XIN SU

DEVELOPMENT OF LATE TERTIARY AND QUATERNARY COCCOLITH ASSEMBLAGES IN THE NORTHEAST ATLANTIC

Dissertation
zur Erlangung des Doktorgrades
der mathematisch-naturwissenschaftlichen Fakultät
der Christian-Albrechts-Universität zu Kiel
Zum Druck genehmigt am 10.12.1995

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4. Variations in accumulation rates of coccolith species and variations in benthic $\partial^{18}O$ data at site 659 (Tiedemann et al., 1994) were used to examine the response of the coccolith flora to climatic changes.

Fluctuation rates of these two data were further characterized by employing a statistical method. High $\partial^{18}O$ fluctuation rates together with evidence from published paleoclimatical studies reflect climatic instability during the Late Pliocene and Quaternary. A high coccolith fluctuation rate of a species is related to a large variability in production levels, which is caused by climatically induced complex changes in the marine ecosystem.

For most time intervals fluctuation rates of coccolith species correspond to those of $\partial^{18}O$. In the Pliocene, low coccolith fluctuation rates parallel low $\partial^{18}O$ fluctuation rates,

indicating that coccolith species show small variations in production during stable climatic conditions. In the Quaternary strongly increased $\partial^{18}O$ fluctuation rates are paralleled by increased coccolith fluctuation rates, suggesting that coccolith species show large-amplitude variations of production in response to increased climatic instability. Rapid and abrupt changes of the coccolith assemblages in the Quaternary are probably correlated to the increased climatic instability. Furthermore, in the Quaternary the coccolith fluctuation rates in high latitudes are higher than those in low latitudes, indicating stronger ecological stress and probably reflecting latitudinal differences in climatic variability. In the Quaternary, extinction rates of coccolith species are higher than in the Pliocene, possibly due to their failure to adapt to the increased climatic and ecological instability.

However, coccolith fluctuation rates during a few time intervals where species evolve or where some genetic variations within species occur, do not correspond to the $\partial^{18}O$ fluctuation rates. Appearance rates of coccolith species do not parallel the $\partial^{18}O$ fluctuation rate curve. Therefore, biologically derived variations in abundances cannot be directly correlated with global climatic changes.

Zusammenfassung

Im Rahmen der vorliegenden Arbeit wurden qualitative und quantitative Untersuchungen an spättertiären und quartären kalkigen Nannofossilien der DSDP/ODP Bohrungen 664, 659, 608, 609, und 610 aus dem Nordost-Atlantik durchgeführt, um die Entwicklung der Coccolithen-Gemeinschaften zu rekonstruieren und um die Anpassungen von Coccolithophoriden an sich verändernden globalen Klima- und Lebensbedingungen während der letzten 5,2 Millionen Jahren zu erarbeiten.

Es wurden folgende Ergebnisse erzielt:

1. Mit Hilfe hochauflösender stratigraphischer Untersuchungen konnte die zeitliche und räumliche Verbreitung der Coccolithen-Arten vom tropischen bis zum nördlichen Nordost-Atlantik seit dem Pliozän rekonstruiert werden.

2. Den größten Anteil an der Coccolithen-Gemeinschaft haben Arten-Gruppen der Familie Noelaerhabdaceae, vor allem die Gattungen *Reticulofenestra*, *Gephyrocapsa,* sowie *Pseudoemiliania lacunosa* und *Emiliania huxleyi*. Anhand der Veränderungen in ihren Akkumulationraten konnten die Entwicklungsprozesse der Gemeinschaften erkannt werden: der Niedergang und das Aussterben der miozänen Arten (hauptsächlich Arten der Gattungen *Reticulofenestra*, *Discoaster* und *Sphenolithus*), das Aufblühen der pliozänen und quartären Arten, besonders die Evolution der Gattung *Gephyrocapsa.* Diese Prozesse veränderten die Artenvergesellschaftung und bewirken die Entwicklung der Coccolithen-Gemeinschaften.

3. Durch die Unterschiede in den Häufigkeiten dominanter Arten konnten acht Entwicklungs-Stadien der Coccolithen-Gemeinschaften unterschieden werden. Im frühen Pliozän dominieren Coccolithen der Gattung *Reticulofenestra* die Gemeinschaft. Das Quartär ist durch wechselnde Dominanzen von *P. lacunosa* und *Gephyrocapsa*-Arten gekennzeichnet. Im Holozän dominiert die neuentwickelte Art *E. huxleyi* die Coccolithen-Gemeinschaft. Die Entwicklung der quartären Coccolithen-Vergesellschaftungen geht deutlich schneller voran als die im Pliozän.

Die acht Entwicklungs-Stadien sind durch verschiedene geographische Veränderungen in den Gemeinschaften gekennzeichnet. Im frühen Pliozän wurden *Discoaster* spp. und *Sphenolithus* spp. häufig im äquatorialen Atlantik und selten im nördlichen Atlantik beobachtet. Im späten Quartär sind *G. oceanica* und *G. margereli* die dominierenden Arten der äquatorialen Gemeinschaften, während der nördliche Atlantik von *G. caribbeanica* allein dominiert wird. Dazwischen erscheinen relativ gleichförmige Gemeinschaften.

4. Um die Anpassung der Coccolithen-Flora an das sich verändernde Klima zu ermitteln, wurden Variationen in den Akkumulationraten der Coccolithen-Arten mit $\partial^{18}O$ Daten von benthischen Foraminiferen an Site 659 (Tiedemann et al., 1994) verglichen.

Mit Hilfe eines statistischen Modells wurden die Fluktuationsraten dieser Daten erfaßt. Hohe $\partial^{18}O$ Fluktuationsraten geben zusammen mit Paläoklima-Daten aus der Literatur deutliche Hinweise auf eine klimatische Instabilität seit dem späten Pliozän. Hohe Fluktuationsraten von Coccolithen-Arten sind auf starke Änderungen in ihrer Produktion zurückzuführen. Diese werden von klimainduzierten Veränderungen im marinen Ökosystem verursacht.

In den meisten Zeiträumen sind die Fluktuationsraten der Coccolithen-Arten mit denen der $\partial^{18}O$-Daten vergleichbar. Während des Pliozäns korrelieren niedrige $\partial^{18}O$-Fluktuationsraten mit niedrigen Coccolithen-Fluktuationsraten. Diese sind auf geringe Veränderungen der Coccolithen-Produktivität unter stabilen Klimabedingungen zurückzuführen. Die im Quartär beobachteten, zunehmenden Coccolithen-Fluktuationsraten verlaufen parallel mit einer dramatischen Zunahme in den $\partial^{18}O$-Fluktuationsraten. Die hohen Coccolithen-Fluktuationsraten sind durch die Reaktion der Arten in ihrer Produktivität an die zunehmende Instabilität des Klimas zu erklären. Im Quartär zeigen die nach Norden zunehmenden Coccolithen-Fluktuationsraten stärkeren ökologischen Streß im nördlichen Atlantik an und spiegeln in ihren geographischen Variationen die Klimaveränderlichkeit wider. Die Aussterbensraten der Coccolithen-Arten im Quartär sind höher als im Pliozän. Auch dies ist vermutlich auf die zunehmende klimatische und ökologische Instabilität zurückzuführen.

In Zeiträumen, in denen sich Arten entwickeln oder genetische Veränderungen einzelner Arten stattfinden, stimmt die Coccolithen-Fluktuationrate nicht mit den $\partial^{18}O$-Fluktuationsraten überein. Das Auftreten neuer Coccolithen-Arten verläuft nicht parallel zu den $\partial^{18}O$-Fluktuationsraten. Es zeigt sich, daß biologisch verursachte Veränderungen in den Coccolithen-Häufigkeiten nicht immer mit globalen Klimaänderungen korrelierbar sind.

摘要

本文为对北大西洋深海钻探项目（DSDP/ODP）664、659、608、609、610站位样品中晚第三纪和第四纪超微化石组合的研究，旨在探求其演化进程及与全球气候变化的关系。

在对该化石组合定性和定量分析的基础上，对约48个化石种或种群的时代和生态分布及其在生物地层学方面的应用进行了研究和讨论。

该化石组合的主要组份为：*Reticulofenestra* 和 *Gephyrocapsa* 中的不同种，以及 *Pseudoemiliania lacunosa* 和 *Emiliania huxleyi* 两种。根据这些种类沉积积累速率的变化，可识别出超微化石组合的演化过程：上新世期间中新世延续分子（*Reticulofenestra*，*Discoaster* 和 *Sphenolithus*）的逐渐衰退和上新世分子（*Pseudoemiliania lacunosa* 和 *Gephyrocapsa* 中一些种）的逐渐兴起；及第四纪期间 *Gephyrocapsa* 的迅速演变。这些生物演化过程导致了该化石组合的主要成份随时间迁移而不断更新，从而推动了该化石组合的发展进化。

综合对化石群绝对和相对丰度的分析，进一步识别出上新世至全新世化石组合的八个演化阶段。每一阶段的超微化石组合都具有独自的特征优势分子及相应的地理差异。老优势种不断地被新兴的优势种所取代，上新世的 *Reticulofenestra* 被第四纪 *Gephyrocapsa* 所替换，*Emiliania huxleyi* 为当代超微浮游生物群的优势种。第四纪超微化石组合演化的特征还在于 *Pseudoemiliania lacunosa* 与 *Gephyrocapsa* 一些种的频繁交替取代，显示出比上新世化石组合明显加快的发展速度。

由这些优势种及常见种的生态习性不同而形成的各阶段的生物地理差异也可明显识别。在早上新世，*Discoaster* 和 *Sphenolithus* 为低纬度地区常见种类，而 *R. productella* 为高纬度地区常见种。晚更新世期间，*G. margereli* 和 *G.oceanica* 为热带和亚热带优势种，而 *G. caribbeanica* 为过渡带地区绝对优势种。

对六个优势种积累速率变化和659站底栖有孔虫氧同位素（得自Tiedemann等，1994）分析表明，在大部分时间段内化石积累速率的波动率与古氧同位素波动率有相对应的联系，从而揭示超微浮游生物对由气候演变引起的古生态整体环境变化的灵敏反应。上新世期间化石积累速率的低波动率与当时氧同位素的低波动率相对应，表明小幅度的超微浮游生物生产率变化与缓和的气候浮动有关；第四纪期间化石积累速率的波动率与古气候波动率均显著上升，揭示随着不断加剧的气候不稳定性，超微浮游生物也发生大幅度的生产率变动。同时超微浮游生物在高纬度地区的波动率要大于在低纬度地区，清楚地反映出高纬度地区强烈的古海洋条件变化使得那里的超微浮游生物承受了比低纬度区生物更大的生态压力。许多超微化石种的绝灭可能与其不能适应连续增强的生态不稳定性有关，因此第四纪的超微化石种绝灭率高于上新世。第四纪 *Gephyrocapsa* 物种和生态的高度分异可能与当时大规模冰期及间冰期的频繁交替和较大的古海洋地理差异相关。因而第四纪古气候的极不稳定性可能是引起此时超微化石组合迅速发展的主要原因。

研究也表明，在有生物演化发生的少量时间段内，化石积累速率的波动率与古氧同位素波动率并不一一对应；新种的出现率与古气候波动率也难以相互联系。说明由生物演化引起的化石丰度变化不能与气候变化进行简单直接的对比。

CHAPTER 1   INTRODUCTION

1.1   Purpose of this study

Coccoliths are the calcareous remains of coccolithophorids which are single celled marine algae (Prymnesiophyceae Hibbert, 1976). Coccolithophorids constitute a major component of the modern phytoplankton, and coccoliths have been a major component of pelagic sediments since the Jurassic. Coccoliths play an important role in biostratigraphy, biogeography and the reconstruction of paleoceanography.

Recent studies of coccolithophorids have revealed new knowledge about their significance in Earth science, for example, in the modern world ocean blooms of *Emiliania huxleyi* are observed. This species is considered to be the most important contributor to the oceanic biomass of $CaCO_3$ (Holligan et al., 1983, 1993; Balch et al., 1991). Coccolithophorids produce several biochemical compounds, besides alkenones and some unique pigments, dimethysulfide (a source molecule for cloud nucleation) (Volkman et al., 1980, 1995; Marlowe et al., 1984, 1990; Charlson et al., 1987). Therefore, it is suggested that coccolithophorids have importance in biogeochemical cycles, including the global cycle of $CaCO_3$, and are related to "global change" (Ackleson et al., 1988; Winter and Briano, 1989; Westbroek et al., 1989, 1993; Holligan, 1992; Robertson et al., 1993).

Coccolithophorids live in the euphotic zone of sea water directly influenced by surface temperature and climate, and are therefore very sensitive to climatic changes. Most extant coccolithophorid species have appeared during the Pliocene and Quaternary. However, relatively little is known about the development of coccolith assemblages in response to climatic changes since the Pliocene.

Hence, the purpose of this study is to investigate Late Tertiary and Quaternary coccolith assemblages from the Northeast (NE) Atlantic with the aim to identify the mechanisms of their development, especially the ecological impact of paleoclimatic changes.

To achieve these aims a number of analytical methods were used including: 1) qualitative analyses of coccolith species; 2) quantitative analyses of occurrences and abundances of species; 3) stratigraphical analyses of sediment samples; 4) statistical analyses to correlate coccolith occurrences and climatic records (Figure 1.1). These methods are described in chapter 2 in detail.

This study is connected with a biometrical investigation of C. Samtleben and K.-H. Baumann on *Gephyrocapsa* with the purpose to evaluate the morphological development and biological evolution of the genus, since *Gephyrocapsa* species are the most abundant and important taxa of Quaternary coccolithophorid floras. Results of the study are cited and marked with (S&B) in the present study.
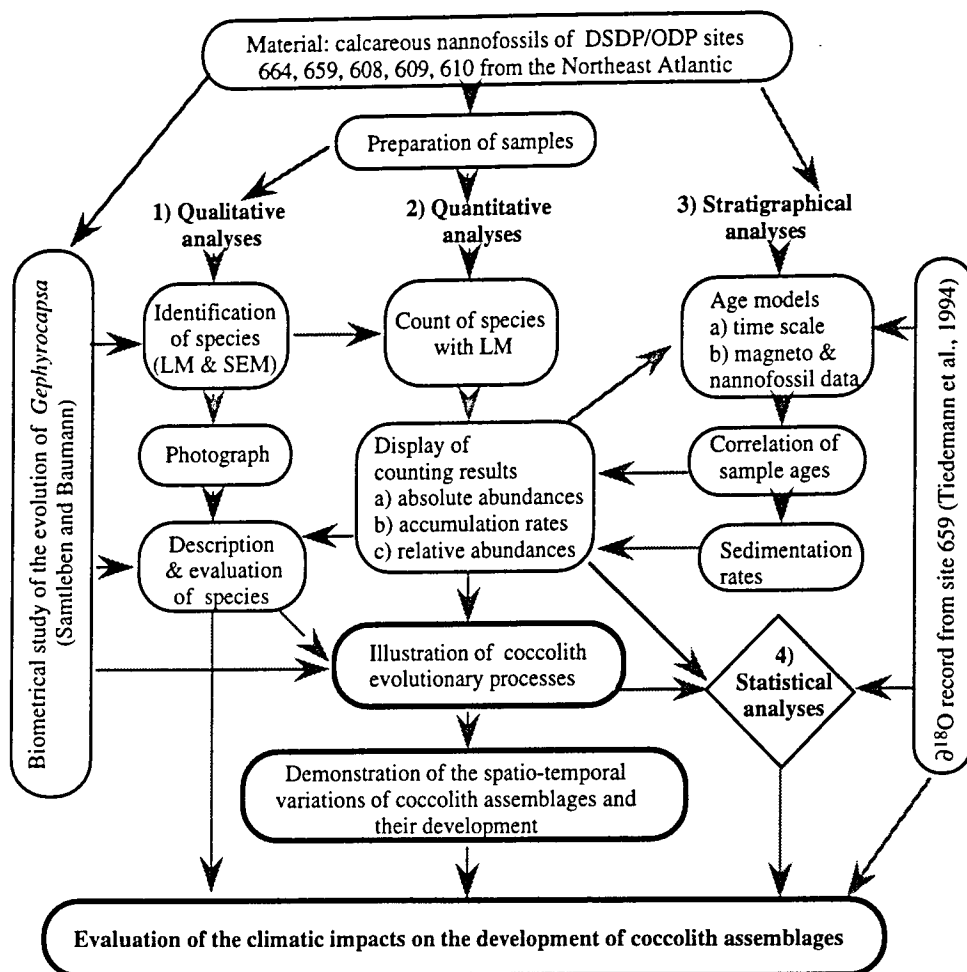
Figure 1.1 Summary of approaches and methods used for studying the development of coccolith assemblages correlated to climatic changes (see details in the text; LM: light microscope, SEM: scanning electron microscope).

