 2.1]), resulting in a biased stratigraphic and regional distribution of this taxon. Erwin and Droser (1993) coined the term "Elvis taxa" for taxa that disappear, to be replaced by unrelated, but strikingly similar impersonators. Especially taxa that bear a simple morphology and often lack sufficient features for discrimination, like many calcareous dinoflagellate cysts, are predestined to be Elvis taxa. Therefore, Elvis taxa are probably an unrecognized problem within the Calciodinelloideae as many simply spherical calcareous cysts generally have few and hard to discriminate characteristics. One example is *Fuettererella deflandrei* (Kamptner, 1956) Hildebrand-Habel and Streng (in review), a species characterized by its spherical single layered cyst, a monoplacoid apical archeopyle, tangential ultrastructure, and an uncharacteristic surface pattern. Kohring (1993a) regarded the species *Pirumella johnstonei* (Bolli, 1974) Lentini and Williams, 1993, and *Orthopithonella minuta* Fütterer, 1990 to be junior synonyms of *F. deflandrei*, species that superficially resemble each other, however minor but substantial differences exist that legitimate to retain and maintain both species as separate taxa (see Systematic Paleontology, Discussion of *Orthopithonella? minuta* Fütterer, 1990). Accordingly, *F. deflandrei* would be the Elvis taxon of *P. johnstonei* and *O.? minuta*. Another example is *Caracomia arctica* (Gilbert and Clark, 1983) Streng et al., 2002 which has been regarded as a single species until, recently Streng et al. (2002) [Chapter 2.1] figured out that two separate species were included in *C. arctica*, i.e., *C. arctica*, and *C. stella* Streng et al., 2002, both showing distinct regional and ecological preferences. In contrast to the concept of Elvis taxa of Erwin and Droser (1993), which implicates by definition a chronologically appearance of taxa typically separated by an extinction event, the described examples within the Calciodinelloideae typically overlap stratigraphically or even appear simultaneously. The

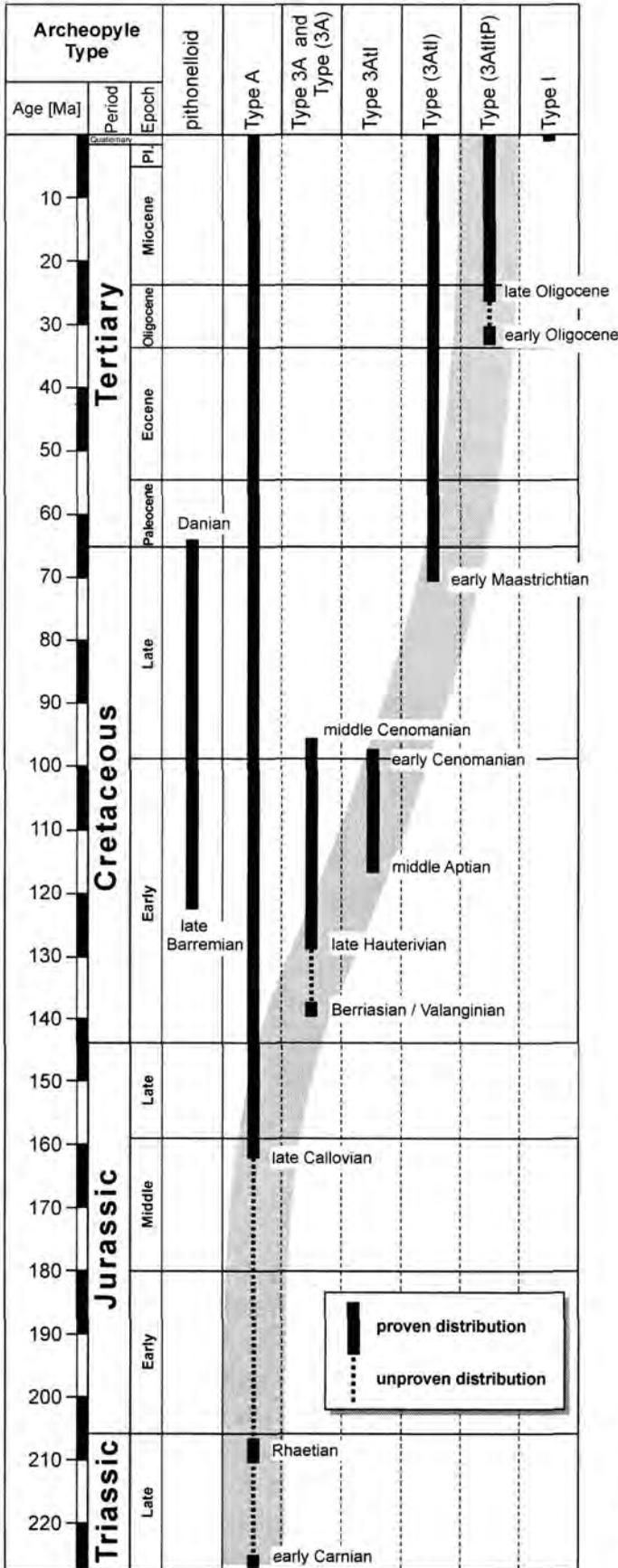


Figure 12. Stratigraphic distribution of archeopyle types of the Calciadinelloideae. Shaded area marks a presumed phylogenetic trend which is characterized by a steady increase of the number of plates involved in the archeopyle.

species *Cervisiella operculata* n. comb., and *Calciodinellum clamosum* n. sp. for example, formerly united within the single species *Operculodinella operculata* (Bramlette and Martini, 1964) Hildebrand-Habel et al., 1999, have both their main appearance in the Paleocene. Even more of such Elvis taxa in a broader sense, are probably still unrecognized within the Calciodinelloideae, biasing stratigraphic and regional distributions. Modern biology denotes extant species, which can hardly or not be separated by morphological characters, but are clearly distinguished genetically, as sibling species. A term that probably would also be appropriate for the examples of calcareous dinoflagellate taxa discussed above, especially to the co-occurring species. However, the concept of sibling species implies a close phylogenetic relationship between those species, a factor that cannot be unambiguously proven in potential fossil calcareous dinoflagellate taxa.

Future investigations must focus and solve the problems and discrepancies described above to prove or to disprove the monophyly of the Calciodinelloideae which would be the base of phylogenetic consistent subdivision. We regard the archeopyle of each species and its correct assignment to a distinct archeopyle type to be at least one appropriate and significant tool to achieve this aim.

CONCLUSIONS

Archeopyle types of the Calciodinelloideae.—Three of the four major archeopyle categories defined by Evitt (1967) for organic-walled dinoflagellates have been found to occur within the Calciodinelloideae, i.e., apical, intercalary, and combination archeopyles (Fig. 13). However, it remains a puzzling fact that the most common archeopyle types of the Calciodinelloideae, i.e., monoplacoid apical archeopyles and mesoepicystal archeopyles, barely occur in the organic-walled Peridinales and *vice versa*. Hence, the position of the calcareous dinoflagellate cysts within the Peridinales, which is already exceptional because of the calcareous wall and unique types of reduced tabulation, becomes even more remarkable, suggesting a separate phylogeny and a higher taxonomic rank for the Calciodinelloideae than previously assumed.

Archeopyles of calcareous cysts that cannot be assigned to one of the major groups are, analogous to the organic-walled cysts, categorized under "miscellaneous archeopyles". Species with a pithonelloid wall, whose dinoflagellate affinity and accommodation within the Calciodinelloideae is still questionable, are regarded as a separate group and are not classified in one of the categories of Evitt (1967). Those species bear a small circular, "apically" located aperture.

Stratigraphic distribution of archeopyle types.—Regarding the stratigraphic distribution of the different archeopyle types of calcareous dinoflagellate cysts, a distinct evolutionary trend is obvious. The oldest assemblages, from the Triassic to the late Cretaceous, are clearly dominated by cysts with an apical archeopyle and a monoplacoid operculum. Archeopyles arising from the loss of a compound operculum are only known from the middle Cretaceous. Combination archeopyles with a simple polyplacoid operculum appear in the early Maastrichtian (*C. albatrosianum* by Hildebrand-Habel et al., 1999), and became more abundant during the Tertiary. The first true epicystal archeopyles are known from the late Oligocene (*Lebessphaera?* sp. B, described herein). *Pernambugia?* *patata* n. sp. with its unique epicystal-like archeopyle is already found in the early Oligocene, though. Generally, a phylogenetic trend is evident in the stratigraphic distribution of archeopyle types of calcareous dinoflagellate cysts which is characterized by a steady increase of the number of plates involved in the archeopyle (Fig. 12). Archeopyles that involve only three apical plates and archeopyles with

compound opercula are obviously evolutionary intermediate stages or precursors of simple mesoepicystal archeopyles.

Archeopyle-cyst relations.—Another puzzling fact is that obviously all species of calcareous dinoflagellate cysts that have a multi-layered wall and whose archeopyles could be identified, have a Type A archeopyle. In contrast, single layered species show all types of archeopyles. But if an archeopyle involves more than one plate is the cyst always single-layered. No relation is evident between tabulation and archeopyle type.

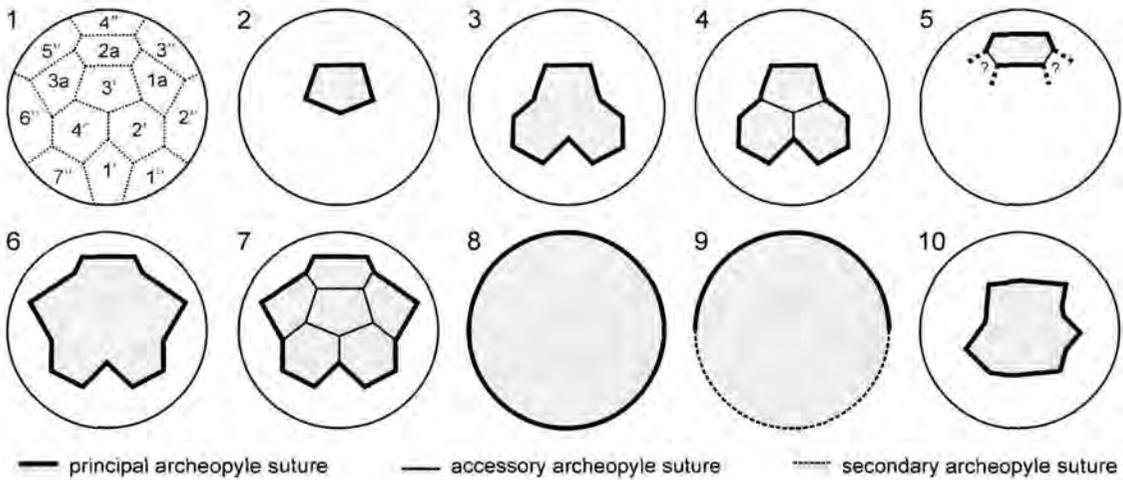


Figure 13. Schematic overview of all observed archeopyle types within the Calciodinelloideae. 1, Labeled epicyst in apical view for orientation; 2, monoplacoid apical archeopyle, Type A; 3, polyplacoid apical archeopyle with simple operculum, Type (3A); 4, polyplacoid apical archeopyle with compound operculum, Type 3A; 5, intercalary archeopyle, Type I; 6, mesoepicystal archeopyle with simple operculum, Type (3AtI); 7, mesoepicystal archeopyle with compound operculum, Type 3AtI; 8, epicystal archeopyle, Type (tAtItp); 9, epicystal archeopyle, Type (tAtItp) with principal and secondary archeopyle suture; 10, irregularly shaped archeopyle of uncertain affinity, "tremic" archeopyle.

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Appendix A. List of valid fossil calcareous dinoflagellate taxa

Alphabetic list of valid fossil calcareous dinoflagellate taxa (only Calciodinelloideae) according to the index of Williams et al. (1998) excluding subspecies and forms. New taxonomic data from more recent literature are incorporated. Species only known from thin sections are not taken into account, as archeopyle characteristics for those species are unknown. This concerns species of the following genera: *Carpistomiosphaera* Nowak, 1968, *Colomisphaera* Nowak, 1968, *Committosphaera* Řehánek, 1985, and *Hemistomiosphaera*, Nowak, 1968. Furthermore, the problematicum *Schizosphaerella punctulata* Deflandre and Dangeard, 1938 is believed to be not a dinoflagellate cyst, because it has a test built of two overlapping valves connected by a simple hinge, a construction that is inexplicable for calcareous dinoflagellate cysts. Likewise, *Thoracosphaera wombatensis* Bralower et al., 1991 more likely represents a species of *Schizosphaerella*. *Calcicarpinum? fallax* Taugourdeau-Lantz and Rosset, 1966 is too large to be a dinoflagellate cyst (>1500 µm), it is presumably a calcified megaspore.

The generic position of species that need future reallocation, e.g., because of intrageneric differences concerning the archeopyle, are marked by a question mark following the generic epithet. For each species, the recognized archeopyle type is given.

Legend: A = apical archeopyle involving the single plate 3'; 3A = apical archeopyle involving plates 2'-4'; I = intercalary archeopyle including at least plate 2a; 3AtI = combination archeopyle involving plates 2'-4' and all intercalary plates; E = epicystal archeopyle; O = archeopyle type not identified, although archeopyles have been observed; X = species without an observed archeopyle; P = pithonelloid species with an apical circular aperture (accommodation of pithonelloid species within the Calciodinelloideae is questionable); "?" indicates uncertainty of the individual archeopyle type.

<i>Alasphaera tuberculata</i> (Pflaumann and Krasheninnikov, 1978) Keupp, 1981	A
<i>Amphora coronata</i> Willems, 1994	O
<i>Bicarinellum calvum</i> Keupp, 1979b	A
<i>Bicarinellum castaninum</i> Deflandre, 1948	A
<i>Bicarinellum cristatum</i> Keupp, 1982	X
<i>Bicarinellum eulineatum</i> Keupp, 1987	X
<i>Bicarinellum jurassicum</i> (Deflandre, 1948) Keupp, 1984	O
<i>Bicarinellum pulchrum</i> Keupp and Kowalski, 1992	?A
<i>Bicarinellum tricarinelloides</i> Versteegh, 1993	A
<i>Bicarinellum tumulosum</i> Willems, 1988	X
<i>Bitorus bulbjergensis</i> Kienel, 1994	?3A
<i>Bitorus truncus</i> Hildebrand-Habel and Willems, 1999	?3A
<i>Bitorus turbiformis</i> Keupp, 1992a	3A
<i>Calcicarpinum bivalvum</i> Versteegh, 1993	A
<i>Calcicarpinum perfectum</i> Versteegh, 1993	A
<i>Calcicarpinum primum</i> Keupp, 1995b	X
<i>Calcicarpinum tetraedricum</i> Deflandre, 1948	X
<i>Calcicarpinum tetramurum</i> Kienel, 1994	A
<i>Calcigonellum? ansatum</i> Hildebrand-Habel and Willems, 1999	3AtI
<i>Calcigonellum? granulatum</i> Kohring, 1993a	3AtI
<i>Calcigonellum infula</i> Deflandre, 1948	E
<i>Calcigonellum? minutum</i> Keupp, 1987	A
<i>Calciodinellum albatrosianum</i> (Kamptner, 1963) Janofske and Karwath in Karwath, 2000	3AtI
<i>Calciodinellum clamosum</i> n. sp.	3AtI

<i>Calciodinellum elongatum</i> (Hildebrand-Habel et al., 1999) Meier et al., 2002	3AtI
<i>Calciodinellum kerguelensis</i> n. sp.	3AtI
<i>Calciodinellum levantinum</i> Meier et al., 2002	3AtI
<i>Calciodinellum limbatum</i> (Deflandre, 1948) Kohring, 1993a	?3AtI
<i>Calciodinellum operosum</i> Deflandre, 1947	3AtI
<i>Calciperidinium asymmetricum</i> Versteegh, 1993	I
<i>Calcipterellum colomii</i> Deflandre, 1948	3AtI
<i>Caracomia arctica</i> (Gilbert and Clark, 1983) Streng et al., 2002	3AtI
<i>Caracomia stella</i> Streng et al., 2002	3AtI
<i>Carinasphaera cimbra</i> Kohring, 1993a	X
<i>Carinellum conulum</i> Keupp, 1981	X
<i>Carinellum hyalinum</i> Keupp, 1987	O
<i>Carinellum lenticulare</i> Keupp, 1987	?A
<i>Carinellum monocarinatum</i> Keupp, 1981	O
<i>Carinellum parasolis</i> Keupp, 1984	O
<i>Carinellum turbosimile</i> Kienel, 1994	X
<i>Centosphaera barbata</i> Wind and Wise in Wise and Wind, 1977	?A
<i>Cervisiella operculata</i> (Bramlette and Martini, 1964) n. comb.	A
<i>Cervisiella saxea</i> (Stradner, 1961) Hildebrand-Habel et al., 1999	A
<i>Congruentia eocaenica</i> Kohring in Keupp et al., 1991	?A
<i>Cubodinellum renei</i> Keupp, 1987	?A
<i>Cubodinellum sulcatum</i> Zügel, 1994	X
<i>Cylindrodinellum scriblitimum</i> Zügel, 1994	X
<i>Dimorphosphaera aequatoriana</i> Keupp, 1979b	?A
<i>Echinodinella erinacea</i> Keupp, 1980a	3A
<i>Echinodinella levata</i> Keupp, 1981	3A
<i>Follisdinellum splendidum</i> Versteegh, 1993	O
<i>Fuettererella belliata</i> n. sp.	A
<i>Fuettererella conforma</i> Kohring, 1993a	X
<i>Fuettererella deflandrei</i> (Kamptner, 1956) Hildebrand-Habel and Streng (in review)	A
<i>Fuettererella elliptica</i> Kohring, 1993a	A
<i>Fuettererella flora</i> (Fütterer, 1990) Hildebrand-Habel and Streng (in review)	A
<i>Fuettererella fungiforma</i> Hildebrand-Habel and Willems, 1999	X
<i>Fuettererella tesserula</i> (Fütterer, 1977) Kohring, 1993a	A
<i>Gonellum calcipterelloides</i> Keupp, 1987	O
<i>Gonellum kurtii</i> Keupp, 1987	O
<i>Gonellum prismaticum</i> Keupp, 1991a	O
<i>Heptasphaera michaelii</i> Keupp, 1979b	A
<i>Heptasphaera paulaworstelliae</i> Bolli, 1978b ex Lentin and Williams, 1985	A
<i>Keuppisphaera radiata</i> (Keupp, 1987) Lentin and Williams, 1989	A
<i>Lebessphaera urania</i> Meier et al., 2002	E
<i>Lentodinella danica</i> Kienel, 1994	?P
<i>Leonella granifera</i> (Fütterer, 1977) Janofske and Karwath in Karwath, 2000	A
<i>Melodomuncula berlinensis</i> Versteegh, 1993	A

<i>Nephrodinella reniformis</i> Keupp, 1981	O
<i>Normandia circumperforata</i> Zügel, 1994	P
<i>Operculodinella costata</i> Kienel, 1994	3Atl
<i>Operculodinella hydria</i> Kienel, 1994	3Atl
<i>Operculodinella reticulata</i> Kienel, 1994	3Atl
<i>Orthocarinellum biconvexum</i> Kienel, 1994	O
<i>Orthocarinellum conosimile</i> Kohring, 1993a	X
<i>Orthocarinellum galerum</i> Keupp, 1987	X
<i>Orthopithonella gustafsonii</i> (Bolli, 1974) Lentin and Williams, 1985	3Atl
<i>Orthopithonella? aequilamellata</i> Willems, 1988	A
<i>Orthopithonella? aspera</i> Fütterer, 1990	?A
<i>Orthopithonella? collaris</i> Wendler et al., 2001	O
<i>Orthopithonella? compsa</i> (Keupp, 1982) Lentin and Williams, 1985	?A
<i>Orthopithonella? congruens</i> Fütterer, 1990	A
<i>Orthopithonella? duplicata</i> Kohring, 1993a	?A
<i>Orthopithonella? geometrica</i> (Jafar, 1983) Janofske, 1987	O
<i>Orthopithonella? globosa</i> (Fütterer, 1984) Lentin and Williams, 1985	A
<i>Orthopithonella? minuta</i> Fütterer, 1990	O
<i>Orthopithonella? misurinae</i> Janofske, 1992	?A
<i>Orthopithonella? multipora</i> Kienel, 1994	?A
<i>Orthopithonella? ornata</i> Zügel, 1994	O
<i>Orthopithonella? porata</i> (Keupp, 1982) Lentin and Williams, 1985	A
<i>Orthopithonella? porifera</i> Keupp and Kowalski, 1992	?A
<i>Orthopithonella? pycnothecata</i> (Keupp, 1978) Lentin and Williams, 1985	X
<i>Orthopithonella? reticulata</i> Zügel, 1994	X
<i>Orthopithonella? veeversi</i> (Bolli, 1974) Lentin and Williams, 1985	?A
<i>Orthopithonella? weileri</i> Kohring, 1993a	O
<i>Orthotabulata obscura</i> Kienel, 1994	X
<i>Pentadinellum cretaceum</i> Keupp, 1992b	?A
<i>Pentadinellum oblatum</i> Keupp, 1991b	?A
<i>Pentadinellum vimineum</i> (Keupp, 1987) Keupp, 1992b	A
<i>Pernambugia tuberosa</i> (Kamptner, 1963) Janofske and Karwath in Karwath, 2000	E
<i>Pernambugia? patata</i> n. sp.	E
<i>Pirumella albiensis</i> (Keupp and Kowalski, 1992) Williams et al., 1998	O
<i>Pirumella amplicrostallina</i> (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1985	A
<i>Pirumella bassriverensis</i> (Olsson and Youssefnia, 1979) Lentin and Williams, 1993	X
<i>Pirumella cookii</i> (Bolli, 1974) Lentin and Williams, 1993	A
<i>Pirumella cumulosa</i> (Zügel, 1994) Williams et al., 1998	X
<i>Pirumella cylindrica</i> (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1993	A
<i>Pirumella echinosa</i> (Keupp, 1982) Lentin and Williams, 1993	O
<i>Pirumella edgarii</i> (Bolli, 1974) Lentin and Williams, 1993	A
<i>Pirumella fusiformis</i> (Rögl, 1976) Lentin and Williams, 1993	X
<i>Pirumella heitzleri</i> (Bolli, 1974) Lentin and Williams, 1993	A
<i>Pirumella hystrichosphaeroidea</i> (Zügel, 1994) Williams et al., 1998	X

<i>Pirumella irregularis</i> (Akselman and Keupp, 1990) Williams et al., 1998	X
<i>Pirumella johnstonei</i> (Bolli, 1974) Lentin and Williams, 1993	A
<i>Pirumella krasheninnikovii</i> (Bolli, 1974) Lentin and Williams, 1993	A
<i>Pirumella labyrinthica</i> (Zügel, 1994) Williams et al., 1998	O
<i>Pirumella laquaeta</i> (Keupp and Mutterlose, 1994) Williams et al., 1998	X
<i>Pirumella lepidota</i> (Keupp, 1982) Lentin and Williams, 1993	O
<i>Pirumella loeblichii</i> (Bolli, 1974) Lentin and Williams, 1993	A
<i>Pirumella longiporosa</i> (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1993	?A
<i>Pirumella loricata</i> (Krasheninnikov and Basov, 1983) Lentin and Williams, 1993	O
<i>Pirumella mcnightii</i> (Bolli, 1974) Lentin and Williams, 1993	A
<i>Pirumella microspinosa</i> (Zügel, 1994) Williams et al., 1998	X
<i>Pirumella miniaperta</i> (Krasheninnikov and Basov, 1983) Lentin and Williams, 1993	?A
<i>Pirumella multistrata</i> (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1993	?A
<i>Pirumella nonarenziae</i> (Bolli, 1974) Williams et al., 1998	?A
<i>Pirumella ossis</i> (Kienel, 1994) Williams et al., 1998	O
<i>Pirumella pachystrata</i> (Zügel, 1994) Williams et al., 1998	O
<i>Pirumella paradoxa</i> (Keupp, 1991a) Williams et al., 1998	X
<i>Pirumella parva</i> (Fütterer, 1984) Lentin and Williams, 1993	A
<i>Pirumella pinguis</i> (Keupp and Ilg, 1989) Lentin and Williams, 1993	X
<i>Pirumella piriformis</i> (Keupp, 1977) Lentin and Williams, 1993	X
<i>Pirumella porosa</i> (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1993	?A
<i>Pirumella prasina</i> (Janofske, 1992) Williams et al., 1998	X
<i>Pirumella quiltyi</i> (Bolli, 1974) Lentin and Williams, 1993	?A
<i>Pirumella rhombica</i> (Janofske, 1987) Lentin and Williams, 1993	?A
<i>Pirumella robinsonii</i> (Bolli, 1974) Lentin and Williams, 1993	A
<i>Pirumella rockeri</i> (Bolli, 1974) Lentin and Williams, 1993	?A
<i>Pirumella scobidota</i> (Zügel, 1994) Williams et al., 1998	X
<i>Pirumella sicelis</i> (Kohring, 1993b) Williams et al., 1998	X
<i>Pirumella sliteri</i> Bolli, 1980	O
<i>Pirumella spathula</i> (Keupp and Ilg, 1989) Lentin and Williams, 1993	?A
<i>Pirumella sphenifera</i> (Keupp, 1987) Lentin and Williams, 1993	X
<i>Pirumella spinosa</i> (Keupp, 1979b) Lentin and Williams, 1993	X
<i>Pirumella squalida</i> (Krasheninnikov and Basov, 1983) Lentin and Williams, 1993	X
<i>Pirumella squamosa</i> (Krasheninnikov and Basov, 1983) Lentin and Williams, 1993	?A
<i>Pirumella stellata</i> (Zügel, 1994) Williams et al., 1998	X
<i>Pirumella strobila</i> (Keupp, 1979b) Lentin and Williams, 1993	X
<i>Pirumella tanyphloia</i> (Keupp, 1979b) Lentin and Williams, 1993	?A
<i>Pirumella thayeri</i> (Bolli, 1974) Lentin and Williams, 1993	?A
<i>Pirumella titanoplax</i> (Rögl, 1976) Williams et al., 1998	O
<i>Pirumella toichohadra</i> (Keupp, 1995b) Williams et al., 1998	X
<i>Pirumella transitoria</i> (Krasheninnikov and Basov, 1983) Lentin and Williams, 1993	A
<i>Pirumella usheri</i> (Krasheninnikov and Basov, 1983) Lentin and Williams, 1993	?A
<i>Pirumella williamsenonii</i> (Bolli, 1978b) Williams et al., 1998	?A
<i>Pirumella zuegelii</i> Williams et al., 1998	O

<i>Pithonella atopa</i> Keupp in Keupp and Kienel, 1994	P
<i>Pithonella cardiiiformis</i> Zügel, 1994	P
<i>Pithonella caucasia</i> Keller, 1946	P
<i>Pithonella discoidea</i> Willems, 1992	P
<i>Pithonella lamellata</i> Keupp in Keupp and Kienel, 1994	P
<i>Pithonella microgranula</i> Zügel, 1994	P
<i>Pithonella multicava</i> Borza, 1972	P
<i>Pithonella ovalis</i> (Kaufmann in Heer, 1865) Lorenz, 1902	P
<i>Pithonella pyramidalis</i> Willems, 1994	P
<i>Pithonella siniformis</i> Řehánek and Mišik, 1991	X
<i>Pithonella sphaerica</i> (Kaufmann in Heer, 1865) Zügel, 1994	P
<i>Pithonella? organica</i> Hultberg, 1985	?A
<i>Praecalcionellum dolium</i> (Keupp, 1979b) n. comb.	?A
<i>Praecalcionellum duopylum</i> Willems, 1995	A
<i>Praecalcionellum mutterlosei</i> (Keupp, 1979b) Lentin and Williams, 1993	A
<i>Praecalcionellum polymorphum</i> (Keupp, 1980a) Lentin and Williams, 1993	A
<i>Praecalcionellum schizosaeptum</i> Versteegh, 1993	A
<i>Praecalcionellum sulcatum</i> (Keupp, 1979a) n. comb.	?A
<i>Praecalcionellum triangulare</i> (Keupp, 1980a) Keupp, 1992b	?A
<i>Pseudopithonella striatula</i> Versteegh, 1993	A
<i>Retesphaera diadema</i> Hildebrand-Habel et al., 1999	A
<i>Ruegenia areata</i> Keupp et al., 1992	?A
<i>Ruegenia crassa</i> Kienel, 1994	?3A
<i>Ruegenia hadra</i> Keupp et al., 1992	?A
<i>Ruegenia inaequilamellata</i> Willems, 1992	O
<i>Ruegenia kyrta</i> Keupp et al., 1992	?A
<i>Ruegenia nodosa</i> Keupp et al., 1992	X
<i>Ruegenia oranensis</i> Keupp and Kohring, 1993	X
<i>Saumuria cingulofera</i> Zügel, 1994	X
<i>Saumuria distincta</i> Zügel, 1994	O
<i>Saumuria obscura</i> Zügel, 1994	O
<i>Scripsiella regalis</i> (Gaardner, 1954) Janofske, 2000	?E
<i>Scripsiella trochoidea</i> (von Stein, 1883) Loeblich III, 1965	3AtI
<i>Septiareata pyramiforma</i> Kienel, 1994	X
<i>Sliteria pentagonalis</i> Krasheninnikov and Basov, 1983	X
<i>Tetramerosphaera lacrimula</i> Willems, 1985	A
<i>Tetratropis corbula</i> Willems, 1990	A
<i>Tetratropis patina</i> Willems, 1990	A
<i>Thoracosphaera? eichstaettensis</i> Keupp, 1978	X
<i>Thoracosphaera? prolata</i> Bukry and Bramlette, 1969	O
<i>Vertebrellum holotabulatum</i> Zügel, 1994	X
<i>Wallia melloi</i> Keupp, 1990	P
<i>Wallidinellum dalei</i> Keupp, 1991b	?3AtI

Appendix B. Glossary of newly proposed terms

Archeopyle area.-An archeopyle area is a defined field on the epicyst of a calcareous dinoflagellate cyst within which excystment occurs. This area is distinguished from the adjacent cyst surface by a different crystallographic surface pattern, although a gradual transition between both is possible. The archeopyle area generally reflects tabulation, the archeopyle does not, as it is generally smaller than the area. Species bearing an archeopyle area do obviously not release a predetermined operculum in the common sense but probably lose parts of the archeopyle area or dissolve the area for excystment.

Mesoepicystal archeopyle.-One of the most common and important archeopyle types within the calcareous dinoflagellate cysts. It is characterized by the loss of three apical plates (2'-4') and all intercalary plates, which represent the central part of the epicyst (general archeopyle formula $3A_{2'-4'}tI$). This type is unknown within the organic-walled dinoflagellates.

Appendix C. Key to the hierarchical order of archeopyles

The different known archeopyles of calcareous dinoflagellate cysts are categorized in major categories, which are subdivided in different archeopyle types (Evitt, 1967, 1985), which themselves again may be split in several variations. Currently four categories and seven archeopyle types are recognized within the calcareous dinoflagellate cysts.

Legend: A = apical plate; I = intercalary plate; P = precingular plate; cipher preceding plate abbreviation designates number of plates involved, no cipher means one plate; t = total, meaning all plates of the corresponding plate series are involved; parentheses indicate a simple operculum (operculum comprises a single piece); missing parentheses indicate a compound operculum (operculum disarticulates into several opercular pieces). Example: Type (3AtI) stands for an archeopyle that involves three apical and all intercalary plates and bears a simple operculum.

Category	Type	Variation
Apical archeopyles	Type A	e.g., operculum superimposed
	Type 3A	no variations designated
	Type (3A)	no variations designated
Intercalary archeopyles	Type I	no variations designated
Combination archeopyles	Type 3AtI *	no variations designated
	Type (3AtI) *	e.g., archeopyle bordered by distinct rim
	Type (3AtItP) **	e.g., no cingular displacement
Miscellaneous archeopyles	no types designated	e.g., irregular archeopyle outline

*) mesoepicystal archeopyle - **) epicystal archeopyle

Calcareous dinoflagellate associations and Maastrichtian-Tertiary climatic change in a high latitude core (ODP Hole 689B, Maud Rise, Weddell Sea)

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Palaeogeography, Palaeoclimatology, Palaeoecology (in review)

ABSTRACT.—The distribution of calcareous dinoflagellates has been analyzed for the Maastrichtian to Miocene interval of ODP Hole 689B (Maud Rise, Weddell Sea). The investigation thus represents a primary evaluation of the long-term evolution in high latitude calcareous dinoflagellate assemblages during the transition from a relatively warm Late Cretaceous to a cold Neogene climate. Major assemblage changes during this interval occurred in characteristic steps: (1) an increase in relative abundance of tangentially structured species - particularly *Cervisiella operculata* - at the K/T boundary; (2) a diversity decrease and several first and last appearances across the middle-late Eocene boundary, possibly attributed to increased climate cooling; (3) a diversity decrease associated with the dominance of *Calciodinellum levantinum* in the late early Oligocene; (4) the reappearance and dominance of *Pirumella edgarii* in the early Miocene, probably reflecting a warming trend; (5) monogeneric assemblages dominated by *Caracomia* spp. denoting strong middle Miocene cooling. The results not only extend the biogeographic ranges of many taxa into the Antarctic region, but also indicate that the evolution of high latitude calcareous dinoflagellate assemblages parallels the changing environmental conditions in the course of the Cenozoic climate transition. Therefore, calcareous dinoflagellates contribute to our understanding of the biotic effects associated with paleoenvironmental changes and might possess the potential for reconstructing past conditions. The flora in the core includes one new taxon: *Caracomia arctica* forma *spinosa* n. form. Additionally, two new combinations are proposed: *Fuettererella deflandrei* (Kamptner, 1956) n. comb. and *Fuettererella flora* (Fütterer, 1990) n. comb.