1.2 Previous research

Most studies of Cenozoic nannofossils in the North Atlantic deal with nannofossil stratigraphy and only a few of them deal with coccolith paleoceanographic indications (McIntyre, 1967; McIntyre et al., 1967, 1972; Martini, 1971; Backman, 1979, 1984; Müller, 1979).

Studies of upper Cenozoic coccoliths in the NE Atlantic are also biostratigraphical investigations.

Pujos-Lamy (1977) suggested 20 coccolith intervals for the last 1.3 m.y. by using coccolith events (FAD/LAD, increase/decrease in abundances, dominance) in three cores from the NE Atlantic.

Bréhéret (1978) distinguished three Quaternary coccolith assemblages (for the last 0.44 m.y.) from two cores in the NE Atlantic, which were further subdivided into seven units for biostratigraphical purposes.

Weaver (1983) investigated four species (*E. huxleyi, G. muellerae, G. caribbeanica* and *G. aperta*) in sediments of eight cores from the Kings Trough Region of the NE Atlantic; five coccolith intervals were identified between oxygen isotope stages 1 to 13.

Backman and Shackleton (1983) studied the biochronology of Pliocene and lower Quaternary calcareous nannofossils, including nannofossils from six cores in the NE Atlantic, and determined the age data of a number of coccolith events (FAD/LAD).

Coccolith biostratigraphy of DSDP sites 606 - 610 was studied by Takayama and Sato (1987) and nannofossil zones (NN1 to NN21) were recognized. Nannofossil biostratigraphy of ODP sites 657 - 668 was investigated by Manivit (1989) and thirty zones were recognized in the Neogene and Quaternary sequences.

Hine (1990) studied Quaternary calcareous nannoplankton from the NE Atlantic (sites 658, 659, 607, 609, 610) to produce a high resolution stratigraphy. She suggested several floral zones and events for a nannoplankton stratigraphy in the NE Atlantic with an average time resolution of one event every 100 ky.

Several studies of *Discoaster* from the NE Atlantic were carried out for various purposes. For example, Backman et al. (1986) studied paleoclimatic and paleoceanographic implications of *Discoaster* accumulation data from DSDP site 552. The biochronological and paleonenvironmental implications of *Discoaster* abundance variations at site 606 were also investigated by Backman (1987). Chepstow-Lusty et al. (1989) suggested variations in abundances of Pliocene *Discoaster* species from the North Atlantic to be caused by orbital forcing.

1.3   Basic information about climatic changes and coccolith development

1.3.1   Climatic system

The earth's climatic system is composed of five components: the atmosphere (the gaseous envelope of the earth); the hydrosphere (oceans, lakes, rivers, etc.); the biosphere (plants, animal life); the cryosphere (snow, ice); and the lithosphere (rocks, sediments). Each of them exhibits internal processes, internal forcings, and interacts in various ways with the other components of the climatic system (GARP, 1975; Bergman et al., 1981; Gates, 1981). Climate evolution is governed both by external and internal forcings, such as solar radiation, land-ocean distribution changes due to continental drift, and aerosol changes due to volcanism (Joussaume, 1994).

According to the recent astronomic theory of paleoclimate (Berger, 1988), a development of the Milankovitch theory (1941), solar radiation is the most important source of energy and is practically the only source for driving climatic processes. Thus, the major paleoclimatic variations are attributed to changing solar insolation due to the earth's orbital variations, or orbital cycles.

1.3.2 $\partial^{18}O$ records and climatic changes

The measurement of stable isotopes ^{16}O and ^{18}O from the calcite tests of foraminifera is a common method of determining past oceanic temperatures. Many foraminifera incorporate both oxygen isotopes into the carbonate of their tests in equilibrium with the surrounding sea waters (Emiliani, 1955). Generally, the $^{18}O/^{16}O$ ratios provide several types of information about climatic changes.

1) The $^{18}O/^{16}O$ ratios in foraminiferal tests reflect isotopic abundances in sea water and vary in correspondence to the storage of isotopically lighter oxygen in glaciers and ice caps at high latitudes. A larger $^{18}O/^{16}O$ ratio in sea water corresponds to the growth of ice-sheets, whereas a smaller ratio corresponds to the reduction of ice-sheets. This has been the case since the middle Pliocene (Shackleton and Opdyke, 1973; Shackleton and Hall, 1984).

2) The $^{18}O/^{16}O$ ratios in foraminiferal tests are also related to water temperature. Carbonate formed in warm waters has a lower value of the isotopic composition than carbonate formed in colder waters (approximately 0.22 ‰ $\partial^{18}O$ per °C).

Thus, foraminiferal $\partial^{18}O$ records serve as proxy records of past temperature changes in sea waters. Planktonic foraminifera provide a record of changes in the near-surface waters, and benthic foraminifera provide that of deep-water alterations. Variations in benthic $\partial^{18}O$ records correspond to those in planktonic $\partial^{18}O$ records. In consequence, based on variations in foraminiferal $\partial^{18}O$, a number of oxygen isotope stages, cold/warm stages or glacial/interglacial stages, have been established and are commonly used in stratigraphy.

The benthic $\partial^{18}O$ records are used as a proxy record of ice-volume (Shackleton, 1967; Imbrie at al., 1984; Williams et al., 1988; Ruddiman et al., 1989) and as indirect evidence for changing sea-levels. The magnitude of this glacio-eustatic effect as a result of glacial-interglacial oscillations over the last 1 m.y. has been estimated as being between 1.2 - 1.8 ‰ $\partial^{18}O$ or as sea-level changes of between 110 - 164 metres (William and Fillon, 1984; Shackleton, 1987).

Recently, it has been found that the fluctuations of the benthic oxygen isotope record are sensitive mainly to northern hemisphere ice sheet variations and to changes in deep water temperatures. These variations are in response to astronomic forcing of the earth's insolation, and benthic $\partial^{18}O$ data are used for studying orbital cycles and astronomical time scales

(Imbrie et al., 1980, 1984, 1992, 1993; Ruddiman et al., 1981, 1989; Raymo et al., 1989; Martinson et al., 1987; Shackleton et al, 1990, 1994; Tiedemann et al., 1994).

1.3.3 Coccolithophorids and their fossil record

As a pelagic phytoplankton group, coccolithophorids are photosynthesising organisms which live in the photic zone of oceans (Figure 1.2). Coccolithophorids are a part of the marine ecosystem, and therefore are sensitive to the changes of various ecological factors in the marine environment.

The ecological factors which act on coccolithophorids are light, temperature, salinity, sea water stratification, turbulence, and nutrient availability (Paasche, 1964, 1969; McIntyre et al. 1970; Honjo and Okada, 1974; Bukry, 1974; Brand, 1984; Fisher and Honjo, 1991; Winter et al., 1994). These factors are physico-chemical parameters connected to oceanography. Biological parameters are genetic variations of coccolithophorids, life cycles, bloom zones, and tolerance to changing environmental stress as well as the relationship among coccolithophorid species and between coccolithophorids and other groups of organisms, e.g. diatoms (Brand, 1981, 1994; Hurbult, 1983; Young and Westbroek, 1991) and zooplankton grazers.

Coccolith assemblages preserved in sediments are fossil records of former coccolithophorid floras. Occurrences and abundances of coccolith species change substantially through geological time as the result of changing paleoceanographic conditions (McIntyre, 1967; McIntyre et al., 1970, 1972; Haq, 1980; Xu and Su, 1987; Roth, 1989, 1994) and biological evolution of coccolithophorids. Therefore, variations in coccolith fossil abundance reflect the ecological impact of paleoclimatic changes.

When interpreting coccolith records the following points should be borne in mind.

1) A coccolith assemblage in sediment is not a complete record of the former living community, since the latter has changed through a series of biological, physical and chemical processes after death. These processes include: a) grazing by zooplankton and selective destruction, b) sedimentation of coccoliths or transit from the surface waters to the sediment (Samtleben et al., 1995), c) chemical dissolution or selective preservation, d) diagenetic effects (Berger and Roth, 1975; Steinmetz, 1994). As shown in Figure 1.2, the majority of coccoliths reach the sea floor in faecal pellets of grazing zooplankton, which accelerate the sinking rates of coccoliths and protect them from dissolution (Roth et al., 1975; Honjo, 1976; Pilskaln and Honjo, 1987; Samtleben and Bickert, 1990; Steinmetz, 1991). The accelerated sinking rates of the faecal pellets help to minimize lateral drift by ocean currents and ensure that a death assemblage on the sea floor has its origin in the overlying surface waters. However, several warm-water species (e.g. *G. oceanica, U. tenuis, U. sibogae*) have been

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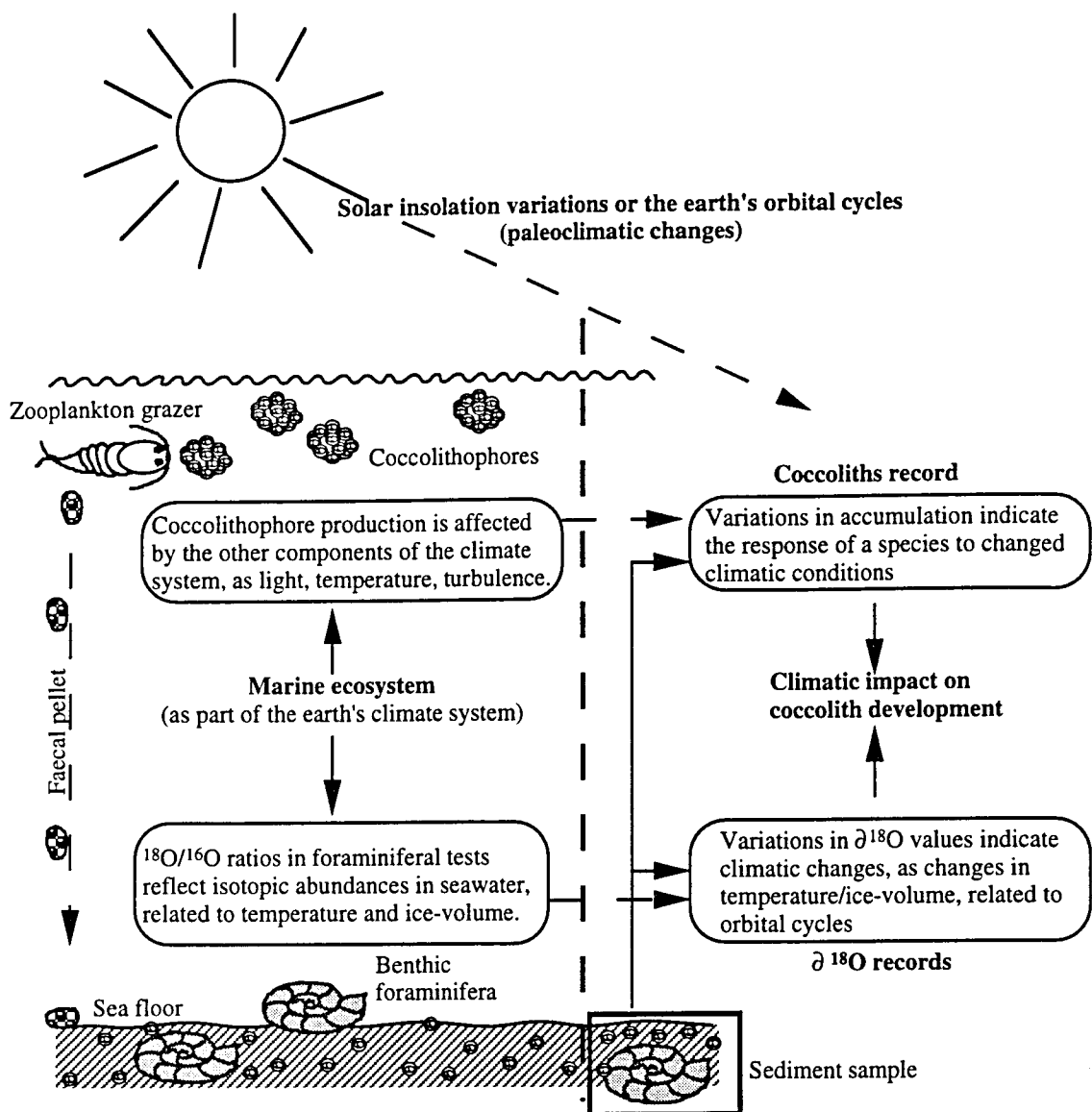
Figure 1.2 Generalized illustration of the ecosystem of living coccolithophorids and benthic foraminifera, and a correlation of the information about climatic changes provided by $\partial\,{}^{18}O$ records and by coccolith accumulation records. The transport of coccoliths from the photic zone to bottom sediments is after Honjo (1976).

drifted as death assemblages with the Atlantic drift into the surface waters of the Norwegian-Greenland Sea (Samtleben and Schröder, 1992). Owing to selective dissolution, many delicate coccoliths, including nearly all holococcoliths and several heterococcoliths (e.g. most species of *Syracosphaera*) dissolve, and only coccoliths with robust interlocking crystals, e.g. *Calcidiscus, Reticulofenestra, Gephyrocapsa, Coccolithus, Discoaster, Helicosphaera*, are resistant to dissolution and preserved in sediments (Adelseck et al., 1973; Berger and Roth, 1975). Therefore, only a small portion of living coccolithophorid species has a substantial fossil record.

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2) Distributions and abundances of coccolith species in sediments have also changed as a result of biological evolution. Generally, two broad levels of evolutionary processes are recognized: a) genetic changes, dealing with systematic changes in homologous alleles in local populations; b) evolution of major groups, which involves changes in the characteristics that distinguish major groups such as genera and families (Levinton, 1989; Grant, 1991). Genetic alterations within a species can lead to a change in ecological affinity of the species without attendant changes in morphological features, i.e. *Coccolithus pelagicus* which was abundant in the tropics during the early Cenozoic and migrated toward the poles during the late Cenozoic (Haq and Lohmann, 1976; Samtleben, 1978). Furthermore, genetic changes can induce changes in both morphology and ecological preferences and form a new species. For example, from about 0.36 to 0.27 Ma B.P. the warm-water species *Gephyrocapsa margereli* evolved into *G. muellerae* which has a smaller bridge angle than *G. margereli* and prefers cold waters (Samtleben, 1980). Thus, biological evolution can drive changes in biogeographical distributions and abundances of coccolithophores, which are not directly related to climatic changes.

In summary, variations in benthic $\partial^{18}O$ values are related to variations in temperature/ice-volume induced by climatic changes. Variations in coccolith occurrences and abundances are the result of both changing ecological conditions and biological evolution. Therefore, it is hopped to reconstruct the development of coccolith assemblages by analysing coccolith occurrences and abundances in sediments. These variations can reflect the changes in the marine ecosystem due to climatic fluctuations in the past. Information supplied by coccolith records should show a certain correlation with information provided by $\partial^{18}O$ records, as they are records of the same climatic system. This correlation should enable a deeper understanding of the climatic impact on the development of coccolith assemblages.

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CHAPTER 2   MATERIAL AND METHODS

2.1   Sites and samples

Upper Tertiary-Quaternary sediments from five DSDP/ODP sites located in the NE Atlantic were selected to investigate spatial and temporal variations in coccolith assemblages. The five DSDP/ODP sites: 664, 659 of Leg 108 and 608, 609, 610 from Leg 94 are aligned in a northerly direction in the NE Atlantic Ocean from about 0° to 53°N (Figure 2.1).

The objective of Leg 94 of the Deep Sea Drilling Project (DSDP) was to investigate high-latitude climatic changes in the northern hemisphere during the Neogene (Ruddiman et al., 1987). Leg 108 was designed to examine ocean-atmosphere circulation changes over Africa and in low latitudes (Ruddiman et al., 1988). According to the published results of Leg 94 and Leg 108, the Upper Tertiary-Quaternary strata of the five sites have high, continuous sedimentation rates with few interruptions by turbidites and hiatuses, also nannofossils from these sites are not strongly affected by carbonate dissolution. A variety of data sources, including magnetic data and stable isotopes, are available for stratigraphical analyses or comparisons with the coccolith data in this study. Therefore, these sites provide very good sources and data for the purposes of this study.
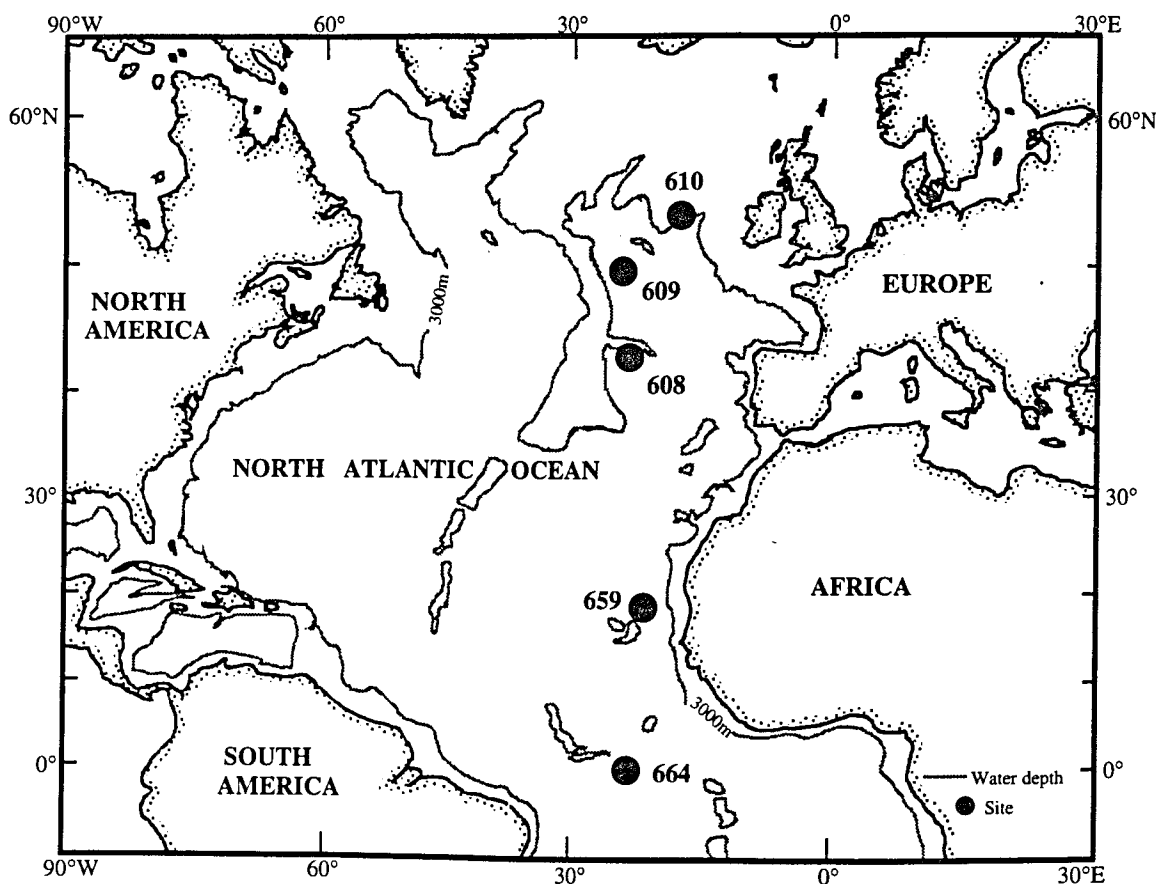

Figure 2.1 Location of ODP/DSDP sites studied.

2.1.1 Sites and lithology of sediments

Locations and sampling intervals of the investigated sites are given briefly in Table 2.1.

Leg	Site	Location			Sample			
		Latitude N	Longitude W	Water depths (m)	Core interval (mbsf)	Age interval (Ma)	Number of samples	Time resolution (in mean value: kyr/sample interval)
108	664D	0°06.44′	23°13.65′	3807	0.01-234.43	0-5.85	189	31
108	659	18°04.63′	21°01.57′	3070	0.01-157.06	0-5.94	150	39
94	608	42°50.21′	23°05.25′	3526	0.03-156.51	0-5.77	198	29
94	609	49°52.67′	24°14.29′	3884	0.12-313.54	0-5.52	203	27
94	610A	53°13.30′	18°53.21′	2417	0.01-199.70	0-4.96	164	30

Table 2.1 Summary of investigated DSDP/ODP sites and samples.

Site 664D is located in the central equatorial Atlantic on the eastern side of the mid-Atlantic Ridge, just north of the Romanche Fracture Zone. The investigated core sections are composed primarily of nannofossil and foraminifer-nannofossil oozes of late Miocene, Pliocene, and Quaternary age.

Site 659 lies on top of the Cape Verde Plateau near the eastern Atlantic continental margin. The studied core sections consist of interbedded nannofossil ooze and silt-bearing to silty nannofossil ooze or foraminifer-bearing nannofossil ooze, with minor portions of silt and clay. The upper part of the seismic record at this site is finely laminated (3 - 20 cm spacing) and the susceptibility curves of Holes 659A, 659B, and 659C can be correlated (Bloemendal et al., 1988). This correlation allows the composition of a complete core down to a composite depth of about 204 mbsf (Bloemendal et al., 1988; Ruddiman et al., 1988; Tiedemann, 1991). This composite depth model was improved by Tiedemann et al. (1994) by the correlation of core sections in Holes 659A, 659B, and 659C from 41 to 146 m composite-depth. In the present study, most samples are from Hole 659A and only a few samples are from Hole 659B (sections 5H, 6H). The composite-depths of samples from 41 to 146 m are constructed following the model of Tiedemann et al. (1994); while those from 0 to 41 m and from 146 to 156 m are after Tiedemann (1991). The results of the composition in this study agree well with the results of Tiedemann et al. (1994).

Site 608 is on the southern flank of the King's Trough. Most of the Pliocene consists of a sequence of chalks to oozes. Glacial-interglacial carbonate cycles begin at around 76 m sub-bottom in the lower Pliocene and continue to the top of the hole. The initiation of glaciation recorded at this location is at about 2.6 Ma (corr.) (Ruddiman et al., 1987).

Site 609 lies on the eastern flank of the Mid-Atlantic Ridge. The Quaternary to upper Pliocene sediments (0-171 m sub-bottom) are alternations of calcareous muds, marly nannofossil oozes, and nannofossil oozes. These sediment changes have been interpreted as

being due to alternations of glacial polar waters with interglacial temperate waters. These alternations began on a large scale at about 2.6 Ma (corr.) in the North Atlantic. The Pliocene to upper Miocene (171-399.4 m sub-bottom) consists of nannofossil oozes and chalks.

Site 610 is located on the western side of the Rockall Trough at the crest of the Feni Ridge. The sediment interval 0 to 135 m sub-bottom in Hole 610A consists of alternating calcareous mud and foraminifer-nannofossil ooze of Quaternary and late Pliocene age. The cycles are considered to be related to glacial-interglacial oscillations since 2.6 Ma (corr.). All sediments below 135 m are white to pale grey and green nannofossil oozes and chalk.

2.1.2   Sample density and time resolution

As shown in Table 2.1, sampling intervals are about one sample per meter for Quaternary samples and one sample per 1.5 m for Pliocene samples, which represents an average time resolution of one sample every 30 kyr. More samples were added to get intervals of one sample per 0.5 m for several Quaternary sediment sections in which distinct changes in coccolith assemblages were observed.

2.2   Stratigraphy

2.2.1   Age models

Construction of age models is very important for estimating ages of coccolith events and the correlation of coccolith assemblages from different sites. In order to establish exact age models, it is necessary to use an accurate time scale with reliable stratigraphical data.

Time scale

Recently, instead of the commonly used time scale of Berggren (1985), two new time scales have become more widely accepted and used: the magnetostratigraphic time scale of Cande and Kent (1992) and the Late Neogene time scale of Shackleton et al. (1994). Differences between these two time scales in the Neogene are small. However, the Shackleton's one is an astronomical time scale calibrated according to orbital variations and is more accurate for Neogene geological time resolution. Therefore, in this study, age models are reconstructed using the time scale of Shackleton et al. (1994).

Tiedemann et al. (1994) suggested an astronomical time scale for the Pliocene-Quaternary Atlantic $\partial^{18}O$ records of ODP site 659 and a number of age data, including the LAD of several nannofossil species. Ages of several data are slightly different from those given by Shackleton et al. (1994). In this investigation, site 659 is the key-site used to depict

the linkage between paleoclimatic changes and coccolith development. Thus, some age data proposed by Tiedemann et al. (1994) were also used (Table 2.2).

Magnetic reversals, biostratigraphical data, stratigraphical boundaries	This work	Tiedemann et al. [1994]	Shackleton et al. [1994]	Cande & Kent [1992]	Young et al. [1994]	Berggren et al. [1985]
	Age (Ma)	Age (Ma)	Age (Ma)	Age (Ma)	Age (Ma)	Age (Ma)
FAD *E. huxleyi*	0.30				2.80 (1)	0.275
LAD *P. lacunosa*	0.49				0.46 (1)	0.474
Brunhes/Matuyama	0.78	0.78	0.780	0.78		0.78
Top Jaramillo	0.99	0.99	0.990	0.984		0.91
Bottom Jaramillo	1.07	1.07	1.070	1.049		0.98
Top Cobb Mountain	1.22			1.201		
Bottom Cobb Mountain	1.23			1.212		
LAD *C. macintyrei*	1.58	1.58±0.02	1.600		1.45 (1)	1.45
Top Olduvai	1.77	1.78	1.770	1.757		1.66
Bottom Olduvai	1.95	1.94	1.950	1.983		1.88
LAD *D. brouweri*	1.96	1.97±0.02	1.961		1.89 (1)	1.90
Top Reunion	2.18			2.197		
Bottom Reunion	2.21			2.229		
LAD *D. pentaradiatus*	2.50	2.52			2.35 (1)	2.40
Matuyama/Gauss	2.60		2.600	2.6		2.47
LAD *D. tamalis*	2.83	2.83			2.65 (1)	2.60
Top Kaena	3.04		3.040	3.054		2.92
Bottom Kaena	3.11		3.110	3.127		2.99
Top Mammoth	3.23		3.233	3.221		3.08
Bottom Mammoth	3.33		3.331	3.325		3.18
Gauss/Gilbert	3.59	3.59±0.03	3.594	3.553		3.40
LAD *S. abies&neoabies*	3.62				3.45 (1)	3.47
Top Cochiti	4.17	4.17±0.03	4.199	4.033		3.88
Bottom Cochiti	4.32		4.316	4.134		3.97
Top Nunivak	4.48		4.479	4.265		4.10
Bottom Nunivak	4.62		4.623	4.432		4.24
Top Sidufjall	4.78		4.781	4.611		4.40
Bottom Sidufjall	4.88		4.878	4.694		4.47
Top Thvera	4.98		4.977	4.812		4.57
FAD *C. rugosus*	5.20	5.23±0.01			4.66 (2)	4.50
LAD *D. quinqueramus*	5.47				4.98 (2)	5.60
Top C3 An.1n	5.88		5.875	5.705		5.35

Table 2.2 Comparison of time-scales. Reference (1): Takayama (1993). (2): Backman et al. (1990).

Recalibrated age data

Since the time scale of Shackleton et al. (1994) is a very new one, many age data in previous literature use the time scale of Berggren et al. (1985). In order to avoid confusion, these age data were recalibrated to correspond to the time scale of Shackleton et al. (1994) by using the reference timetable of Wei (1994); and are marked "(corr.)".

For example, the Late Tertiary and Quaternary geological time scale summarized by Harland et al. (1989) is utilized in this study (Table 2.3). According to this scale, the age of the Pliocene-Pleistocene boundary is 1.75 Ma (corr.), the age of the Upper Pliocene-Lower

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Pliocene boundary is 3.59 Ma (corr.) and that of the Miocene-Pliocene boundary is 5.72 Ma (corr.). The dates of 1.75, 3.59, and 5.72 are recalibrated from the original data of 1.64, 3.46, and 5.2 Ma in the study of Harland et al. (1989). Thus, the coccolith records in this investigation begin with the Early Pliocene.

Era	Sub-era Period	Epoch		Harland et al. (1989) Age (Ma)	This work Age (Ma)
Late Cenozoic	Quaternary	Holocene		0.01	0.01
		Pleistocene			
				1.64	1.75
	L.Tertiary / Neogene	Pliocene	Plio 2	3.40	3.59
			Plio 1		
				5.2	5.72
		Miocene			

Table 2.3 Late Tertiary and Quaternary geological time scale (after Harland et al., 1989).