INTRODUCTION

Dinoflagellates are generally unicellular algae that live in most aquatic environments. As part of their life-cycle, some dinoflagellates produce 'dinosporin' cysts that may be fossilized (so called 'organic-walled dinoflagellate cysts'). Some marine taxa, which constitute the calcareous dinoflagellates, incorporate calcite into their walls. Most Recent calcareous dinoflagellates probably represent resting cysts ('calcareous dinocysts'). However, the coccoid shell of *Thoracosphaera heimii* is formed during the vegetative stage and so is not a cyst (Young et al., 1997). It is unknown whether the fossil taxa were calcareous resting cysts or vegetative shells. They are therefore referred to as 'calcareous dinoflagellates'. These calcareous dinoflagellates extend back to Late Triassic (Janofske, 1992) and may occur in rock-forming quantities (e.g., Willems, 1988). It has become evident that they are cosmopolitan and occur at virtually all latitudes in many different marine environments, ranging from inner neritic to open oceanic (Zonneveld et al., 1999). However, data on the ecological preferences of the group and/or of its individual species is still sparse. Most information concentrates

on few stratigraphic intervals and paleogeographic regions. The most detailed paleoecologic information on calcareous dinoflagellates is available from the Cretaceous of Europe (e.g., Keupp, 1981, 1987, 1991a, 1992b, 1993, 1995a,b; Keupp and Mutterlose, 1984, 1994; Keupp and Kowalski, 1992; Kienel, 1994; Zügel, 1994; Willems, 1996; Hildebrand-Habel and Willems, 1997) and the Quaternary Equatorial and South Atlantic Ocean (e.g., Höll et al., 1998, 1999; Zonneveld et al., 1999; Esper et al., 2000; Karwath et al., 2000; Vink et al., 2000, 2002). Notably less is known about calcareous dinoflagellates in the Tertiary Period.

Since Recent calcareous dinoflagellates are phytoplanktonic organisms, it is probable that changes in Tertiary calcareous dinoflagellate assemblages reflect past changes in conditions in the uppermost water column. Indeed, a first evaluation of Maastrichtian to Miocene calcareous dinoflagellates from the mid-latitudinal DSDP Site 357 (Rio Grande Rise, western South Atlantic Ocean) indicates that major assemblage changes occurred at the Cretaceous-Tertiary (K/T) boundary and at times of strong cooling events in the Tertiary (Hildebrand-Habel and Willems, 2000).

Although there is some information on Tertiary calcareous dinoflagellates available (e.g., from the Atlantic Ocean: Fütterer, 1977, 1984, 1990; Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000; from Europe: Weiler, 1990; Kohring, 1993a; Keupp and Kohring, 1994; from North Africa: Kohring 1993a; Keupp and Kohring, 1993), remarkably little is known about high latitude assemblages. The only thorough examinations of high latitude calcareous dinoflagellates have been carried out on the Pliocene-Pleistocene of the central Arctic Ocean (Gilbert and Clarke, 1983) and on the K/T boundary of Maud Rise (eastern Weddell Sea) (Fütterer, 1990). Other studies on calcareous dinoflagellates from high latitudes add specific taxonomic information (e.g., Streng et al., 2002 [**Chapter 2.1**]) or identify absolute abundance variations within the group of organisms in short stratigraphic intervals (e.g., early late Eocene: Vonhof et al., 2000).

In this study we have analyzed Maastrichtian to Miocene calcareous dinoflagellate associations of Ocean Drilling Program (ODP) Hole 689B (Leg 113, Maud Rise). Maud Rise is an isolated aseismic ridge in the eastern Weddell Sea that has probably formed by the interaction of a spreading ridge with a hot-spot (Shipboard Scientific Party, 1988). It rises more than 2500 m above the deep oceanic basins (Diester-Haass, 1995) and represents one of the few topographic highs within Antarctic waters where it is possible to obtain sedimentary sequences in the open ocean at depths shallow enough to preserve calcareous sediments. Upper Cretaceous and Cenozoic sediments at Site 689 were deposited in a pelagic, open-ocean environment at lower to middle bathyal depths, sinking from 500-1000 m to the present depth of about 2000 m over the last 65 m.y. (Shipboard Scientific Party, 1988).

We chose Hole 689B because it represents one of the otherwise best-studied high latitude cores and correspondingly many secondary data are available from this core. Furthermore, we intend to supplement the data already available on calcareous dinoflagellates of the K/T boundary of Maud Rise (ODP Holes 689B and 690C) by Fütterer (1990). In our examination of ODP Hole 689B, we have evaluated how the transition from a warm Cretaceous to a cold Neogene affected the calcareous dinoflagellate associations in high latitudes and determined their stratigraphic applicability for much of the Tertiary.

CLASSIFICATION OF FOSSIL CALCAREOUS DINOFLAGELLATES

Until recently, the classification of fossil calcareous dinoflagellates followed a systematic concept established by Keupp (1987) and Kohring (1993a), who regarded the wall structure as the most

important feature for classification. Indeed, Janofske (1996) and Montresor et al. (1997) proved the crystallographic orientation of the calcite crystals to be a genetically fixed morphological feature. Following upon the concept of Keupp (1987) and Kohring (1993a), Young et al. (1997) introduced four types of wall structure: oblique = formed of elements with their *c*-axes oblique to the wall and variably aligned relative to each other; pithonelloid = formed of elements with their *c*-axes oblique to the wall and sub-parallel to each other; radial = formed of elements with their *c*-axes perpendicular to the wall; tangential = formed of elements with their *c*-axes tangential to the wall. Fensome et al. (1993), however, considered wall structure to be subsidiary to tabulation when analyzing possible phylogenetic affinities. Streng et al. (2002) [Chapter 2.1] assumed both tabulation and wall structure to be of major taxonomic relevance for calcareous dinoflagellates and proposed a classification concept which includes the following attributes to distinguish between genera: type of tabulation (especially of the archeopyle), number of wall layers (and whether number is constant), and ultrastructure of the individual layers.

MATERIAL AND METHODS

The 21 investigated samples are from Ocean Drilling Program (ODP) Hole 689B (Fig. 1), part of Leg 113 in the eastern Weddell Sea ($64^{\circ}31.009'S$, $03^{\circ}05.996'E$). The Hole was drilled in a water depth of 2080 m near the crest of Maud Rise (Shipboard Scientific Party, 1988). The recovered core of 297.3 m consists exclusively of pelagic, biogenic sediments of late Campanian? / early Maastrichtian to Quaternary age. Hiatuses or highly condensed sequences occur throughout the core (Fig. 2).

The studied stratigraphic interval covers the early Maastrichtian to late Miocene. The three lithological units are: lower Maastrichtian to upper Eocene sediments of nannofossil ooze and chalk with varying amounts of foraminifera, upper Eocene to upper Miocene sediments of primarily biosiliceous and calcareous oozes, and uppermost Miocene biosiliceous oozes.

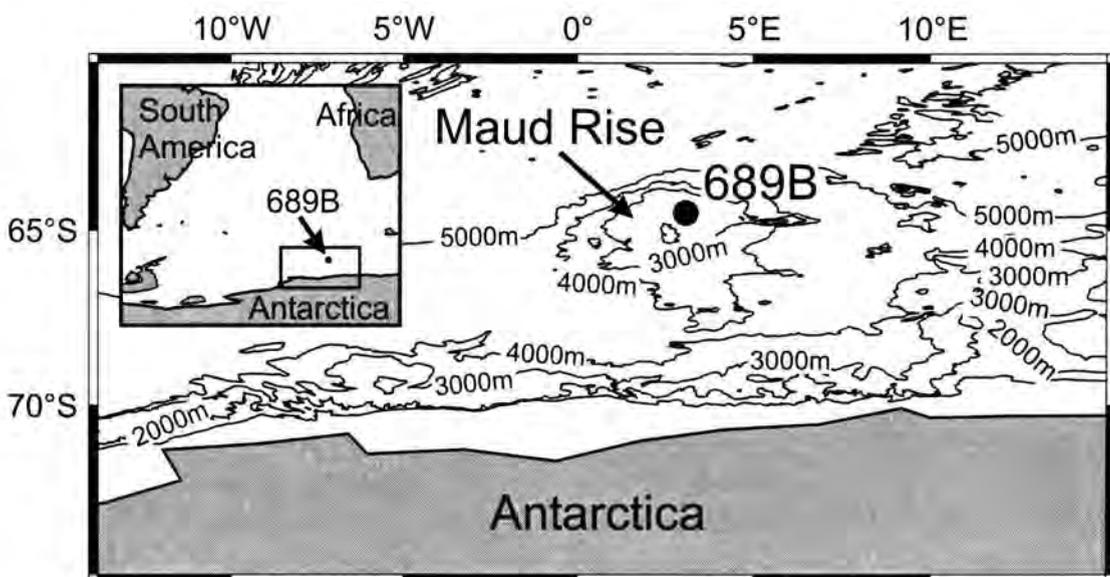


Figure 1. Geographic location of ODP Hole 689B on Maud Rise. Bathymetry after GEBCO (1997).

The sample material was disintegrated by repeated freezing and thawing in dematerialized water buffered with ammonia to prevent dissolution. Afterwards, the disintegrated material was wet-sieved through 125 μm and 20 μm screens and dried.

Although most calcareous dinoflagellates are 20-75 μm (Wendler and Willems, 2002), we preferred using mesh sizes of 20 and 125 μm , because some Cretaceous species (e.g., *Pirumella krasheninnikovii*) are larger. For some of the Tertiary samples, however, the >63 μm fraction had been previously separated by wet sieving by D. Fütterer (Alfred Wegener Institute for Polar and Marine Research, Bremerhaven). In these samples, we were only able to examine the fraction <63 μm (asterisks in Table 1).

A microspatula of the dried sediment was evenly scattered on a picking tray and the number of specimens per 50 fields of view at a magnification of 128 \times was counted using a binocular microscope. Estimates of the calcareous dinoflagellate abundance in the studied size fraction were recorded as follows: 0 = Absent, R = Rare (1-10 specimens), F = Few (11-30 specimens), C = Common (31-70 specimens), A = Abundant (71-150 specimens), VA = Very abundant (>150 specimens).

Table 1. Preservation of calcareous dinoflagellates and abundance estimates in the studied size fraction of 20-125 μm , or 20-63 μm , respectively.

Stratigraphy	Sample	preservation	abundance
late Miocene	689B-4H-2, 71-73 cm	0	0
middle Miocene	689B-5H-3, 68-70 cm*	G	R
middle Miocene	689B-7H-4, 70-72 cm	G	R
early Miocene	689B-8H-2, 71-73 cm	G	R
late Oligocene	689B-9H-1, 71-73 cm*	M	F
early Oligocene	689B-11H-3, 70-72 cm*	P	F
early Oligocene	689B-13H-3, 71-73 cm*	X	C
late Eocene	689B-14H-6, 70-72 cm*	G	C
late Eocene	689B-15H-4, 42-44 cm*	M	C
middle Eocene	689B-17H-2, 58-60 cm	M	C
middle Eocene	689B-18H-3, 70-72 cm*	M	C
middle Eocene	689B-20H-1, 70-72 cm*	M	C
middle Eocene	689B-22X-2, 70-72 cm	M	C
late Paleocene	689B-23X-2, 70-72 cm	M	C
late Paleocene	689B-24X-1, 51-53 cm*	G	A
early Paleocene	689B-25X-4, 30-31 cm*	G	VA
late Maastrichtian	689B-25X-5, 79-81 cm*	P	A
late Maastrichtian	689B-26X-1, 43-45 cm	P	A
late Maastrichtian	689B-27X-1, 79-81 cm	M	C
early Maastrichtian	689B-29X-1, 80-82 cm	P	C
early Maastrichtian	689B-30X-3, 77-79 cm	M	C

*=studied size fraction 20-63 μm ; X=Excellent, G=Good, M=Moderate, P=Poor; 0=Absent, R=Rare (1-10 specimens per 50 fields of view at 128 \times), F=Few (11-30 specimens per 50 fields of view at 128 \times), C=Common (31-70 specimens per 50 fields of view at 128 \times), A=Abundant (71-150 specimens per 50 fields of view at 128 \times), VA=Very abundant (>150 specimens per 50 fields of view at 128 \times).

The first 100 recorded specimens were picked with an eyelash. In the Miocene samples, calcareous dinoflagellates were rare so that only 20-40 specimens were picked in the time available. The selected specimens were mounted on aluminum stubs provided with double-sided adhesive tape, sputter-coated

with gold, and examined under a CamScan-44 scanning electron microscope (SEM). Subsequently, numerous specimens were broken with a scalpel and sputter-coated again to investigate the wall structure.

Some specimens were additionally prepared for crystallographic analysis in polarized light, following the procedure of Janofske (1996). By wetting its gelatinous surface, isolated specimens were attached to a strip of a developed negative film and subsequently sputter-coated with gold. After SEM examination, the film strip was embedded in low-viscosity Spurr's resin. The hardened sample was cut into 3 μm thin sections using a rotation microtome. The thin sections were embedded in Canada balsam and examined under a Zeiss Axioplan light microscope, to determine the four wall types after Young et al. (1997).

In total, about 2000 specimens were examined. Taxonomic information on the species recorded is given in the Appendices. The studied material is deposited in the collection of the Division of Historical Geology and Paleontology, University of Bremen, Germany.

RESULTS

Although only the $<63 \mu\text{m}$ fraction was studied in some samples, the assemblages were not markedly different from those in the 20-125 μm fractions. A comparison of calcareous dinoflagellate counts in samples of the two size fractions within the same stratigraphic interval shows that differences in diversity and wall type distribution are small to negligible. However, a possible size increase of individual species, as has for example been documented in the high-resolution investigation of Vonhof et al. (2000), cannot be ruled out. Nevertheless, the long-term assemblage changes in ODP Hole 689B are distinct and correspond to changes as observed in high latitude Maastrichtian to Miocene assemblages of the SE Indian Ocean (Hole 747A, Kerguelen Plateau) (Streng et al., *subm. B [Chapter 2.4]*).

Preservation and abundance

Organic-walled dinoflagellate cysts are not present in ODP Hole 689B (Mohr, 1990). Calcareous dinoflagellates occur (in varying numbers) in most of the samples studied, however. Preservation is variable (Tab. 1). In the Maastrichtian, preservation is poor to moderate, but improves significantly in the Tertiary. Paleocene, Eocene, and Miocene preservation is predominantly moderate to good; Oligocene assemblages show considerable variation from poor to excellent preservation.

Although Maastrichtian calcareous dinoflagellates are common to abundant in the studied size fraction (Tab. 1), optical smear slide analyses indicate that they only accounted for about 5 % of the total sediment in the latest Maastrichtian of Hole 689B (Fütterer, 1990). In the Paleocene, there was a marked increase to 10-15 % of the total sediment. Calcareous dinoflagellates were still common in the late Paleocene to early Oligocene, but decreased markedly in the late Oligocene. They were rare in the Miocene, and no specimens have been found in the radiolarian-bearing diatom ooze of upper Miocene sample 689B-4H-2, 71-73 cm.

Diversity

A total of 29 calcareous dinoflagellate taxa have been identified in the early Maastrichtian to late Miocene interval (Fig. 2; Plates 1-4; Appendices A and B). Diversity ranged from four to six in the early Maastrichtian, but increased to six to eleven in the latest Maastrichtian (Fig. 3). The samples

spanning the K/T boundary have the highest species richness (8-11 species). Diversity remained relatively high during the Paleocene and middle Eocene (7-10 species), declined in the late Eocene (3-6 species), and slightly increased to 7 species in the early Oligocene. Relatively low diversity characterized the late early Oligocene to Miocene (2-4 species).

During most of the Maastrichtian and in the late Oligocene to Miocene, the highest diversity was found within the oblique and radial wall types (Fig. 2). From the latest Maastrichtian to the early Oligocene, the highest diversity was found within the tangential wall type.

Stratigraphic distribution pattern of species and wall types

The calcareous dinoflagellates show stratigraphic variability in species assemblages (Fig. 2) and the relative abundance of wall types (oblique, radial, tangential; Fig. 3). The early Maastrichtian assemblage was strongly dominated by *Pirumella krasheninnikovii* (oblique; >90 % of the entire assemblage). In the late Maastrichtian, other species, particularly *Orthopithonella? congruens* (radial) and *Fuettererella flora* (tangential), increased in relative abundance. Although the oblique wall type was still the most abundant, the radial wall type slightly increased and the tangential wall type appeared.

Only two species, *Pirumella cf. loeblichii* (oblique) and *Orthopithonella? congruens* (radial), became extinct at the K/T boundary, *Orthopithonella? aff. gustafsonii* (radial) and *Centosphaera barbata* (tangential) extended to the earliest Danian. Even though there was not a mass extinction or marked decrease in species richness at the K/T boundary, there was a pronounced change in the assemblages. With an increase in absolute and relative abundance of *Cervisiella operculata* (tangential) in the earliest Tertiary, the dominant wall type shifted from oblique to tangential. In the lower Paleocene sample 689B-25X-4, 30-31 cm, *C. operculata* constitutes 66 % of the total calcareous dinoflagellate assemblage. Additionally, *Pirumella krasheninnikovii* (oblique), the most common Maastrichtian species, almost vanished across the K/T boundary.

During the Paleocene, the tangential wall type remained most prominent, but the oblique wall type slightly increased, due to the appearance of *Pirumella parva* (oblique). The initial dominance of *Cervisiella operculata* (tangential) declined through an increase in abundance of other tangential species in the late Paleocene, particularly *Fuettererella flora*. In the Eocene, the oblique and radial wall types continued to increase in abundance. *C. operculata* did not continue into the middle Eocene of Hole 689B. The most important middle Eocene species included *Fuettererella flora* (tangential), "*Rhabdothorax*" spp. (?radial), and *Pirumella parva* (oblique). From the middle to late Eocene, the calcareous dinoflagellate association changed. In the latest middle Eocene sample 689B-17H-2, 58-60 cm, three species last appeared: *Pirumella krasheninnikovii* (oblique), *Pirumella multistrata* (oblique), and *Fuettererella flora* (tangential) and three species first appeared: *Calcigonellum infula* (tangential), *Calciodinellum operosum* (tangential), and *Calciodinellum levantinum* (tangential). The quantitatively most important radially and obliquely structured species of the late Eocene were the same as in the middle Eocene: "*Rhabdothorax*" spp. (?radial), and *P. parva* (oblique). The species richness within these two wall types, however, decreased by one to three species. The most abundant late Eocene species within the tangential wall type were *C. levantinum* and *C. operosum*.

In the early Oligocene, *Pirumella parva* (oblique) represented the most common species (43 % of the assemblage), followed by *Calciodinellum levantinum* (tangential; 25 % of the assemblage).

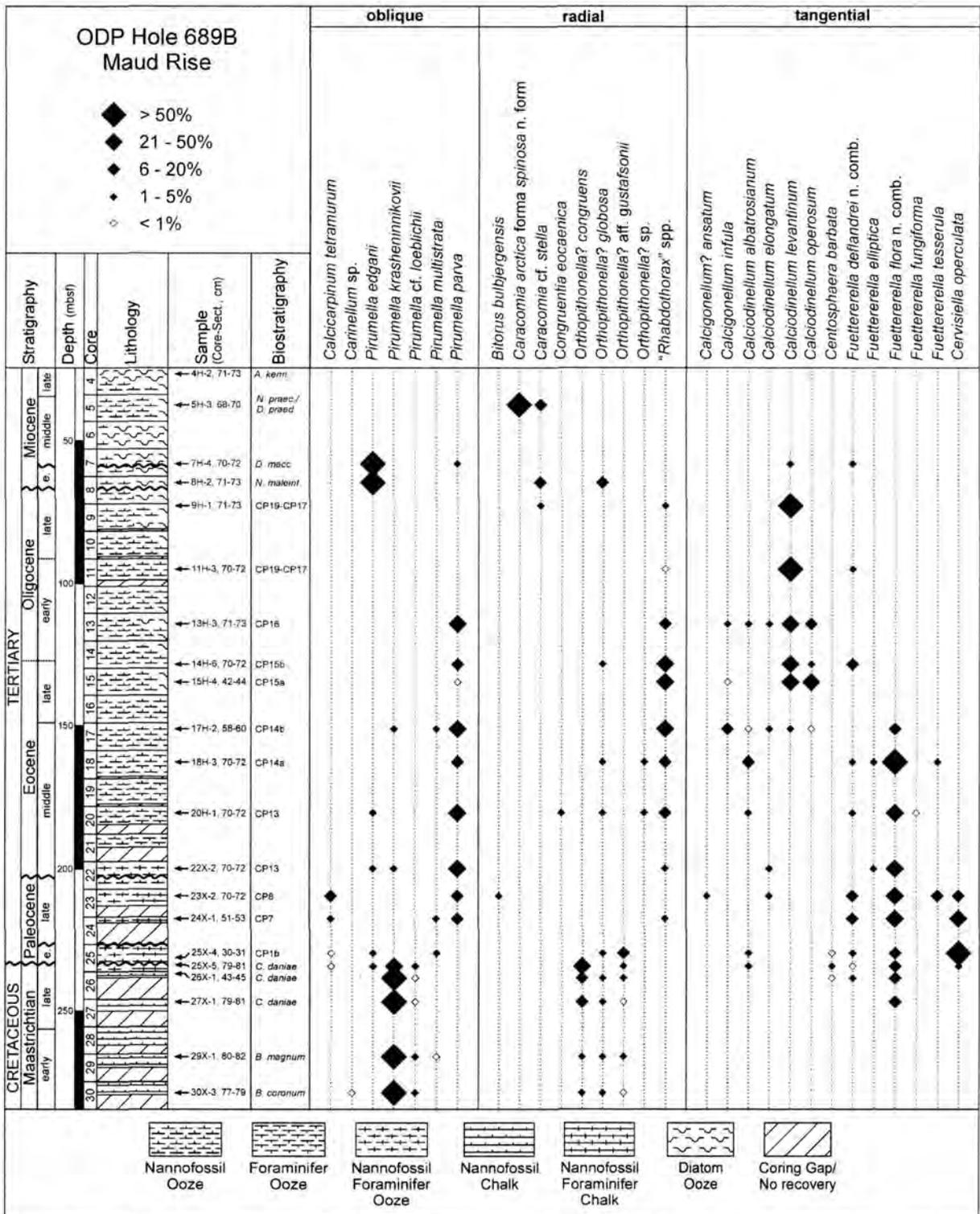


Figure 2. Lithology and percentage occurrence of calcareous dinoflagellate species in ODP Hole 689B. Calcareous dinoflagellates have been grouped into three categories according to their wall types (oblique, radial, and tangential) following Young et al. (1997). Neogene diatom zonation after Gersonde and Burckle (1990), Paleogene and Maastrichtian nannoplankton zonation after Wei and Wise (1990) and Pospichal and Wise (1990a,b). *A. kenn.* = *Asteromphalus kennettii*, *N. praec.* = *Nitzschia praecurta*, *D. praed.* = *Denticulopsis praedimorpha*, *D. macc.* = *Denticulopsis maccollumii*, *N. maleint.* = *Nitzschia maleinterpretaria*, *C. daniae* = *Cribosphaerella daniae*, *B. magn.* = *Biscutum magnum*, *B. coron.* = *Biscutum coronum*. Lithology after Shipboard Scientific Party (1988).

Approaching the boundary between the early and late Oligocene, *C. levantinum* comprised 99 % of the total assemblage. This dominance continued in the late Oligocene.

Across the Oligocene-Miocene boundary, the abundance of *Calciodinellum levantinum* (tangential) decreased drastically and *Pirumella edgarii* (oblique), which reappeared for the first time since the middle Eocene, accounted for 84 % of the total assemblage. In the late middle Miocene another wall type dominated: in sample 689B-5H-3, 68-70 cm, only two radially structured species were present (*Caracomia arctica* forma *spinosa* and *Caracomia* cf. *stella*). No calcareous dinoflagellates have been found in the upper Miocene sample.

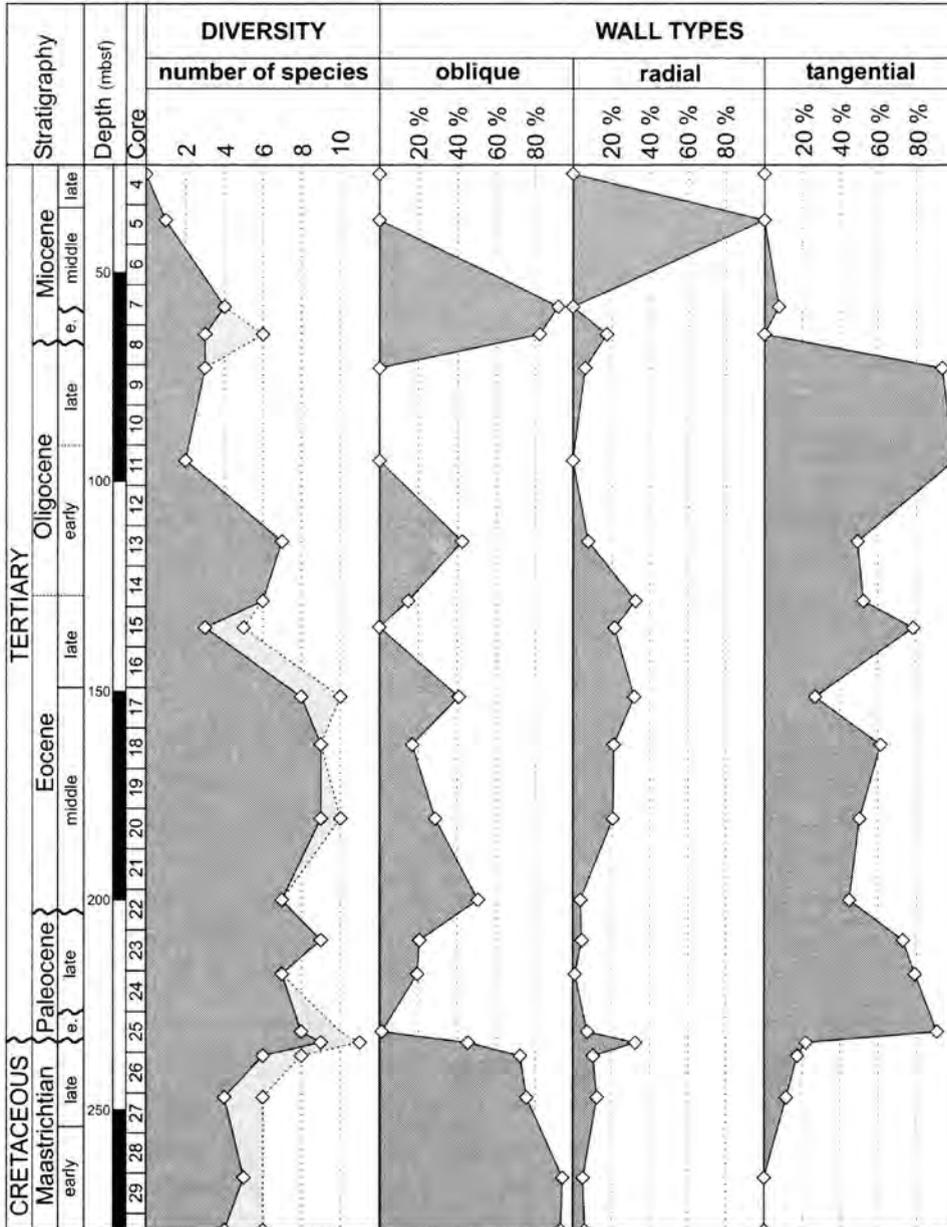


Figure 3. Calcareous dinoflagellate diversity (number of species) in ODP Hole 689B: light grey shade indicates rare species discovered in subsequent analyses (<1 % of association). Wall types after Young et al. (1997): relative abundances (%) of calcareous dinoflagellate wall types (oblique, radial, and tangential). Squares show the sample positions.

DISCUSSION

Our examination of ODP Hole 689B provided the opportunity to study calcareous dinoflagellate assemblage changes from a warm Cretaceous to a cold Neogene in high latitudes (Fig. 4). Comparison with published data on the long-term distribution of Cretaceous and Tertiary calcareous dinoflagellate taxa (e.g., Fütterer, 1977, 1984; Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000) indicates that fluctuations were common throughout this time interval. Since the majority of taxa were long-ranging, these fluctuations were generally not due to earliest or latest appearances, but represented quantitative changes in species abundances or migration between regions. The stratigraphic trends thus reflected paleoenvironmental / paleoclimatic changes rather than evolution, enhancing the usefulness of calcareous dinoflagellates as environmental indicators.

Maastrichtian associations

In general, the Maastrichtian was significantly cooler than the average Late Cretaceous climate: it was marked by gradually decreasing temperatures, punctuated by more rapid cooling near the early-late Maastrichtian boundary (Barrera and Huber, 1990; Barrera, 1994; Li and Keller, 1998). Climate reconstructions based on oxygen isotopes, clay mineralogy, and planktonic microfossil assemblages indicate temperate to cool subtropical conditions with high seasonality in the Maud Rise area during the Maastrichtian (Kennett and Barker, 1990).

Although latitudinal differences in the South Atlantic had an effect on the composition of both the flora and the fauna in the Maastrichtian (e.g., Huber, 1990; Pospichal and Wise, 1990a; Li and Keller, 1998), the associations of calcareous dinoflagellates in high and middle latitudes showed only minor differences. Oceanic assemblages were generally dominated by *Pirumella krasheninnikovii*. This Late Cretaceous dominance has been reported from other South Atlantic sites from 20°-65°S latitude (Bolli, 1978a; Krasheninnikov and Basov, 1983; Fütterer, 1984, 1990; Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000), the eastern North Atlantic (37°N; Pflaumann and Krasheninnikov, 1978), and the eastern Indian Ocean (17°S; Bolli, 1974).

Tangentially structured species first appeared during the late Maastrichtian in the Maud Rise region, whereas they were already present in the early Maastrichtian in the mid-latitudinal South Atlantic Ocean (Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000). Of all four wall types of calcareous dinoflagellates (oblique, radial, tangential, pithonelloid), only the pithonelloid wall type is absent in Hole 689B, possibly due to the oceanic position at this site: pithonelloids were common in the Tethyan Realm in the Cretaceous, though they were probably restricted to the outer shelf (Villain, 1981; Dias-Brito, 1985, 1992, 1995). In the western South Atlantic, pithonelloids appear to have progressively migrated north, being absent in the Albian of offshore southern Brazil, but abundant in the Turonian of offshore northern Brazil (Dias-Brito, 1994, 1995). In the late Albian-early Cenomanian, they migrated into the Boreal Realm from the Tethyan regions (Keupp, 1987; Keupp and Kowalski, 1992; Zügel, 1994). Pithonelloids dominated the Late Cretaceous associations in the Boreal Realm until they became extinct at or immediately above the K/T boundary (e.g., Kienel, 1994; Willems, 1996; Hildebrand-Habel and Willems, 1997; Wendler and Willems, 2002). In the Maastrichtian of the open-oceanic, western South Atlantic DSDP Sites 356 and 357, pithonelloid specimens were present in very low numbers only (Hildebrand-Habel and Willems, 2000). This might either reflect a final retreat from the South Atlantic to more northern regions, or an inshore-offshore gradient in the distribution of pithonelloids.

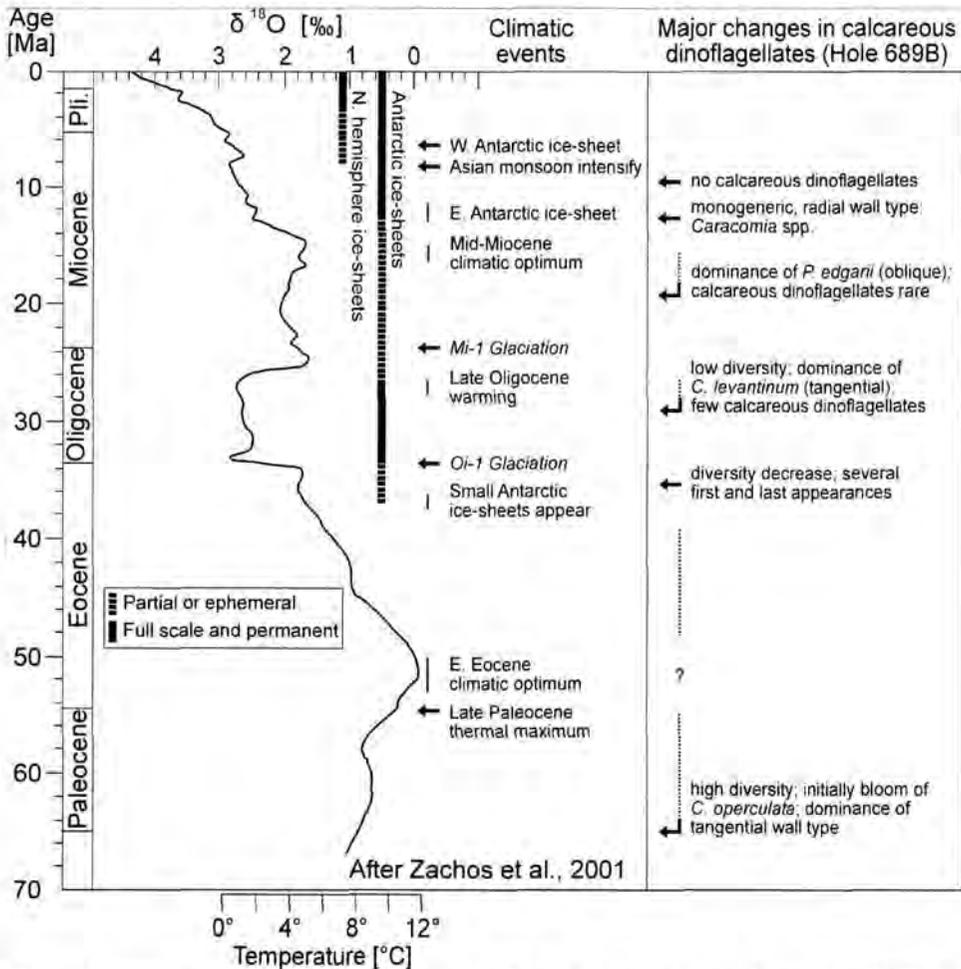


Figure 4. Summary of major calcareous dinoflagellate assemblage changes in ODP Hole 689B in relation to the smoothed composite benthic foraminiferal $\delta^{18}\text{O}$ record for the Cenozoic, the qualitative representation of ice volume in each hemisphere and major climatic events after Zachos et al. (2001).