Magnetochronological and biochronological data

In general, magnetochronological data are more accurate and reliable than biochronological data (Hailwood, 1989; Hills and Thierstein, 1989; Spencer-Cervato et al., 1994). Neogene calcareous nannofossil biochronological data are commonly estimated by correlation with magnetochronological data (Backman, 1990; Takayama, 1993). These nannofossil biochronological data were discussed and summarized during the Fifth International Nannofossils Conference, Salamanca (Spain), 1993 (Young et al., 1994).

In the present study, nearly all available magnetic data from the DSDP/ODP sites were used as basic control points for the reconstruction of age models. Additionally, several nannofossil data determined in this study were selected as age control points and their ages estimated after Backman (1990) and Takayama (1993). All selected magneto- and biochronological data (Table 2.4) were recalibrated to correspond to the time scale of Shackleton et al. (1994), (Table 2.2).

There are still several problems in determining and using biostratigraphical data.

The first problem lies in the identification of species which are used as stratigraphical markers. Morphologically, many species vary within a large range and there are intermediate forms between species within a genus. In the case of evolution, a species develops into another species through a gradual morphological change over a certain transition period. This results in a morphological overlap between the species and its descendant. The intermediate forms, e.g. coccoliths in the overlapping area of *G. lumina* and *G. oceanica* (Figure 3.9 in chapter 3, Figures 4.2a-e in chapter 4), may be identified as either one of these two species by various authors who make mostly typological identification, and so the levels of the FAD of *G. oceanica* or the LAD of *G. lumina* can vary from author to author.

| Magnetic reversals & biostratigraphical data | Sub-top and sub-bottom in site | | | | | This work |
	Site 664 Depth (mbsf)	Site 659 Depth (mbsf)**	Site 608 Depth (mbsf)	Site 609 Depth (mbsf)	Site 610 Depth (mbsf)	Age (Ma)
FAD *E. huxleyi*		10.34-11.06	5.70-7.02	17.43-18.13	17.01-18.02	0.30
LAD *P. lacunosa*	15.02-16.52	15.09-15.79	9.02-9.52	22.63-23.63	25.11-26.61	0.49
Brunhes/Matuyama	27.9	24.80	15.49-17.59	42.79-44.29	41.61-43.31	0.78
Top Jaramillo	35.8	30.60	17.59-19.09	55.99-57.49	52.76-54.38	0.99
Bottom Jaramillo	38.2	33.00	20.59-21.99	63.49-65.59	55.88-57.98	1.07
Top Cobb Mountain			21.99-23.59	74.41-75.19	61.24-62.74*B	1.22
Bottom Cobb Mountain			23.59-25.09	75.89-76.69	62.74-64.23*B	1.23
LAD *C. macintyrei*	60.44-61.94	45.87-46.67	33.73-34.21			1.58
Top Olduvai		51.56*B		118.09-119.59	92.56-94.39	1.77
Bottom Olduvai		56.16*B		131.41-133.09	97.88-98.38	1.95
LAD *D. brouweri*	77.43-78.85	(?53.87)-57.05	41.32-42.32			1.96
Top Reunion			66.0-67.54*A	144.91-145.69	105.95-107.48	2.18
Bottom Reunion			68.80-70.30*A	146.41-147.19	107.48-109.25	2.21
LAD *D. pentaradiatus*	107.46-107.84	72.98-73.68				2.50
Matuyama/Gauss			84.79-86.29	171.19-171.86	126.68-128.18	2.60
LAD *D. tamalis*	124.22-125.84	82.28-83.28	89.82-90.82			2.83
Top Kaena			92.29-94.39	211.4-213.5*B	150.38-153.98	3.04
Bottom Kaena			100.39-101.89	217.99-219.89	153.98-155.48	3.11
Top Mammoth			103.66-103.99		156.98-158.48	3.23
Bottom Mammoth			106.99-108.49		161.50-163.58	3.33
Gauss/Gilbert		102.47-103.87*C	109.31-109.99	238.71-240.21	168.08-169.58	3.59
LAD *S. abies&neoabies*	153.72-155.02	104.56-107.05				3.62
Top Cochiti		117.00-119.18*C		256.39-257.89	176.18-177.68	4.17
Bottom Cochiti				261.07-262.57	179.18-180.28	4.32
Top Nunivak				264.60-265.99	190.28-192.38	4.48
Bottom Nunivak				271.97-273.47	195.38-196.88	4.62
Top Sidufjall				277.05-278.75	196.88-198.38	4.78
Bottom Sidufjall				281.87-282.83		4.88
Top Thvera				285.7-286.97*B		4.98
FAD *C. rugosus*	206.5-208.01	148.39-149.39	146.92-147.92			5.20
LAD *D. quinqueramus*	218.30-219.80	150.85-153.31	153.52-154.52			5.47
Top C3 An.1n				330.91-333.08		5.88

Table 2.4 Magneto- and biostratigraphical control points used for construction of age models of sites. Magnetic data are after Clement and Robinson (1987). Tauxe et al. (1989) and Tiedemann et al. (1994); data with * are transferred from Hole A/B/C. depths (mbsf)** of site 659 are composite depths.

The second problem lies in determining levels of the FAD/LAD of stratigraphical markers. Commonly, the FAD of a species is observed only when it becomes more common in sediments; and a species often becomes very rare in sediments before its extinction. An extinct species can also be found in younger sediments due to reworking or disturbances. For these reasons, determinations of the FAD/LAD levels depends mostly on the abundance patterns around the appearances or extinctions of stratigraphical markers. For example, recognition of the LAD of *G. caribbeanica* in the studied cores is relatively easy, since its extinction is characterized by an abrupt decrease in abundance (Figure 3.10); while the LAD of *R. pseudoumbilicus* is difficult to determine, due to its abundance fluctuating over a long

period (Figure 3.21). Various extinction patterns of coccolith species indicated by absolute abundance patterns have been observed in this study. These patterns agree well with those in the study of Backman (1986), who found several Neogene species to have different extinction patterns with changing accumulation rates in sediments.

Furthermore, different ecological affinities of fossil species also cause difficulties in use of their FAD/LAD in certain areas. For example, *Discoaster brouweri* is abundant in low latitudes whereas it is rare in high latitudes. Therefore, the LAD of *D. brouweri* can only be used in low latitudes, i.e. for the construction of age models of sites 664, 659 and 608 in this study (Table 2.4).

2.2.2   Age-depth correlation

Using the selected time scale and chronological data from the five studied sites, ages of samples from each site were calibrated by interpolation of the depths and ages of the control points used in the sites (Figures 2.2a-e). Some remarks on the use of these data are given below.

Site 664D: Only a few magnetochronological data for site 664 (Figure 2.2a) are available, namely the boundary of Brunhes/Matuyama and Jaramillo-top and bottom. Therefore, the age model for this site was constructed mainly by using nannobiochronological data: mostly the LAD of *Discoaster* forms. Fortunately, this site is located in the tropical area and these *Discoaster* species are abundant with relatively distinct LAD levels. However, the FAD of *E. huxleyi* recorded in this study seems to be too young (5.52 m) and may be unreliable. This may be caused by strong dissolution around the sample interval (see also Figure 3.8 in chapter 3). Hence, the FAD of *E. huxleyi* was not used in the age model.

Site 659:   The stratigraphy of site 659 is shown in Figure 2.2b. Although this stratigraphy was made by using magneto- and biostratigraphical data, its results agree well with that given by Tiedemann et al. (1994). This agreement in stratigraphy is very important and provides the possibility of correlating changes in coccolith assemblages with climatic changes as suggested by Tiedemann et al. (1994) in the same time levels (chapter 5) .

Site 608:   There are several problems with the stratigraphy of site 608 (Figure 2.2c). Firstly, both magneto- and biostratigraphical levels between the core depth interval of 40 m and 55 m are not reliable. Results of counting analyses in this study show a strong reworking in this interval (Figure 4.2c). Certain forms of *Gephyrocapsa* that occur only in younger sediments were observed in these samples (S&B). These observations suggest a mixing of older and younger samples, which is probably caused by coring or sampling. A further analysis of this study shows that using the magnetic reversals of Olduvai events would create
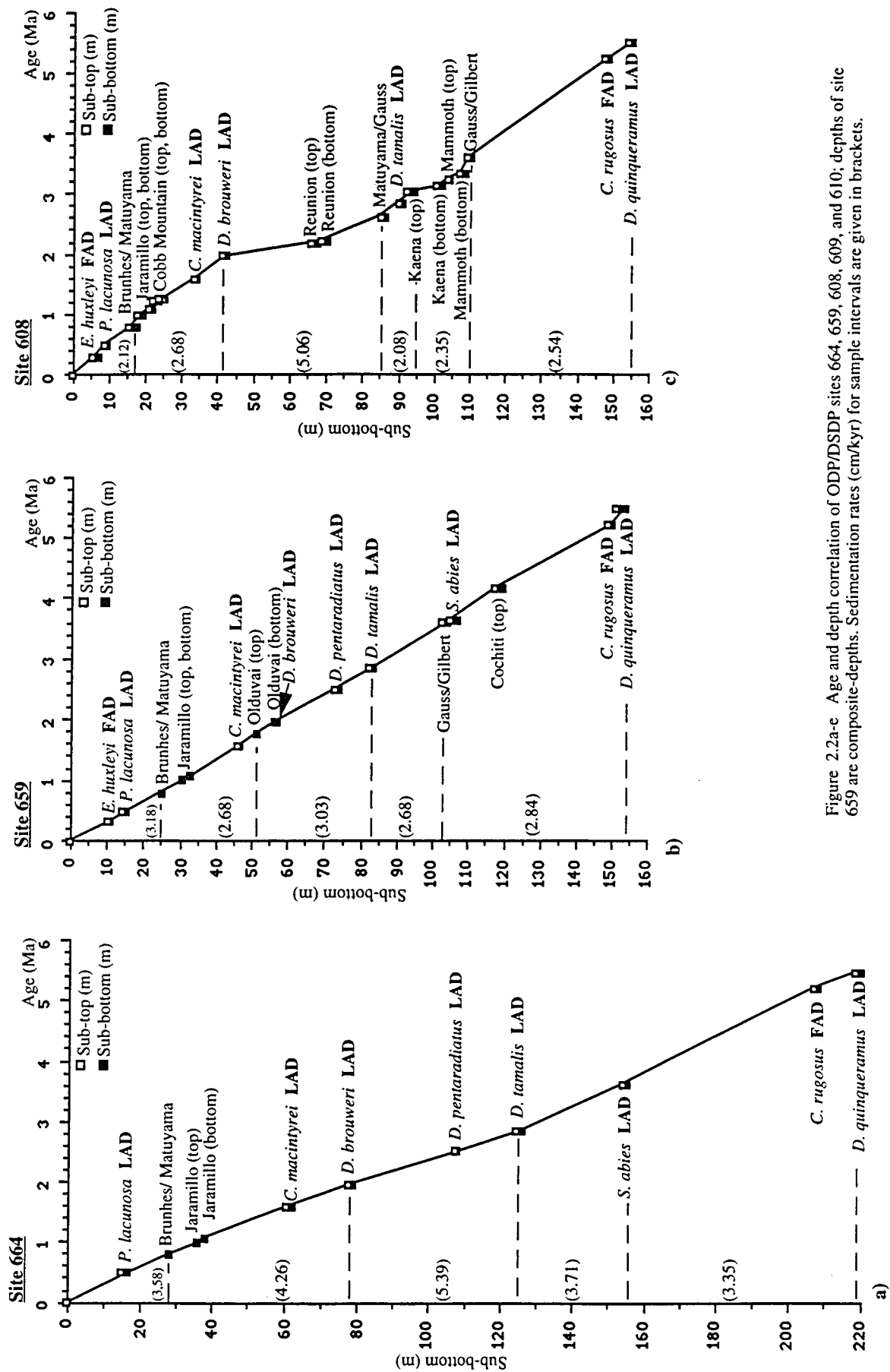
Figure 2.2a-e   Age and depth correlation of ODP/DSDP sites 664, 659, 608, 609, and 610; depths of site 659 are composite-depths. Sedimentation rates (cm/kyr) for sample intervals are given in brackets.

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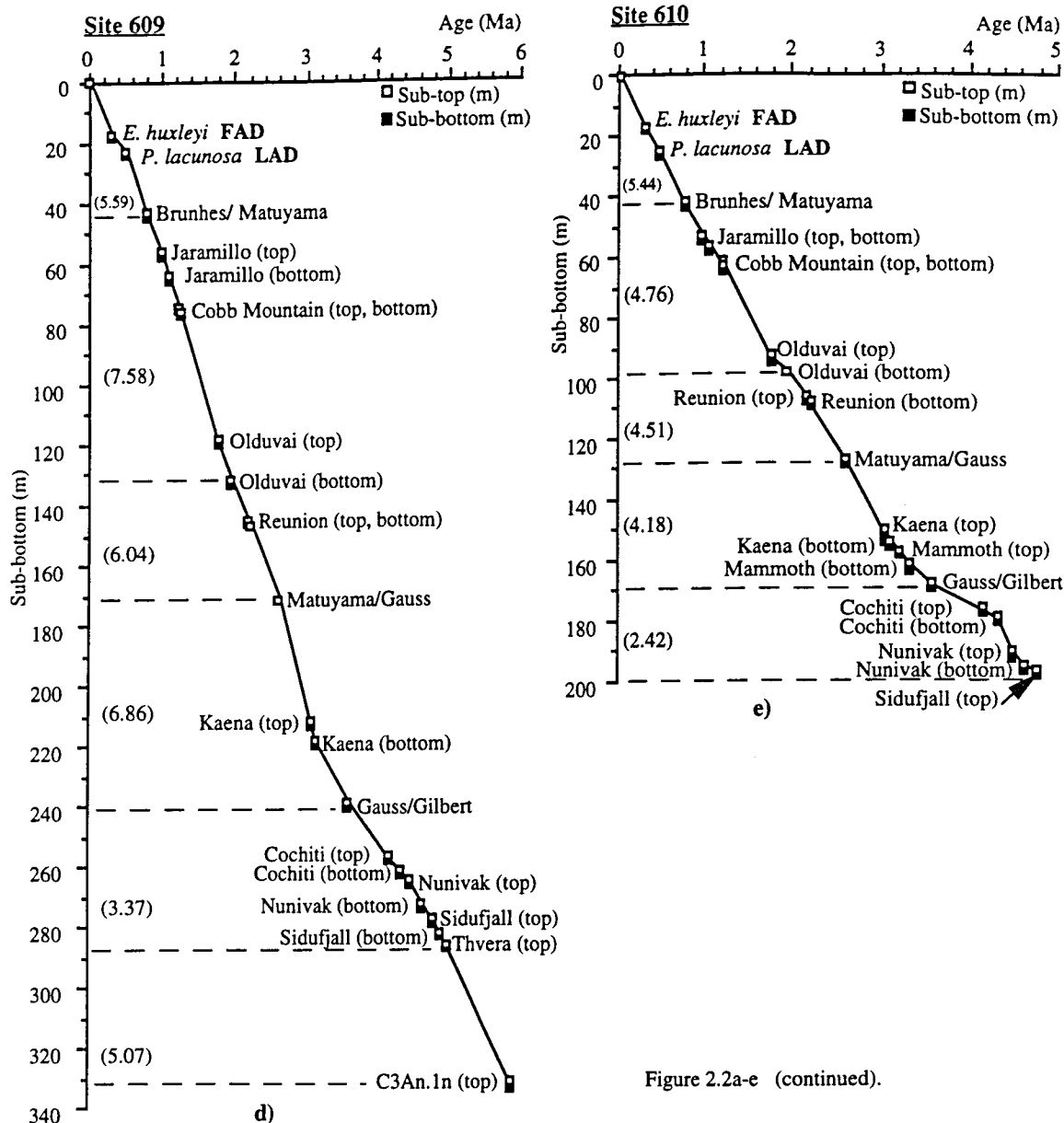
Figure 2.2a-e (continued).

difficulties in correlation of coccolith events with those at other sites, a better correlation can be achieved by using the LAD of *D. brouweri* at this site. There are no good stratigraphical data available for samples below the Gauss/Gilbert reversal. Additionally, the LAD of *S. abies* group is clearly not usable in this area. Therefore, based on further observations the FAD of *C. rugosus* and the LAD of *D. quinqeramus* were used as control points.

Sites 609 and 610: These two sites (Figures 2.2d-e) supply abundant magnetic data. However, many nannobiostratigraphical data, e.g. the LAD of *Discoaster* species and the LAD of *C. macintyrei*, are not usable owing to their earlier disappearances in these areas. Therefore, age models for these two sites were constructed mainly by using magnetic data and only two fossil data: the LAD of *P. lacunosa* and the FAD of *E. huxleyi*.

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2.2.3 Sedimentation rates

The sedimentation rates at the five studied sites were interpolated linearly from the magneto- and nannobiostratigraphic control points used in the age models. Sedimentation rates for various sample intervals in these sites are given in Figures 2.2a-e and they were used for the calculation of accumulation rates (section 2.4).

2.3 Qualitative analyses

2.3.1 Investigation by microscope

A light microscope (LM) was used to observe coccoliths in this study. As given in section 2.1.2, a great number of samples were taken to obtain a relatively high time resolution of sediments. Preparing samples for LM is easier, quicker and more economical than for a scanning electron microscope (SEM). The features of calcareous nannofossils observed under polarized light allow identification to a relatively reliable degree. For these reasons, in this study, observations and counts of coccoliths were made mainly by means of LM.

The magnification (x1000 in this study) and resolution of LM are limited, which can cause difficulties in identifying certain coccolith species. For example, a safe identification of small sized species, such as *Emiliania huxleyi* and small *Gephyrocapsa* species, can only be made by using SEM. In these cases, counts of species with LM have usually been supported by using SEM or SEM micrographs.

2.3.2 Separating and grouping methods

Two methods, separating and grouping, are commonly used in identifying coccoliths.

The first method is separating. In effect, the most difficult problem in identification is to separate species within a genus, which are morphologically very similar to each other. Usually, these species show a great deal of morphological variation and these variations overlap, forming series of intergradations between distinct individuals/end-members of different species.

Figure 2.3 illustrates two examples of morphological overlapping in coccolith length and opening widths of two species. A and B are separate species, but they vary greatly in coccolith lengths and opening widths. The overlap between coccolith lengths is in the range 4.5 to 5.5 μm (Figure 2.3b) and between opening widths in the range 35 to 45% (Figure 2.3c). Distinct individuals of A (smaller than 4.5 μm in Figure 2.3b) are never confused with the end-members of B (larger than 5.5 μm). However, coccoliths falling within the overlapping
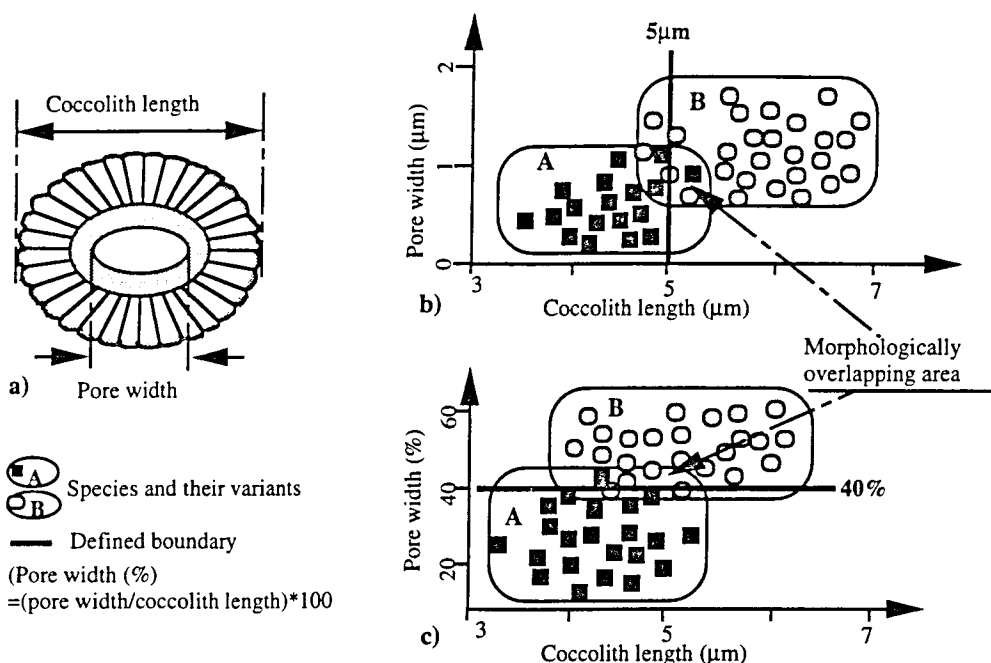
Figure 2.3 Method for separating morphologically related species in counting analyses. a) biometrical features; b) variations of species A and B have partly overlapping coccolith lengths; c) A and B have overlapping pore widths. According to results of biometrical studies, separating A from B can be made by definite criteria or boundaries, such as a certain value of coccolith length (b); or a certain value of pore width (c).

area are intergradations between A and B and are impossible to separate, when these forms are chiefly identified by features as coccolith lengths and central opening widths. Such a case is commonly seen within the genera: *Gephyrocapsa, Reticulofenestra,* and *Calcidiscus.*

During the last decades, a number of biometrical analyses have been carried out on these genera, for example, the studies of *Reticulofenestra* by Backman (1980) and Young (1990); the study of *Gephyrocapsa* by Samtleben (1980); and the studies of *Calcidiscus* by Janin (1981) and Knappertsbusch (1990). These studies suggested a number of reliable boundaries, usually size diagnoses, for separating forms and species within these genera. These size diagnoses can be easily recognized and determined by means of LM.

For these reasons, in the present study, separating intergrading species was made by means of biometrically defined boundaries. Detailed problems and their resolutions are given in chapter 3.

Grouping was used for species that are impossible to separate accurately by means of LM, e.g. small *Gephyrocapsa* species which can only be accurately separated by biometrical analysis with SEM (S&B). Therefore, all small *Gephyrocapsa* species are grouped together. Additionally, several taxa having similar distributions, but few ecological or stratigraphical applications, are grouped and identified only at genus level. *Scyphosphaera* spp., *Amaurolithus* spp., etc., fall into this category.

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2.4   Quantitative analyses

Quantitative analyses are commonly used in microfossil research for investigating and depicting changes in microfossil assemblages, especially those changes in connection with climate or paleoceanography. Usually, two quantitative analyses are used: relative abundance counts and absolute abundance counts.

2.4.1   Absolute abundances

An absolute abundance count has been chosen for the present study. The absolute abundance of a species is determined as the number of specimens per gram sediment, that is, fossil specimens are treated as sediment particles. Thus, coccolith absolute abundances are directly controlled by sedimentary processes, such as export production, dissolution of carbonate, and terrigenous dilution. All these processes are influenced by past oceanic conditions. Variations in coccolith absolute abundances can provide evidence of the links between coccolithophores and environment, including past climate.

An accurate and appropriate method for preparing samples for an absolute quantitative study of coccoliths is necessary. Several methods were selected from literature (Backman and Shackleton, 1983; Wei, 1988; Beaufort, 1991) and tested. These tests showed that Beaufort's method produces a random distribution of particles and reproducible results and that counting results derived from this method are more accurate than those from other methods.

The method of Beaufort is a random settling technique adapted from Moore (1973), which is commonly used in the study of Radiolaria. The reliability of Moore's method has been tested by a number of studies. These tests found an accurate absolute number of fossils derived from this method representative of the original material (Laws, 1983; Granlund, 1984). The random settling technique is also widely used in analysing diatoms to obtain random distributions of diatoms on slides and reproducible results (Meng, 1994).

In the present study, the method of Beaufort (1991) is used but has been slightly modified for preparing a large number of samples. The procedures are described below:

A certain amount of dry sediment sample is weighed and diluted in a beaker with a given volume of distilled water (buffered to a pH of 9), it is then subjected to ultrasound for about 10 sec and stirred thoroughly for several minutes to obtain a homogenized suspension of sediment. The suspension is carefully poured into another beaker into which a coverglass attached to a platform has been placed (Figure 2.4). The beaker is then left in an oven (40°C) for several days. Coccoliths, together with other sediment particles, will randomly settle on the coverglass and the water will slowly evaporate. After the water level has dropped below the coverglass, the coverglass is dry and covered with thin sediment coating. The dry
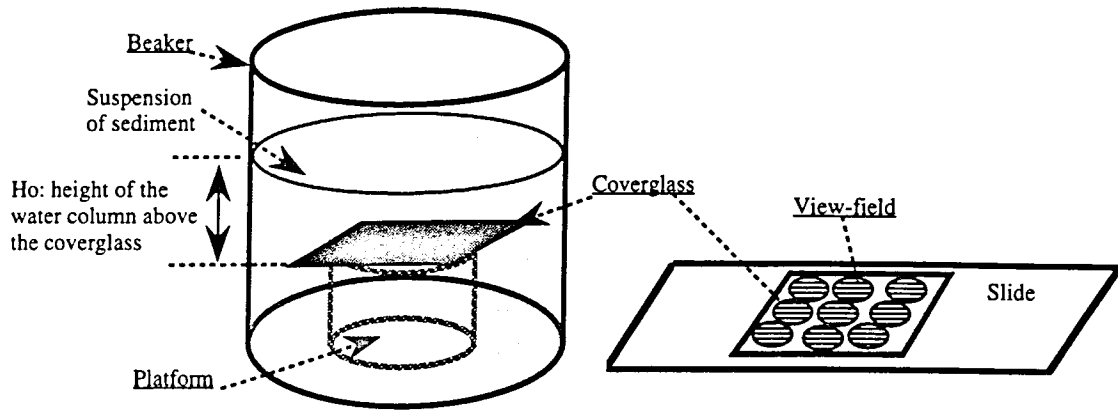
Figure 2.4 Method for preparing samples used in this study, which is a modification of the method of Beaufort (1991).

coverglass is then mounted on a slide and counting analyses using LM can then be carried out.

In this study, all fossil taxa represented in a view-field were identified and usually more than 400 coccoliths on a slide were counted.

The absolute abundance of a species (AA) can then be calculated with formula (1):

$$AA \text{ (number of coccoliths / gram sediment)} = (A * Vs)/(N * S * G * Ho) \qquad (1)$$

G = Weight of a sample

Vs = Volume of the sediment suspension

Ho = Height of the water column above the coverglass

S = Surface area of a view-field

N = Number of viewfields investigated

A = Number of coccoliths counted.

2.4.2 Relative abundances

The counting results have been also used for the calculation of the relative abundance of a species (RA) by using formula (2):

$$RA \text{ (\%)} = (A / Asum) * 100 \qquad (2)$$

A = Number of coccoliths of a species

Asum = Number of coccoliths of all taxa.

2.4.3 Accumulation rates

Coccoliths are sediment particles and therefore coccolith accumulation rates (AR coccoliths) of a species can be calculated as:

$$AR_{coccoliths} \text{ (number of coccoliths} * cm^{-2} * kyr^1)$$
$$= AR_{bulk} \text{ (g} * cm^{-2} * kyr^1) * AA \text{ (number of coccoliths} * g^{-1}) \qquad (3.1)$$

According to Ehrmann and Thiede (1985), the accumulation rates of sediment bulk can be calculated as:

$$AR_{bulk} \text{ (g} * cm^{-2} * kyr^{-1}) = LSR \text{ (cm} * kyr^{-1}) * DBD \text{ (g} * cm^3) \qquad (3.2)$$
$$DBD \text{ (g} * cm^{-3}) = WBD \text{ (g} * cm^{-3}) - \{Dcorr. \text{ (g} * cm^{-3}) * POR \text{ (\%)} * 100^{-1}\} \qquad (3.3)$$

LSR = linear sedimentation rates
DBD = Dry-bulk density of a sample
WBD = Wet-bulk density of a sample
POR = Porosity of a sample
Dcorr. = Density corrector for porewater (Dcorr. is 1.0363 in the North Atlantic Ocean, after Boyce, 1976).

The physical properties of the sediments from the studied sites are available from the Initial Reports of DSDP Leg 94 (Ruddiman et al., 1987) and of ODP Leg 108 (Ruddiman et al., 1988). Data of linear sedimentation rates for the five studied sites and of coccolith absolute abundances are given in Figure 2.3 and Tables 3.6-3.10 in the appendix.

The accumulation rate of a coccolith species is treated as an input of this species to ocean sediments. It is mainly controlled by the primary abundance or production of the species in the former coccolithophorid flora. It is also controlled by various parameters in sedimentary processes, such as destruction by grazing zooplankton, dissolution of carbonate, terrigenous dilution, or the input of other fossil groups in a given time interval. Thus, variations in the accumulation rates of a species are closely related to variations in past oceanic conditions. Coccoliths accumulation data are used for depicting variation patterns of coccolith species correlated to past climatic changes (chapter 4, 5).

2.5   Statistical analyses

A statistical method, the coefficient of variation, was introduced to analyse and compare variability of coccolith accumulation rates and that of benthic $\partial^{18}O$ data from site 659 (Tiedemann et al., 1994) during the last 5.2 m.y.

In statistics, the coefficent of variation is used to measure the relative variation of a sample population (Devore and Peck, 1986). A high coefficent indicates an unstable sample population and a low one indicates a stable population.