Biotic changes during the latest Maastrichtian have often been postulated and could illustrate environmental pressure preceding the K/T mass extinction (e.g., Brinkhuis and Zachariasse, 1988; Keller and Barrera, 1990; Eshet et al., 1992; MacLeod et al., 1997). An oxygen isotopic decrease may indicate a warming of about 4°C of surface and intermediate waters in the Weddell Sea beginning about 500 k.y. prior to the K/T boundary (Stott and Kennett, 1990a). This possible warming did not seem to cause significant changes in the marine biota of the Weddell Sea (Stott and Kennett, 1990a; Kennett and Barker, 1990). In the South Atlantic DSDP Hole 525A, however, a decline in planktonic foraminifer species richness by 11 (about 20 %) has been associated with the warming event (Li and Keller, 1998). On the other hand, coccolithophorid associations did not change significantly during the latest Maastrichtian world-wide (Pospichal, 1996). Stable isotope data indicate that a subsequent cooling of about 3°C , beginning 200 k.y. prior to the K/T boundary, preceded the mass extinction event in the Maud Rise region (Kennett and Barker, 1990).

The species composition of South Atlantic calcareous dinoflagellate associations was generally stable prior to the K/T boundary (Fütterer, 1990; Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000). However, the increase in the previously uncommon tangential wall type in the South

Atlantic might be attributed to climatic changes in the latest Maastrichtian. Likewise, the first appearance of the dominant Danian species *Cervisiella operculata* in the latest Maastrichtian of both Tethyan and Boreal Realms (e.g., Verbeek, 1977; Kienel, 1994) and Hole 689B may be related to environmental modifications preceding the K/T boundary.

Turnover at the K/T boundary

Although the exact causes, time-scale and magnitude of biotic turnover at the Cretaceous-Tertiary transition are contentious, it is widely accepted that the changing environmental conditions resulted in considerable modifications of the biosphere (e.g., MacLeod et al., 1997). Most marine planktonic organisms, particularly the calcareous plankton, suffered major reductions in abundance and diversity (e.g., Thierstein 1982; Jiang and Gartner 1986; Keller et al. 1995; Henriksson 1996; MacLeod et al. 1997). The taxa surviving the mass extinctions are usually considered to be eurytopic generalists or 'disaster' species, with special adaptations to deal with environmental factors which produce high levels of biological stress (Tappan, 1979; Harries et al., 1996). Calcareous dinoflagellates were exceptionally abundant in the calcareous nannoplankton survivor assemblages (Henriksson, 1996; MacLeod et al., 1997). The abundance increase of calcareous dinoflagellates is a near global phenomenon and has been recorded as the so-called '*Thoracosphaera*'-bloom in numerous nannoplankton studies (e.g., Thierstein, 1981; Perch-Nielsen et al., 1982; Eshet et al., 1992). The magnitude of the early Paleocene abundance increase varied with latitude: calcareous dinoflagellates dominated the calcareous nannoplankton assemblages in lower latitudes (Perch-Nielsen et al., 1982; Jiang and Gartner, 1986; Pospichal 1996), accounted for about 50 % of mid-latitude assemblages (Perch-Nielsen et al., 1982), but did not show a mass occurrence in higher latitudes (Pospichal and Wise, 1990b; Pospichal 1996). Although calcareous dinoflagellates did not form a dominant element of the calcareous nannoplankton assemblage in high latitudes, they nonetheless exhibited an abundance increase above the K/T boundary in Hole 689B (Fütterer, 1990).

Cervisiella operculata represented the quantitatively most important species contributing to the abundance increase of calcareous dinoflagellates above the K/T boundary. In the Weddell Sea region, it appeared at or directly below the K/T boundary, the latter possibly being attributable to bioturbation (Fütterer, 1990). Since this species was already present in the early Maastrichtian in the middle latitudes of the South Atlantic Ocean (Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000), it is likely to have migrated southwards into the higher latitudes, where it could flourish after the decline of other phytoplankton. The opportunistic *C. operculata* probably profited from the abundant nutrient supplies, which remained untapped as a consequence of the reduced surface-water productivity (Hollander et al., 1993).

With the dominance of *Cervisiella operculata* at the K/T boundary, the calcareous dinoflagellate association significantly changed. The main Maastrichtian species became finally being replaced by *C. operculata* and other tangentially structured species. It is still unclear whether or not there was a mass extinction of calcareous dinoflagellates. Most studies support the idea of a low extinction rate with the majority of taxa crossing the K/T boundary (Kienel, 1994; Willems, 1996; Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000; Wendler and Willems, 2002). In his study of Weddell Sea assemblages, however, Fütterer (1990) concluded that no latest Maastrichtian taxa survived into the late Paleocene. This conclusion contradicts our results and literature data, which indicate that most late Maastrichtian species sporadically occurred above the K/T boundary and only a few species disappeared. The inconsistent occurrence of some of the survivor species in the Tertiary can easily be

explained by their low numbers (i.e., an effect of dilution or reduced population size). However, the convergent evolution of morphologically analogous taxa in the Tertiary cannot be strictly excluded.

Paleocene recovery and climatic warming

Once the environmental conditions had taken a turn towards normalcy after the K/T boundary, the surviving species formed a Paleocene association that gradually displaced the dominating 'disaster'-species (Jiang and Gartner, 1986). A first postextinction return of surface-water productivity to more 'normal' levels, as measured in the carbon isotope signal, the barium accumulation rates, and the CaCO₃ content, occurred near the nannofossil NP1/NP2 Zone boundary (after Martini, 1971), about 500 k.y. after the K/T event (Zachos et al., 1989). An initial stabilization of the organic-walled dinoflagellate, planktonic foraminifera, and coccolithophorid assemblages is indicated by a decrease in Cretaceous taxa and relatively stable species populations for a similar time interval (Keller et al., 1990; Eshet et al., 1992; Pospichal, 1996). A final change in coccolithophorid assemblages towards a stable Paleocene population composition, however, apparently occurred at about NP3/NP4 (Wei and Pospichal, 1991). Calcareous dinoflagellate assemblages experienced an initial recovery in the NP3 as indicated by the increase in abundance of additional species which suppressed the dominance of *Cervisiella operculata* (Hildebrand-Habel et al., 1999).

With 9-10°C, the surface-water temperatures on Maud Rise may have been lower in the earliest Paleocene than in the Late Cretaceous (Stott et al., 1990). The stable oxygen isotope data from Sites 689 and 690 on Maud Rise reflect the widely recognized extensive global warming in the course of the Paleocene (e.g., Miller et al., 1987) and indicate a temperature increase of about 3°C between the early and late Paleocene and maximum temperatures of 16-18°C during the Paleocene-Eocene transition

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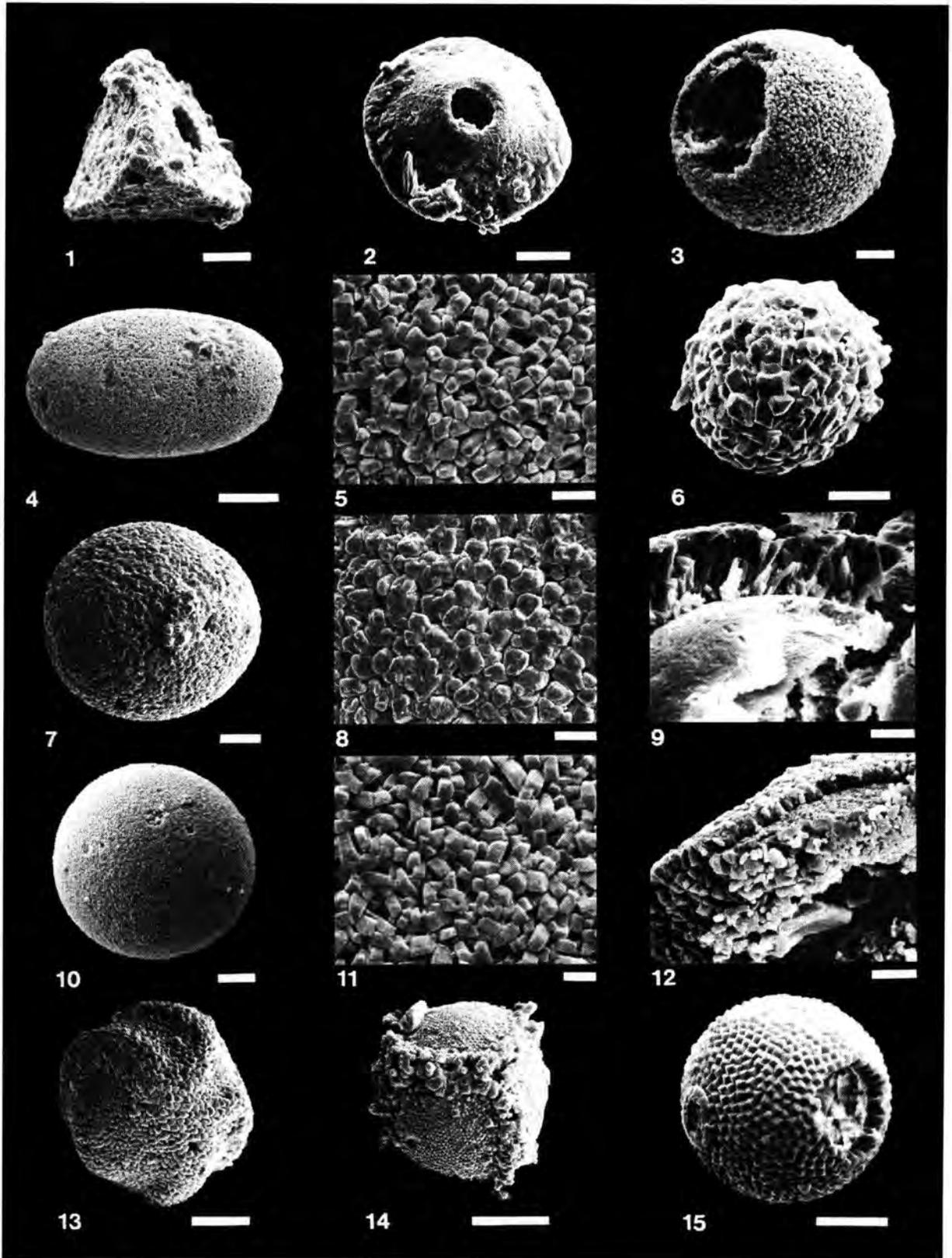
Plate 1. Figs. 1-12, Cysts with oblique wall structure

Fig. 1, *Calcicarpinum tetramurum* Kienel, 1994. Apical archeopyle, Type A. Cyst no. 139/2; core 113-689B-23X-2, 70-72 cm; scale bar = 10 µm. Fig. 2, *Carinellum* sp. Apical archeopyle, Type A. Cyst no. 126/4; core 113-689B-30X-3, 77-79 cm; scale bar = 10 µm. Fig. 3, *Pirumella edgarii* (Bolli, 1974) Lentini and Williams, 1993. Apical archeopyle, Type A. Cyst no. 159/1; core 113-689B-8H-2, 71-73 cm; scale bar = 10 µm. Figs. 4, 5, *Pirumella krasheninnikovii* (Bolli, 1974) Lentini and Williams, 1993. Fig. 4: cyst no. 129/9; core 113-689B-27X-1, 79-81 cm; scale bar = 30 µm. Fig. 5: cyst no. 133/9; core 113-689B-25X-5, 130-132 cm; detail of the outer surface; scale bar = 3 µm. Fig. 6, *Pirumella* cf. *loeblichii* (Bolli, 1974) Lentini and Williams, 1993, sensu Keupp, 1981. Cyst no. 133/84; core 113-689B-25X-5, 130-132 cm; scale bar = 10 µm. Figs. 7-9, *Pirumella multistrata* (Pflaumann and Krasheninnikov, 1978) Lentini and Williams, 1993. Cyst no. 128/6; core 113-689B-25X-5, 130-132 cm. Fig. 7: scale bar = 10 µm. Fig. 8: detail of the outer surface; scale bar = 3 µm. Fig. 9: cross-section of the wall; scale bar = 3 µm. Figs. 10-12, *Pirumella parva* (Fütterer, 1984) Lentini and Williams, 1993. Figs 10, 11: cyst no. 137/60; core 113-689B-24X-1, 51-53 cm. Fig. 10: scale bar = 10 µm. Fig. 11: detail of the outer surface; scale bar = 1 µm. Fig. 12: cyst no. 147/9; core 113-689B-17H-2, 58-60 cm; cross-section of the wall; scale bar = 3 µm.

Figs. 13-15, Cysts with radial wall structure

Fig. 13, *Bitorus bulbjergensis* Kienel, 1994. Cyst no. 139/97; core 113-689B-23X-2, 70-72 cm; scale bar = 10 µm. Fig. 14, *Congruentia eoacaenica* Kohring in Keupp et al., 1991. Cyst no. 144/9; core 113-689B-20H-1, 70-72 cm; scale bar = 10 µm. Fig. 15, *Orthopithonella? congruens* Fütterer, 1990. Apical archeopyle, Type A. Cyst no. 133/57; core 113-689B-25X-5, 130-132 cm; scale bar = 10 µm.

Plate 1



(Stott et al., 1990). According to Stott and Kennett (1990b), the planktonic foraminiferal assemblages showed little latitudinal variation during the early Paleocene. With some of the lower latitude forms lacking, however, they recognized the development of a more 'high-latitude' character in the assemblages of the Maud Rise region in the middle Paleocene.

The calcareous dinoflagellates of Hole 689B developed a somewhat high-latitude association by the late Paleocene, with an increase in the relative abundance of *Fuetererella flora* and *Pirumella parva*. These species were absent or rare in the late Paleocene of the mid-latitude South Atlantic (Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000).

The Paleocene-Eocene thermal maximum (PETM) was associated with a distinct negative $\delta^{13}\text{C}$ shift in the oceans (Stott et al., 1990), which was connected to changes in ocean circulation and chemistry and a reorganization of global carbon cycling (e.g., Röhl et al., 2000). These changes caused a major extinction amongst benthic foraminifera (e.g., Oberhänsli et al., 1991; Thomas and Shackleton, 1996; Aubry et al., 1998; Katz et al., 1999; Röhl et al., 2000), while the calcareous plankton underwent significant turnover and diversification (Zachos et al., 1993; Kelly et al., 1996). The organic-walled dinoflagellate cysts also underwent distinct perturbations during the LPTM: as a result of very warm temperatures along with an increase in the supply of nutrients to the marginal oceans, the assemblages became dominated by the genus *Apectodinium* on a global scale (e.g., Crouch et al., 2001).

Eocene onset of cooling

Since a hiatus spans the lower Eocene of Hole 689B, the consequences of the early Eocene climatic maximum cannot be investigated. Although the sea surface temperatures remained fairly warm at high latitudes (Kennett and Stott, 1990), a long-term cooling trend was initiated near the early-middle Eocene boundary and continued during the middle and late Eocene (Zachos et al., 2001).

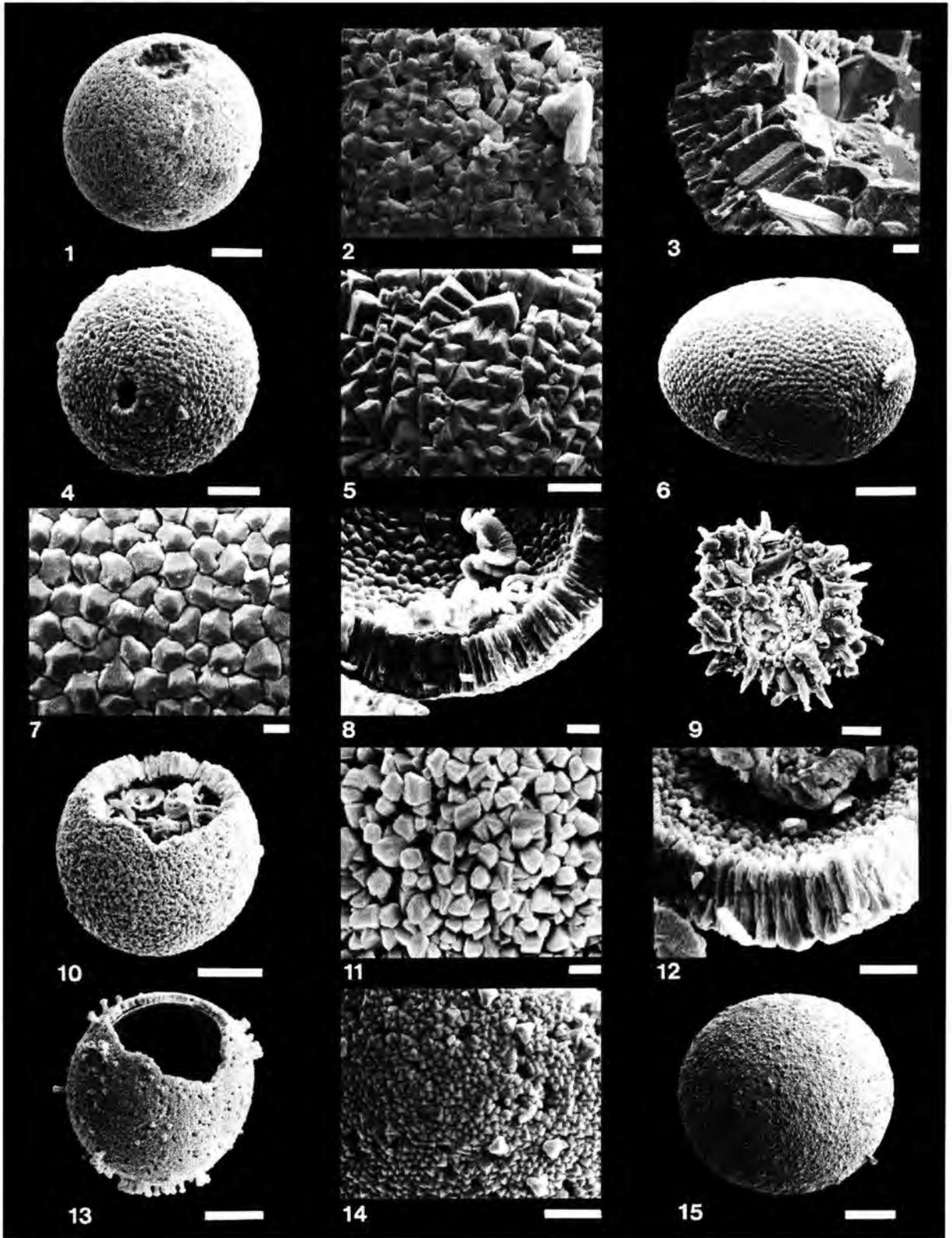
The middle Eocene coccolithophorid assemblages of Hole 689B had a temperate climatic character and formed part of a high-latitude biogeographic province, which contained only a few warm-water taxa (Wei and Wise, 1990). The calcareous dinoflagellate associations exhibited little

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Plate 2. Figs. 1-15, Cysts with radial wall structure

Figs. 1-3, *Orthopithonella? globosa* (Fütterer, 1984) Lentini and Williams, 1985. Damaged apical archeopyle, Type A. Cyst no. 130/2; core 113-689B-27X-1, 79-81 cm. Fig. 1: scale bar = 30 μm . Fig. 2: detail of the outer surface; scale bar = 3 μm . Fig. 3: cross-section of the wall; scale bar = 3 μm . Figs 4, 5, *Orthopithonella? aff. gustafsonii* (Bolli, 1974) Lentini and Williams, 1985. Secondary opening, no archeopyle visible. Cyst no. 135/63; core 113-689B-25X-4, 30-31 cm. Fig. 4: scale bar = 10 μm . Fig. 5: detail of the outer surface; scale bar = 3 μm . Figs 6-8, *Orthopithonella? sp.* Figs 6, 7: cyst no. 145/35; core 113-689B-18H-3, 70-72 cm. Fig. 6: scale bar = 10 μm . Fig. 7: detail of the outer surface; scale bar = 1 μm . Fig. 8: cyst no. 143/54; core 113-689B-20H-1, 70-72 cm; cross-section of the wall; scale bar = 3 μm . Fig. 9, "*Rhabdothorax*" spp. Cyst no. 143/66; core 113-689B-20H-1, 70-72 cm; scale bar = 10 μm . Figs. 10-12, *Caracomia cf. stella* Streng et al., 2002. Combination archeopyle, Type (3AtI). Cyst no. 159/11; core 113-689B-8H-2, 71-73 cm. Fig. 10: scale bar = 10 μm . Fig. 11: detail of the outer surface; scale bar = 1 μm . Fig. 12: cross-section of the wall; scale bar = 3 μm . Figs. 13-15, *Caracomia arctica* forma *spinosa* n. form. Figs 13, 14: holotype; cyst 163/2; core 113-689B-5H-3, 68-70 cm. Fig. 13: ventral-apical view showing the combination archeopyle, Type (3AtI) and the inner organic layer; scale bar = 10 μm . Fig. 14: detail of the outer surface; scale bar = 3 μm . Fig. 15, paratype; cyst 163/9; core 113-689B-5H-3, 68-70 cm; scale bar = 10 μm .

Plate 2



change from the late Paleocene, although five species did not continue into the middle Eocene and four species appeared in the middle Eocene.

By the mid-middle Eocene, the maximum surface-water temperature may have decreased to 12–13°C, and across the middle-late Eocene boundary, the temperature probably dropped about 2°–3°C at Site 689 (Stott et al., 1990; Kennett and Stott, 1990). The sea surface temperature continued to decrease during the late Eocene, but generally temperate climatic conditions continued to prevail (Kennett and Barker, 1990) and surface-water productivity increased in the Antarctic (Diester-Haass et al., 1993; Diester-Haass, 1995): this probably resulted from a slight increase in upwelling intensity (Kennett and Barker, 1990). Biosiliceous organisms thrived, but the species richness in Hole 689B declined for the calcareous plankton (Stott and Kennett, 1990b; Wei and Wise, 1990).

Due to the extinction of several taxa and the appearance or increase of others, the calcareous dinoflagellate associations in Hole 689B changed significantly between the middle and late Eocene. Although these changes were less pronounced in the middle latitudes, there were differences in the species composition (Hildebrand-Habel and Willems, 2000). Unlike in the mid-latitudes though, the species richness of calcareous dinoflagellates declined during the late Eocene in Hole 689B.

$\delta^{18}\text{O}$ records from Hole 689B indicate that following at least two closely spaced, late Eocene extraterrestrial impact events, accelerated cooling took place (Vonhof et al., 2000). $\delta^{13}\text{C}$ data suggest that the cooling was associated with a surface-water productivity increase, and a concurrent pulse-like increase of percentage of calcareous dinoflagellates in the >63 μm fraction occurred (Vonhof et al., 2000). A subsequent analysis of sample material provided by Vonhof et al. showed that the species spectrum in the >63 μm fraction corresponds to the assemblage we recorded in the 20–63 μm fraction of sample 689B-14H-6, 70–72 cm, 30 cm above the impact layer (Hildebrand-Habel, unpubl. data). The species particularly increasing in abundance in the >63 μm fraction is *Pirumella parva* (Vonhof et al., 2000, Fig. 2).



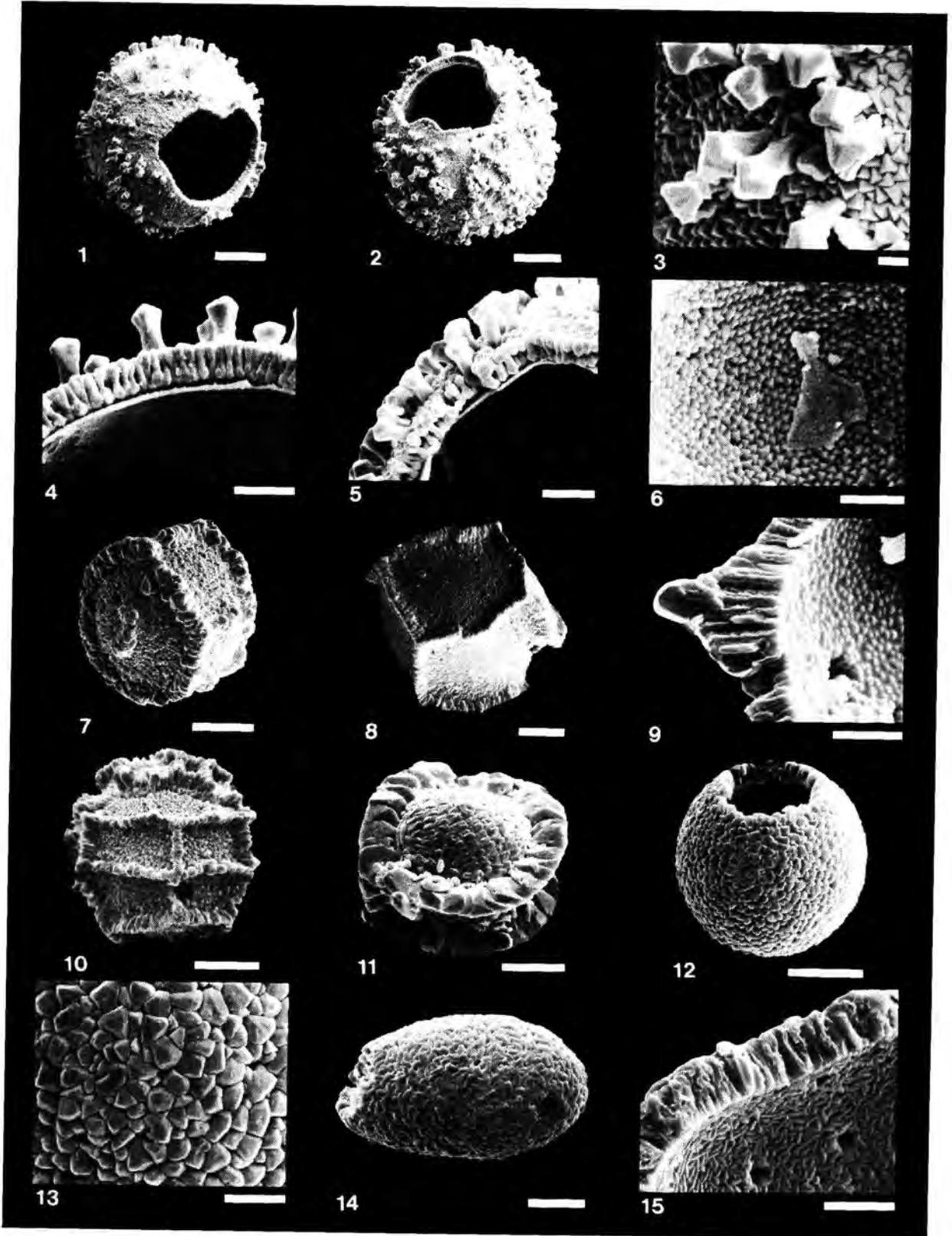
Plate 3. Figs. 1-6, Cysts with radial wall structure

Figs. 1-6, *Caracomia arctica* forma *spinosa* n. form; Core 113-689B-5H-3, 68-70 cm. Fig. 1: left lateral-apical view showing the combination archeopyle, Type (3Atl); paratype; cyst 163/7; scale bar = 10 μm . Figs. 2, 3: paratype; cyst 163/10. Fig. 2: lateral-ventral view showing the combination archeopyle, Type (3Atl); scale bar = 10 μm . Fig. 3: detail of the outer surface; scale bar = 1 μm . Fig. 4: paratype; cyst 163/17; cross-section of the wall; scale bar = 3 μm . Fig. 5: paratype; cyst 163/18; cross-section of the wall; scale bar = 3 μm . Fig. 6: paratype; cyst 163/6; detail of the inner surface; scale bar = 3 μm .

Figs. 7-15, Cysts with tangential wall structure

Fig. 7, *Calcigonellum? ansatum* Hildebrand-Habel and Willems, 1999. Cyst no. 139/88; core 113-689B-23X-2, 70-72 cm; scale bar = 10 μm . Figs. 8, 9, *Calcigonellum infula* Deflandre, 1948, emend. Keupp, 1984. Core 113-689B-25X-4, 30-31 cm. Fig. 8: cyst no. 147/36; scale bar = 10 μm . Fig. 9: cyst no. 147/72; cross-section of the wall; scale bar = 3 μm . Fig. 10, *Calciodinellum operosum* Deflandre, 1947, emend. Montresor et al., 1997. Cyst no. 153/51; core 113-689B-13H-3, 71-73 cm; scale bar = 10 μm . Fig. 11, *Centosphaera barbata* Wind and Wise in Wise and Wind, 1977. Lateral-apical view showing two strongly recrystallized tabulation ridges. Cyst no. 133/97; core 113-689B-25X-5, 130-132 cm; scale bar = 10 μm . Figs. 12, 13, *Fuettererella deflandrei* (Kamptner, 1956) n. comb. Apical archeopyle, Type A. Cyst no. 151/57; core 113-689B-14H-6, 70-72 cm. Fig. 12: scale bar = 10 μm . Fig. 13: detail of the outer surface; scale bar = 3 μm . Figs. 14, 15, *Fuettererella elliptica* Kohring, 1993a. Fig. 14: cyst no. 145/88; core 113-689B-18H-3, 70-72 cm; scale bar = 10 μm . Fig. 15: cyst no. 141/8; core 113-689B-22X-2, 70-72 cm; cross-section of the wall; scale bar = 3 μm .

Plate 3



Association changes during the Oligocene cooling

At Site 689, the Eocene-Oligocene (E/O) boundary is marked by a rapid, strong positive shift in $\delta^{18}\text{O}$ isotope values (Kennett and Stott, 1990; Stott et al., 1990). This shift represents a climate change of great consequences, coupled with a strong drop of sea surface temperatures and substantial ice-sheet growth on East Antarctica (e.g., Salamy and Zachos, 1999; Barker et al., 1999; Shipboard Scientific Party, 2001). In the Weddell Sea, planktonic foraminifera and coccolithophorids decreased in diversity, but there was an increase in relative abundance of cool water taxa (Stott and Kennett, 1990b; Wei and Wise, 1990; Wei et al., 1992). The gradual replacement of calcareous primary producers by siliceous organisms suggests a stronger upwelling intensity in the Weddell Sea area and continued cooling during the Oligocene (Kennett and Barker, 1990; Stott and Kennett, 1990b; Salamy and Zachos, 1999).

Despite the major environmental and biotic changes across the E/O boundary, the calcareous dinoflagellates in Hole 689B did not initially show a marked change in the early Oligocene. In the late early Oligocene, however, there were significant differences, with a strong decrease in species richness and abundance, the dominance of *Calciodinellum levantinum*, and the abundance decrease or extinction of several species. During the late Oligocene, the association of calcareous dinoflagellates remained relatively stable, with continued dominance of *C. levantinum*.