The Pliocene and Quaternary coccolith accumulation (ARcoccoliths) data and $\partial^{18}O$ data are, in terms of statistics, records of a variable through time (Swan and Sanilands, 1995). These two data sets are subdivided by using the same time intervals which is 0.25 m.y. per interval for Quaternary samples and 0.5 m.y. per interval for Pliocene ones. This is made on the basis of the good agreement in the stratigraphy of site 659 with the study of Tiedemann et al. (1994) and the close stratigraphical correlations between the studied sites. Thus, variations in accumulation rates of a species through a given time interval is a time series X_t (X_1, X_2, ..., X_n), and variations in the $\partial^{18}O$ data through the same time interval is also a time series Y_t (Y_1, Y_2, ..., Y_n). The coefficient of variation (CV) of these two time series in a given time interval are calculated by the equations (4.1 - 4.3):

1) Equation for sample mean:

$$\overline{X} = \frac{1}{n} \sum_{i=1}^{n} X_i \qquad\qquad \overline{Y} = \frac{1}{n} \sum_{i=1}^{n} Y_i \qquad\qquad (4.1)$$

2) Equation for sample standard deviation:

$$Sx = \sqrt{\frac{1}{n-1} \sum_{i=1}^{n} (X_i - \overline{X})} \qquad Sy = \sqrt{\frac{1}{n-1} \sum_{i=1}^{n} (Y_i - \overline{Y})} \qquad (4.2)$$

3) Equation for sample coefficent of variation (CV):

$$CVx \,(\%) = (Sx \div \overline{X}) * 100 \qquad CVy \,(\%) = (Sy \div \overline{Y}) * 100 \qquad (4.3)$$

In the case of this study, a high ARcoccoliths coefficent is related to a large-amplitude variation in production levels and a low one is related to a steady productivity of the species. Also, a high $\partial^{18}O$ coefficent is induced by large-amplitude variations in $\partial^{18}O$ and a low one is related to small-amplitude variations in $\partial^{18}O$. Therefore, in the present study, ARcoccoliths coefficients and $\partial^{18}O$ coefficients are called coccolith fluctuation rates and $\partial^{18}O$ fluctuation rates. Further interpretations are given in chapter 5.

CHAPTER 3   DESCRIPTION OF INVESTIGATED TAXA

3.1. Classification system

Recently, Jordan and Kleijne (1994) suggested a new classification system for extant coccolithophores. The majority of species found in this investigation still live today, this makes the use of the new system for these taxa possible (Table 3.1). However, a few extinct taxa, for example *Discoaster* spp. and *Sphenolithus* spp., do not appear in this classification system. In these cases, the classification of Tappan (1980) was used.

3.2   Descriptions and illustrations

Instead of biological species determined by living coccospheres, life cycles etc., species mentioned in this study are "palaeontological species", as only separate coccoliths are preserved in sediments and can be identified mainly by morphological features.

A detailed description is unnecessary, since most species found in this study have been described in previous literature. Only a few of the important and most abundant genera, such as *Reticulofenestra* and *Gephyrocapsa*, are described, in order to discuss the identification of various species.

Family Calciosolenianceae Kamptner 1937
Genus *Scapholithus* Deflandre, in Deflandre and Fert 1954
Scapholithus fossilis Deflandre, in Deflandre and Fert 1954

1954 *Scapholithus fossilis* Deflandre: 165, pl. 8, figs. 12, 16-17.

Description: Deflandre, in Deflandre and Fert, 1954: 165.

Remarks: This is a "palaeontological species" determined by morphology only. Reinhardt (1972) pointed out that the *Scapholithus* forms identified by Deflandre (1954) are coccoliths from two separate biological species: *Calciosolenia murrayi* Gran 1912 and *Anoplosolenia brasiliensis* (Lohmann 1919) Deflandre 1952, which are distinguished by having or not having long polar spines on the coccospheres. In sediments, only isolated coccoliths are found and it is impossible to identify them in term of biological species.

Occurrence: Rare in Pliocene and Quaternary sediments of all sites studied (Tables 3.6-3.10 in the appendix).

Classification system

Kingdom Protista Haecker 1866
Phylum Prymnesiophyta Hibberd 1976

Class Prymnesiophyceae Hibberd 1976

Order Coccolithophorales Schiller 1926

Family Calciosoleniaceae Kamptner 1937
   Genus *Scapholithus* Deflandre,
            in Deflandre and Fert 1954
     S. fossilis Deflandre,
             in Deflandre and Fert 1954

Family Ceratolithaceae Norris 1965
   Genus *Amaurolithus* Gartner and Bukry 1975
     Amaurolithus spp.
   Genus *Ceratolithus* Kamptner 1950
     Ceratolithus spp.

Family Coccolithaceae Poche 1913
   Genus *Calcidiscus* Kamptner 1950
     C. leptoporus (Murray and Blackman 1898)
            Loeblich and Tappan 1978
     C. macintyrei (Bukry and Bramlette 1969)
            Loeblich and Tappan 1978
   Genus *Coccolithus* Schwarz 1894
     C. pelagicus (Wallich 1877) Schiller 1930
   *Genus *Coronocyclus* (Hay, Mohler and
            Wade 1955) Stradner 1968
     Coronocyclus spp.
   Genus *Hayaster* Bukry 1973
     H. perplexus (Bramlette and Riedle 1954)
            Bukry 1973
   Genus *Neosphaera* Lecal-Schlauder 1950
     N. coccolithomorpha Lecal-Schlauder 1950
   Genus *Oolithotus* Reinhardt,
            in Cohen and Reinhardt 1968
     O. fragilis (Lohmann 1912)
            Martini and Müller 1972
   Genus *Umbilicosphaera* Lohmann 1902
     U. sibogae (Werbe-van Bosse 1901)
            Gaarder 1970

Family Helicosphaeraceae Black 1971,
            emend. Jarfar and Martini 1975
   Genus *Helicosphaera* Kamptner 1954
     H. carteri (Wallich 1877) Kamptner 1954
     H. sellii Bukry and Bramlette 1969
     Helicosphaera spp.

Family Noelaerhabdaceae Jerkovic 1970
   Genus *Emiliania* Hay and Mohler, in: Hay et al. 1967
     E. huxleyi (Lohmann 1902)
            Hay and Mohler, in Hay et al. 1967
   Genus *Gephyrocapsa* Kamptner 1943
     G. caribbeanica Boudreaux and Hay 1967
     G. lumina Bukry 1973
     G. oceanica Kamptner 1943
     G. margereli-muellerae group:
     G. margereli Breheret 1978
     G. muellerae Breheret 1978
     Gephyrocapsa forma V

     Gephyrocapsa spp. 1 (small species):
     G. aperta Kamptner 1963
     G. ericsonii McIntyre and Bé 1967
     G. rota Samtleben 1980
     G. sinuosa Hay and Beaudry 1973
     Gephyrocapsa forma D
     Gephyrocapsa forma F
     Gephyrocapsa forma H
     Gephyrocapsa forma P
     Gephyrocapsa forma V
     Gephyrocapsa forma Q
   *Genus *Pseudoemiliania* Gartner 1968
     P. lacunosa (Kamptner 1963) Gartner 1969
   Genus *Reticulofenestra* Hay, Mohler and Wade 1966
     R. asanoi Sato and Takayama 1991
     R. minuta Roth 1970
     R. minutula (Gartner 1967) Haq and Berggren 1978
     R. perplexa (Burns 1975) Wise 1983
     R. productella (Bukry 1975) Gallagher 1989
     R. pseudoumbilicus (Gartner 1967) Gartner 1969

Family Pontosphaeraceae Lemmermann 1908
   Genus *Pontosphaera* Lohmann 1902
     P. japonica (Takayama 1967) Nishida 1971
     P. syracusana Lohmann 1902
     Pontosphaera spp.
   Genus *Scyphosphaera* Lohmann 1902
     Scyphosphaera spp.

Family Rhabdosphaeraceae Ostenfeld 1899
   Genus *Rhabdosphaera* Haeckel 1894
     R. claviger Murray and Blackman 1898

Family Syracosphaeraceae Lemmermann 1908
   Genus *Syracosphaera* Lohmann 1902
     S. pulchra Lohmann 1902
     Syracosphaera spp.

GENERA INCERTAE SEDIS
   Genus *Umbellosphaera* (Paasche 1955)
     emend. Gaarder, in Heidmal and Gaarder 1981
     Umbellosphaera spp.

*Order Discoasterales Hay 1977

*Family Discoasterceae Tan Sin Hok 1927
   *Genus *Discoaster* Tan 1927
     D. brouweri (Tan 1927) emend.
            Bramlette and Riedel 1954
       D. asymmetricus morphotype
       D. tamalis morphotype
       D. triradiatus morphotype
     D. pentaradiatus (Tan 1927)
            Bramlette and Riedel 1954
     D. quinqueramus Gartner 1969
     D. surculus Martini and Bramlette 1963
     D. variabilis group
     Discoaster spp.

*Family Sphenolithaceae Deflandre 1952
   *Genus *Sphenolithus* Deflandre, in Grasse 1952
     S. abies group

Table 3.1 Classification system (mainly after Jordan and Kleijne, 1994; those with * after Tappan, 1980).

Family Ceratolithaceae Norris 1965

Genus *Amaurolithus* Gartner and Bukry 1975

Description: Gartner and Bukry, 1975: 454.

Remarks: Specimens of *Amaurolithus* are determined at genus level only (*Amaurolithus* spp.), because of their sporadic occurrence. *Amaurolithus* is horseshoe-shaped and seems to be similar to *Ceratolithus*, however *Amaurolithus* differs from the latter by being dark between crossed nicols. Several forms of *Amaurolithus*, for example *A. amplificus*, appear to show slightly birefringence. This indicates that *Ceratolithus* may have evolved from *Amaurolithus*.

Occurrence: Sporadic in Lower Pliocene sediments of sites 664, 659, 608 (Tables 3.6-3.8).

Genus *Ceratolithus* Kamptner 1950

Plate 7, Figure 41

Description: Kamptner, 1950: 154.

Remarks: Species of *Ceratolithus* are identified mainly as *Ceratolithus* spp., since they occur very sporadically. Only *C. rugosus* Bukry and Bramlette (1968), a robust form with parallel horns, was determined separately for stratigraphical purposes.

C. *cristatus* has been found in the coccospheres of ring-shaped coccoliths in Pacific, North Atlantic, and Mediterranean Sea (Norris, 1965; Knappertsbusch, 1990, Winter and Siesser, 1994). These coccospheres with *C. cristatus* were observed to be formed in a phase of life cycle of *Neosphaera coccolithomorpha* (Abcober and Jordan, 1995).

Occurrence: Sporadic in the Pliocene and Quaternary of sites 664, 659, 608 (Tables 3.6-3.8). As given above, the FAD of *C. rugosus* was used in the stratigraphy of sites 664, 659, 608 (Table 2.4 in chapter 2).

Family Coccolithaceae Poche 1913

Genus *Calcidiscus* Kamptner 1950

1950 *Calcidiscus* Kamptner: 153.
1954 *Cyclococcolithus* Kamptner: 23, 74, 75.
1958 *Tiarolithus* Kamptner: 70, 81, 85.
1963 *Cycloplacolithus* Kamptner: 167, 194, 197.
1968 *Cycloplacolithella* Haq: 13, 20, 25.
1970 *Cyclococcolithina* Wilcoxon: 82.
1978 *Calcidiscus* Kamptner, Loeblich and Tappan: 1390-1392.

Description: Circular placoliths with small central pores. Elements are imbricated dextrally in the distal shield and sinistrally in the proximal shield. The suture lines on the distal surface of
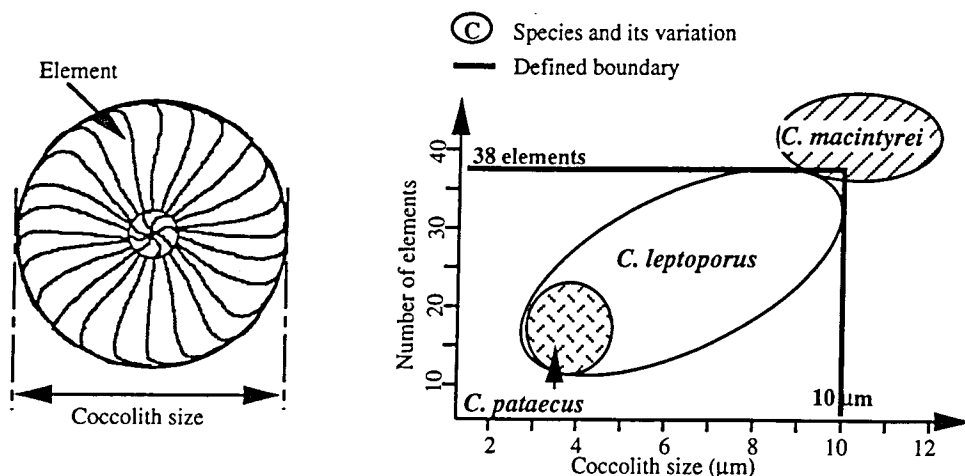
Figure 3.1 *Calcidiscus leptoporus* and *C. macintyrei* separated by differences of coccolith size and number of elements. *Coccolithus pataecus* is considered as a synonym of *C. leptoporus* in this study.

the distal shield are straight for approximately one-half the distance from the central column, then curve sinistrally; the proximal surface of both shields shows straight suture lines.

Remarks: Coccoliths of two species, *C. leptoporus* and *C. macintyrei*, are found in this study. They vary in coccolith size and the number of elements. Moreover, a morphological overlapping between *C. leptoporus* and *C. macintyrei* was observed. According to biometrical studies (Janin, 1980; Knappertsbusch, 1990) *C. leptoporus* differs from *C. macintyrei* by being smaller than 10 μm and having fewer than 38 elements. These criteria are used for separating *C. leptoporus* from *C. macintyrei* (Figure 3.1).

Calcidiscus leptoporus (Murray and Blackman 1898) Loeblich and Tappan 1978

Plate 1, Figure 3, Plate 5, Figure 5, Plate 7, Figures 35-36

*1898 *Coccosphaera leptopora* Murray and Blackman: 430, 439, pl. 15, figs. 1-7.
1967 *Cyclococcolithus leptoporus* (Murray and Blackman) Kamptner; McIntyre and Bé: 569, pl. 7, figs. a-b.
1967 *Coccolithus pataecus* Gartner: 4, pl. 5, figs. 6-8.
1972 *Cyclococcolithina leptopora* (Murray and Blackman) Wilcoxon: 82.
1978 *Calcidiscus leptoporus* (Murray and Blackman) Loeblich and Tappan: 1391.
1990 *Calcidiscus leptoporus* (Murray and Blackman) Loeblich and Tappan; Knappertsbusch: 85-86, pls. 1-2.

Description: McIntyre and Bé, 1967: 569.

Remarks: *C. leptoporus* can be subdivided into several morphotypes by differences in coccolith size and number of elements by using SEM. However, the number of elements in small coccoliths is not clearly recognizable under LM, so a subdivision of this species was not made in this study.