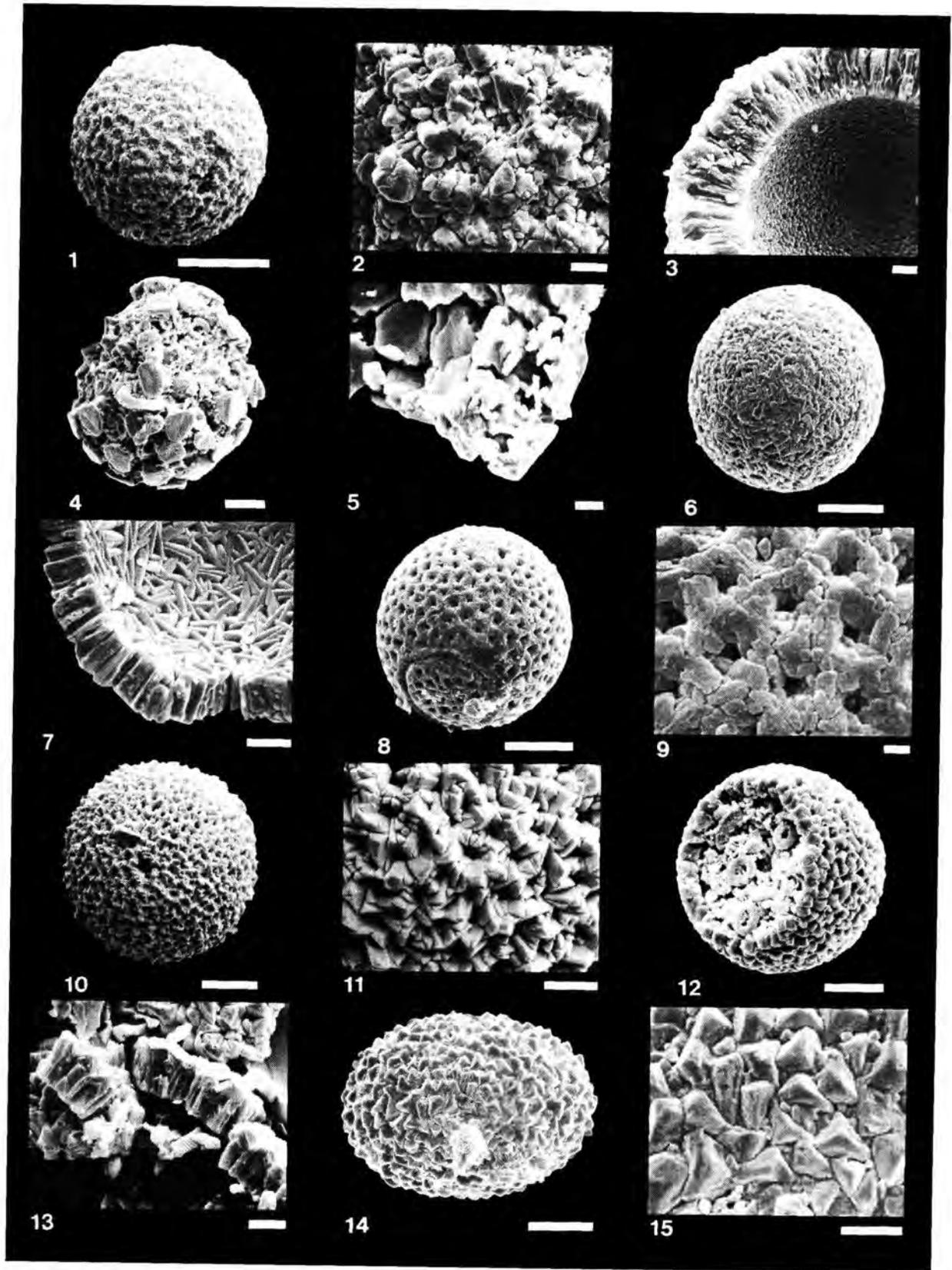
The growing biological stress induced by the changing environmental factors probably caused *Pirumella parva* to migrate into more northern regions, since it has been recorded from the late Oligocene of the Rio Grande Rise, mid-latitude western South Atlantic Ocean (Hildebrand-Habel and Willems, 2000).

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Plate 4. Figs. 1-15, Cysts with tangential wall structure

Figs. 1-3, *Fuettererella flora* (Fütterer, 1990) n. comb. Figs 1, 2: cyst no. 133/40; core 113-689B-25X-5, 130-132 cm. Fig. 1: scale bar = 30 μm . Fig. 2: detail of the outer surface; scale bar = 3 μm . Fig. 3: cyst no. 135/87; core 113-689B-25X-4, 30-31 cm; cross-section of the wall; scale bar = 3 μm . Figs. 4, 5, *Fuettererella fungiforma* Hildebrand-Habel and Willems, 1999. Cyst no. 144/8; core 113-689B-20H-1, 70-72 cm. Fig. 4: scale bar = 10 μm . Fig. 5: cross-section of the wall; scale bar = 3 μm . Figs. 6, 7, *Fuettererella tesserula* (Fütterer, 1977) Kohring, 1993a. Core 113-689B-23X-2, 70-72 cm. Fig. 6: cyst no. 139/23; scale bar = 10 μm . Fig. 7: cyst no. 139/13; cross-section of the wall and the inner surface; scale bar = 3 μm . Figs. 8, 9, *Cervisiella operculata* (Bramlette and Martini, 1964) Hildebrand-Habel et al., 1999. Apical operculum, archeopyle Type A. Cyst no. 137/19; core 113-689B-24X-1, 51-53 cm. Fig. 8: scale bar = 10 μm . Fig. 9: detail of the outer surface; scale bar = 1 μm . Figs. 10, 11, *Calciodinellum albatrosianum* (Kamptner, 1963) Janofske and Karwath in Karwath, 2000. Cyst no. 143/85; core 113-689B-20H-1, 70-72 cm. Fig. 10: scale bar = 10 μm . Fig. 11: detail of the outer surface; scale bar = 3 μm . Figs. 12, 13, *Calciodinellum levantinum* Meier et al., 2002. Fig. 12: cyst 149/73; core 113-689B-15H-4, 42-44 cm; combination archeopyle, Type (3AtI); scale bar = 10 μm . Fig. 13: cyst 147/89; core 113-689B-17H-2, 58-60 cm; cross-section of the wall; scale bar = 3 μm . Figs. 14, 15, *Calciodinellum elongatum* (Hildebrand-Habel et al., 1999) Meier et al., 2002. Cyst no. 141/23; core 113-689B-22X-2, 70-72 cm. Fig. 14: scale bar = 10 μm . Fig. 15: detail of the outer surface; scale bar = 3 μm .

Plate 4



Neogene to modern dominances

An important hiatus, linked with an intensification of circum-Antarctic deep-water circulation, is present across the Oligocene-Miocene boundary in Hole 689B (Shipboard Scientific Party, 1988; Kennett and Barker, 1990). During the early Miocene, planktonic foraminifera and coccolithophorids at Maud Rise exhibited a slight increase in species richness (Kennett and Barker, 1990) and radiolarian faunas had a more cosmopolitan character (Lazarus and Caulet, 1993). These biotic changes indicated a warmer period with a rather poorly developed latitudinal gradient (Gallagher et al., 2001). This warming was reflected by a change in the calcareous dinoflagellate association, with the obliquely structured *Pirumella edgarii* returning to the Maud Rise region after it had left in the middle Eocene, and immediately dominating the assemblage. This early Miocene increase in the oblique wall type has also been recorded in the middle latitudes, where it is accompanied by an increase in *Pirumella parva* (Hildebrand-Habel and Willems, 2000).

Although the middle Miocene is often regarded as a time of renewed cooling and substantial ice build-up on Antarctica (e.g., Shackleton and Kennett, 1975; Miller et al., 1987; Berger and Wefer, 1996), the prevailing dominance of *P. edgarii* at Hole 689B during the early middle Miocene provides evidence of ameliorated climatic conditions in the Weddell Sea area. Site 689 clay mineral data also suggest that a major cooling of Antarctica occurred after the early middle Miocene (Robert and Maillot, 1990). During the middle Miocene cool phase, coccolithophorid and planktonic foraminiferal assemblages, when present, became essentially monospecific (Kennett and Barker, 1990). Comparably, the calcareous dinoflagellate assemblage became monogeneric and dominated by *Caracomia arctica* forma *spinosa* in the late middle Miocene. The bipolar *Caracomia arctica* has apparently been restricted to cold and polar waters and may thus be used as a cold water indicator (Streng et al., 2002 [Chapter 2.1]).

By the mid-late Miocene, only biosiliceous sediments were deposited on Maud Rise (Kennett and Barker, 1990) and no calcareous dinoflagellates have been preserved. In Pliocene to Pleistocene sediments, calcareous nannofossils are generally absent (Wei and Wise, 1990). On Maud Rise, a thin calcareous ooze of Quaternary age is widespread, but was not sampled at Site 689 (Shipboard Scientific Party, 1988). It could well contain calcareous dinoflagellates, since they have been found in calcareous surface sediment samples of Maud Rise (Streng et al., 2002). The assemblages contain only *Caracomia arctica* (Streng et al., 2002 [Chapter 2.1]). Thus, modern calcareous dinoflagellate assemblages in high latitudes do not compare with mid and low latitudes, in which the cosmopolitan vegetative-coccolith *Thoracosphaera heimii* dominates within both the plankton and the sediment. Although *T. heimii* appeared in the latest Maastrichtian / earliest Paleocene (Hildebrand-Habel et al., 1999), it has not been observed in Hole 689B. *Caracomia arctica* first appears in the late Oligocene (Streng et al., subm. B [Chapter 2.4]) and seems to be the sole calcareous dinoflagellate species able to - at least to some degree - clear the hurdle of physical limitations on carbonate secretion in cold environments.

CONCLUSIONS

Calcareous dinoflagellates, the only dinoflagellates recorded in ODP Site 689 so far, were substantially influenced by the consequences of the K/T boundary event and the long-term change from a relatively warm Late Cretaceous to a cold Neogene climate. Probably driven by the resulting

environmental changes, the calcareous dinoflagellates in Hole 689B developed distinct stratigraphic distribution patterns, in many respects differing significantly from those in lower latitudes.

Maastrichtian oceanic assemblages showed little latitudinal variation and a fairly uniform and stable species spectrum. The appearance and increase in tangentially structured species, however, may have indicated some environmental changes in the late Maastrichtian. The K/T boundary was marked by a major change in species composition, but a low species' extinction rate. Directly above the K/T boundary, there was a strong abundance increase in the opportunistic species *Cervisiella operculata*, although less pronounced than in the lower latitudes.

The dominance of *C. operculata* declined in the early Paleocene and by the late Paleocene, the calcareous dinoflagellate assemblages had a high-latitudinal aspect, as indicated by the high relative abundances of *Fuftererella flora* and *Pirumella parva*. The assemblages remained stable prior to the late Eocene, although some species did not continue into the middle Eocene. As in the mid-latitudes (Hildebrand-Habel and Willems, 2000), major changes characterized the middle-late Eocene boundary on Maud Rise, probably reflecting increased cooling. Cooling across the Eocene-Oligocene boundary had little effect on the calcareous dinoflagellates, but there were significant changes in the late early Oligocene. A decrease in species richness associated with the dominance of *Calciodinellum levantinum* typified the assemblages. *Pirumella parva* disappeared from the high latitudes and may have migrated into the middle latitudes during the Oligocene.

The reappearance and dominance of the obliquely structured *Pirumella edgarii* possibly denoted a slight warming trend in the early Miocene. This dominance indicated that the warming trend continued into the early middle Miocene. Later, the strong middle Miocene climate cooling was reflected in the assemblages which contained only *Caracomia* spp. No calcareous dinoflagellates have been recovered from the late Miocene. The Pliocene-Pleistocene was most likely also barren of these organisms, due to the predominance of biosiliceous sediments. Surface sediment samples of Maud Rise contain specimens of *Caracomia arctica*, however, stressing its preference for cold and polar oceans (Streng et al., 2002 [Chapter 2.1]).

Despite the fact that a lot of basic research on calcareous dinoflagellates remains to be done, the response of high-latitudinal assemblages to climatic changes in the Cenozoic emphasizes the potential of this group to provide essential and unique information on the biotic effects underlying paleoenvironmental changes and, more importantly, climatic changes.

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Appendix A. List of calcareous dinoflagellate taxa found in ODP Hole 689B in alphabetical order of generic epithets

Bitorus bulbjergensis Kienel, 1994
Calcicarpinum tetramurum Kienel, 1994
Calcigonellum? ansatum Hildebrand-Habel and Willems, 1999
Calcigonellum infula Deflandre, 1948, emend. Keupp, 1984
Calciodinellum albatrosianum (Kamptner, 1963) Janofske and Karwath *in* Karwath, 2000
Calciodinellum elongatum (Hildebrand-Habel et al., 1999) Meier et al., 2002
Calciodinellum levantinum Meier et al., 2002
Calciodinellum operosum Deflandre, 1947, emend. Montresor et al., 1997
Caracomia arctica forma *spinosa* n. form
Caracomia cf. *stella* Streng et al., 2002
Carinellum sp.
Centosphaera barbata Wind and Wise *in* Wise and Wind, 1977
Congruentia eocaenica Kohring *in* Keupp et al., 1991
Fuettererella deflandrei (Kamptner, 1956) n. comb.
Fuettererella elliptica Kohring, 1993a
Fuettererella flora (Fütterer, 1990) n. comb.
Fuettererella fungiforma Hildebrand-Habel and Willems, 1999
Fuettererella tesserula (Fütterer, 1977) Kohring, 1993a
Cervisiella operculata (Bramlette and Martini, 1964) Streng et al., *subm.* A
Orthopithonella? congruens Fütterer, 1990
Orthopithonella? globosa (Fütterer, 1984) Lentin and Williams, 1985
Orthopithonella? aff. gustafsonii (Bolli, 1974) Lentin and Williams, 1985
Orthopithonella? sp.
Pirumella edgarii (Bolli, 1974) Lentin and Williams, 1993
Pirumella krasheninnikovii (Bolli, 1974) Lentin and Williams, 1993
Pirumella cf. *loeblichii* (Bolli, 1974) Lentin and Williams, 1993, *sensu* Keupp, 1981
Pirumella multistrata (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1993
Pirumella parva (Fütterer, 1984) Lentin and Williams, 1993
 "Rhabdothorax" spp.

Appendix B. Systematic paleontology

Division DINOFLAGELLATA (Bütschli, 1885) Fensome et al., 1993
 Subdivision DINOKARYOTA Fensome et al., 1993
 Class DINOPHYCEAE Pascher, 1914
 Subclass PERIDINIPHYCIDAE Fensome et al., 1993
 Order PERIDINIALES Haeckel, 1894
 Suborder PERIDINIINEAE Autonym
 Family PERIDINIACEAE Ehrenberg, 1831
 Subfamily CALCIODINELLOIDEAE Fensome et al., 1993

Genus *Caracomia* Streng et al., 2002

Diagnosis (Streng et al., 2002: 398 [Chapter 2.1]).—"Spherical to ovoid cysts with single-layered calcareous wall; wall-forming crystals radially arranged; morphological long-axes of crystals correspond to crystallographic *c*-axes; combination archeopyle polygonal in outline; simple operculum includes apical (2'-4') and intercalary plates (1a-3a); tabulation typically restricted to operculum."

Caracomia arctica (Gilbert and Clark, 1983) Streng et al., 2002

Diagnosis (Streng et al., 2002: 398 [Chapter 2.1]).—"Species of *Caracomia* with wall built of elongated, rod-shaped crystals; wall-forming crystals generally increase in thickness towards distal and proximal ends; operculum polygonal in outline comprising apical and intercalary plate homologs."

Caracomia arctica forma *spinosa* new form

Plate 2, Figures 13-15; Plate 3, Figures 1-6

Diagnosis.—Form of *Caracomia arctica* with distally lengthened individual crystals.

Description.—Spherical to subspherical cysts with diameters of 26.7–56.9 μm , and an average size of 36 μm . The single-layered wall, 1.4–3.7 μm thick (excluding spines), consists of radially oriented calcite crystals (both morphological long-axes and crystallographic *c*-axes). The crystals are rod- to bone-shaped in habit and typically increase in thickness towards their proximal and distal ends (Pl. 3, Figs. 4, 5). The proximal and distal surfaces exhibit a pattern of densely packed trigonal ends of wall-forming crystals, however, they are occasionally interrupted by irregularly disseminated pores (Pl. 2, Fig. 14; Pl. 3, Fig. 6). The relatively smooth distal surface may be modified by the growth of individual crystal tops (Pl. 2, Fig. 14). In its final stage, the crystal growth results in the development of trigonal spines (Pl. 3, Fig. 3). The number of spines varies from one (Pl. 2, Fig. 15) to more than two hundred (Pl. 3, Fig. 2). In some cases, rows of spines seem to delineate plate boundaries, however, a tabulation exceeding cryptotabulation remains unproven. The polygonal combination archeopyle is situated apically or slightly ventrally. The simple polyplacoid operculum comprises plates 2'-4' and 1a-3a [archeopyle formula: (3AtI)]. A principal archeopyle suture is always present (Pl. 2, Fig. 15). Typically, a 0.2–0.35 μm thick rough inner organic layer is preserved (Pl. 3, Figs. 4, 5).

Etymology.—From *spinus* (Latin) = spiny; based on the development of individual spines on the distal surface.

Types.—Holotype: cyst 163/2, SEM micrographs 219/3/1-5; 219/4/1-5; 378/1/1-5 (Pl. 2, Figs. 13, 14); type locality and stratum: Queen Maud Rise, Weddell Sea, ODP Leg 113, sample 113-689B-5H-3, 68-70 cm; latest middle Miocene diatom zones *Nitzschia praeurta*/*Denticulopsis praedimorpha* (Gersonde and Burckle, 1990); paratypes: cyst 163/9, SEM micrographs 220/3/5; 220/4/1-6; 379/2/6; 379/3/1-6; 383/2/4-6 (Pl. 2, Fig. 15); cyst 163/7, SEM micrographs 220/2/2-5; 220/3/1-2; 379/1/6; 179/2/1-5 (Pl. 3, Fig. 1); cyst 163/10, SEM micrographs 220/5/1; 379/4/1-5; 382 (Pl. 3, Figs. 2, 3); cyst 163/17, SEM micrographs 221/1/4-5; 221/2/1-2; 380/2/6; 380/3/1-4 (Pl. 3, Fig. 4); cyst 163/18, SEM micrographs 221/2/3-4; 380/3/5-6; 380/4/1 (Pl. 3, Fig. 5); cyst 163/6, SEM micrographs 220/1/2-5; 220/2/1; 379/1/2-5 (Pl. 3, Fig. 6).

Dimensions of holotype.—The diameter of the cyst (apical-antapical) is 34.1 μm ; wall thickness, excluding spines is 2.1 μm ; maximum wall thickness including spines is 4.36 μm .

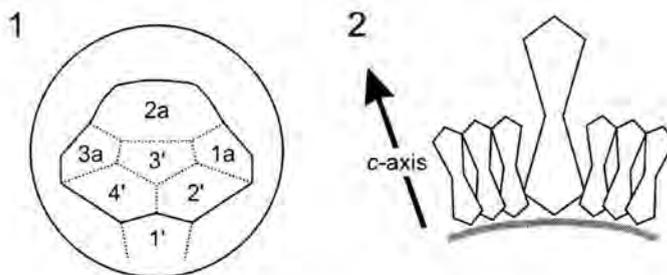


Figure 5. Schematic drawings of *Caracomia arctica* forma *spinosa* n. form. 1, apical view showing archeopyle and involved plates; 2, cross section of wall showing crystal arrangement and inner organic layer

Discussion.—Apart from the development of spines, *Caracomia arctica* forma *spinosa* corresponds to the autonym *C. arctica* forma *arctica* in having: a spherical to ovoid cyst, a cryptotabulation, a polyplacoid operculum, an archeopyle formula (3AtI), a radial wall type, rod- to bone-shaped habit of crystals, equilateral

trigonal crystal tops, and a commonly preserved organic layer. *Caracomia arctica* forma *spinosa* differs from the autonym, however, in the frequent occurrence of pores. A diagenetic overgrowth on crystals, producing a somewhat coarser surface texture, has been described for *Caracomia arctica*. However, *C. arctica* forma *arctica* never exhibits a comparable development of spines.

Occurrence.—*Caracomia arctica* forma *spinosa* has only been found in the middle Miocene of ODP Hole 689B. *C. arctica* occurs from late Oligocene to ?Recent and is restricted to polar and cold oceans (Streng et al., 2002 [Chapter 2.1]).

Caracomia stella Streng, Hildebrand-Habel and Willems, 2002

Diagnosis (Streng et al., 2002: 399 [Chapter 2.1]).—"Species of *Caracomia* with a relatively thick wall typically penetrated by numerous pores; wall-forming crystals rod-like; each single crystal is constructed of a sequence of several tiny crystallites; operculum simple, polygonal in outline, comprising plates 2'-4' and 1a-3a."

Caracomia cf. *stella* Streng, Hildebrand-Habel and Willems, 2002

Plate 2, Figures 10-12

Description.—Spherical cysts with diameters of 31.6-59.1 μm (average 39 μm). The single-layered wall, 3.6-4.2 μm thick, consists of radially oriented crystals (both morphological long-axes and crystallographic *c*-axes). The stem-like crystals increase in thickness towards their distal ends (Pl. 3, Fig. 12). Both proximal and distal surfaces exhibit a pattern of triradiate crystal tops. However, strong diagenetic alteration results in an irregular pattern particularly on the outer surface (Pl. 3., Fig. 11). The polygonal archeopyles are 3.7-4.7 μm in diameter.

Discussion.—*Caracomia* cf. *stella* is comparable to *C. stella* Streng et al., 2002 regarding the polygonal combination archeopyle (3AtI) and the massive, single-layered wall of densely packed crystals with a radial orientation. It differs, however, in the structure of the stem-like crystals that consist of a succession of epitaxially grown tiny rhombohedrons in *C. stella*. Additionally, the wall in *C. stella* is pierced by numerous, equally distributed pores. However, the specimens of *C. cf. stella* reveal strong diagenetic overprints (Pl. 2, Figs. 11, 12) and the secondary growth of crystals may have obscured the wall structure. *C. stella* has as yet only been described from low and middle latitudes.

Genus *Carinellum* Keupp, 1981

Diagnosis (Keupp, 1981: 51).—"Monocarinate calcareous dinoflagellate cyst with a conical epittract and a hemispherical to plane hypottract. The single- to double-layered wall is constructed in 'Kreuzbalken-Struktur' (X-like crossing calcitic stems). The enclosed organic capsule is globular."

Carinellum sp.

Plate 1, Figure 2

Description.—Monocarinate cysts with maximum diameters of 36.3-43.3 μm (average 41.5 μm). A cingular rim of coarser crystals separates the weakly conical epittract from the weakly conical to hemispherical hypottract. A slight depression in this cingular rim might indicate the position of the sulcus (Pl. 1, Fig. 2). The single-layered wall consists of irregularly oblique oriented thin-stemmed crystals. The distal fusion of crystals results in a smooth outer surface. The archeopyles of 8.9-9.5 μm are positioned centrally in the apex and involve the single plate 3'.

Discussion.—The shape of the cysts is similar to *Carinellum hyalinum* Keupp, 1987 and *Carinellum lenticulare* Keupp, 1987. *C. hyalinum* has a comparable wall structure of distally fusing crystallites, but the stemmed crystals are coarser. Additionally, *C. hyalinum* differs from *Carinellum* sp. in possessing a longitudinal ventral ridge on the hypocyst and partly on the epicyst. *C. lenticulare* differs in having a wide depression in a subcingular ledge and an eccentric archeopyle that is positioned dorsally.

Genus *Fuettererella* Kohring, 1993a

Diagnosis (Kohring, 1993a, p. 88).—"Calcareous dinoflagellate cyst with a pseudoorthopithonelloid outer wall, however wall crystals with the *c*-axis parallel to the cysts surface."

Fuettererella deflandrei (Kamptner, 1956) new combination

Plate 3, Figures 12, 13

Orthopithonella deflandrei (Kamptner 1956). KOHRING, 1993a, p. 30, pl. 4, figs f-k. [Comment: this combination was not validly published in Keupp, 1992a, since this author did not fully reference the basionym].

Basionym.—*Thoracosphaera deflandrei* Kamptner, 1956. Österreichische Botanische Zeitschrift 103, pp. 448-455, figs 1-4; holotype, fig. 1.

Discussion.—Based on SEM studies, Keupp (1992a) and Kohring (1993a) considered *Thoracosphaera deflandrei* as belonging to the genus *Orthopithonella* Keupp in Keupp and Mutterlose, 1984. According to the emended diagnosis of the genus in Keupp and Versteegh (1989), *Orthopithonella* comprises spherical cysts with only rudimentary tabulation, an archeopyle formed from the loss of apical plates 2'-4' and a predominantly single-layered, calcareous wall consisting of crystals with radially oriented *c*-axes. However, in the original examination of *Thoracosphaera deflandrei*, Kamptner (1956) applied crystallographic methods and observed a symmetric extinction cross and a positive optic sign under the light microscope in crossed nicols and with gypsum plate. He concluded that the optical axis of each element is oriented parallel to the sphere's surface. Since the crystallographic features do not correspond to those of *Orthopithonella*, the species should not be included in that genus. Based on its ultrastructural characteristics, i.e., crystals with tangentially oriented *c*-axes but radially oriented morphological long-axes, we assign it to the genus *Fuettererella*.

Fuettererella flora (Fütterer, 1990) new combination

Plate 4, Figures 1-3

Basionym.—*Orthopithonella flora* Fütterer, 1990. Proceedings of the Ocean Drilling Program, Scientific Results 113, p. 538, pl. 3, figs 1-7; holotype, pl. 3, figs 1, 3.

Discussion.—Comparable to other calcareous dinoflagellates with elongate crystals oriented perpendicularly to the cysts' surfaces, *Fuettererella flora* was originally interpreted as possessing a radial wall structure and was thus assigned to the genus *Orthopithonella*. However, our subsequent light-optical analysis of material from the type area revealed a tangential orientation of the *c*-axes in *F. flora*. *Fuettererella flora* has a spherical operculum situated in the apical area, crystals with radially oriented morphological long-axes, and exhibits a symmetric extinction cross and a positive optic sign under the light microscope in crossed nicols and with gypsum plate. The characteristic 'pseudo-radial', in fact tangential wall structure necessitates the new combination *Fuettererella flora*.

Genus *Orthopithonella* Keupp in Keupp and Mutterlose, 1984 emend. Streng et al., 2002

Original diagnosis (translated from Keupp in Keupp and Mutterlose, 1984: 158).—"Cysts with predominantly single-layered calcareous walls, built of blocky to rod-like, radially arranged crystallites (*c*-axis perpendicular to surface). Generally no paratabulation."

Emended diagnosis (Streng et al., 2002: 401 [Chapter 2.1]).—"Single-layered calcareous dinoflagellate cyst with radially oriented crystallographic *c*-axes of wall forming crystals; compound operculum disarticulates in several opercular pieces; polygonal archeopyle reflects tabulation and involves apical and intercalary plates."

Orthopithonella? sp.

Plate 2, Figures 6-8

Description.—Ovoid cysts with a longitudinal diameter of 43.3-58.6 µm and a minimum diameter of 29.7-48.9 µm. The length/width ratio is 1.1-1.5. The single-layered wall is 5.4-6.1 µm thick and consists of long-

stemmed skeletal-like crystals. The morphological long-axes of the crystals are radially oriented; the crystallographic orientation, however, needs to be confirmed by light microscope examination. A pattern of densely packed trigonal ends of wall-forming crystals characterizes the proximal and distal surfaces. On the outer surface, the crystal tops interfinger and show different stages of diagenetic overgrowth and recrystallization. No archeopyles have been observed.

Discussion.—The ovate shape of *Orthopithonella?* sp. distinguishes this taxon from all other elongated calcareous dinoflagellate species. However, as no additional information on the archeopyle type and the crystallographic orientation of the wall-forming crystals is available, no specific identification has been attempted and the species is questionably assigned to *Orthopithonella*.

Genus "*Rhabdothorax*" Kamptner ex Gaarder and Heimdal, 1973

Remarks.—Kamptner (1958) introduced the generic name "*Rhabdothorax*" for oval to subspherical calcareous tests with flat polygonal crystallites that possess a distal spine. However, Kamptner (1958) omitted to provide a Latin diagnosis to make this genus available. A Latin diagnosis was later provided by Gaarder and Heimdal (1973, p. 97) who thereby validated the genus (*Rhabdothorax* Kamptner ex Gaarder and Heimdal, 1973). Recently, Janofske (2000) inferred that *Rhabdothorax* is a junior synonym of *Scrippsiella* Balech ex Loeblich III, 1965 [see discussion of "*Rhabdothorax*" spp.].

"*Rhabdothorax*" spp.

Plate 2, Figure 9

Description.—Spherical to subspherical cysts with diameters of 27.8-67.5 μm (including spines; average 44.3 μm). The single-layered wall has a maximum thickness of 6.1-11.8 μm (average 9.7 μm). It consists of crystallites with a basal plate that has a polygonal to triangular outline and a distal spine. The spines are radially oriented and characterized by high morphological variability. All six specimens analyzed in polarized light possess a radial wall structure. Under the SEM, all tests exhibit strong secondary growth of crystals. The archeopyles are 16.8-39.9 μm in diameter (average 25.7 μm).

Discussion.—Numerous authors have included various types of spinose cysts of uncertain affinity in *Rhabdothorax* using open nomenclature (e.g., Keupp and Kowalski, 1992; Keupp and Kohring, 1993; Kienel, 1994; Vink et al., 2000). Janofske (2000) emended the species belonging to *Rhabdothorax*, i.e., *R. regale* (Gaarder, 1954) Gaarder in Gaarder and Heimdal, 1973 (senior synonym of *R. geremus* Kamptner, 1967) and *R. erinaceus* (Kamptner, 1937) Kamptner, 1958, and concluded that *Rhabdothorax* is a junior synonym of *Scrippsiella* Balech ex Loeblich III, 1965, as the type of *Rhabdothorax*. *R. erinaceus*, is a junior synonym of *Scrippsiella trochoidea* (von Stein, 1883) Loeblich III, 1965 emend. Janofske, 2000. *R. regale* was newly combined to *Scrippsiella regalis* (Gaarder, 1954) Janofske, 2000. Consequently, the genus *Rhabdothorax* became obsolete. Accordingly, all morphotypes of *Rhabdothorax* published under open nomenclature should now be referred to as *Scrippsiella* sp. However, in contrast to the radial wall structure of our specimens of "*Rhabdothorax*" spp., *Scrippsiella* is characterized by a tangential ultrastructure (see Janofske, 2000). Consequently, the accommodation of all specimens of "*Rhabdothorax*" spp. within *Scrippsiella* is problematic. Since the vast morphological variability observed within this group and the diagenetic alteration of all specimens did not allow a clear determination, we maintain the name "*Rhabdothorax*" as an informal name to accommodate spinose calcareous dinoflagellates of uncertain affinity and possibly radial wall structure.

Long-term evolution of calcareous dinoflagellate associations
since the Late Cretaceous:
comparison of a high and a low latitude core from the Indian Ocean

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ABSTRACT.—A high and a low latitude core of the Ocean Drilling Program from the eastern and southern Indian Ocean were studied to obtain a general overview of the evolution of calcareous dinoflagellate cyst associations in this region and their possible reaction to known major Cenozoic climatic changes. Despite a relatively low sample density several shifts in calcareous dinoflagellate assemblages could be linked to periods of major climatic or environmental changes at the Cretaceous/Tertiary transition, in the early Oligocene, and in the Neogene. Coherences between changes in the climate and in the associations appear to be more distinctive in high latitudes than in low latitudes. For the first time, shifts in the stratigraphic distribution pattern of different archeopyle types have been evaluated. The ratio between small and large archeopyles turned out to be a possible tool for the reconstruction of the large-scale climatic evolution in high latitudes, with small archeopyles correlating with warmer periods and large archeopyles characterizing colder conditions. Altogether 65 taxa have been distinguished of which several rare or problematic taxa, which may partly represent new species, are informally described or described using open nomenclature. Additionally, the problematic species *Thoracosphaera? prolata* and its relation to and potential synonymy with *Calciadinellum elongatum* is discussed in detail.

INTRODUCTION

During the last years, large amounts of data have been published on the ecology of calcareous dinoflagellate cysts (e.g., Höll et al., 1998, 1999; Vink et al., 2002) and their use as proxies in paleoceanography (e.g., Esper et al., 2000; Vink et al., 2001). However, as those studies concentrate mainly on the Quaternary, investigations of calcareous dinoflagellate cyst associations covering longer time periods within the Cenozoic are still scarce and only comprise studies by Fütterer (1977, 1984), Hildebrand-Habel et al. (1999), and Hildebrand-Habel and Willems (2000). Especially high latitude assemblages are poorly studied and still many questions need to be addressed, e.g., how do high latitude associations differ from those of middle or low latitudes, do typical high latitude associations exist and how do high latitude assemblages of calcareous dinoflagellate cysts react to climatic changes during the Cenozoic compared to those of lower latitudes? Additionally, all previous studies on long-term assemblage changes concentrated on the Atlantic Ocean. This study is the first record of Cenozoic calcareous dinoflagellate cyst associations of high and low latitudes in the Indian Ocean. It supplements the results on calcareous dinoflagellate distributions of Fütterer (1990) and Hildebrand-Habel and Streng (in review) [Chapter 2.3] from the high latitudinal eastern Weddell Sea and of Hildebrand-Habel et al. (1999) and Hildebrand-Habel and Willems (2000) from the mid-latitudinal

South Atlantic Ocean. A comprehensive evaluation of all available information on changes in calcareous cyst associations during the Cenozoic should provide a funded basis for subsequent detailed and high-resolution studies of selected stratigraphic intervals.

LOCALITIES AND MATERIAL

The studied samples originate from two cores of the Ocean Drilling Program (ODP), Hole 747A, Kerguelen Plateau, southern Central Indian Ocean (ODP Leg 120), and Hole 761B, Wombat Plateau, eastern Indian Ocean (ODP Leg 122) (Fig. 1). A single sample from ODP Leg 120, Hole 747C (sample 120-747C-1R-4, 66-67 cm) is used to supplement the poor Oligocene recovery of Hole 747A. To avoid confusion in the following, data from this sample are regarded as to belong to Hole 747A.