Coccolithus pataecus (Gartner) was commonly found in the NE Atlantic samples. The shield of this species is about 3 - 5 μm and consists of approximately 10 - 25 elements. This
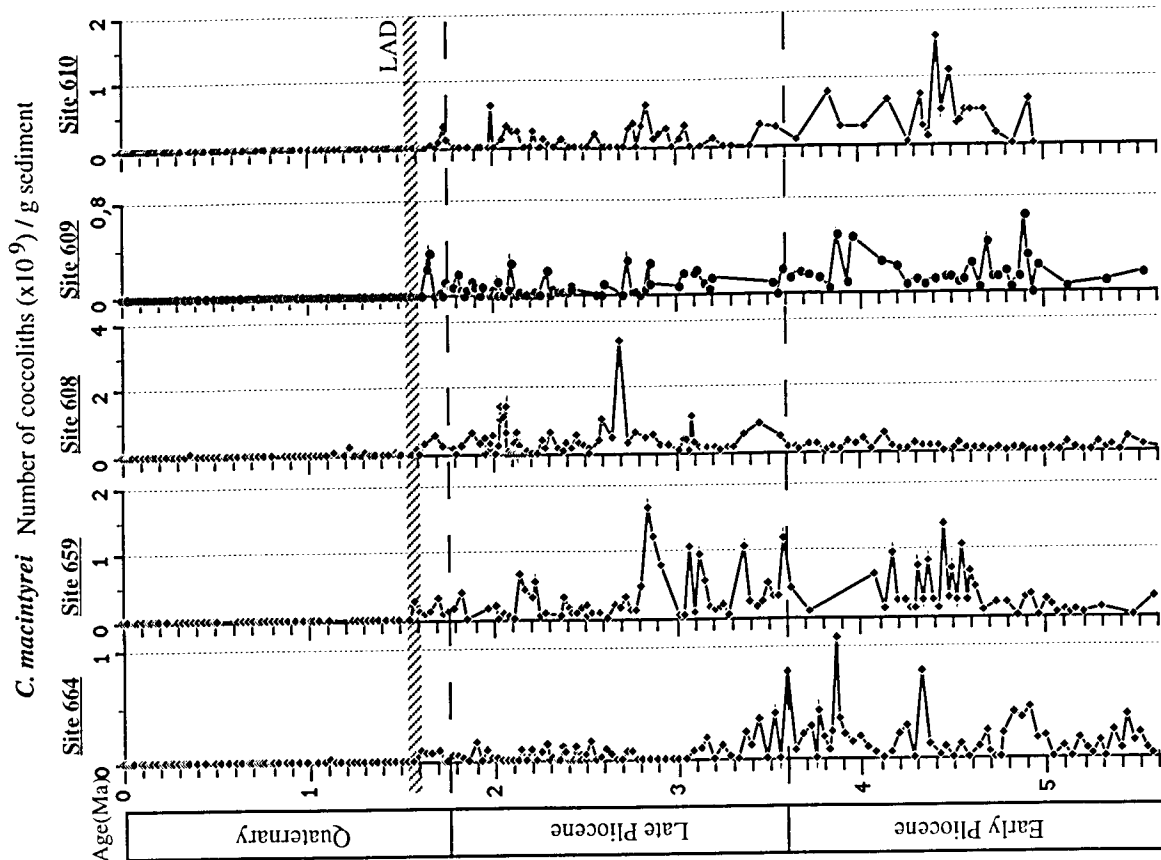
Figure 3.3 Absolute abundance plots of *C. macintyrei* at DSDP/ODP Sites 664, 659, 608, 609, 610. Its LAD is marked by the shaded area.

Figure 3.2 Absolute abundance plots of *C. leptoporus* at DSDP/ODP Sites 664, 659, 608, 609, 610. Several abundance peaks (I - VI) are marked with shaded areas.

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form is very similar to small coccoliths of *C. leptoporus* and differs from the latter only by its elliptical shape and poorly defined interference figure between crossed nicols. Usually, a variation of coccolith shape from elliptical to circular is considered as an intra-specific one (Perch-Nielsen, 1985). Knappertsbusch (1990) regarded *C. pataecus* as a synonym of *C. leptoporus*. These suggestions are used in this study (Figure 3.1).

Ecology: *C. leptoporus* lives today in the upper photic layer and is a cosmopolitan species with a wide temperature range (5 - 30°), (McIntyre and Bé, 1967; McIntyre et al., 1970; Okada and McIntyre, 1979; Knappertsbusch, 1990). Various morphotypes of *C. leptoporus* are considered to be temperature related ecophenotypes (Kleijne, 1993). Furthermore, Baumann (1990) showed, that in the Quaternary sediment from the northern North Atlantic the larger sized variant of *C. leptoporus* (form B) occurs only during the interglacial period.

Occurrence: Common in Pliocene and Quaternary sediments of all studied sites (Figure 3.2), this indicates it to have been a cosmopolitan species since the Pliocene, and its paleoecology to be in agreement with its present day ecology.

Calcidiscus macintyrei (Bukry and Bramlette 1969) Loeblich and Tappan 1978
Plate 5, Figure 8, Plate 7, Figure 34

*1967 *Coccolithus leptoporus var.* A McIntyre, Bé and Preikstas: 9, pl. 4, figs. C-D.
1969 *Cyclococcolithus macintyrei* Bukry and Bramlette: 132, pl. 1, figs. 1-3.
1978 *Calcidiscus macintyrei* (Bukry and Bramlette) Loeblich and Tappan 1978: 1392.

Description: McIntyre, Bé and Preikstas, 1967: 9.

Remarks: Differences between this species and *C. leptoporus* have been noted above.

Biostratigraphy: Tiedemann et al. (1994) suggested an age of 1.58 Ma for the LAD of *C. macintyrei.*

Occurrence: Rare to common in Pliocene and lower Quaternary sediments of all sites (Figure 3.3). The LAD of this species is distinct and nearly synchronous in sites 664, 659 and 608. It was used as a control point for the stratigraphy of these three sites. It disappears a little earlier from the northern areas, so its LAD was not usable for the stratigraphy of sites 609 and 610.

Genus *Coccolithus* Schwarz 1894
Coccolithus pelagicus (Wallich 1877) Schiller 1930
Plate 5, Figure 11, Plate 7, Figure 37

*1877 *Coccosphaera pelagica* Wallich: 348, pl. 17, figs. 1-2, 5, 8-11.
1930 *Coccolithus pelagicus* (Wallich) Schiller: 246-247, figs. 123a-d.
1967 *Coccolithus pelagicus* (Wallich) Schiller; McIntyre, Bé and Preikstas: 11, pl. 8, figs. A-C.
1973 *Coccolithus pliopelagicus* Wise: 593, pl. 8, figs. 1-6.
1980 *Coccolithus pelagicus* (Wallich) Schiller; Backman: 8, pl. 1, figs. 1-2, 5-7, pl. 2, fig. 1.

Description: McIntyre, Bé and Preikstas, 1967: 11.

Remarks: Here, differences between *C. pelagicus* and *C. pliopelagicus* (Wise, 1973) were considered as intra-specific variations, the latter was regarded as a synonym of *C. pelagicus*, based on the suggestion of Backman (1980) and observations in this study.

Size variations of this form, both in the size of the shield and the central opening, exist between samples. This agrees with observations of previous studies (Backman, 1980; Baumann, 1990).

Ecology: The extant *C. pelagicus* is recorded as a typical cold-water form. McIntyre and Bé (1967) gave a temperature range of 6 - 14°C (optimum about 9°C). It was also found in colder waters of about 1°C in the North Atlantic (Okada and McIntyre, 1979), and -1.7°C in the Denmark Trough (Braarud, 1979). Samtleben and Schröder (1992) showed that *C. pelagicus* represents the polar species group and predominates in the East Greenland Current.

Occurrence: In the Pliocene: sparse to rare at site 664, common at sites 659, 608, 609, dominant at site 610. In the Quaternary: absent at site 664, rare to absent at sites 659, 608, 609, common to rare at site 610 (Figure 3.4). An increase in abundance towards the northern areas through time can be observed.

In this study, its more frequent occurrence in the northern areas during the Quaternary agrees with the record of its ecology. However, together with warm water forms such as *Discoaster* and *Sphenolithus,* it does occur abundantly in the tropical and transitional Pliocene sediments (sites 664, 659, 608). This agrees with the results of Samtleben (1978), who suggested that the ecological affinities of *C. pelagicus,* at least its preferred water temperature, have changed since the end of the Pliocene, without however, any attendant changes in morphological features.

Genus *Coronocyclus* (Hay, Mohler and Wade 1966) emend. Stradner 1968
Plate 5, Figure 2

Description: Stradner, 1968: 28.

Remarks: Circular cycloliths with wide central openings were identified at the genus level, *Coronocyclus* spp. They are easily recognized by their very wide openings and narrow rims.

Occurrence: Rare to common in Pliocene sediments of all studied sites (Tables 3.6-3.10).

Genus *Hayaster* Bukry 1973
Hayaster perplexus (Bramlette and Riedel 1954) Bukry 1973

*1954 *Discoaster perplexus* Bramlette and Riedel: 400, pl. 39, fig. 9.
1973 *Hayaster perplexus* (Bramlette and Riedel) Bukry: 308.
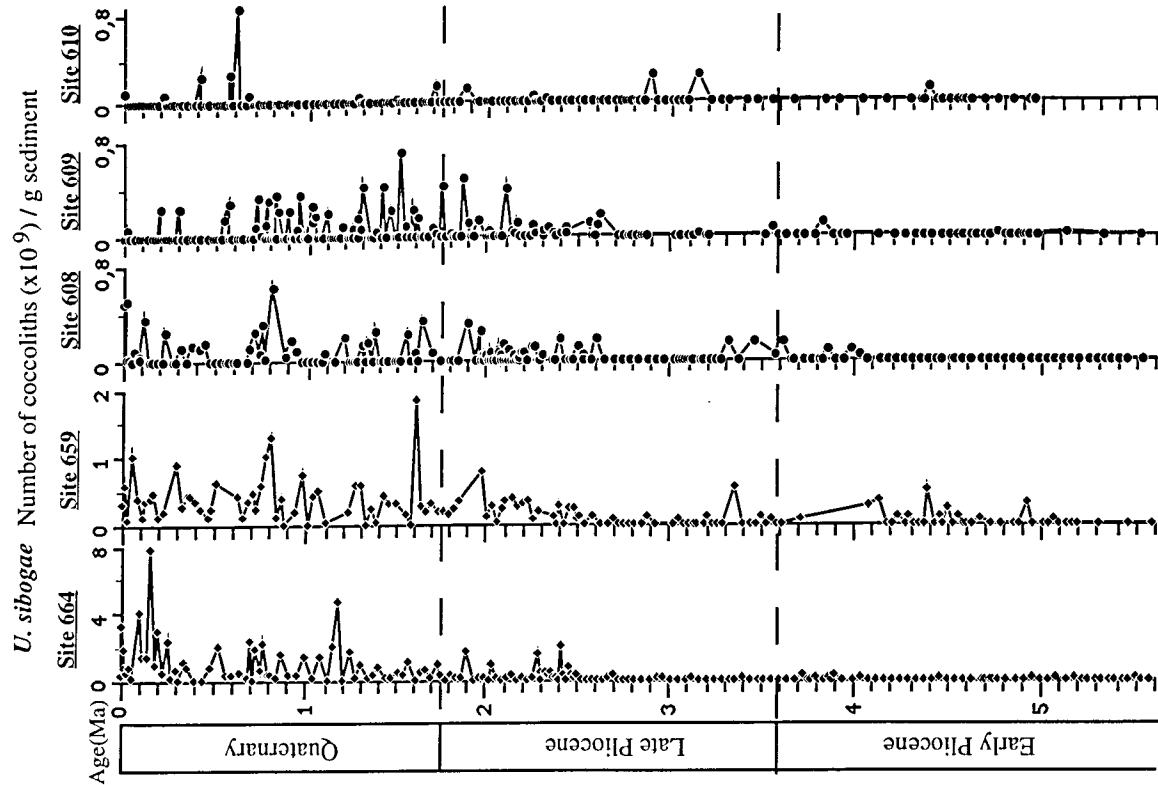
Figure 3.5 Absolute abundance plots of *U. sibogae* at DSDP/ODP Sites 664, 659, 608, 609, 610.
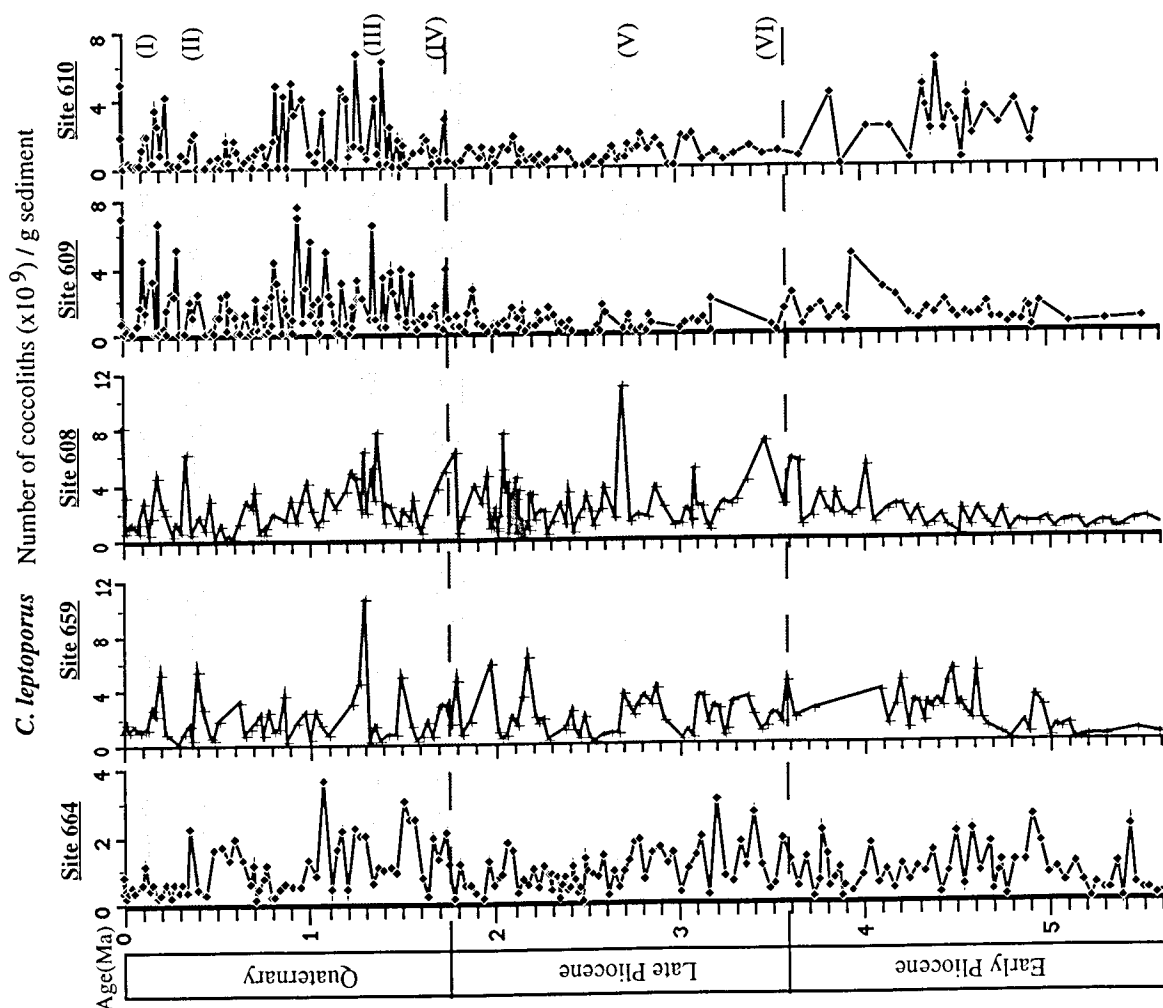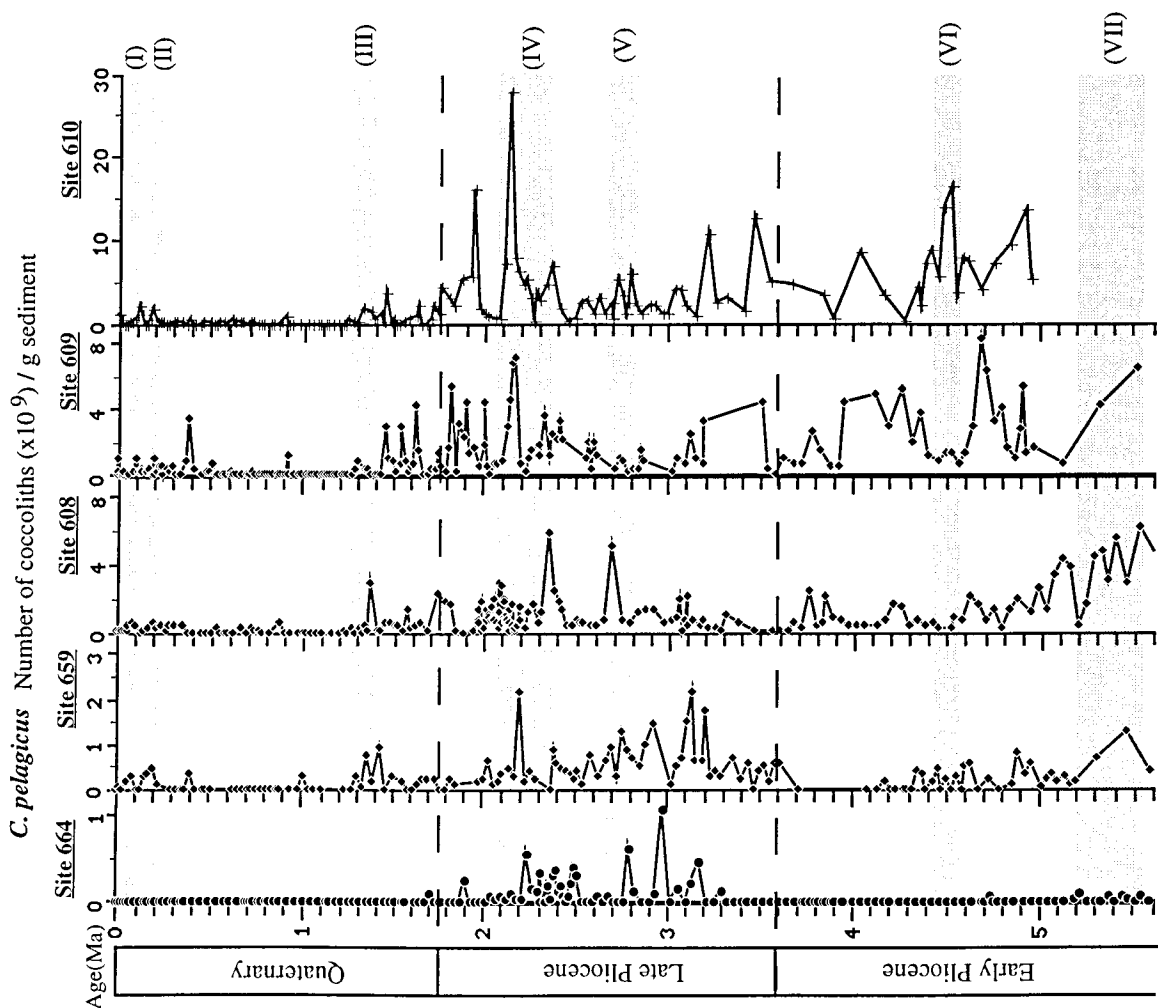