The Kerguelen Plateau is a broad NW-SE directed topographic high, located between 54°-57°S and 61°-84°E, separated from the Antarctic continent through the Princess Elizabeth Trough. Site 747 (54°48.68' S, 76°47.64' E) is located in the central zone of the Kerguelen Plateau at a water depth of about 1,700 m, approximately 300 km SE of Heard Island. The central Kerguelen Plateau formed 120-110 my ago by excessive volcanic activity at the axis of the spreading ridge that separated India from Antarctica (Munschy et al., 1992). Sedimentation rates at Site 747 varied notably. They were relatively high in the Maastrichtian (about 20 m/my), whereas the early Cenozoic evolution of the Kerguelen Plateau is characterized by a continuous sedimentation at a very low rate (less than 1 m/my) and two major hiatuses (63.8-58 my and 52.6-37.8 my) related to recurrent faulting and subsidence, resulting in a condensed succession (Shipboard Scientific Party, 1989). The break-up of the North Kerguelen Plateau and the Broken Ridge in the middle Eocene (43-42 my) had been accompanied by a sedimentation change due to an intensification of the physical oceanic regime (Munschy et al., 1992). With the beginning of the late Oligocene, the sedimentation rate increased to about 5 m/my and remained constant until the Holocene, except for a brief hiatus of 2.5 my at the Miocene-Pliocene boundary (Shipboard Scientific Party, 1989). The samples of Hole 747A consist of cream-colored foraminifer-diatom oozes (sections 1H-5, 2H-4, 3H-3, 4H-1 and 4H-3), white nannofossil oozes (sections 4H-6, 6H-1, 7H-4, 9H-5, 12H-2, 14H-2 and 14H-5), and white to pale brown nannofossil chalks (sections 1R-4, 19X-2, 20X-1 and 21X-1).

The Wombat Plateau is a small W-E directed elevation extending from about 16.5°S to 17.0°S and from 114.5° E to 115.5°E. It is the northern part of the Exmouth Plateau, a large marginal plateau offshore NW Australia from which it is separated by the Wombat half-graben. The Exmouth Plateau is part of the north-western Australian margin and is underlain by continental crust (Exon et al., 1992). Site 761 is located in the north-eastern section of the central part of the Wombat Plateau in a water depth of 2189 m, about 530 km NW of Port Hedland (Western Australia). The Exmouth Plateau was part of the northern shore of eastern Gondwana during the early and middle Mesozoic, until Late Triassic to Late Jurassic rifting processes caused the break-up of the northern margin. Subsequent rapid subsidence of the plateau during the Cretaceous led to a change in sedimentation: the Triassic to early Cretaceous detrital, terrestrially influenced sedimentation was successively replaced by hemipelagic marls and chalks in the mid-Cretaceous. Eupelagic sedimentation of oozes and chalks subsequently dominated the Cenozoic (Exon et al., 1992). Sedimentation rates of the studied section of Site 761 varied significantly: relative high sedimentation rates during the uppermost Cretaceous (20 m/my) dropped drastically in the initial Paleocene, and the Cretaceous/Tertiary (K/T) boundary itself

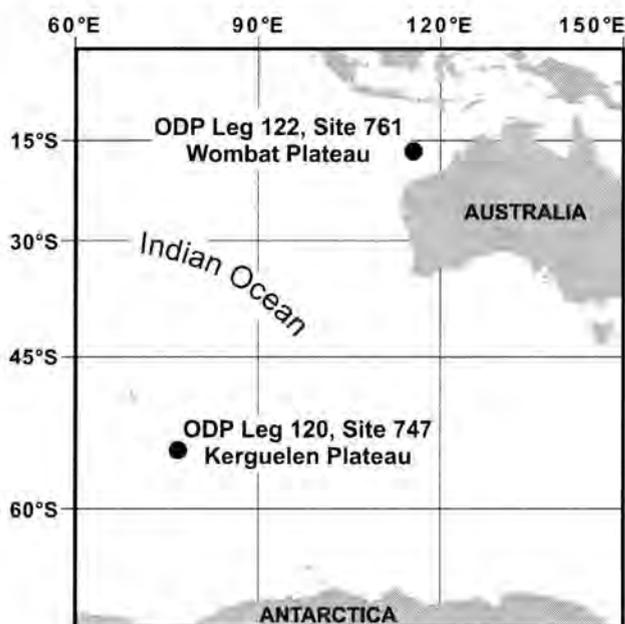


Figure 1. Location of the two studied ODP Sites in the eastern and southern Indian Ocean.

is represented by a slight hiatus. Until the middle Eocene, sedimentation had been generally of medium rate, decreasing from 12 m/my in the lower Paleocene to a minimum of 2.5 m/my in the Eocene. After a major hiatus (middle Eocene to upper Oligocene), Neogene sedimentation rates are generally lower with an average of 1.5 m/my and the sedimentation was interrupted by three minor short hiatuses between the Pliocene and Miocene (Shipboard Scientific Party, 1990). The examined samples of Hole 761B consist of white to light gray or greenish-gray colored oozes (sections 2H-3 to 16X-2) and white to gray chalks (sections 18X-2 to 25X-3).

METHODS

The individual samples were suspended in tap water buffered with ammonia to prevent dissolution and repeatedly frozen and thawed to achieve complete disintegration. Afterwards, the material was washed through a 125 μm and a 20 μm sieve. The residue was dried and the fraction between 20 and 125 μm was used to pick the specimens under a binocular microscope. The selected specimens were mounted on aluminum stubs, sputter-coated with gold, and photographed under a scanning electron microscope (SEM) at the University of Bremen (CamScan-44).

Frequencies of calcareous dinoflagellate cysts at Site 747 (Fig. 2) were determined as follows: about 1 cm^3 of each sample was dried, weighed and sieved as described above. Afterwards the separated fractions were dried and weighed individually. The dry 20-120 μm fraction was homogenized and about 70 μg of the dried fraction separated, weighed and transferred to a picking tray. Every object resembling a cyst of this microsplit was picked under a binocular, mounted on an SEM stub and studied under the SEM. With the obtained number of cysts and the weights of the individual fractions the frequency of calcareous cysts in each sample (cysts per gram sediment) was calculated. Frequencies of calcareous dinoflagellate cysts at Site 761 were estimated during picking of the individual samples. A fixed volume of each sample was homogeneously distributed on a picking tray which is subdivided into 45 squares of 1 cm^2 . The total number of specimens of calcareous

dinoflagellate cysts of 4 squares were counted using a binocular microscope and classified in four categories as follows: rare = 1-20 specimens, few = 21-100 specimens, common = 101-200 specimens, and abundant = more than 200 specimens.

The studied material is repositied in the collection of the Division of Historical Geology/Paleontology, University of Bremen, Germany.

RESULTS AND DISCUSSION

Early Maastrichtian to Quaternary assemblages of calcareous dinoflagellate cysts of two ODP cores, Hole 747A, central Kerguelen Plateau and Hole 761B, Wombat Plateau (Fig. 1), were studied at a relatively low sample density to obtain a general overview of the evolution of this group during the Cenozoic and to map differences in stratigraphic and latitudinal distribution patterns, as well as to link observed shifts in associations and abundance to major climatic changes. As both studied cores are characterized by different hiatuses though, a direct comparison is possible for some stratigraphic intervals only (compare Fig. 5).

Abundance of calcareous dinoflagellate cysts

The absolute abundance of calcareous dinoflagellate cysts in Hole 747A shows remarkable variability from less than 100 to a maximum of more than 50,000 cysts per gram sediment (Fig. 2). Major changes in cyst frequency occur between the early Maastrichtian and early Paleocene as well as between the early Eocene and early Oligocene. Both times of changes were accompanied by drastic changes in the sedimentation rate, though, which might have contributed to the changes in absolute cyst abundance (see 2 Localities and material). Calcareous cysts were again common in the middle Miocene, but abundance gradually decreased towards the core top, with a minimum in the latest Pliocene and Pleistocene.

The relative abundance of calcareous dinoflagellate cysts in Hole 761B generally varies from rare to few, interrupted by three major peaks where calcareous cysts are common to abundant. Comparable to Hole 747A, a major abundance peak occurred in the early Paleocene. However, in contrast to Hole 747A, the abundance peak in Hole 761B did not correlate with a significant decrease in the sedimentation rate. The abundance increase in both cores is mainly due to the numerous appearance of a single species, i.e., *Cervisiella operculata*. However, different from Hole 761B, the high abundance of *C. operculata* in the Paleocene of Hole 747A was accompanied by an additional taxon, *Fuetererella flora*, a species which is only of minor quantitative importance in the Paleocene of Hole 761B.

The second abundance peak in Hole 761B occurred in the middle Eocene, and the third in the Pleistocene, with the latter being attributed to the high abundance of *Calciodinellum albatrosianum*. In contrast to the general abundance decrease since the early Miocene and the minimum in the Pleistocene in Hole 747A, a general abundance increase was observed in Hole 761B since the middle Miocene, with a maximum in the Pleistocene.

Discussion.—The significant abundance increase of calcareous cysts following the Cretaceous/Tertiary boundary coincides with a drastic abundance decrease and the mass extinction of species of other calcareous phytoplankton (e.g., Henriksson, 1996). This increase of calcareous dinoflagellate cysts, which is also known as '*Thoracosphaera*' bloom (Thierstein, 1981; Eshet et al., 1992), has been

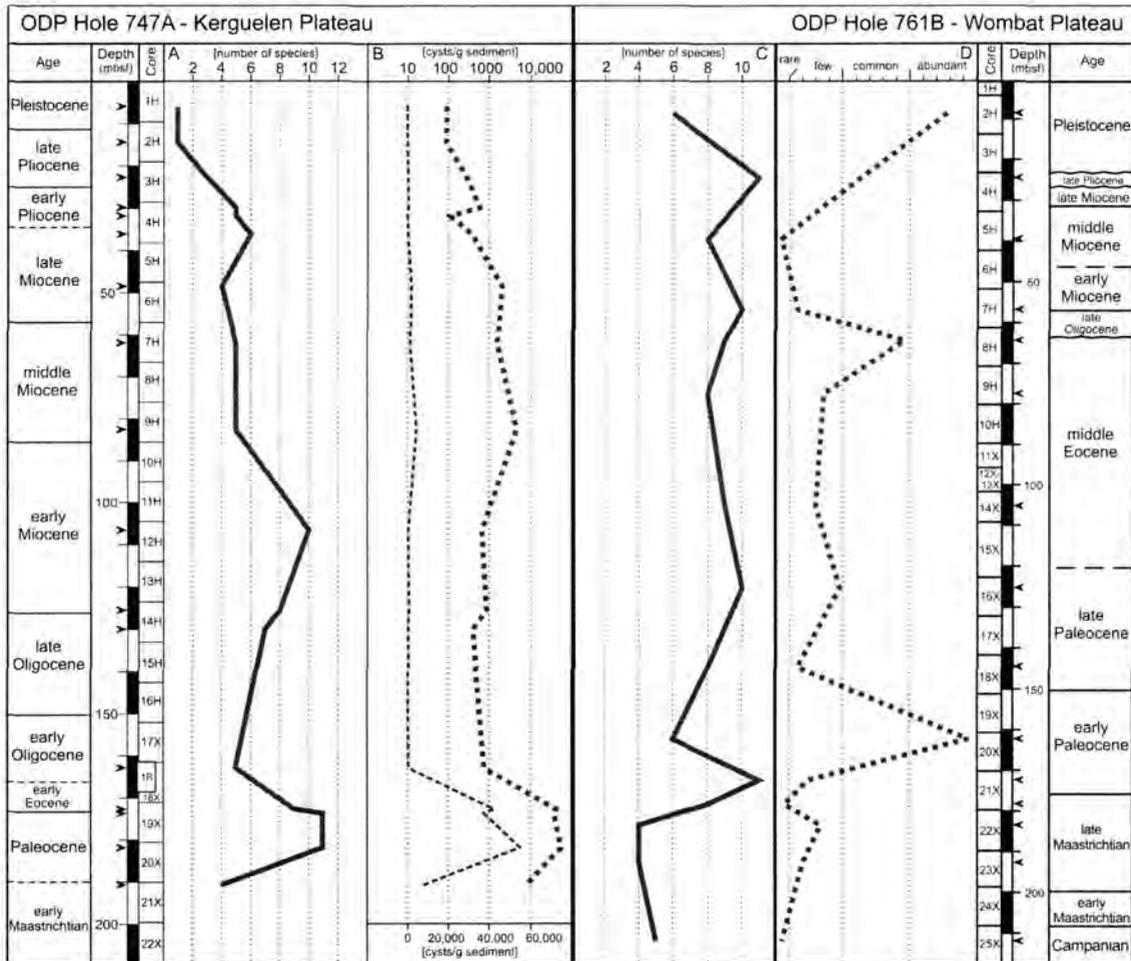


Figure 2. Abundance of calcareous dinoflagellate cysts (B and D) and diversity (number of species) (A and C) in ODP Hole 747A (left half) and ODP Hole 761B (right half). B) Absolute abundance of cysts (cysts / g sediment). D) Relative abundance of cysts (rare to abundant). Note logarithmic (upper scale; dotted line) and normal scaling (lower scale; dashed line) in B.

reported from many oceanic sections world-wide (e.g., Thierstein, 1981; Perch-Nielsen et al., 1982; Fütterer, 1990; Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000). It obviously varied in intensity with the latitude, being more pronounced in lower latitudes than in higher latitudes (e.g., Hildebrand-Habel and Streng, in review [Chapter 2.3]). '*Thoracosphaera*' bloom generally means the acme of *Cervisiella operculata* (former *Thoracosphaera operculata*), a species that was obviously specially adapted to the higher ecological stress caused by the rapid environmental changes at the K/T transition.

The slight abundance increase in the middle Miocene sample 9H-5 (120-121 cm) of Hole 747A falls in the range of a short decrease in $\delta^{18}\text{O}$ values (Wright and Miller, 1992), indicating the mid-Miocene climatic optimum. The steady decrease in abundance following this event correlates with an increase of $\delta^{18}\text{O}$ values because of the progressing temperature drop and the growth of the Antarctic ice-sheet (Zachos et al., 2001). This late Miocene cooling caused an increase in biosiliceous sedimentation (Shipboard Scientific Party, 1989) and a distinct deterioration of the living conditions for calcareous dinoflagellates in high latitudes at Site 747, as reflected in the steady abundance decrease. Obviously, the low latitude assemblages of Hole 761B were also affected by this cooling, but in contrast to the high latitudes, the low latitude assemblages experienced an increase in abundance

during the late Neogene, implying an improvement of the living conditions for calcareous dinoflagellates in low latitudes, although diversity decreased.

Diversity

In total, 35 morphotypes of calcareous dinoflagellate cysts (excluding *Thoracosphaera heimii*) have been distinguished in the studied samples of Hole 747A. The species richness of the individual samples varies significantly throughout the section, ranging from monospecific associations to assemblages with a maximum of 11 morphotypes (Fig. 2). With four taxa, the diversity was relatively low in the early Maastrichtian, but increased drastically to 11 in the Paleocene. Early Oligocene diversity was again relatively low (5 morphotypes) and increased anew in the late Oligocene and early Miocene (up to 10 morphotypes). A steady decrease in diversity has been observed in the younger samples, culminating in monospecific associations in the latest Pliocene and Pleistocene.

In Hole 761B, the total number of calcareous dinoflagellate taxa (47) is much higher than in Hole 747A. Additionally, the species richness of the individual samples generally exceeds those of Hole 747A. However, like in Hole 761B, diversity was very low in the samples preceding the K/T boundary (4 to 5 morphotypes), although an increase already occurred in the sample closest to the boundary. With 11 taxa, diversity reached a maximum in the early Danian. Diversity remained relatively high throughout the remaining Cenozoic (8 to 11 taxa), except for the Pleistocene, which had a relatively low species richness of 6 taxa.

Discussion.—The general diversity increase after the K/T boundary may be attributed to the same reasons as the abundance increase discussed above. The drastic abundance decrease or even extinction of most of the calcareous nannofossil taxa at the K/T event (Henriksson, 1996), made a rapid increase in abundance and diversity of calcareous dinoflagellate cysts possible, most likely due to missing competitors and/or predators. Generally spoken, some calcareous dinoflagellate taxa of this period, in particular *C. operculata* and *F. flora*, reacted opportunistically like typical disaster taxa with a high reproductive rate.

The low species richness in the early Oligocene of Hole 747A may correspond to the early Oligocene glaciation. Low diversity during this time has also been reported for high latitude planktonic foraminifera associations (Jenkins, 1993). Analogous to those associations, the diversity of calcareous cyst associations slightly increased after the glaciation event.

The observed drastic decrease in species richness since the Pliocene at both sites can be explained by the progressing water-mass cooling of the southern hemisphere (e.g., Kennett, 1982) linked with the onset of the northern hemisphere glaciation. However, in contrast to the low latitudes where species richness of calcareous dinoflagellate cysts halved since the late Pliocene, changes in high latitudes were more severe and produced monospecific associations, with *Caracomia arctica* being the sole calcareous dinoflagellate species capable of tolerating a cold environment (Streng et al., 2002; Hildebrand-Habel and Streng, in review [Chapters 2.1 and 2.3]).

Shifts in associations of calcareous dinoflagellates

Major shifts in the associations of calcareous dinoflagellates since the late Cretaceous have generally been attributed to principal changes in the paleoenvironment induced by severe climatic or oceanographic changes (Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000). Because of the low sample density in this study, fluctuations in the associations of calcareous

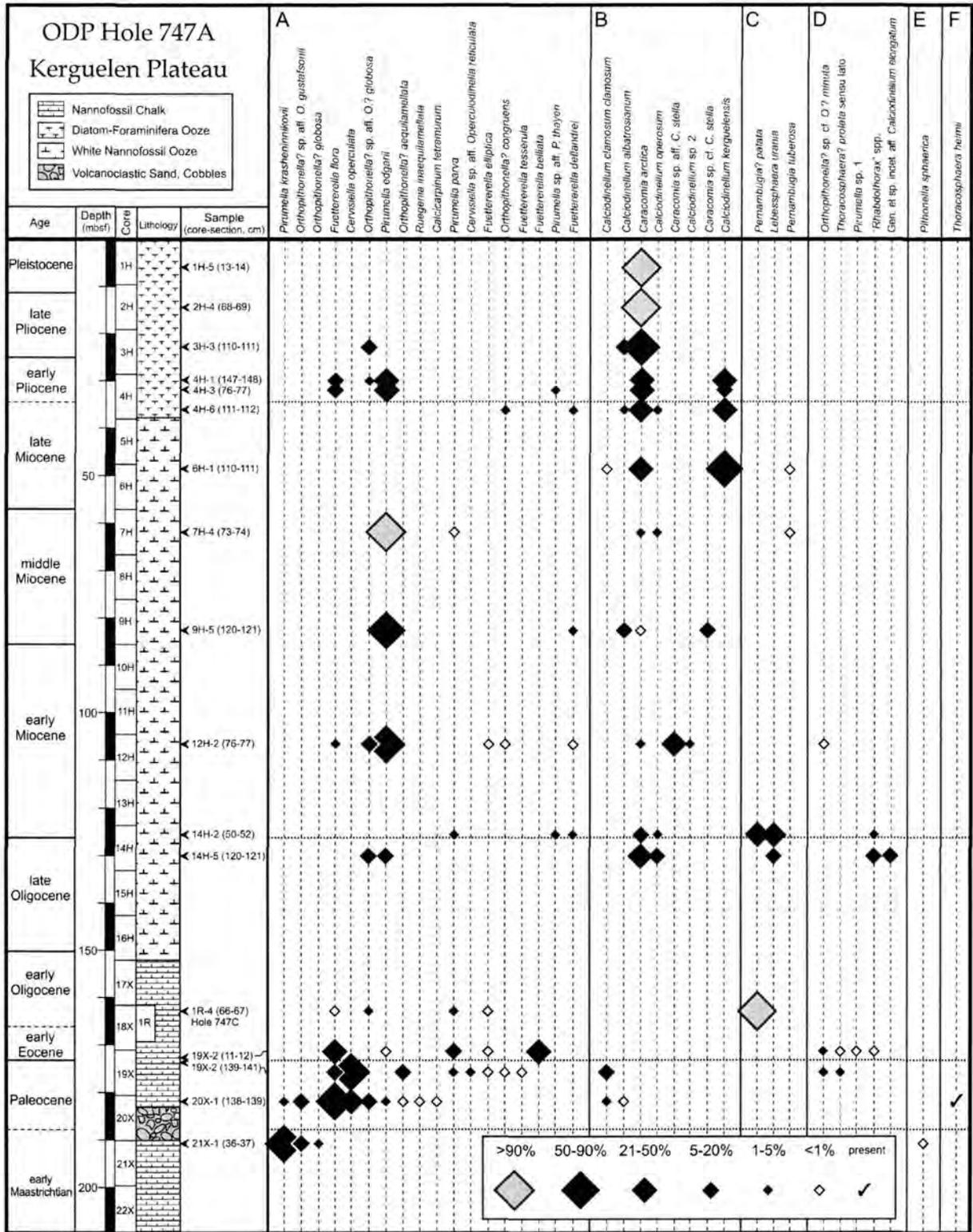


Figure 3. Stratigraphy, general lithology and percentage occurrence of calcareous dinoflagellate taxa in ODP Hole 747A. Calcareous dinoflagellates have been grouped according to their archeopyle type as follows: A) taxa with a small apical archeopyle involving the single plate 3' (= Type A); B) taxa with a mesoepicystal archeopyle involving three apical and all intercalary plates (= Type 3AtI); C) taxa with an epicystal archeopyle involving all apical, intercalary and preangular plates; D) taxa with an unknown archeopyle type; E) pithonelloid species with small circular aperture; F) shells of the coccooid stage of *Thoracosphaera heimii*.

dinoflagellates are not surprising. Consequently, uncertainties exist regarding the significance of the observed shifts. However, since calcareous dinoflagellate taxa are generally long-ranging (e.g., Hildebrand-Habel and Willems, 2000) and shifts in associations are obviously linked to large-scale environmental changes, an influence of environmental changes on the associations cannot be dismissed.

The Cretaceous/Tertiary transition

In both holes, the Cretaceous/Tertiary transition is characterized by a pronounced change in calcareous dinoflagellate assemblages (Figs. 3, 4). Maastrichtian assemblages were characterized by a low diversity and the dominance of *Pirumella krasheninnikovii*, a species which is typical for oceanic sediments of this time. Early Paleocene assemblages, on the contrary, were highly diverse and dominated by *Cervisiella operculata*. However, no mass extinction event of calcareous dinoflagellate taxa occurs at the K/T boundary which would be comparable to other calcareous micro-organisms. Although some taxa disappear at or prior to the boundary, many taxa manage to persist into the Paleocene. Whereas typical late Cretaceous taxa, for instance *P. krasheninnikovii* and *Orthopithonella? congruens*, if persisting, drastically decrease in abundance.

Discussion.—Both sites show the same changes in associations and abundance of calcareous dinoflagellate cysts that have already been reported elsewhere from the Cretaceous-Tertiary transition (Hildebrand-Habel et al., 1999; Hildebrand-Habel and Streng, in review [Chapter 2.3]). These remarkable changes are mainly due to the nearly world-wide occurring 'Thoracosphaera' bloom discussed above. However, in contrast to all other oceanic assemblages studied so far, the early Paleocene assemblage in Hole 747A is not dominated by *C. operculata*, but by *Fuettererella flora* with 52 percent of the association. *C. operculata* is present only with 21 percent and untypically achieves its highest abundance in the late Paleocene. Similar results have been reported by Hildebrand-Habel and Streng (in review) from Maud Rise (Weddell Sea, South Atlantic Ocean), where *F. flora* and *C. operculata* also dominate the early and late Paleocene. Both taxa seem to represent essential elements of a typical high latitude association of calcareous dinoflagellate cysts in the Paleocene as already suggested by Hildebrand-Habel and Streng (in review) [Chapter 2.3]. The existence of characteristic early Paleocene high latitudinal nannofossil assemblages suggests that the transition from a low latitudinal thermal gradient in the Late Cretaceous to a more significant latitudinal thermal gradient occurred already in the Danian (Wei and Pospichal, 1991).

The Paleocene-Eocene transition at Site 747

Discussion.—The late Paleocene-early Eocene interval was a time of major changes in oceanic circulations and global climate, as reflected in an evolutionary radiation and increased diversity of marine biotas (e.g., Berggren et al., 1998), however, no corresponding changes in calcareous dinoflagellate associations are obvious in Hole 747A. Although *C. operculata* abruptly disappeared at the end of the Paleocene and *Fuettererella belliata* appeared with already relatively high abundance in the early Eocene, these changes do not seem to be directly linked with the severe climatic warming at this time. However, a more detailed study of the late Paleocene-early Eocene interval might also reveal significant changes in the calcareous dinoflagellate associations.

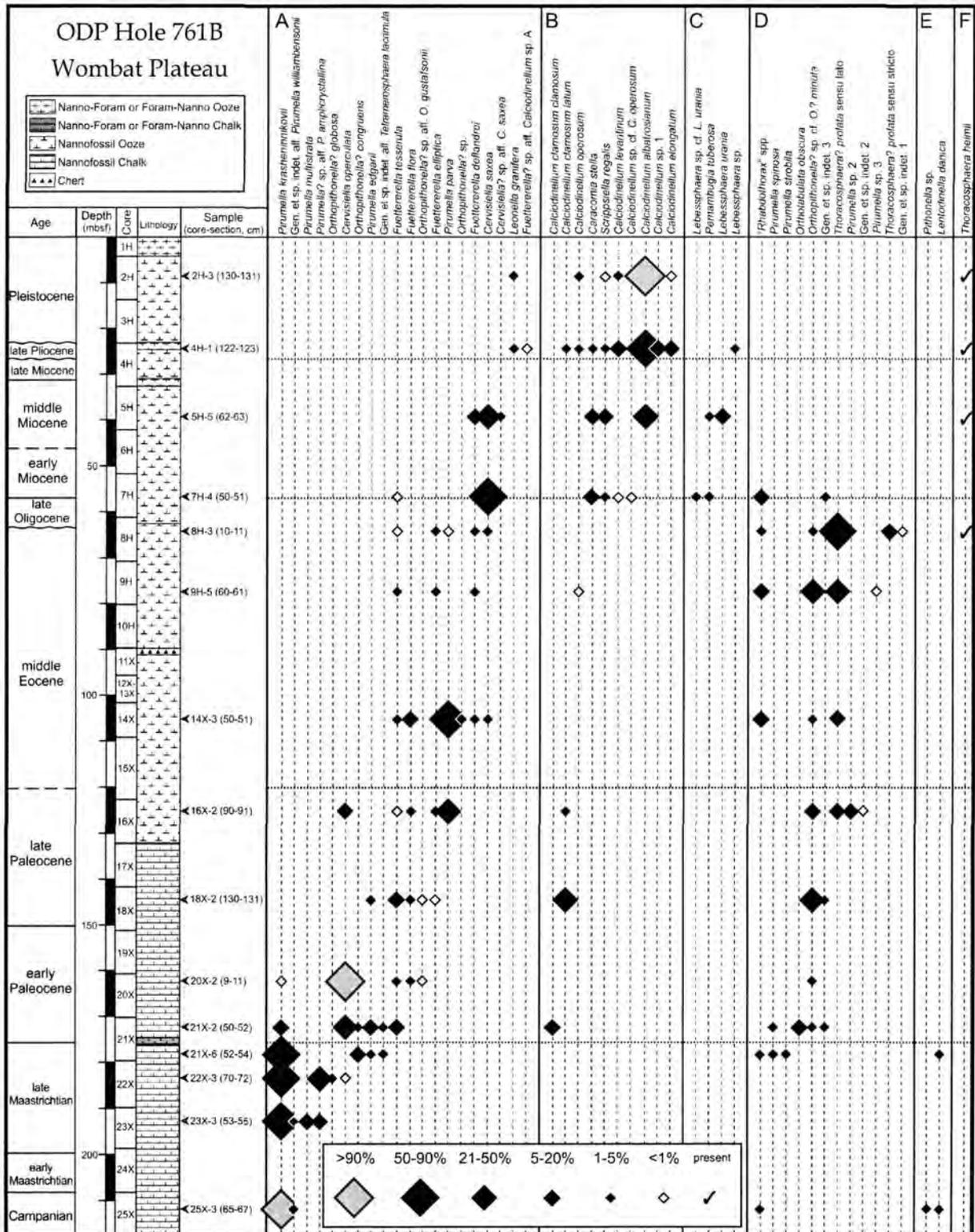


Figure 4. Stratigraphy, general lithology and percentage occurrence of calcareous dinoflagellate taxa in ODP Hole 761B. Calcareous dinoflagellates have been grouped according to their archeopyle type as follows: A) taxa with a small apical archeopyle involving the single plate 3' (= Type A); B) taxa with a mesoepicystal archeopyle involving three apical and all intercalary plates (= Type 3AtI); C) taxa with an epicystal archeopyle involving all apical, intercalary and precingular plates; D) taxa with an unknown archeopyle type; E) pithonelloid species with small circular aperture; F) shells of the coccoid stage of *Thoracosphaera heimii*.

Early Oligocene of Site 747

The early Oligocene assemblage of Site 747 is remarkable: it is characterized by a low diversity and the domination of a single species, i.e., *Pernambugia? patata*, which forms 93 % of the association (Fig. 3). *P.? patata* is a problematic species, since it is obviously a stress form. It is characterized by an irregular shape and an unique type of epicystal archeopyle. It has only been found at Site 747 as yet (Streng et al., subm. A [Chapter 2.2]).

Discussion.—The Eocene-Oligocene transition is characterized by a lowering of atmospheric temperatures, ocean cooling associated with stronger thermal stratification and the initiation of the Antarctic Circumpolar Current as well as the initiation of Antarctic glaciation (Jenkins, 1993; Berggren et al., 1998). Drastic cooling of early Oligocene surface waters in the southern Indian Ocean is indicated by a sudden increase in the percentage of cold water calcareous nannoplankton taxa, an increase in $\delta^{18}\text{O}$ values of planktonic foraminifera and the increase of biosiliceous sediments on the Kerguelen Plateau (Wise et al., 1992; Zachos et al., 1992). Moreover, typical Antarctic assemblages developed within the radiolarians (Lazarus and Caulet, 1993). We assume that *P.? patata* might be a typical representative of an Antarctic calcareous dinoflagellate cyst assemblage in the southern Indian Ocean and, analogous to the radiolarians, indicative for rapid cooling of surface waters in the early Oligocene.

Middle to late Miocene transition at Site 747

The Miocene of the southern Indian Ocean was characterized by a warming trend in the early Miocene to early mid-Miocene, associated with a reduction of the Antarctic ice cover (Zachos et al., 2001). Subsequently, a cooling trend initiated in the middle Miocene and continued into the late Miocene (Jenkins, 1993). This cooling was accompanied by the reestablishment of a major ice sheet on Antarctica (Zachos et al., 2001). The expansion of the East Antarctic ice sheet in the latest middle Miocene correlated with a decline of surface water temperatures in the Southern Ocean, followed by a progressive glaciation on West Antarctica. Cold Antarctic surface waters expanded northwards and initiated increased upwelling and biogenic productivity in the late Miocene (Kennett, 1977; Jenkins, 1993). Although calcareous dinoflagellate cysts did not contribute to this increase in biogenic productivity, they nonetheless reflected the climatic changes of the period described above: the early and middle Miocene was dominated by a single species, i.e., *Pirumella edgarii*, reflecting the warmer temperatures prior to the intensification of the Antarctic glaciation. The association changed abruptly in the late Miocene: *P. edgarii* disappeared completely, and the cold water species *Caracomia arctica* (Streng et al., 2002 [Chapter 2.1]) became abundant together with another potential cold water taxon, *Calciodinellum kerguelensis* (Fig. 3).

Discussion.—The increased abundance of *C. arctica* and the appearance of *C. kerguelensis* in the late Miocene is interpreted as to reflect the major cooling of the Southern Ocean during this time. This distinct shift in the associations matches the results of Hildebrand-Habel and Streng (in review) [Chapter 2.3] from the eastern Weddell Sea, Site 689. Likewise to Hole 747A, the early and middle Miocene of Hole 689B was dominated by *P. edgarii*, which was followed by a dominance of *C. arctica* in the latest middle Miocene, after the mid-Miocene climatic optimum. The coincident results from different regions suggest that the described change in associations from a dominance of *P. edgarii* to a dominance of *C. arctica* is characteristic for the Miocene of high latitudes and marks the distinct climatic change at the mid-Miocene climatic optimum.

The abrupt common occurrence of *C. kerguelensis* and *C. arctica* at the same time during the late Miocene indicates that *C. kerguelensis* might be, just like *C. arctica*, specially adapted to cool temperate regions. In contrast to *C. arctica*, however, *C. kerguelensis* obviously did not succeed to adapt to the increased cooling at the beginning of the late Pliocene.

Pliocene to Pleistocene at Site 747

The Pliocene-Pleistocene evolution of calcareous dinoflagellate cyst associations of Hole 747A is characterized by two major changes. The species composition drastically changed from the late Miocene to early Pliocene and from the early Pliocene to late Pliocene. Early Pliocene assemblages are typified by a quantitatively balanced occurrence of four main taxa (*Pirumella edgarii*, *Caracomia arctica*, *Calciodinellum kerguelensis* and *Fuetererella flora*). They thus differ from the late Miocene assemblages which were dominated by *C. arctica* and *C. kerguelensis*, and from the early late Pliocene to Pleistocene assemblages which were dominated by *Caracomia arctica*. It is worth noting that two species disappeared at the end of the early Pliocene: 1) *Calciodinellum kerguelensis*, a species that had appeared in the late Miocene and probably was adapted to the cold environment to a certain degree, and 2) *Pirumella edgarii*, a species that dominated throughout the early and middle Miocene. *P. edgarii* had been absent in the late Miocene, but had reappeared in high abundance in the early Pliocene before it finally disappeared in the late Pliocene.

Discussion.—The described major shifts in calcareous dinoflagellate cyst associations from the early to late Pliocene occurred simultaneously with a rapid increase in $\delta^{18}\text{O}$ values reflecting the onset of the northern hemisphere glaciation and an intensified general cooling trend (e.g., Zachos et al., 2001), accompanied by a world-wide lowering of the sea level. A slight warming in the early Pliocene, however, preceded the Pliocene cooling (e.g., Thiede and Vorren, 1994; Jenkins, 1993). It caused a temporary increase in surface water temperatures of 4°C in the southern Indian Ocean (Bohaty and Harwood, 1998). The balanced early Pliocene assemblages and the reappearance of *Pirumella edgarii* correlate with this warming trend, whereas the rapid late Pliocene cooling is reflected in the diversity decrease and dominance of the cold water species *Caracomia arctica* (see also Hildebrand-Habel and Streng, in review [Chapter 2.3]).

Neogene and Quaternary of Site 761

Quaternary mid- and low-latitude pelagic assemblages of Atlantic calcareous dinoflagellate cysts are typically dominated by few species. *Calciodinellum albatrosianum*, *Calciodinellum levantinum* (= *Sphaerodinnella tuberosa* of many authors, see Meier et al., 2002), and *Leonella granifera* are the most common taxa (e.g., Höll et al., 1999; Esper et al., 2000; Vink et al., 2000). *Calciodinellum operosum*, *Pernambugia tuberosa*, *Scrippsiella* spp. and a few additional taxa occur only subsidiary, infrequently or regionally restricted. The Pleistocene assemblage of Hole 761B, dominated by *C. albatrosianum*, is no exception. These "modern" assemblages differ distinctly from known pre-Quaternary (= "fossil") assemblages, and it has been puzzling when the change from "fossil" to "modern" assemblages took place. The Neogene assemblages of Hole 761B provide a first clue to this problem. The early Miocene is dominated by typical "fossil" taxa, with *Cervisiella saxea* being the most common species. Modern species (*Scrippsiella regalis* and *Pernambugia tuberosa*) constitute only about 5 percent of the association. In the middle Miocene, the proportion of modern taxa increases to 37 percent, mainly due to the occurrence of *C. albatrosianum* in relatively high numbers (26 percent of association) and the decline of *C. saxea*. The late Pliocene assemblage can

already be compared with the modern associations, since it is essentially composed of modern taxa (82 percent) and characterized by a dominance of *C. albatrosianum*. Another puzzling change becomes obvious when comparing the cyst size of specimens of *C. albatrosianum* from the middle Miocene as part of a "fossil" assemblage with those from the late Pliocene and Pleistocene, representing "modern" assemblages. With diameters of 31.6 to 47.5 μm (mean = 38.6 μm), middle Miocene cysts of *C. albatrosianum* are distinctly larger than those from the late Pliocene and Pleistocene, which have diameters of 24.2 to 36.3 μm (mean = 28.4 and 28.2 μm) (Fig. 5). Additionally, the range of the cyst diameters gradually narrowed from 15.9 μm in the middle Miocene to 8.5 μm in the Pleistocene.

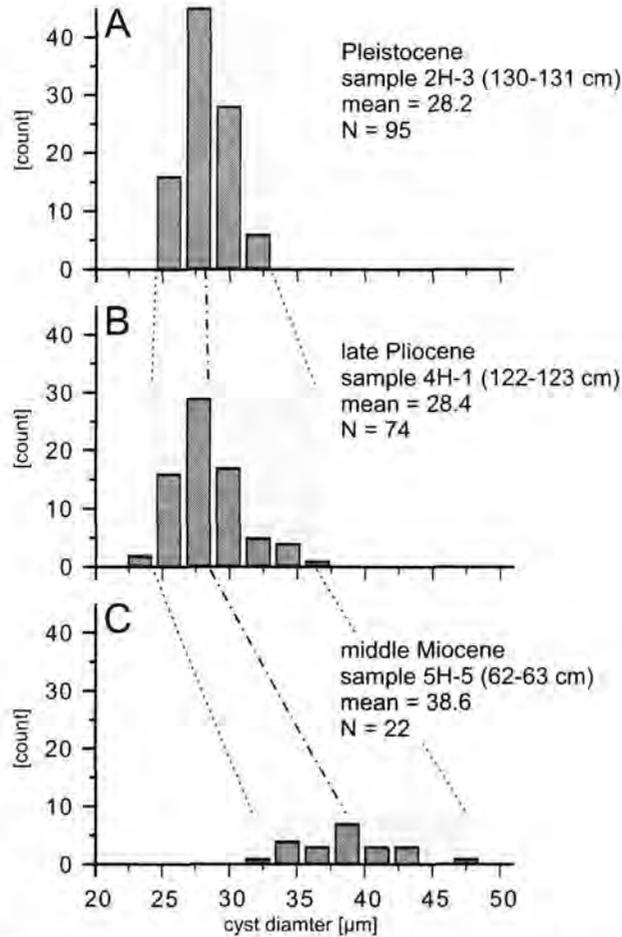


Figure 5. Frequency distribution of cyst diameters of *Calciadinellum albatrosianum* in three succeeding samples of the Neogene of Hole 761B (Wombat Plateau) illustrating the general decrease of the diameter and its range (shaded area) from the middle Miocene to the Pleistocene.

Discussion.—After the mid-Miocene climatic optimum, the climate evolution of the southern hemisphere was mainly influenced by the development of the Antarctic Ice Sheet. Linked with expansions of the Antarctic ice sheet were northward penetrations of the cold Antarctic water masses, also connected to middle and late Miocene cooling in the eastern Indian Ocean, as indicated by the arrival of cool water foraminifera (e.g., Zachariasse, 1992). During the latest Miocene and earliest

Pliocene, glaciation of Antarctica progressed, ocean circulation intensified, the temperature gradient between polar and equatorial regions increased and the sea level experienced a major lowering. Generally warm conditions for the remaining early Pliocene (e.g., Thiede and Vorren, 1994), accompanied by a reduction of the Antarctic ice shield (e.g., Crowley and North, 1991) was broken off by the late Pliocene cooling and the onset of northern hemisphere glaciation. Therefore, two potential reasons might have been the trigger for the development of the typical modern low diversity calcareous dinoflagellate cyst assemblages: 1) the late Miocene cooling and/or 2) the continuation of this trend with the beginning of the late Pliocene. Further studies are needed to clarify if one or both cooling events are responsible for the shift to modern assemblages and to verify a possibly gradual development from "fossil" to "modern" assemblages. Additionally, the significance of variations of the cyst diameter, especially of *C. albatrosianum*, as an indicator of environmental changes has to be proven in further studies from different localities.

Variations in the relative abundance of calcareous dinoflagellate archeopyle types

During the past decades, calcareous dinoflagellate cysts have mainly been classified according to the crystallographic orientation of the wall-forming crystals (e.g., Keupp and Mutterlose, 1984; Keupp, 1987; Kohring, 1993a). Great efforts have been made by Hildebrand-Habel et al. (1999), Hildebrand-Habel and Willems (2000) and Hildebrand-Habel and Streng (in review) [Chapter 2.3] to correlate relative abundance of these wall-types with times of major paleoenvironmental changes. To determine the exact orientation of the c-axes of the wall-forming crystallites and thus the wall-type, the cysts have to be examined in 1.5 to 3 μm thin sections under polarized light using a method introduced by Janofske (1996). This method has been applied to many species recently, but numerous species, especially from the Cretaceous, have still not been examined. The wall-type of these species has generally been interpreted from SEM examinations (morphological cross section of the wall) and comparison with species with a verified wall-type. This lack of reliable information on wall-types arises from the method of Janofske (1996), which is not practicable for all cysts. Especially from double-layered cysts with one thick and one thin layer, no reliable information is obtainable, as the optic sign of the thick wall superimposes that of the thinner layer. Because of the missing information on the wall-types of many species, interpretations concerning fluctuations of wall-types must be regarded as tentatively. Furthermore, the only distinct and pronounced fluctuation of wall-types recognized until now occurs at the Cretaceous-Tertiary transition: the oblique and radial wall types, which prevailed in the latest Cretaceous, gave way to the tangential wall type in the early Paleocene. The duration of the prevalence of the tangential wall-type, however, obviously depends on the individual locality (compare Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2001; Hildebrand-Habel and Streng, in review [Chapter 2.3]).

For the reasons outlined above, fluctuations of the relative abundance of wall-types have not been analyzed in the studied cores of Sites 747 and 761. Instead we focussed on fluctuations in the tabulation reflected by the archeopyle in order to unveil and verify a possible ecological control of these fluctuations. We applied the taxonomic concept of Streng et al. (2002; subm. A [Chapters 2.1 and 2.2]), that regards the tabulation of the archeopyle as a major taxonomic and phylogenetic feature of calcareous dinoflagellate cysts. Currently, seven archeopyle types of calcareous dinoflagellate cysts are distinguished according to the system introduced for organic-walled dinoflagellates by Evitt (1967). These archeopyle types are accommodated in four categories (see Streng et al., subm. A, for details [Chapter 2.2]): apical, intercalary, and combination archeopyles as well as archeopyles of

uncertain affinity. The taxa of Hole 747A and Hole 761B belong to four different archeopyle types: apical archeopyle (Type A), mesoepicystal archeopyle (Type (3AtI)), epicystal archeopyle (Type (3AtItP)) and unidentified archeopyle type. The calcareous dinoflagellate taxa were categorized and plotted according to those four types in Figs. 3 and 4. Pithonelloid taxa were treated separately, since their affiliation with the dinoflagellates is doubtful (Fensome et al., 1993; Streng et al., subm. A [Chapter 2.2]), as well as *Thoracosphaera heimii*, since its calcareous test is not a resting cyst (Tangen et al., 1982). Variations in the relative abundance of archeopyle types are illustrated in Fig. 6, with the four relevant archeopyle types grouped as follows: 1) small archeopyles (apical archeopyles that involve a single plate; Type A), 2) large archeopyles (archeopyles that involve more than one plate, Type (3AtI) = mesoepicystal archeopyle and Type (3AtItP) = epicystal archeopyle) and 3) unknown archeopyle type.

Species with a large archeopyle appear in the early Paleocene of Hole 747A, though in low numbers, and show a first peak in the relative abundance of cysts in the Oligocene due to the mass appearance of *Pernambugia? patata*. However, their first significant contribution to the assemblages in relative as well as in number of species, is in the late Oligocene, where the number of species with a large archeopyle for the first time exceeds the number of species with a small archeopyle. Thenceforward, species with a large archeopyle are prominent members of the associations, though in varying number and relative abundance. Correspondingly, the relative abundance of archeopyle types in Hole 747A shows notable fluctuations throughout the studied section. Small archeopyles dominate the Maastrichtian to early Eocene and the early to middle Miocene. Accordingly, large archeopyles peak in the early Oligocene, earliest and late Miocene, and in the late Pliocene to Pleistocene. A balanced ratio of both archeopyle categories is present in the early Pliocene (compare Fig. 6).

Analogous to Hole 747A, species with a large archeopyle appear in the early Paleocene of Hole 761B and become significant members of the associations (regarding the number species) in the early Miocene. With a dominance of small archeopyles in the Maastrichtian to early Paleocene, the relative abundance of archeopyle types of Hole 761B shows a similar pattern as in Hole 747A. The relative abundance pattern of Hole 761B also corresponds to Hole 747A in the late Pliocene to Pleistocene samples, with a dominance of large archeopyles (Fig. 6). Furthermore, small archeopyles are relative abundant in the middle Eocene and early Miocene. However, late Paleocene to middle Eocene samples have relatively high numbers of species with an unknown archeopyle type, amongst them are the abundant problematic taxa *Thoracosphaera? prolata* and *Orthopithonella? minuta* (see Taxonomic notes). The presence of those species unfortunately biases the fluctuation pattern of the archeopyle types and makes an interpretation impossible.

Discussion.—Fluctuations in the abundance of the prevailing archeopyle type in Hole 747A correlates with general trends in the Cenozoic climatic evolution, with species with small archeopyles being characteristic for warmer periods and species with large archeopyles for colder. Thus, the high relative abundance of species with small archeopyles during the Paleocene and early Eocene corresponds to the Paleogene interval of global warming culminating in the early Eocene climatic optimum (Zachos et al., 2001); the higher abundance of small archeopyles in the early to middle Miocene reaches a maximum just after the mid-Miocene climatic optimum; and the early Pliocene excursion correlates with the subtle warming trend at this time (Ciesielski and Grinstead, 1986; Bohaty and Harwood, 1998; Zachos et al., 2001). High values in the relative abundance of large archeopyles, on the contrary, correlate with major cooling events triggered by the increasing Antarctic glaciation. As such,

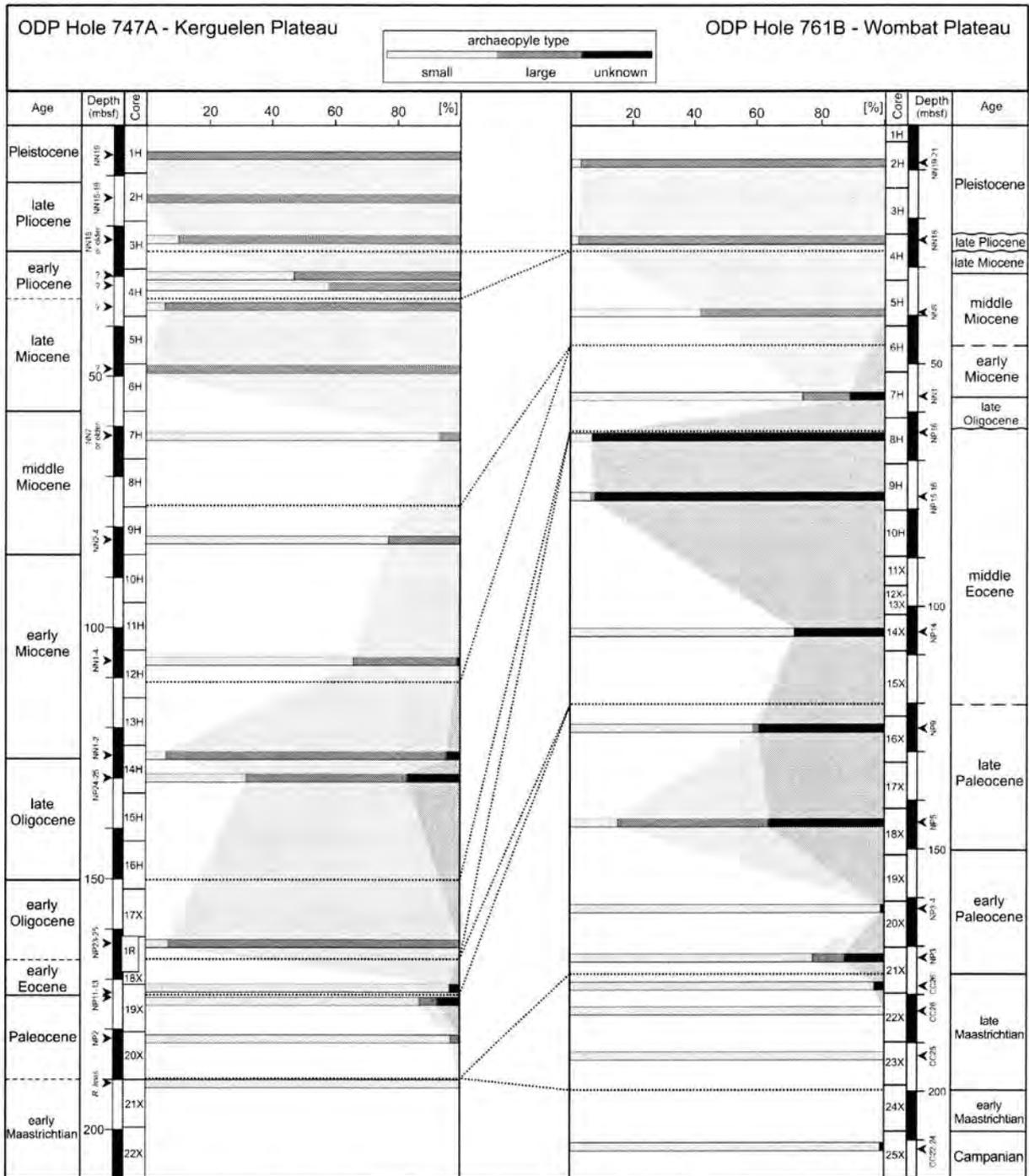


Figure 6. Rough correlation and comparison of the two studied ODP cores regarding relative abundance of calcareous dinoflagellate archeopyle types. Three categories are distinguished: small archeopyle type = archeopyles including a single apical plate; large archeopyle type = archeopyles involving more than one plate; unknown archeopyle type = archeopyle type of individual taxa can not be designated because of unknown number of involved plates or the absence of an archeopyle. Arrows with nannofossil zones indicate sample positions. Nannoplankton zonation according to Martini (1971) and Sissingh (1977).

abundance peaks in the early Oligocene and earliest Miocene follow the first major glaciation episodes (Oi-1 and Mi-1; Zachos et al., 2001). Comparably, the late Miocene and late Pliocene to Pleistocene maxima correspond to the reestablishment of a major ice-sheet on Antarctica after the mid-Miocene

climatic optimum and the continuation and intensification of the general Cenozoic cooling with the onset of the northern hemisphere glaciation, respectively.

Only in the early Paleocene and the late Pliocene to Pleistocene, fluctuations in the relative abundance of archeopyle types in Hole 761B correspond to those in Hole 747A. In contrast to Hole 747A, late Paleocene to middle Miocene fluctuations cannot be connected with climatic variations. This may partly be due to the high abundance of species with an unknown archeopyle type in Hole 761B, biasing the fluctuation. However, in times of low abundance of these problematic species, for instance in the early and middle Miocene, the ratio of small to large archeopyles depicts trends different from Hole 747A. This implies that the correlation of the archeopyle ratio with the climatic development observed in Hole 747A is either of only local reliability or distinctive for high latitudes. The latter possibility is supported by the data of Hildebrand-Habel and Streng (in review) [Chapter 2.3] from Hole 689B, Maud Rise, Weddell Sea. Their results show similar trends, although less clear than in Hole Site 747A.

CONCLUSIONS

The comparison of two cores from the eastern and southern Indian Ocean evinced that the large-scale Cenozoic evolution and composition of calcareous dinoflagellate cyst assemblages seem to be effectively influenced and controlled by the major climatic changes during this time period. The different latitudinal positions of the cores made it possible to investigate the varying developments of typical high and low latitude associations since the beginning of the early Paleocene. Despite the different species composition, high and low latitude associations generally react coevally to climatic and environmental changes, though often in an opposite way or with different intensity. The following time periods of major shifts in calcareous dinoflagellate associations and their relation to severe climatic or environmental changes became obvious:

- 1) Cretaceous/Tertiary transition: Calcareous dinoflagellate cyst associations of both sites respond to the severe environmental deterioration following the K/T boundary with a striking increase in abundance and diversity as well as a major change in the species composition. The opportunistic species *Cervisiella operculata* typically characterizes the early Paleocene assemblages, but in contrast to low latitudes where it exclusively dominates the associations, high latitude assemblages are additionally influenced by a high abundance of *Fuettererella flora*. These two species probably represent typical components of a high latitude association in the early Paleocene. No mass extinction event of calcareous dinoflagellate cysts was recognized at the K/T boundary.
- 2) Early Oligocene: The early Oligocene assemblage of the high latitudinal site is dominated by *Pernambugia? patata*, a stress species probably indicating the early Oligocene temperature drop and the onset of continental ice accumulation on Antarctica.
- 3) Neogene: The development of the associations during the Neogene is quite opposite at the two sites. The high latitude site clearly illustrates the overall progressive cooling trend by a general decrease in abundance and diversity. Additionally, the species composition of the individual intervals revealed "warmer" and "colder" associations. Higher abundance of *Pirumella edgarii* are probably indicative of warmer periods, i.e., the early and middle Miocene and the early Pliocene, whereas *Caracomia arctica* and *Calciodinellum kerguelensis* are characteristic for colder periods, like the late Miocene and late Pliocene to Pleistocene. The low latitude site, on the contrary, experienced a general increase in the abundance of cysts during the Neogene and a concomitant reduction of diversity towards the typical

modern associations. The change to the modern association occurred in the time frame of late middle Miocene to early late Pliocene.

Besides the observed fluctuations in the associations, shifts in the stratigraphic distribution pattern of the ratio of small to large archeopyles also revealed a distinct correlation with the Cenozoic climatic development, particularly in high latitudes. Taxa with small archeopyles seem to prevail during warmer periods, like the late Cretaceous and the Paleocene, whereas taxa with large archeopyles are representative for cooler periods, like the late Miocene and late Pliocene.

Despite the identification of the distinct correlations as described above, more detailed and higher resolution studies of selected stratigraphic intervals are needed to confirm the observed connection between the association dynamics of calcareous dinoflagellate cysts and the climatic evolution of the Cenozoic.

TAXONOMIC NOTES

Most species found in the analyzed samples of ODP Hole 747A and 761B are well-known. However, some taxa need further explanations, because their accommodation to a distinct genus is only tentative or impossible. Many of these taxa may represent new species, but the lack of a sufficient number of specimens on one hand and uncertainties concerning the crystallographic ultrastructure on the other, allow only an informal description or a description using open nomenclature. Species are sorted according to the different archeopyle categories summarized in Streng et al. (subm. A) [Chapter 2.2].

Species with an apical archeopyle including the single plate 3'

Cervisiella sp. aff. *Operculodinella reticulata* Kienel, 1994

Plate 1, Figure 9

Remarks.—The three specimens of *Cervisiella* sp. aff. *Operculodinella reticulata* form a transition between *Cervisiella operculata* (Bramlette and Martini, 1964) Streng et al. (subm. A) [Chapter 2.2] and *Operculodinella reticulata* Kienel, 1994. The outer cyst surface is characterized by an irregular pattern of numerous pseudo-pores which are surrounded by strong ridges. This pattern is generally similar to that of *C. operculata*, however, *C. sp. aff. O. reticulata* bears less pseudo-pores and a more solid development of ridges. Size and number of pseudo-pores and ridges, in turn, resemble those of *O. reticulata*, but pseudo-pores of *O. reticulata* are arranged in regular rows, which run parallel to the equatorial plane and ascend in the sulcal area, reflecting possibly a reduced tabulation.

Cysts of *Cervisiella* sp. aff. *Operculodinella reticulata* are spherical in shape (39.6, 39.8 and 47.4 μm in diameter) and bear a circular to slightly angular apically situated archeopyle measuring 35 to 42% of the cyst diameter. As the archeopyle is comparable to that of *C. operculata*, the three specimens have been assigned to the genus *Cervisiella* and probably represent an extremely rough-textured variation of *C. operculata*.

Range.—Late Paleocene of Hole 747A, Kerguelen Plateau.

Cervisiella? sp. aff. *Cervisiella saxea* (Stradner, 1961) Hildebrand-Habel et al., 1999

Plate 1, Figure 11

Remarks.—The single specimen of *Cervisiella?* sp. aff. *C. saxea* is spherical in shape with a diameter of 34.9 μm and has a 3.1 μm thick single-layered wall. The circular archeopyle measures 10.5 μm in

diameter and represents the single plate 3'. The cyst resembles *C. saxea* concerning size, archeopyle type and the general habit of the crystallites, however crystallites of *Cervisiella?* sp. aff. *C. saxea* are more prominent and show a coarser, probably diagenetically altered habit.

Occurrence.—Middle Miocene (NN6) of Hole 761B, Wombat Plateau.

Fuettererella? sp. aff. *Calciodinellum* sp. 1

Plate 1, Figure 5

Remarks.—The single specimen of *Fuettererella?* sp. aff. *Calciodinellum* sp. 1 is spherical, 29.0 μm in diameter, and strikingly resembles *Calciodinellum* sp. 1 (Pl. 3, Figs. 6-9), but bears a circular 9 μm wide archeopyle. The archeopyle outline and the probably tangential ultrastructure (see Remarks on *Calciodinellum* sp. 1) suggest the accommodation of this specimen in the genus *Fuettererella*.

Occurrence.—Late Pliocene (NN16) of Hole 761B, Wombat Plateau.

Gen. et sp. indet. aff. *Pirumella williamsenii* (Bolli, 1978b) Williams et al., 1998

Plate 1, Figure 21; Plate 2, Figure 7

Orthopithonella williamsenii (Bolli, 1978b). WILLEMS, 1988 p. 449-451, pl. 4, figs. 17-19; HILDEBRAND-HABEL AND WILLEMS, 1997, p. 185, pl. 3, figs. 7-8.

Remarks.—*Pirumella williamsenii* (Bolli, 1978b) is a problematic taxon as it probably accommodates several different species. Bolli (1978b) described *P. williamsenii* from late Jurassic strata as having a loose crystal arrangement with large interspaces on the outer cyst surface, a 10 μm thick outer and much thinner inner layer of about 2 μm . Keupp (1981) and Keupp and Ilg (1989) assigned specimens to *P. williamsenii* that closely resemble the type material of Bolli (1978b), however no information on the number of wall layers is given. Keupp (1987) and Keupp and Kowalski (1992) assigned single-layered specimens to *P. williamsenii*, which show a much coarser crystal arrangement than the type material. *P. williamsenii* sensu Kohring (1993a) is single layered and exhibits no interspaces. In contrast, Willems (1988) and Hildebrand-Habel and Willems (1997) described clearly double-layered specimens as *P. williamsenii*, whereas both layers are more or less equal in thickness. However, none of the depicted specimens of the mentioned authors exactly corresponds to the description given by Bolli (1978b) or the information given is insufficient for an exact assignment. Therefore, *P. williamsenii* can be subdivided into four morphotypes which are separated morphologically as well as stratigraphically: 1) *P. williamsenii* sensu stricto introduced by Bolli (1978b) from the late Jurassic. Tentatively assigned to this morphotype are the specimens described by Keupp (1981) and Keupp and Ilg (1989) from the early Hauterivian and Callovian, respectively. 2) *P. williamsenii* sensu Keupp (1987) from the Albian is single-layered and bears coarse crystallites. 3) *P. williamsenii* sensu Willems (1988) (described as *Orthopithonella williamsenii* Willems, 1988 n. comb.) known from the middle Coniacian to late Santonian is characterized by its double-layered wall and a potential radial ultrastructure. 4) *P. williamsenii* sensu Kohring (1993a) from the middle Eocene is single-layered and shows no interspaces between the crystals.

The three specimens from the Wombat Plateau correspond to the description and depicted specimens of the third morphotype, *P. williamsenii* sensu Willems (1988). The cysts are spherical or slightly ovoid and have a maximum diameter of 41, 54 and 63 μm . The crystals of the double-layered wall appear radially arranged in cross-section. Both layers are similar in thickness, although the dimensions of the outer layer slightly exceeds the inner layer; wall about 6.5 μm thick. Inner wall

built of massive, densely packed rhombohedrons; outer wall, in contrast, constructed of loosely arranged bar-like crystals. The radial ultrastructure of this morphotype is suggested by Willems (1988) by means of SEM examinations of cross-sections of the wall.

Occurrence.—Campanian and late Maastrichtian of Hole 761B, Wombat Plateau.

Gen. et sp. indet. aff. *Tetramerosphaera lacrimula* Willems, 1985

Plate 1, Figure 25; Plate 2, Figure 15

Remarks.—Two specimens were found that superficially resemble *Tetramerosphaera lacrimula* Willems, 1985 concerning the drop-shaped appearance of the cyst and the position of the archeopyle. However, they have a single-layered, relatively thick wall (4.7 μm), in contrast to the double-layered *T. lacrimula*, in which the individual wall layers are typically separated by ridges that reflect a reduced tabulation. The wall of gen. et sp. indet. aff. *T. lacrimula* is built of radially arranged, irregularly shaped rod-like crystallites. The habit of the crystallites might suggest a radial ultrastructure.

Occurrence.—Late Maastrichtian (CC26) and early Paleocene (NP3) of Hole 761B, Wombat Plateau.

Orthopithonella? sp. aff. *Orthopithonella?* *globosa* (Fütterer, 1984) Lentin and Williams, 1985

Plate 1, Figure 24; Plate 2, Figure 2

Orthopithonella sp. cf. *globosa* (Fütterer, 1984). KEUPP, 1990, pl. 15, figs. 5-13; MONNET, 1993, p. 24-25, pl. 4, figs. 10-13.

Orthopithonella? *globosa* (Fütterer, 1984). KOHRING, 1993a, p. 38-40, pl. 29, figs. a-f, pl. 33, figs. a-i; KEUPP AND KOHRING, 1994, p. 166, pl. 2, figs. 5-7.

? *Orthopithonella* cf. *globosa* (Fütterer, 1984). HILDEBRAND-HABEL AND WILLEMS, 1997, p. 185, pl. 3, figs. 5, 6.

Orthopithonella globosa (Fütterer, 1984). HILDEBRAND-HABEL AND WILLEMS, 2000, fig. 5h.

Remarks.—*Orthopithonella?* *globosa* was first described by Fütterer (1984) from the late-middle Maastrichtian and early Danian of the south-eastern Atlantic Ocean (ODP Leg 74). Specimens from the type material are characterized by an exceptionally large size (84-132 μm) and a double-layered wall. The proximal layer is built of massive rhombohedrons and is about three times thicker than the distal layer. Crystallites of the thin distal layer are arranged in a rosette-like pattern on the outer surface. Similar cysts from Eocene to Miocene sediments have been assigned to *O.?* *globosa* by various authors (see synonymy), however, those specimens are significantly smaller (reported range of diameter is 29 to 60 μm) and lack the rosette-like pattern on the outer surface. We consider this morphotype to represent a co-generic, but different species.

In addition to typical specimens of *O.?* *globosa*, several specimens were recognized in Hole 747A and 761B that resemble the morphotype as described above. They are spherical to slightly ovoid in shape and variable in size. The cyst diameter ranges from 35.1 to 67 μm (mean = 53.6, $n = 35$). The wall is built of two layers which are more or less equal in thickness. The inner layer is characterized by radially arranged columnar to short columnar crystals. Crystals of outer layer also appear radial in cross-section, but the distal surface of the outer layer may suggest an oblique ultrastructure, because its pattern of interwoven crystallites is similar to the oblique distal layer of *Pirumella edgarii* (Bolli, 1974) Lentin and Williams, 1993.

Specimens of *O.?* *globosa* of the Holes 747A and 761B differ from the described morphotypes in having large diameters of 109-120 μm and a massive inner layer.

Occurrence.—Early Paleocene (NP2), Oligocene, early Miocene and Pliocene of Hole 747A, Kerguelen Plateau. Late Maastrichtian of Hole 761B, Wombat Plateau.

Orthopithonella? sp. aff. *Orthopithonella gustafsonii* (Bolli, 1974) Streng et al., 2002

Plate 1, Figures 10, 12, 13, 15

Remarks.—*Orthopithonella?* sp. aff. *O. gustafsonii* is characterized by a spherical shape, a single-layered wall built of radially arranged crystallites and a relatively uniform surface pattern of trigonal crystal tips. However, besides this general appearance we recognized three different morphotypes, which are separated stratigraphically and show some morphological differences. Morphotype 1 (Plate 1, Fig. 15) was found in the early Maastrichtian of Hole 747A and is characterized by a less organized appearance of the outer cysts' surface and hourglass-shaped wall-forming crystals in cross-section. Cyst diameter ranges from 33.1 to 49.0 μm (mean = 41.7 μm , $n = 21$). Morphotype 2 (Plate 1, Figs. 10, 12) was detected in Paleocene strata of Hole 747A and Hole 761B. Morphotype 2 is slightly smaller than Morphotype 1 (29.7 to 41.6 μm in diameter; mean = 36.7 μm , $n = 15$) and the wall-forming crystals are of columnar shape in cross section, resembling the inner layer of *Orthopithonella? aequilamellata* (Plate 2, Fig. 1). Morphotype 3 (Plate 1, Fig. 13) from the Paleocene of Hole 747A differs from Morphotype 2 in additionally possessing coarser crystallites. All morphotypes occasionally display a circular archeopyle.

Specimens resembling Morphotypes 1 and 2 were accommodated within *O. gustafsonii* or described as *O. cf. gustafsonii* and *O. aff. gustafsonii*, respectively, by several authors (e.g., Fütterer, 1990; Keupp, 1992b; Keupp and Mutterlose, 1994). Cysts comparable to Morphotype 3 were first described by Kienel (1994) from the Danian of Germany and Denmark as *Orthopithonella cf. gustafsonii* forma *salebra*. However, Streng et al. (2002) [Chapter 2.1] clearly distinguished those specimens from *O. gustafsonii* by means of the archeopyle characteristics.

Fütterer (1990) depicted two specimens from the Maud Rise that closely resemble Morphotype 1 and Morphotype 2, respectively, revealing the same differences concerning the habit of the wall-forming crystals. Additionally, just like Morphotype 1 and 2, the specimens of Fütterer (1990) are from the late Maastrichtian and the Danian.

Occurrence.—Early Maastrichtian (*R. levis* biozone) and Paleocene of Hole 747A, Kerguelen Plateau and late Paleocene (NP5) of Hole 761B, Wombat Plateau.

Orthopithonella? sp.

Plate 1, Figure 29; Plate 2, Figure 8

Remarks.—Four specimens of *Orthopithonella?* sp. were found which are all ovoid in shape, single-layered and bear a subapically situated circular to slightly angular archeopyle. The specimens are 75.4 μm to 60.4 μm long; width of cyst is about 85% of length. The cyst wall is 5.5 to 6.0 μm thick, built of numerous, radially arranged slim crystallites. Outer surface of cyst appears smooth, because of the densely packed, tiny equilateral triradiate crystal tips. Orientation of the crystallographic *c*-axes of wall-forming crystallites unknown.

Occurrence.—Middle Eocene (NP14) of Hole 761B, Wombat Plateau.

Pirumella? sp. aff. *Pirumella amplicrystallina* (Pflaumann and Krasheninnikov, 1978)

Lentin and Williams, 1985

Plate 1, Figure 28; Plate 2, Figure 12

Remarks.—Cysts of *Pirumella?* sp. aff. *P. amplicrystallina* measure 66 to 106 μm in length (mean = 86.9 μm , $n = 29$) and 44 to 66 μm in width (mean = 55.3, $n = 29$); specimens less than 75 μm in length are scarce. Length and width are roughly positively correlated. The elongated cysts are pear- or drop-

shaped, with the antapical side being blunt and the apical side pointed. Therefore, the maximum width is not in medial position, but slightly shifted antapically. The apically situated archeopyle is circular to slightly angular in outline, about 11 to 16 μm in diameter and interpreted to represent the single apical plate 3'. The single-layered wall is 5 to 6 μm thick and appears to be built of obliquely oriented crystals arranged in a loose pattern in surface view, however, in cross-section crystals appear in fact to be radially oriented or possibly slightly oblique.

Specimens of *Pirumella?* sp. aff. *P. amplicrostallina* are similar to several other Maastrichtian species in their general outer appearance, i.e., *Pirumella krasheninnikovii* (Bolli, 1974) Lentin and Williams, 1993, *Pirumella usheri* (Krasheninnikov and Basov, 1983) Lentin and Williams, 1993, and *Pirumella amplicrostallina* (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1985. However, in contrast to *P. krasheninnikovii*, cysts of *P.?* sp. aff. *P. amplicrostallina* are single-layered and the outline is drop- or pear-shaped rather than elliptical. Regarding the pear-shaped outline they resemble *Pirumella usheri* (Krasheninnikov and Basov, 1983) Lentin and Williams, 1993, which has, however, two layers. *P. amplicrostallina* is single-layered, but its outline is elliptical not pear-shaped and the shape appears more compact.

Occurrence.—Late Maastrichtian (CC25 and CC26) of Hole 761B, Wombat Plateau.

Pirumella sp. aff. *Pirumella thayeri* (Bolli, 1974) Lentin and Williams, 1993

Plate 1, Figure 17

Obliquipithonella thayeri (Bolli, 1974). VERSTEEGH, 1993, p. 373, pl. 7, figs. 3-4.

Remarks.—A single specimen of *Pirumella* sp. aff. *P. thayeri* was found, which is similar to a specimen described as "*Obliquipithonella*" *thayeri* by Versteegh (1993) from the late Pliocene. Both specimens resemble the type material of Bolli (1974), but since *P. thayeri* has as yet only been reported from the Late Jurassic and Early Cretaceous, a reappearance in the Pliocene is unlikely. Therefore, no distinct allocation of these specimens has been attempted, especially because *P. thayeri* is a poorly defined morphotype and probably accommodates more than one biological species.

Occurrence.—Early Pliocene of Hole 747A, Kerguelen Plateau.

Species with a combination archeopyle - Mesoepicystal archeopyles

Calciodinellum? sp. 1

Plate 3, Figures 6-9

Remarks.—*Calciodinellum?* sp. 1 is generally very similar to *C. levantinum* regarding cyst size and general appearance. However, wall-forming crystals of *Calciodinellum?* sp. 1 are typically smaller than in *C. levantinum* and are additionally distally flattened in contrast to the pointed crystal tips of *C. levantinum*. Cysts of *Calciodinellum?* sp. 1 are always spherical, measuring 25.5 μm to 32.3 μm (mean = 28.8 μm , $n = 14$) in diameter; cyst wall is 1.6 to 2.2 μm thick. Archeopyle is mesoepicystal, angular in outline. Cysts are questionably assigned to *Calciodinellum* since the orientation of the c-axes of wall-forming crystals has not been examined. However, as the crystals resemble those of *C. levantinum*, they most probably have a tangential orientation.

Occurrence.—Late Pliocene (NN16) of Hole 761B, Wombat Plateau.

Calciodinellum? sp. 2

Plate 3, Figure 4

Remarks.—Only two specimens of *Calciodinellum?* sp. 2 were found. Both cysts are spherical, measuring 30.0 and 36.2 μm in diameter; cyst walls are 2.0 and 2.5 μm thick. Mesoepicystal archeopyles are angular in outline and comprise 66 and 69% of the cysts' diameter. Wall-forming crystals are radially arranged, longer than wide; distal crystal tips differ in size, generating an irregular pattern on the outer cyst surface. Inner cyst surface appears more regular, formed by equally distributed crystal terminations of similar size. Ultrastructure of wall-forming crystals unknown, the assignment to *Calciodinellum* is therefore only tentative.

Occurrence.—Early Miocene of Hole 747A, Kerguelen Plateau.

Calciodinellum sp. cf. *Calciodinellum operosum* Deflandre, 1947

Plate 3, Figure 13

Remarks.—A single specimen of *Calciodinellum* sp. cf. *C. operosum* was found. It is distinguished from typical representatives of *C. operosum* Deflandre, 1947 by the absence of the sutural ridge which separates the epicyst from the cingulum. Apart from this, the tabulation pattern is identical, as already noted in specimens from the late Miocene of Algeria by Keupp et al. (1991). Furthermore, the relatively large size (53.2 μm) of this specimen is remarkable, which is distinctively larger than other reported sizes of *C. operosum*.

Occurrence.—Early Miocene (NN1) of Hole 761B, Wombat Plateau.

Caracomia sp. cf. *Caracomia stella* Streng et al., 2002

Plate 3, Figures 15, 17, 18

Remarks.—Specimens of *Caracomia* sp. cf. *C. stella* differ from typical cysts of *C. stella* Streng et al., 2002 in the absence of pores and of the characteristic wall with epitaxially grown crystals. More massive, stem-like crystals are developed instead. Only occasionally, the epitaxial growth of the wall-forming crystals is intimated (Plate 3, Fig. 15). The lack of pores as well as the different wall structure are most probably due to a diagenetic overprint. *Caracomia* sp. cf. *C. stella* is ovoid, less frequently spherical in shape; diameters range from 27.9 to 33.0 μm .

Occurrence.—Middle Miocene of Hole 747A, Kerguelen Plateau.

Caracomia sp. aff. *Caracomia stella* Streng et al., 2002

Plate 3, Figures 16, 21, 22

Remarks.—Cysts of *Caracomia* sp. aff. *C. stella* are spherical to slightly ovoid in shape. Diameters of cysts range from 27.1 to 34.4 μm . Archeopyle is mesoepicystal, polygonal in outline. Wall massive, about 3 μm thick, built of stem- to wedge-shaped crystals, which are radially arranged. Outer cyst surface characterized by an irregular pattern of tri- and quadrangular crystal terminations of variable sizes.

Occurrence.—Early Miocene of Hole 747A, Kerguelen Plateau

Species with a combination archeopyle - Epicystal archeopyles

Lebessphaera sp. cf. *Lebessphaera urania* Meier et al., 2002

Plate 4, Figure 4

Remarks.—Specimens of *Lebessphaera* sp. cf. *L. urania* differ from the typical *L. urania* Meier et al., 2002 in the larger size and a more bumpy appearance of the outer cyst surface. The four examined specimens of *L. sp. cf. L. urania* are spherical in shape with a cyst diameter of 45.2 to 56.2 μm . Undehisced cysts show a faint descending cingular displacement (Plate 4, Fig. 4).

Occurrence.—Early Miocene (NN1) of Hole 761B, Wombat Plateau.

Lebessphaera? sp.

Plate 4, Figures 7, 8

Remarks.—Probably a new species of *Lebessphaera*, which is characterized by interfingering crystals with polylobate crystal tips resembling jigsaw pieces. Two specimens were found, which are 29.0 and 38.6 μm in diameter. One specimen shows a descending cingular displacement (Plate 4, Fig. 7).

Occurrence.—Late Pliocene (NN16) of Hole 761B, Wombat Plateau.

Species with unknown archeopyle type

Gen. et sp. indet. aff. *Calciodinellum elongatum* (Hildebrand-Habel et al., 1999) Meier et al., 2002

Plate 4, Figure 23

Remarks.—The three specimens found are ovoid in shape, 24.4 to 30.4 μm wide and about 15% longer than wide. The 2.5–3 μm thick, single-layered wall is built of massive calcite rhombohedrons which form a cobblestone-like pattern on the outer cyst surface. The archeopyle type is unknown, but might possibly be mesoepicystal. Cysts resemble *Calciodinellum elongatum* in size, shape and archeopyle outline, but wall-forming crystals are more similar to *Fuettererella deflandrei*. The habit of crystals suggests a tangential ultrastructure of the specimens.

Occurrence.—Late Oligocene of Hole 747A, Kerguelen Plateau.

Gen. et sp. indet. 1

Plate 4, Figure 20

Remarks.—The single cyst of gen. et sp. indet. 1 is spherical, 37.4 μm in diameter, single-layered, and has a relatively thick wall of 6 μm . The wall is built of columnar, radially oriented crystals of about 1.5 μm width. Length of crystals equals wall thickness. Outer cyst surface characterized by an irregular pattern of crystal terminations of different sizes. Inner surface similar to outer. Archeopyle not present. Ultrastructure of wall unknown, probably radial.

Occurrence.—Middle Eocene (NP16) of Hole 761B, Wombat Plateau.

Gen. et sp. indet. 2

Plate 4, Figure 14

Remarks.—A single cyst of gen. et sp. indet. 2 was found. The specimen is spherical, 50.5 μm in diameter and strikes because of its large wall-forming crystals. Individual crystals of the single-layered wall had been affected by a diagenetic overprint that caused distal and especially proximal growth of

crystals resulting in a relatively thick wall. Inner cyst diameter is less than half of outer cyst diameter. Cyst somewhat resembles *Pirumella loeblichii* (Bolli, 1974) Lentin and Williams, 1993.

Occurrence.—Late Paleocene of Hole 761B, Wombat Plateau.

Gen. et sp. indet. 3

Plate 4, Figures 16, 17

Remarks.—Cysts of gen. et sp. indet. 3 are spherical and single-layered, and had obviously been influenced by diagenetic overgrowth obscuring the primary crystal habit. All cysts appear somewhat spiny due to secondary growth of distal crystal tips. No archeopyle or archeopyle suture is visible in any of the cysts. Sizes of cysts range from 30.8 to 64.3 μm . Ultrastructure of wall unknown.

Occurrence.—Early Paleocene, late Paleocene and early Miocene of Hole 761B, Wombat Plateau.

Orthopithonella? sp. cf. *Orthopithonella?* *minuta* Fütterer, 1990

Plate 5, Figures 15-17

Remarks.—The problematic of *O.?* *minuta* were extensively discussed by Streng et al. (subm. A) [Chapter 2.2]. No distinct archeopyle type can be assigned to *O.?* *minuta*, because the preserved archeopyles generally have an irregular and variable outline that admit no reliable assignment of involved plates.

Tentatively assigned to *O.?* *minuta* are several specimens from Hole 761B and some from Hole 747A that closely resemble the type material of Fütterer (1990). They are spherical and variable in size; cysts' diameters range from 23.7 to 50.6 μm (mean = 33.1 μm , $n = 104$). Single-layered wall is built of short and sturdy crystals which are approximately as wide as long (about 2 μm). Outer cyst surface is characterized by an irregular pattern of trigonal to polygonal crystal terminations. Archeopyles are generally relatively large, circular to irregular circular in outline, most likely involving more than one plate. However, smaller angular archeopyles are observed as well, which are probably the result of wall damages and not related to an archeopyle. Occasionally, an archeopyle suture and a pointed operculum are visible in undehisced cysts (Pl. 5, Fig. 17), most undehisced cysts show no excystment features though. Due to the poor definition and variability of this morphotype, probably more than one species is united within *O.?* sp. cf. *O.?* *minuta*.

Occurrence.—Early Paleocene to early Miocene of Hole 761B, Wombat Plateau, and late Paleocene, early Eocene and early Miocene of Hole 747A, Kerguelen Plateau.

Pirumella sp. 1

Plate 4, Figures 12, 15

Remarks.—The three specimens of *Pirumella* sp. 1 are ovoid in shape with a length-width ratio of about 1:0.88; largest specimen measures 56.3 μm in length, smallest 47.1 μm . Double-layered wall consists of a thin inner layer (about 1 μm thick) and a thick outer layer of about 6 μm . Outer layer is built of massive interlocking and intertwining bar-like crystals which produce a rough distal cyst surface. Inner layer principally similar to outer, but crystals of inner layer are much smaller and less elongated. Crystals of both layers obliquely oriented. No archeopyle was observed.

Occurrence.—Early Eocene of Hole 747A, Kerguelen Plateau.

Pirumella sp. 2

Plate 4, Figures 9, 10

Remarks.—Cysts of *Pirumella* sp. 2 are spherical, measure 31.7 to 49.2 μm in diameter (mean = 39.0, $n = 26$) and have a single-layered 4–5 μm thick wall. Wall built of obliquely oriented plate-like crystals of different sizes, smaller crystals fill the gaps between the larger ones. Distal cyst surface rough, dominated by several large crystal terminations, which appear bar-like. Pattern of proximal surface similar to distal, but with a smoother texture. Ultrastructure of wall interpreted as oblique. None of the specimens exhibits an archeopyle.

Occurrence.—Late Paleocene (NP9) of Hole 761B, Wombat Plateau.

Pirumella sp. 3

Plate 4, Figures 21, 22

Remarks.—A single spherical cyst of *Pirumella* sp. 3 was observed. It measures 30.2 μm in diameter and its wall is 2.7 μm thick. The wall is interpreted as single-layered although it is obviously constructed of a double row of obliquely oriented crystallites. Crystals of the basal, proximal row appear smaller and elongated in contrast to those of the distal row that have a more blocky shape. However, crystals of the proximal row also protrude into the distal row and vice versa. Therefore, no partition into two discrete "layers" is possible. The inner surface is characterized by an irregular pattern of polygonal (about 1 μm in diameter) and elongated polygonal (up to 2.5 μm in length) crystal faces. Outer surface typically has irregularly arranged crystal terminations of uniform size (about 2 μm) and appears coarser and less smooth than the inner surface. No archeopyle is visible.

Occurrence.—Middle Eocene (NP15–NP16) of Hole 761B, Wombat Plateau.

"Rhabdothorax" spp.

Plate 4, Figure 19

Remarks.—The generic name *Rhabdothorax* was introduced by Kamptner (1958) for typically ovoid, but also spherical tests, built of flat polygonal crystallites distally bearing a central spine which may be capitate. However, Kamptner (1958) failed to give a Latin diagnosis to make his new genus available. A Latin diagnosis was later provided by Gaarder and Heimdal (1973, p. 97) who thereby validated the genus (*Rhabdothorax* Kamptner ex Gaarder and Heimdal, 1973). Subsequently, many authors included various types of spiny cysts of uncertain affinity in *Rhabdothorax* using open nomenclature (e.g., Keupp and Kowalski, 1992; Keupp and Kohring, 1993; Kienel, 1994). Recently, Janofske (2000) emended the species belonging to *Rhabdothorax*, i.e., *R. regale* (Gaarder, 1954) Gaarder in Gaarder and Heimdal, 1973 (senior synonym of *R. gerenus* Kamptner, 1967) and *R. erinaceus* (Kamptner, 1937) Kamptner, 1958, and concluded that *Rhabdothorax* is a junior synonym of *Scrippsiella* Balech ex Loeblich III, 1965, since the type of *Rhabdothorax*, *R. erinaceus*, is a junior synonym of *Scrippsiella trochoidea* (von Stein, 1883) Loeblich III, 1965 emend. Janofske, 2000. *R. regale* was newly combined to *Scrippsiella regalis* (Gaarder, 1954) Janofske, 2000. Consequently, the genus *Rhabdothorax* became obsolete. Accordingly, all morphotypes of *Rhabdothorax* published under open nomenclature should now be referred to as *Scrippsiella* sp. However, since *Scrippsiella* is characterized by a tangential ultrastructure (see Janofske, 2000) and some of the specimens published as *Rhabdothorax* sp. were proven to have a radial wall type (Hildebrand-Habel and Streng, in review [Chapter 2.3]) and additionally show morphological differences, an accommodation of those

specimens within *Scrippsiella* is problematic. Therefore, we retain the name "*Rhabdothorax*" as an informal name to unite more-or-less spiny cysts of uncertain affinity.

Occurrence.—Campanian, late Maastrichtian, middle Eocene and early Miocene of Hole 761B, Wombat Plateau, and late Oligocene to early Miocene of Hole 747A, Kerguelen Plateau.

Thoracosphaera? prolata Bukry and Bramlette, 1969

Plate 5, Figures 1-12

Thoracosphaera prolata BUKRY AND BRAMLETTE, 1969, p. 141, pl. 3, fig. 18; JAFAR, 1975, p. 82, pl. 14, fig. 5; ?MÜLLER, 1979, pl. 5, fig. 11; PERCH-NIELSEN, 1985, fig. 75.3; ?SIESSER AND BRALOWER, 1992, pl. 4, fig. 12.

? *Sphaerodinella? tuberosa* forma *elongata* HILDEBRAND-HABEL, WILLEMS, AND VERSTEEGH, 1999, p. 83, pl. 5, figs. 5-7.

Remarks.—*Thoracosphaera? prolata* was first described by Bukry and Bramlette (1969) from middle Eocene sediments of all major oceans and some additional locations. The species was defined to be extremely eccentric with a length-width ratio exceeding 2.0 and an outer surface "with a distinctly sculptured appearance". Since Bukry and Bramlette (1969) used lightmicroscopic methods, they did not provide additional information on archeopyle characteristics or habit of individual wall-forming crystals. Additionally, they reported less elongate forms associated with *T.? prolata*. Subsequently, *T.? prolata* has been reported from the early Eocene (Müller, 1979; Steinmetz and Stradner, 1984), middle Eocene (Bukry, 1971; Shafik, 1975; Jafar, 1979), middle Eocene to early Oligocene (Siesser and Bralower, 1992), middle Miocene (Bukry, 1973), and late Miocene (Jafar, 1975) of all major oceans. Unfortunately, only Jafar (1975), Müller (1979), and Siesser and Bralower (1992) provided illustrations of their material, and only the depicted specimen of Jafar (1975) corresponds to the definition of Bukry and Bramlette (1969). More recently, Hildebrand-Habel et al. (1999) described a morphotype, which is similar to *T.? prolata*, as *Sphaerodinella? tuberosa* forma *elongata* from the middle Eocene of the South Atlantic. They reported length-width ratios of 1.1 to 1.8 and homologized the archeopyle, although irregular in outline, with the plates 2'-4' and 1a-3a. Recently, Meier et al. (2002) discovered ovoid cysts from surface sediments and water samples of the Mediterranean Sea which they interpreted as being identical with the morphotype of Hildebrand-Habel et al. (1999) and therefore established the new combination *Calciodinellum elongatum*, giving the form of Hildebrand-Habel et al. (1999) species rank. Additionally, they considered *T.? prolata* not to be synonymous with *C. elongatum* because of the high length-width ratio of *T.? prolata*. The specimens from the Quaternary of the Mediterranean Sea only show length-width ratios of 1.1 to 1.2 (Meier pers. comm.).

Many specimens were found in Hole 747A and 761B that resemble *T.? prolata* of Bukry and Bramlette (1969), especially in the middle Eocene of Hole 761B. As already mentioned by Bukry and Bramlette (1969), less ovoid specimens also co-occur with extremely elongated morphotypes in Hole 761B. However, the restricted definition of Bukry and Bramlette (1969) concerning the length-width ratio of *T.? prolata* (> 2.0) is unreproducible with the material at hand. Examinations of the length-width ratios in the available material yielded values of 1.0 to 2.4. The frequency distribution of these values allows a distinction into two groups (Fig. 7). The first group shows length-width ratios of 1.0 to 1.7 and the second group of 1.9 to 2.4. The specimens of both groups show the same morphological characteristics, besides the shape, though: a pattern of triradiate crystals tops on the outer cyst surface, a single-layered wall and an apically located archeopyle of indeterminable type. Therefore, the two morphotypes can only be distinguished by the shape. Specimens belonging to the first group most

probably correspond to the specimens described by Hildebrand-Habel et al. (1999) as *Sphaerodinella? tuberosa* forma *elongata*, which would in turn mean that they are co-specific with *Calciodinellum elongatum*. However, since in none of the observed specimens an unequivocal outline of the archeopyle is discernible, we refer to those specimens as *T.? prolata* sensu lato. The specimens depicted by Müller (1979) and Siesser and Bralower (1992) most likely belong to this group, too. Concomitantly, specimens with length-width ratios of >1.8 are referred to as *T.? prolata* sensu stricto, extending the definition of Bukry and Bramlette (1969). As long as the archeopyle characteristics of *T.? prolata* have not unambiguously been proven, it remains dubious if *T.? prolata* is the senior synonym of *C. elongatum* or if the specimens described by Meier et al. (2002) from the Mediterranean Sea represent a separate species. Since the archeopyle outline of *T.? prolata* does not allow an accurate designation of the plate or plates involved, no appropriate genus can be assigned to *T.? prolata*. A generic reallocation, as already proposed by Fütterer (1976), however, is necessary because *Thoracosphaera* is currently regarded as a monospecific genus due to its unique life cycle (Tangen et al., 1982; Fensome et al., 1993).

To solve the uncertainties described above concerning the taxonomic position of *T.? prolata*, a restudy of the type material of Bukry and Bramlette (1969) (Scripps core AMPH 116P, 488 cm) was performed. Unfortunately, the residual type material underwent considerable carbonate dissolution during storage (W. Smith, pers. comm.) and a re-examination of a sample from the type material yielded no specimens of *T.? prolata*.

Occurrence.—Late Paleocene to middle Eocene of Hole 761B, Wombat Plateau and late Paleocene and early Eocene of Hole 747A, Kerguelen Plateau.

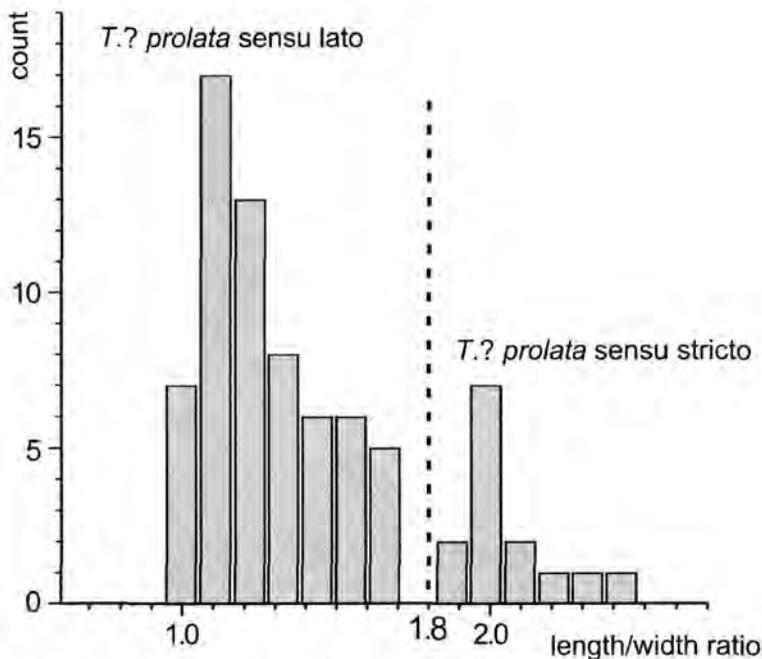


Figure 7. Frequency distribution of the length/width ratio of the problematic species *Thoracosphaera? prolata*. See text for further explanations.

Pithonelloid species with a circular aperture

Pithonella sp.

Plate 2, Figure 18

Remarks.—The single spherical to slightly ovoid specimen of *Pithonella* sp. has a maximum diameter of 41 μm and had obviously been diagenetically altered. The wall-forming crystals show a secondary overgrowth resulting in an oversized appearance. Nevertheless, the typical spiral pithonelloid arrangement of the crystals is still visible, which permits a generic determination.

Occurrence.—Campanian of Hole 761B, Wombat Plateau.

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Plates

Plate 1

Species with an apical archeopyle that involves plate 3' only. Scale bar equals 10 μm , except for 22 and 25-30 = 20 μm . 1, 2, 5, 7, 8, 10, 11, 14, 19-21, 23, 25, 29 = ODP Leg 122, Hole 761B, Wombat Plateau; 3, 4, 6, 9, 12, 13, 15-18, 22, 24, 26-28, 30 = ODP Leg 120, Hole 747A, Kerguelen Plateau.

- 1 *Fuettererella deflandrei* (Kamptner, 1956) Hildebrand-Habel and Streng (in review) (cyst 122-5H-5/X17); middle Miocene.
- 2 *Fuettererella tesserula* (Fütterer, 1977) Kohring, 1993a (cyst 122-8H-3/XIII14), specimen with secondary aperture; middle Eocene.
- 3 *Fuettererella belliata* Streng et al. (subm. A) (cyst 120-19X-2-11/IV2); early Eocene.
- 4 *Fuettererella elliptica* Kohring, 1993a (cyst 120-19X-2-11/XIII12); early Eocene.
- 5 *Fuettererella?* sp. aff. *Calciodinellum* sp. 1 (cyst 122-4H-1/XIII9); late Pliocene.

- 6 *Callicarpinum tetramurum* Kienel, 1994 (cyst 120-20X-1/VI9); early Palaeocene.
- 7 *Cervisiella saxea* (Stradner, 1961) Hildebrand-Habel et al., 1999 (122-8H-3/V14); middle Eocene.
- 8 *Cervisiella operculata* (Bramlette and Martini, 1964) Streng et al. (subm. A) (cyst 122-16X-2/IX3-2); late Palaeocene.
- 9 *Cervisiella* sp. aff. *Operculodinella reticulata* Kienel, 1994 (cyst 120-19X-2-139/140); late Palaeocene.
- 10, 12, 13, 15 *Orthopithonella?* sp. aff. *Orthopithonella gustafsonii* (Bolli, 1974) Streng et al., 2002 (cysts 122-18X-2/IV2, 120-20X-1/V45, 120-20X-1/VI35, 120-21X-1/X38); late Palaeocene (10), early Palaeocene (12, 13), early Maastrichtian (15); see also Plate 2, Figure 9.
- 11 *Cervisiella?* sp. aff. *Cervisiella saxea* (Stradner, 1961) Hildebrand-Habel et al., 1999 (cyst 122-5H-5/V25-2); middle Miocene.
- 14 *Leonella granifera* (Fütterer, 1977) Janofske and Karwath in Karwath, 2000 (cyst 122-4H-1/XIII18); late Pliocene.
- 16 *Pirumella edgarii* (Bolli, 1974) Lentin and Williams, 1993 (cyst 120-7H-4/V1); middle Miocene; see also Plate 2, Figure 4.
- 17 *Pirumella* sp. aff. *Pirumella thayeri* (Bolli, 1974) Lentin and Williams, 1993 (cyst 120-4H-3/XIII10-2); early Pliocene.
- 18, 22 *Fuettererella flora* (Fütterer, 1990) Hildebrand-Habel and Streng (in review) (cysts 120-20X-1/VIII11, 120-19X-2-11/V24); early Palaeocene and early Eocene; see also Plate 2, Figure 6.
- 19 *Pirumella parva* (Fütterer, 1984) Lentin and Williams, 1993 (cyst 122-16X-2/VI9-2); late Palaeocene; see also Plate 2, Figures 10, 13.
- 20 *Pirumella multistrata* (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1993 (cyst 122-23X-3/99); late Maastrichtian.
- 21 Gen. et sp. indet. aff. *Pirumella williamsenii* (Bolli, 1978b) Williams et al., 1998 (cyst 122-25X-3/58), specimen with secondary aperture; Campanian; see also Plate 2, Figure 7.
- 23 *Orthopithonella? congruens* Fütterer, 1990 (cyst 122-21X-6/05); late Maastrichtian.
- 24 *Orthopithonella?* sp. aff. *Orthopithonella? globosa* (Fütterer, 1984) Lentin and Williams, 1985 (cyst 120-14H-5/V20-2), specimen with secondarily enlarged archeopyle; late Oligocene; see also Plate 2, Figure 2.
- 25 Gen. et sp. indet. aff. *Tetramerosphaera lacrimula* Willems, 1985 (cyst 122-21X-2/13); early Palaeocene; see also Plate 2, Figure 15.
- 26 *Pirumella krasheninnikovii* (Bolli, 1974) Lentin and Williams, 1993 (cyst 120-21X-1/II4); early Maastrichtian; see also Plate 2, Figure 3.
- 27 *Orthopithonella? aequilamellata* Willems, 1988 (cyst 120-19X-2-139/V6); late Palaeocene; see also Plate 2, Figure 1.
- 28 *Pirumella?* sp. aff. *Pirumella amplicrystallina* (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1985 (cyst 122-22X-3/IX3-2); late Maastrichtian; see also Plate 2, Figure 12.
- 29 *Fuettererella?* sp. (cyst 122-14X-3/X21); middle Eocene; see also Plate 2, Figure 8.
- 30 *Orthopithonella? globosa* (Fütterer, 1984) Lentin and Williams, 1985 (cyst 120-21X-1/IX1); early Maastrichtian; see also Plate 2, Figures 11, 14.

Plate 1

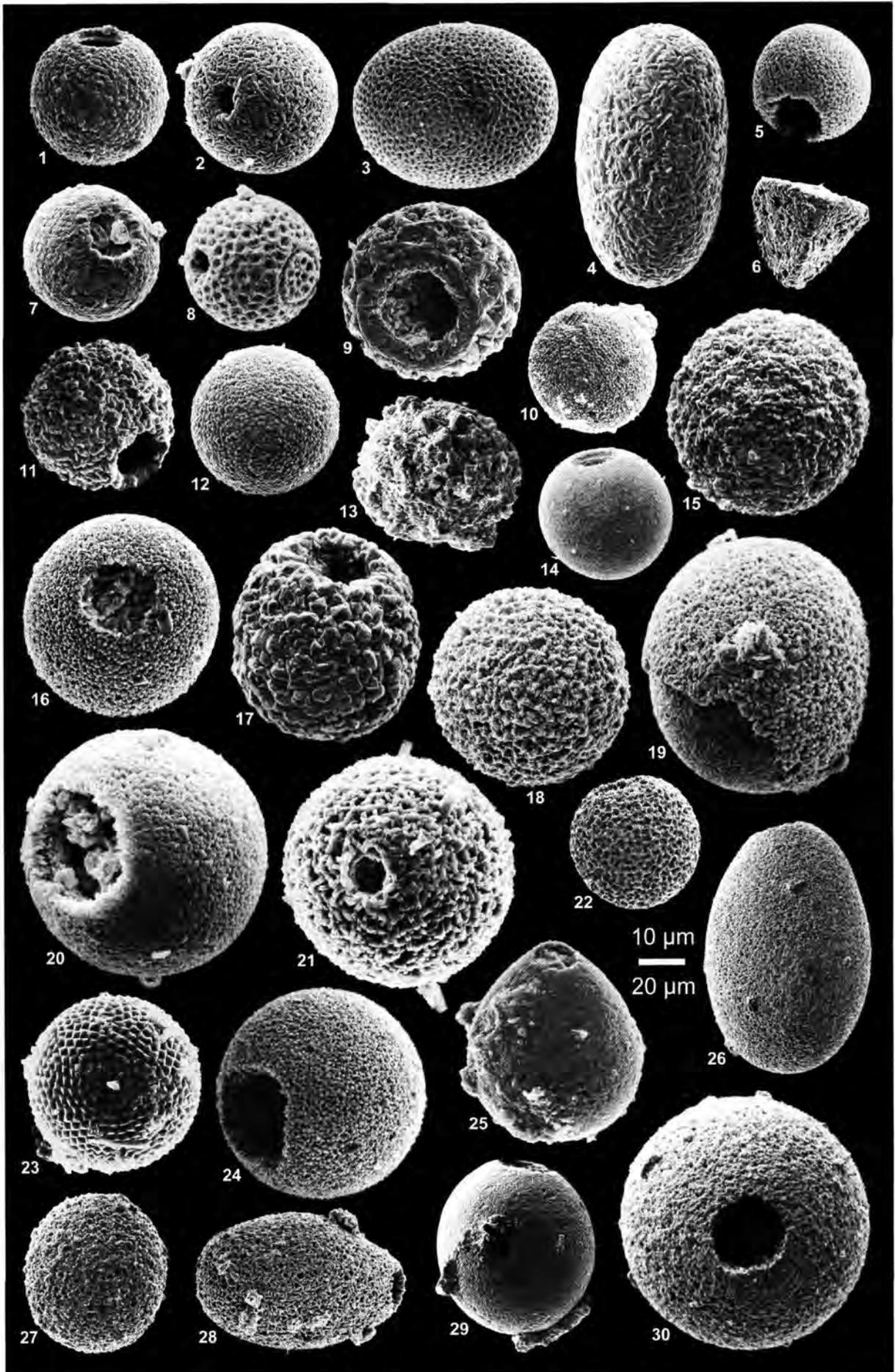


Plate 2

Cross sections of cyst walls and surface pattern of various cysts and pithonelloid species. Scale bar equals 5 μm , except for 11 and 16-18 = 10 μm . 1-6, 9-11, 16 = ODP Leg 120, Hole 747A, Kerguelen Plateau. 7, 8, 12-15, 17, 18 = ODP Leg 122, Hole 761B, Wombat Plateau.

- 1 *Orthopithonella? aequilamellata* Willems, 1988 (cyst 120-19X-2-139/V4); late Palaeocene.
- 2 *Orthopithonella? sp. aff. Orthopithonella? globosa* (Fütterer, 1984) Lentin and Williams, 1985 (cyst 120-12H-2/VII26-2); early Miocene.
- 3 *Pirumella krasheninnikovii* (Bolli, 1974) Lentin and Williams, 1993 (cyst 120-21X-1/XII2); early Maastrichtian.
- 4 *Pirumella edgarii* (Bolli, 1974) Lentin and Williams, 1993 (cyst 120-12H-2/VII8-2); early Miocene.
- 5 *Ruegenia inaequilamellata* Willems, 1992 (cyst 120-20X-1/IX11); early Palaeocene.
- 6 *Fuettererella flora* (Fütterer, 1990) Hildebrand-Habel and Streng (in review) (cyst 120-19X-2-11/V2); early Eocene.
- 7 Gen. et sp. indet. aff. *Pirumella williamsenii* (Bolli, 1978b) Williams et al., 1998 (cyst 122-25X-3/58); Campanian.
- 8 *Fuettererella? sp.* (cyst 122-14X-3/XIV14); late Oligocene.
- 9 *Orthopithonella? sp.* (cyst 120-21X-1/X3); early Maastrichtian.
- 10, 13 *Pirumella parva* (Fütterer, 1984) Lentin and Williams, 1993 (cysts 120-19X-2-11/V31, 122-16X-2/V5-2); early Eocene and late Palaeocene.
- 11, 14 *Orthopithonella? globosa* (Fütterer, 1984) Lentin and Williams, 1985 (cysts 120-21X-1/IX2, 122-22X-3/X10-2); early and late Maastrichtian.
- 12 *Pirumella? sp. aff. P. amplicrystallina* (Pflaumann and Krasheninnikov, 1978) Lentin and Williams, 1985 (cyst 122-22X-3/IV7-2); late Maastrichtian.
- 15 Gen. et sp. indet. aff. *Tetramerosphaera lacrimula* Willems, 1985 (cyst 122-21X-2/13); early Palaeocene.
- 16 *Pithonella sphaerica* (Kaufmann in Heer, 1865) Zügel, 1994 (cyst 120-21X-1/XI5); early Maastrichtian.
- 17 *Lentodinella danica* Kienel, 1994 (cyst 122-21X-6/74); late Maastrichtian.
- 18 *Pithonella sp.* (cyst 122-25X-3/31); Campanian.

Plate 2

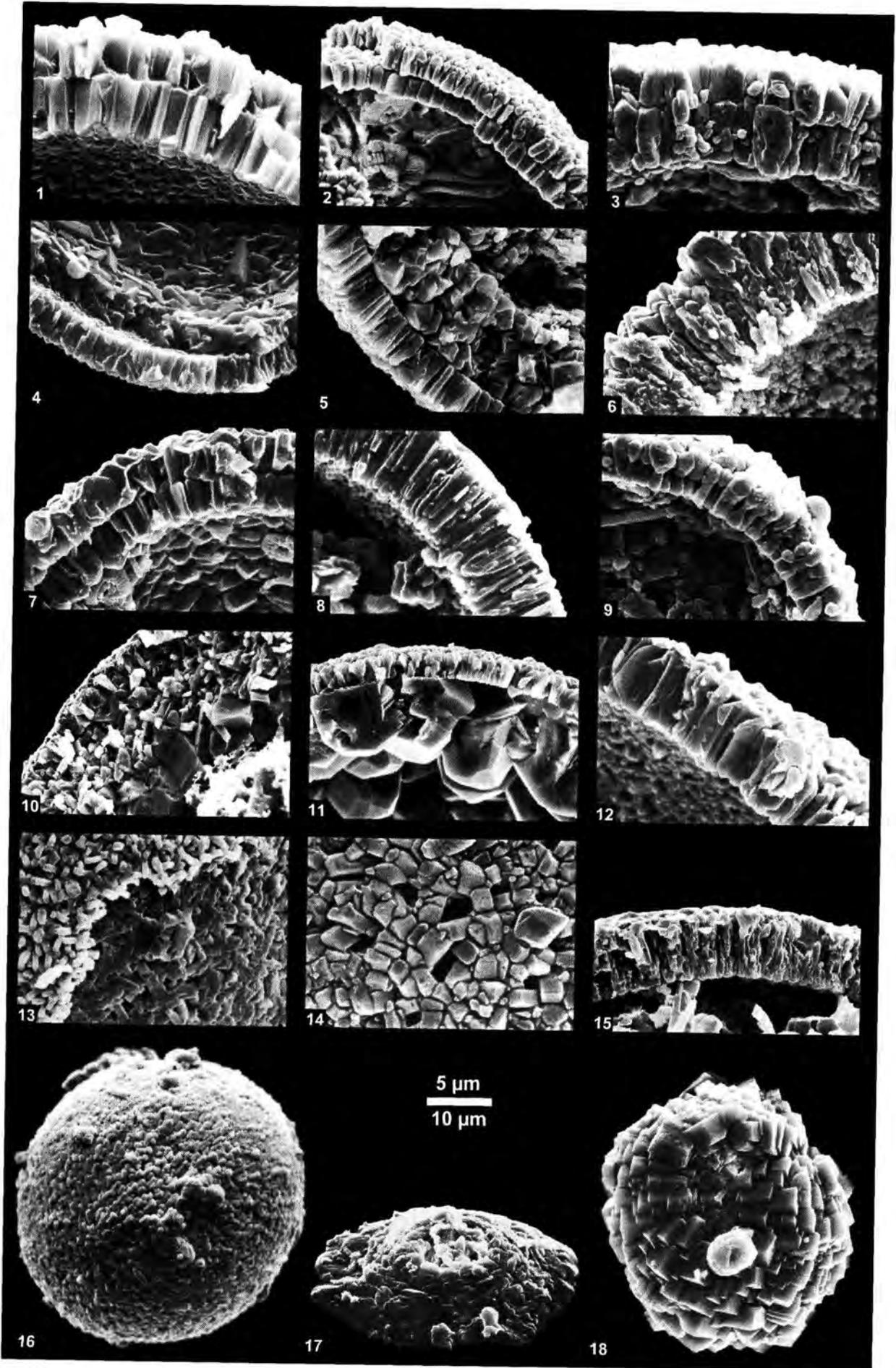


Plate 3

Species with a mesoepicystal archeopyle. Scale bar equals 10 μm for hole cysts and 3 μm for details (9, 15, 21, 22). 1, 3, 5-9, 11, 13, 14, 19 = ODP Leg 122, Hole 761B, Wombat Plateau; 2, 4, 10, 12, 15-18, 20-22 = ODP Leg 120, Site 747, Kerguelen Plateau.

- 1 *Calciodinellum albatrosianum* (Kamptner, 1963) Janofske and Karwath *in* Karwath, 2000 (cyst 122-2H-3/VI14); Quaternary.
- 2 *Calciodinellum operosum* Deflandre, 1947 (cyst 120-14H-2/V6-2); early Miocene.
- 3 *Calciodinellum levantinum* Meier et al., 2002 (cyst 122-2H-3/X18); Quaternary.
- 4 *Calciodinellum* sp. 2 (cyst 120-12H-2/IX12-2); early Miocene.
- 5 *Calciodinellum elongatum* (Hildebrand-Habel et al., 1999) Meier et al., 2002 (cyst 122-2H-3/VI18); Quaternary.
- 6-9 *Calciodinellum* sp. 1 (cysts 122-4H-1/XIV5, 122-4H-1/IV18, 122-4H-1/VI8); late Pliocene.
- 10 *Calciodinellum clamosum clamosum* Streng et al. (subm. A) (cyst 120-20X-1/VIII3); early Palaeocene.
- 11 *Calciodinellum clamosum latum* Streng et al. (subm. A) (cyst 122-18X-2/IV13); late Palaeocene.
- 12 *Calciodinellum kerguelensis* Streng et al. (subm. A) (cyst 120-6H-1/V19); late Miocene.
- 13 *Calciodinellum* sp. cf. *C. operosum* Deflandre, 1947 (cyst 122-7H-4/IV7); early Miocene.
- 14 *Caracomia stella* Streng et al., 2002 (cyst 122-5H-5/ss2); middle Miocene.
- 15, 17, 18 *Caracomia* sp. cf. *C. stella* Streng et al., 2002 (cysts 120-9H-5/VI18, 120-9H-5/V32, 120-9H-5/VIII4); middle Miocene.
- 16, 21, 22 *Caracomia* sp. aff. *C. stella* Streng et al., 2002 (cysts 120-12H-2/VII23-2, 120-12H-2/V7); early Miocene.
- 19 *Scrippsiella regalis* (Gaardner, 1954) Janofske, 2000 (cyst 122-2H-3/IX2), slightly compressed specimen; Quaternary.
- 20 *Caracomia arctica* (Gilbert and Clark, 1983) Streng et al., 2002 (cyst 120-3H-3/X9); late Pliocene.

Plate 3

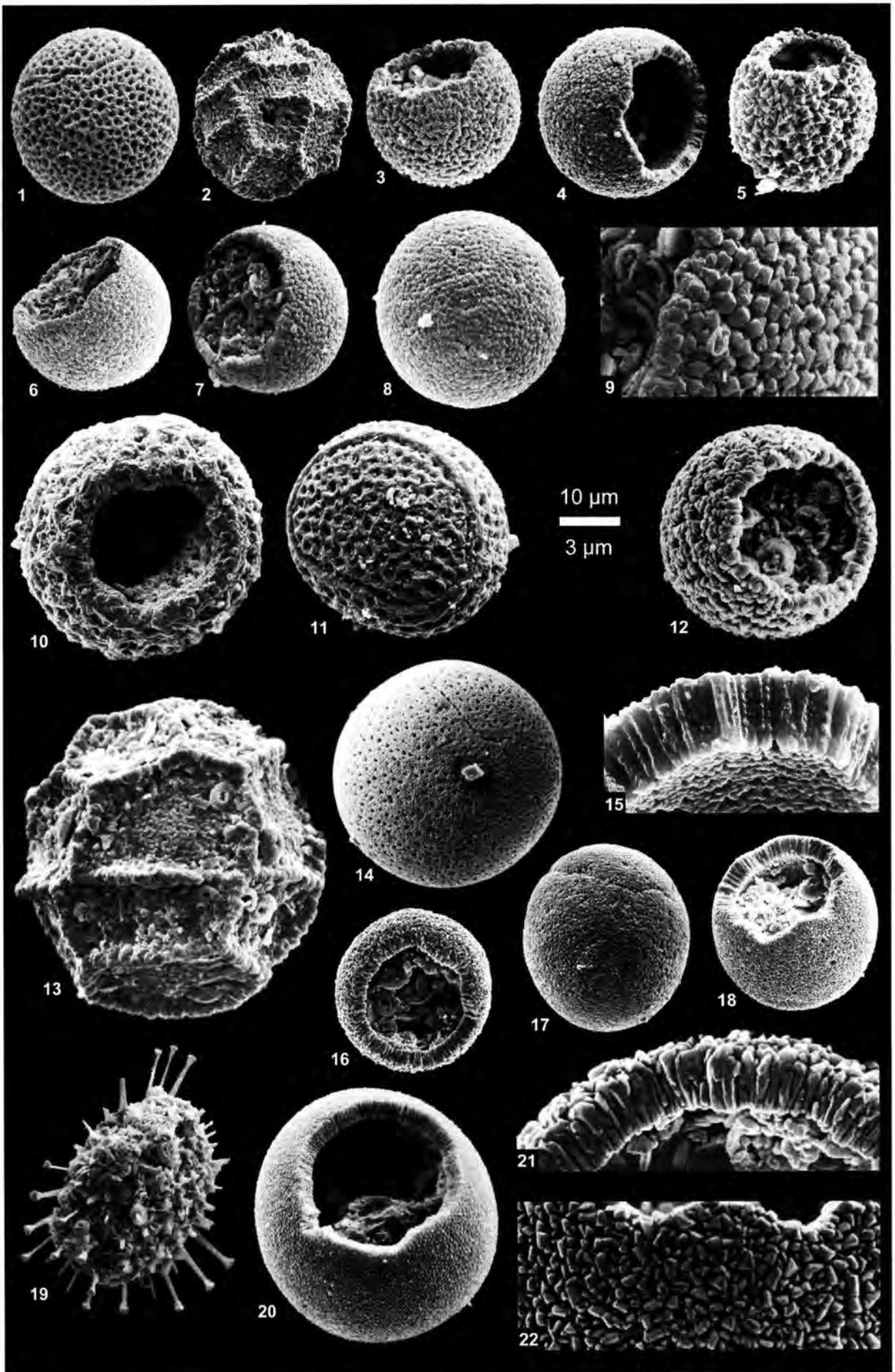


Plate 4

Species with an epicystal archeopyle (1-8) and with unknown archeopyle type (9-23). Scale bar equals 10 μm , except 8, 9, 22 = 3 μm and 12 = 6 μm . 1, 4, 7-11, 13, 14, 16-18, 20-22 = ODP Leg 122, Site 761, Wombat Plateau; 2, 3, 5, 6, 12, 15, 19, 23 = ODP Leg 120, Site 747, Kerguelen Plateau.

- 1 *Pernambugia tuberosa* (Kamptner, 1963) Janofske and Karwath *in* Karwath, 2000 showing archeopyle suture (cyst 122-7H-4/X8); early Miocene.
- 2, 3 *Pernambugia? patata* Streng et al. (subm. A) (cysts 120-1R-4/VI8-3, 120-1R-4/IX7-3); early Oligocene.
- 4 *Lebessphaera* sp. cf. *L. urania* Meier et al., 2002 (cyst 122-7H-4/VI18), oblique ventral view showing faint archeopyle suture and descending cingular displacement; early Miocene.
- 5, 6 *Lebessphaera urania* Meier et al., 2002 (cysts 120-14H-5/VI9-2, 120-14H-2/X32); late Oligocene and early Miocene.
- 7, 8 *Lebessphaera* sp. (cyst 122-4H-1/IV8); late Pliocene; 7, ventral view with descending cingular displacement; 8, detail of outer surface of cyst showing polylobate crystal terminations.
- 9, 10 *Pirumella* sp. 2 (cysts 122-16X-2/XI8-2, 122-16X-2/VII2-2); late Palaeocene.
- 11 *Pirumella strobila* (Keupp, 1979b) Lentin and Williams, 1993 (cyst 122-21X-6/40); late Maastrichtian.
- 12, 15 *Pirumella* sp. 1 (cyst 120-19X-2-11/VI18); early Eocene.
- 13 *Orthotabulata obscura* Kienel, 1994 (cyst 122-21X-2/07); early Palaeocene.
- 14 Gen. et sp. indet. 2 (cyst 122-16X-2/VII5-2); late Palaeocene.
- 16, 17 Gen. et sp. indet. 3 (cysts 122-7H-4/IV6, 122-7H-4/VII25); early Miocene.
- 18 *Pirumella spinosa* (Keupp, 1979b) Lentin and Williams, 1993 (cyst 122-21X-6/09); late Maastrichtian.
- 19 "*Rhabdothorax*" sp. with relatively large circular archeopyle (cysts 120-14H-2/II3-2); early Miocene.
- 20 Gen. et sp. indet. 1 (cyst 122-8H-3/VII12); middle Eocene.
- 21, 22 *Pirumella* sp. 3 with pseudo double-layered wall (22) (cyst 122-9H-5/X1-2); middle Eocene.
- 23 Gen. et sp. indet. aff. *Calciodinellum elongatum* (Hildebrand-Habel et al., 1999) Meier et al., 2002 (cyst 120-14H-5/VI31); late Oligocene.

Plate 4

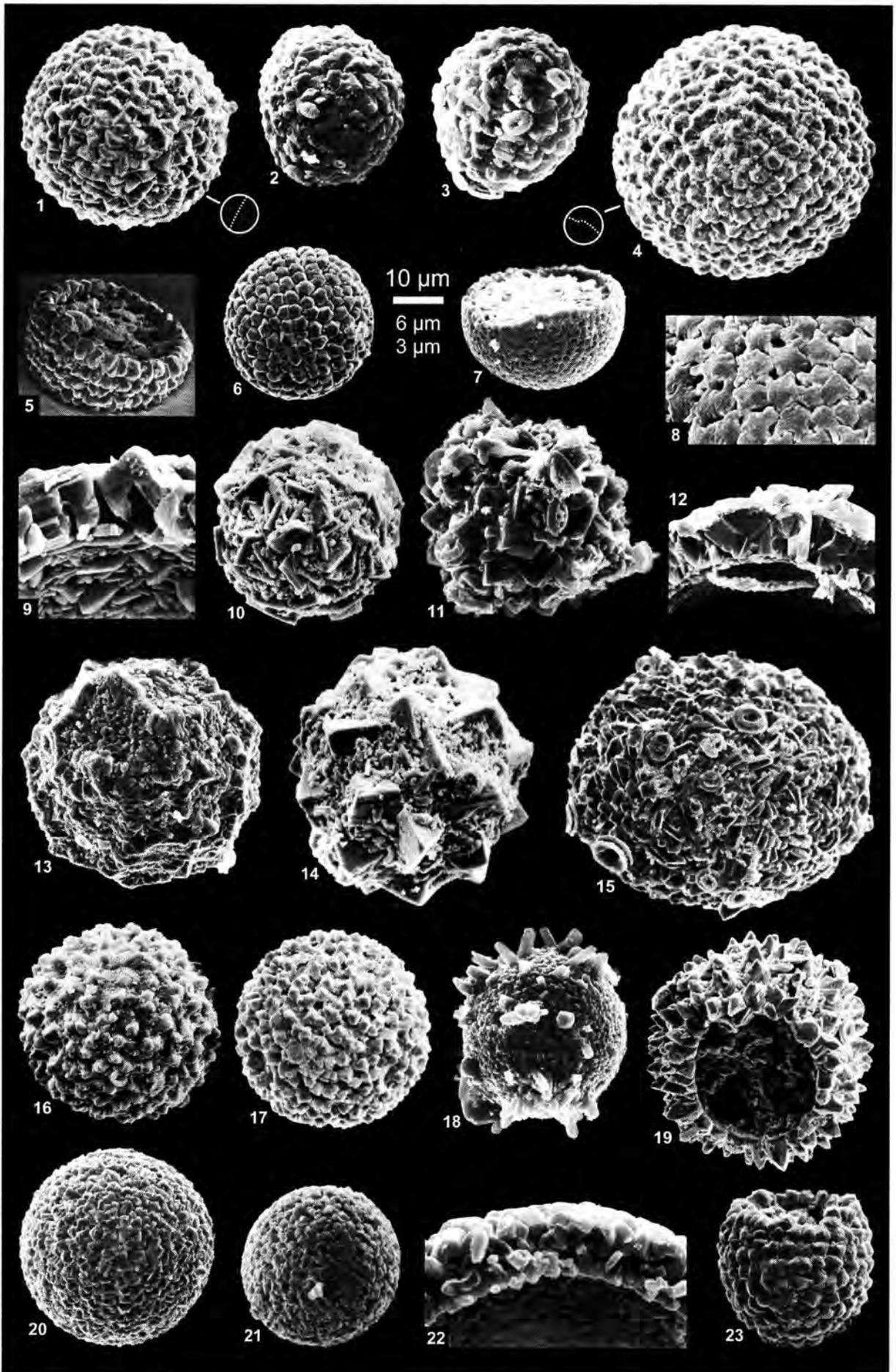
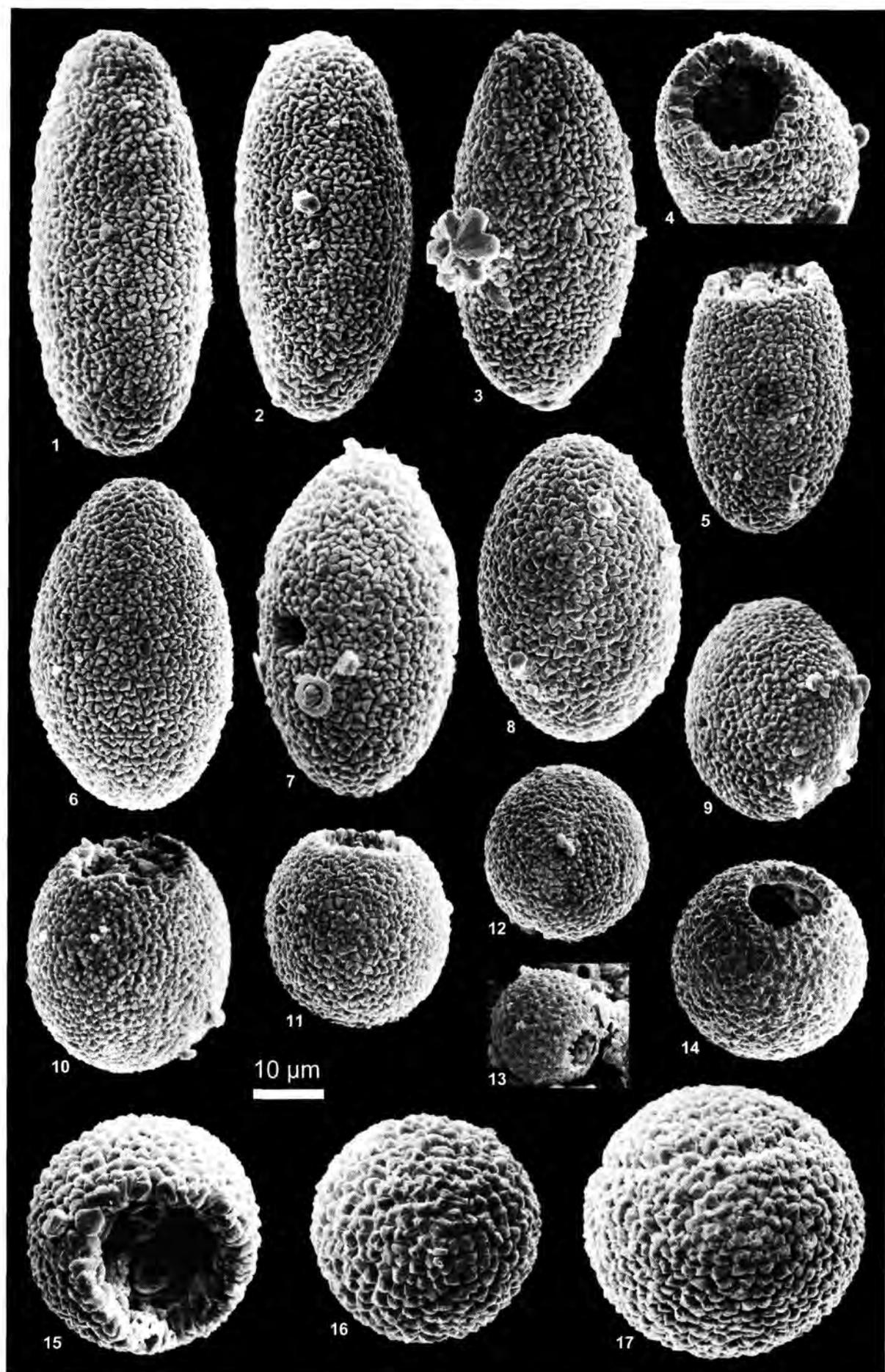


Plate 5

Variability of the problematic taxa *Thoracosphaera? prolata* Bukry and Bramlette, 1969 (1-12) and *Orthopithonella? sp. cf. O.? minuta* Fütterer, 1990 (15-17), as well as the coccoïd stage of *Thoracosphaera heimii* (Lohmann, 1920) Kamptner, 1944 (13-14). Scale bar equals 10 μm . All from ODP Leg 122, Hole 761B, Wombat Plateau.

- 1-5** *Thoracosphaera? prolata* Bukry and Bramlette, 1969 sensu stricto, meaning cysts with length/width ratio > 1.8 ; middle Eocene. 1-3, Undehisced cysts (cysts 122-8H-3/VI25, 122-8H-3/VII2, 122-8H-3/XII3); 4, apical view of dehisced specimen showing archeopyle outline (cyst 122-8H-3/A6); 5, lateral view of dehisced specimen (cyst 122-8H-3/IX10).
- 6-12** *Thoracosphaera? prolata* Bukry and Bramlette, 1969 sensu lato, meaning cysts with length/width ratio < 1.8 ; middle Eocene. 6-9, 12, Undehisced specimens with varying outline (cysts 122-8H-3/X8, 122-8H-3/IV1, 122-8H-3/VII8, 122-8H-3/VIII10, 122-8H-3/IX6); 10, 11, lateral view of dehisced specimens (cysts 122-8H-3/VIII6, 122-8H-3/XIV6).
- 13, 14** *Thoracosphaera heimii* (Lohmann, 1920) Kamptner, 1944; two specimen showing subcircular apertures (cysts 122-4H-1/S1, 122-5H-5/IV1); late Pliocene and middle Miocene.
- 15-17** *Orthopithonella? sp. cf. O.? minuta* Fütterer, 1990; middle Eocene. 15, Oblique apical view with irregular archeopyle outline (cyst 122-9H-5/V3-2); 16, undehisced cyst (cyst 122-9H-5/II3-2); 17, undehisced cyst showing archeopyle suture (cyst 122-9H-5/II-2).

Plate 5



3 Conclusions and future perspectives

The reconstruction of evolutionary trends and the comprehension of phylogenetic lineages of calcareous dinoflagellates require two premises which have to be complied first: 1) A consistent taxonomic concept that applies the various morphologic features of a group to each taxon of this group in the same manner. 2) An established knowledge on spatial as well as stratigraphic distribution of the individual taxa of calcareous dinoflagellates.

In order to obtain an useful and practicable taxonomic concept, the importance of the individual morphological features has to be evaluated and to be ranked according to their significance. In this study, the tabulation of calcareous cysts, especially that of the archeopyle, is regarded to represent the major criterion to distinguish between genera of calcareous dinoflagellates (Streng et al., 2002 [CHAPTER 2.1]; Streng et al., subm. A [CHAPTER 2.2]). This concept has been found to be consistent with phylogenetic lineages and has been applied to emendate quite a number of species in the course of this study (Streng et al., subm. A [CHAPTER 2.2]). However, still many genera need emendation as they are defined by the ultrastructure of the wall only, unifying different types of archeopyles as well as different types of external tabulation (e.g., the genus *Ruegenia*). Furthermore, with the emendation of the genus *Orthopithonella* herein, a variety of species that formerly belonged to *Orthopithonella* need reallocation. Additionally, a great number of taxa evinced to have even no known archeopyle or bear an archeopyle which cannot be related to distinct plates with certainty. All these taxa need intensive reexamination using the type material as well as potential new material to verify or to abolish their current affiliation. However, their reallocation is hampered and aggravated by one main aspect: The ultrastructure of the individual wall layers of a calcareous cyst is still regarded as an important taxonomic feature in terms of the wall type being consistent within a genus. The reported wall types of most of the taxa which need reallocation, however, must be regarded as tentative as they have been suggested from SEM examinations only. Therefore, the wall types of the individual taxa must be approved first by light microscope investigations of thin sections, to assure the proposed allocation. However, not only the inability to assess the ultrastructure of distinct double-layered species using thin section but also the phylogenetic significance of the wall structure in general, have led to a controversy of the real taxonomic importance of the wall structure. To unravel this difficulty, further genetic investigations on modern taxa with different wall types are inevitable. These investigations will probably also shed some light on the taxonomic and phylogenetic significance of the different archeopyle types and other morphologic features of calcareous dinoflagellates.

Spatial and stratigraphic distribution of fossil calcareous dinoflagellates is quite satisfactory at least for some regions and stratigraphic intervals: E.g., the Cretaceous and Paleogene of the European Boreal Realm was investigated in detail mainly through studies of Keupp and Kohring, respectively (Keupp, 1980a, 1981, 1982, 1984, 1987, 1991a, 1992b, 1995a, b; Keupp and Ilg, 1989; Keupp and Kowalski, 1992; Keupp and Mutterlose, 1984, 1994; Kohring, 1993a, Keupp and Kohring, 1994); the same applies to the Cenozoic of the South Atlantic (Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000; Hildebrand-Habel and Streng, in revision [CHAPTER 2.3]), the Jurassic and the Cretaceous as well as the Cenozoic of the eastern Indian Ocean (Bolli, 1974; Streng et al., subm. B [CHAPTER 2.4]). However, still many regions have been widely unrecognized and uninvestigated. Especially the Pacific Ocean represents a blank area in the investigation of fossil calcareous

dinoflagellates. Reports of fossil calcareous dinoflagellates in the Pacific Ocean are restricted to studies on calcareous nannoplankton and are limited to a few species, localities and time slices: the Danian of the southeast Pacific Ocean (Rögl, 1976), the Paleocene of the central Pacific Ocean (Kamptner, 1963), the middle Eocene of the central and southwest Pacific Ocean (Wei and Pospichal, 1991; Bukry and Bramlette, 1969; Shafik, 1975), and the middle Miocene of the western Pacific Ocean (Bukry, 1973). No specific investigation on the spatial distribution and diversity of calcareous dinoflagellates of this vast area has ever been performed for any time period. Another blank area may represent the sediments of the present shelf areas and former epicontinental and semi-enclosed seas. Investigations in the Mediterranean Sea have evinced a high diversity and a variety of as so far endemic species especially in near coast neritic environments of the Pliocene and Pleistocene (Versteegh, 1993; Rehakova, pers. comm.). Therefore, the younger sediments of many neritic environments, like the Caribbean Sea, the Gulf of Mexico, or the South China Sea, bear a high potential to enlarge our knowledge on the morphological variability and diversity of calcareous dinoflagellates.

Stratigraphic distribution patterns of calcareous dinoflagellate associations have shown to depict the long-term climatic evolution during the Cenozoic (Hildebrand-Habel et al., 1999; Hildebrand-Habel and Willems, 2000; Hildebrand-Habel and Streng, in revision [CHAPTER 2.3]; Streng et al., subm. B [CHAPTER 2.4]). Now, high resolution investigations of selected stratigraphic intervals covering distinct climatic events, like the Paleocene/Eocene transition with the Late Paleocene Thermal Maximum and the Early Eocene Climatic Optimum, or the Eocene/Oligocene transition, are needed to prove the applicability of calcareous dinoflagellates to depict short-termed climatic developments in the fossil record. High resolution investigations from the Late Quaternary have already revealed that changes in the absolute abundance of calcareous dinoflagellates are an useful tool for the reconstruction of paleoenvironmental changes during the glacial/interglacial cycles (Esper et al., 2000; Vink et al., 2000).

Another quite special difficulty arose during the last years through the results of culturing experiments of calcareous dinoflagellates. Fossil dinoflagellate cysts are generally regarded as resting cysts resulting from sexual reproduction (Fensome et al., 1993). However, investigations of Janofske and Karwath (1999) on the cyst production of some modern calcareous dinoflagellates, i.e., *Calciadinellum albatrosianum*, *Leonella granifera*, and *Pernambugia tuberosa*, has shown that the encystment process for at least these species cannot be connected to a sexual phase of the life cycle, as already demonstrated, e.g., for *Scrippsiella* cf. *lachrymosa* (Olli and Anderson, 2002). Additionally, the cyst stage of *Leonella granifera* appears to be the dominant stage of its life cycle, similar to the vegetative cyst stage of *Thoracosphaera heimii* (see CHAPTER 1). These results call the general opinion that all fossil calcareous cysts are hypnozygotes (resting cysts) into question and imply the possibility that many calcareous cysts represent indeed vegetative cysts. However, as the cysts of the three species examined by Janofske and Karwath (1999) comprise the three different wall types (radial, oblique, and tangential) and also the three major archeopyle types (apical, mesoepicystal, and epicystal), neither the wall type nor the archeopyle type can provide a potential clue to discriminate between probable resting or vegetative cysts in the fossil record. Further culturing experiments on modern taxa have to evince and to discriminate the different probabilities of cyst formation within the calcareous dinoflagellates.

Generally, the calcareous dinoflagellates still provide the possibility of a variety of investigations, including biological and paleontological, evolutionary and phylogenetic, climatological and oceanographical, as well as genetic aspects, which implies that our knowledge of calcareous dinoflagellates is far from being complete.

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