Figure 3.4 Absolute abundance plots of *C. pelagicus* at DSDP/ODP Sites 664, 659, 608, 609, 610. Several main abundance peaks (I - VII) are marked with shaded areas.

Description: Circular placoliths constructed of two shields, in which the distal shield is significantly larger than the proximal shield. Each shield bears radial elements delimited by straight suture lines.

Remarks: This form can be easily recognized by its circular outline, straight rays and the feature of being dark between crossed nicols. Jordan and Kleijne (1994) transferred this species into the family Coccolithaceae since coccoliths of this species are constructed of two shields and have a similar morphology to placoliths of *Oolithotus*. Their suggestion is accepted in this study.

Occurrence: In the Pliocene: rare at sites 664, 659, 608, 609 (Tables 3.6-3.9).

Genus *Neosphaera* Lecal-Schlauder 1950

Neosphaera coccolithomorpha Lecal-Schlauder 1950

Plate 5, Figure 9

*1950 *Neosphaera coccolithomorpha* Lecal-Schlauder: 163-167, figs. 4-6.
1967 *Cyclolithella annulus* Cohen; McIntyre and Bé: 568; pl. 5, figs. a-c.
1977 *Neosphaera coccolithomorpha* Lecal-Schlauder; Okada and McIntyre: 16-17, pl. 6, figs. 1-2.
1993 *Neosphaera coccolithomorpha* var. *coccolithomorpha* Kleijne: 191-193, pl. 3, fig. 3.
1993 *Neosphaera coccolithomorpha* var. *nishidae* Kleijne: 193-194, pl. 3, fig. 4.

Description: Okada and McIntyre, 1977: 16-17.

Remarks: This species was subdivided into two variants by differences in opening size (Kleijne, 1993). However, such a subdivision was not made here, due to difficulties in identification under LM.

Ecology: According to McIntyre and Bé (1967), this species lives today in the North Atlantic within a temperature range of 20 - 29°C (optimum 22 - 28°C); it is the most abundant species in tropical areas, a common species in subtropical areas, and absent in the northern North Atlantic. Kleijne (1993) suggested the distribution of the species to vary with its ecotypes, i.e. the forms with a larger opening live in the warm Indian Ocean and Red Sea, while the forms with a smaller opening occur at higher latitudes of the North Atlantic.

Occurrence: In the Pliocene and Quaternary: common to rare at site 664; rare to sparse at sites 659, 608, 609, absent at site 610 (Tables 3.6-3.10). Generally this agrees with its ecology as observed by McIntyre and Bé (1967).

Genus *Oolithotus* Reinhardt, in Cohen and Reinhardt 1968

Oolithotus fragilis (Lohmann 1912) Martini and Müller 1972

Plate 5, Figure 7

*1912 *Coccolithophora fragilis* Lohmann: 49, 54, fig. 11.
1977 *Oolithotus fragilis* (Lohmann) Okada and McIntyre: 11-12. pl. 4, fig. 3.

Description: Okada and McIntyre, 1977: 11-12.

Remarks: This species was separated into two species or forms, by differences in the size of their coccospheres and in the ultrastructure of the proximal shield (Okada and McIntyre, 1977; Kleijne, 1993). Since in sediments only isolated coccoliths are found and the ultrastructure of the shield is not determinable by using LM, a subdivision of this species was not made here.

Occurrence: In Pliocene and Quaternary sediments: rare to occasionally common at sites 664, 659, 608, sporadic at sites 609, 610 (Tables 3.6-3.10).

Genus *Umbilicosphaera* Lohmann 1902

Umbilicosphaera sibogae (Weber-van Bosse 1901) Gaarder 1970

Plate 5, Figure 1, Plate 7, Figure 32

*1901 *Coccosphaera sibogae* Weber-van Bosse: 137, 140, pl. 17, figs. 1-2.
1902 *Umbilicosphaera mirabilis* Lohmann: 139-140, pl. 5, figs. 66, 66a.
1970 *Umbilicosphaera sibogae* (Weber-van Bosse) Gaarder: 122-126, figs. 9c-d.
1977 *Umbilicosphaera sibogae* (Weber-van Bosse) Gaarder; Okada and McIntyre: 13, pl. 4, fig. 2.
1977 *Umbilicosphaera sibogae foliosa* (Kamptner) Okada and McIntyre: 13, pl. 4, fig. 1.

Description: Okada and McIntyre, 1977: 13.

Remarks: Two variants of this species were suggested: *U. sibogae* with larger openings and *U. sibogae foliosa* with smaller openings (Okada and McIntyre, 1977; Kleijne, 1993). However, Inouye and Pienarar (1984) showed that these two coccolith types may be produced by one cell. Therefore, no subdivision of this species has been made here.

Ecology: According to McIntyre and Bé (1967), it is a common species in the subtropic floral assemblage in the North Atlantic and has a temperature range of 18 - 25 °C.

Occurrence: Sparse in lower-middle Pliocene sediments of all sites. In upper Pliocene and Quaternary sediments: common at sites 664, 659; rare at sites 608, 609, sparse at site 610 (Figure 3.5). An increase in abundance towards the tropical areas indicates its paleoecology to be in agreement with its present day ecology.

Family Helicosphaeraceae Black 1971, emend. Jarfar and Martini 1975

Genus *Helicosphaera* Kamptner 1954

1954 *Helicosphaera* Kamptner: 21,73.
1967 *Helicopontosphaera* Hay and Mohler, in Hay et al.: 448.
1975 *Helicosphaera* Kamptner; Jafar and Martini: 386-389.

Description: Jafar and Martini, 1975: 386-389.

Remarks: Here, only two species of this genus, *H. carteri* and *H. sellii*, are identified separately, other helioliths are determined as *Helicosphaera* spp., which occur very sporadically and have no remarkable significance for ecology or biostratigraphy.

Helicosphaera carteri (Wallich 1877) Kamptner 1954

Plate 4, Figures 1-2, Plate 7, Figure 38

*1877 *Coccosphaera carterii* Wallich: 347-348, pl. 17, figs. 3-4, 6-7, 12s, 17.
1902 *Coccolithophora wallichi* Lohmann: 138, pl. 5, figs. 58-59.
1954 *Helicosphaera carteri* (Wallich) Kamptner: 21-23, 73-74, figs. 17-19.
1967 *Helicosphaera kamptneri* Hay and Mohler: 448, pls. 10-11, fig. 5.
1969 *Helicopontosphaera wallichii* (Lohmann) Boudreaux and Hay: 272, pl. 6, fig. 9.
1970 *Helicopontosphaera hyalina* Gaarder: 113, figs. 1-3a.
1984 *Helicosphaera carteri* (Wallich) Kamptner; Theodoridis: 131-132, pl. 23, figs. 5-9, pl. 27, fig. 7.
1990 *Helicopontosphaera carteri* var. *hyalina* (Gaarder) Jordan and Young: 15-16.

Description: Theodoridis, 1984: 131-132.

Remarks: Recently, differences in the central areas and wings between forms *H. carteri*, *H. wallichii* and *H. hyalina* have been considered as intra-specific variations; the latters are regarded as synonyms of *H. carteri* (Theodoridis, 1984; Jordan and Young, 1990).

Ecology: *H. carteri* lives today in the North Atlantic within a temperature range of 15 - 26°C (optimum 21 - 26°C), according to McIntyre and Bé (1967). It occurs commonly in the recent subtropical and transitional floral communities in the North Atlantic and is absent in the subarctic areas (Okada and McIntyre, 1977).

Occurrence: In Pliocene and Quaternary sediments: rare and occasionally common at sites 664, 659, 608, 609, rare at site 610 (Figure 3.6). This agrees with its present day ecology.

Helicosphaera sellii (Bukry and Bramlette 1969) Jafar and Martini 1975

Plate 4, Figure 3, Plate 7, Figure 39

*1969 *Helicopontosphaera sellii* Bukry and Bramlette: 134, pl. 2, figs. 3-7.
1975 *Helicosphaera sellii* (Bukry and Bramlette) Jafar and Martini: 391.
1984 *Helicosphaera sellii* (Bukry and Bramlette) Jafar and Martini; Theodoridis: 128-129, pl. 26, fig. 7.

Description: Theodoridis, 1984: 128-129.

Remarks: This species differs from *H. carteri* in always having two larger elliptical central openings with a bar inclined to the short axis, and a gradually terminating wing.

Biostratigraphy: An age of 1.55 Ma (corr.) for the LAD of *H. sellii* was suggested by Takayama (1993).

Occurrence: Rare to occasionally common in Pliocene and lower Quaternary sediments of all sites (Figure 3.7). The LAD of *H. sellii* seems to be non-synchronous in the sites studied,

Figure 3.7 Absolute abundance plots of *H. sellii* at DSDP/ODP Sites 664, 659, 608, 609, 610. Its LAD is marked by the shaded area.

Figure 3.6 Absolute abundance plots of *H. carteri* at DSDP/ODP Sites 664, 659, 608, 609, 610.

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varying from 1.4 to 1.58 Ma. This agrees with the study of Backman and Shackleton (1983), who suggested that this event is non-synchronous and can be used only with extreme caution.

Family Noelaerhabdaceae Jerkovic 1970

Remarks: Four genera *Reticulofenestra, Pseudoemiliania, Gephyrocapsa,* and *Emiliania* are included in this family. Morphologically they are closely related and are the ancestors and descendants of an evolutionary lineage (see also Figure 4.1, chapter 4). *Reticulofenestra* is the earliest genus and has its origin in the Eocene. In the Early Pliocene, *Reticulofenestra* gives rise to *Pseudoemiliania* and *Gephyrocapsa,* and lastly *Emiliania* evolves from *Gephyrocapsa* (Thierstein et al., 1977; Samtleben, 1980; Gallagher, 1987; Young, 1990).

Genus *Emiliania* Hay and Mohler, in Hay et al., 1967

Description: Hay and Mohler, in Hay et al., 1967: 477.

Emiliania huxleyi (Lohmann 1902) Hay and Mohler, in Hay et al., 1967
Plate 1, Figures 1-2, Plate 7, Figure 1

*1902 *Pontosphaera huxleyi* Lohmann: 129-130, pl. 4, figs. 1-9, pl. 6, fig. 69.
1943 *Coccolithus huxleyi* (Lohmann) Kamptner: 44.
1967 *Coccolithus huxleyi* (Lohmann) Kamptner; McIntyre and Bé: 568, pl. 5, fig. d, pl. 6, figs. a-b, pl. 12, fig. b.
1967 *Emiliania huxleyi* (Lohmann) Hay and Mohler: 477, pl. 10, figs. 1-2, pl. 11, figs. 1-2.
1991 *Emiliania huxleyi* (Lohmann) Hay and Mohler; Young and Westbroek: 21-22, pl. 1, figs 1-12, pl. 2, figs. 1-10, pl. 3, figs. 1-8.

Description: Young and Westbroek, 1991: 21-22.
Remarks: *E. huxleyi* is characterized by its "I-shape" elements. However, when observed with LM, only the "I-shape" elements of larger specimens can be seen. In counting analyses with LM, coccoliths of this species were distinguished from *Reticulofenestra minuta* by its narrower rim and poorly defined birefringence between crossed nicols, and from *Reticulofenestra productella* by a larger central opening. It differs from the same sized *Gephyrocapsa* forms by having no bridge. However, when the latter have lost their bridges, distinguishing them can be problematic. *E. huxleyi* evolved from *Gephyrocapsa,* most likely from *Gephyrocapsa margereli* (Thierstein et al., 1977; Samtleben, 1980).

In this study, various forms of this species, such as the warm-water or cold-water forms of McIntyre and Bé (1967), or forms A, B, C of Young and Westbroek (1991), were observed with SEM, but cannot be distinguished under LM.

E. huxleyi Number of coccoliths (x10⁹) / g sediment
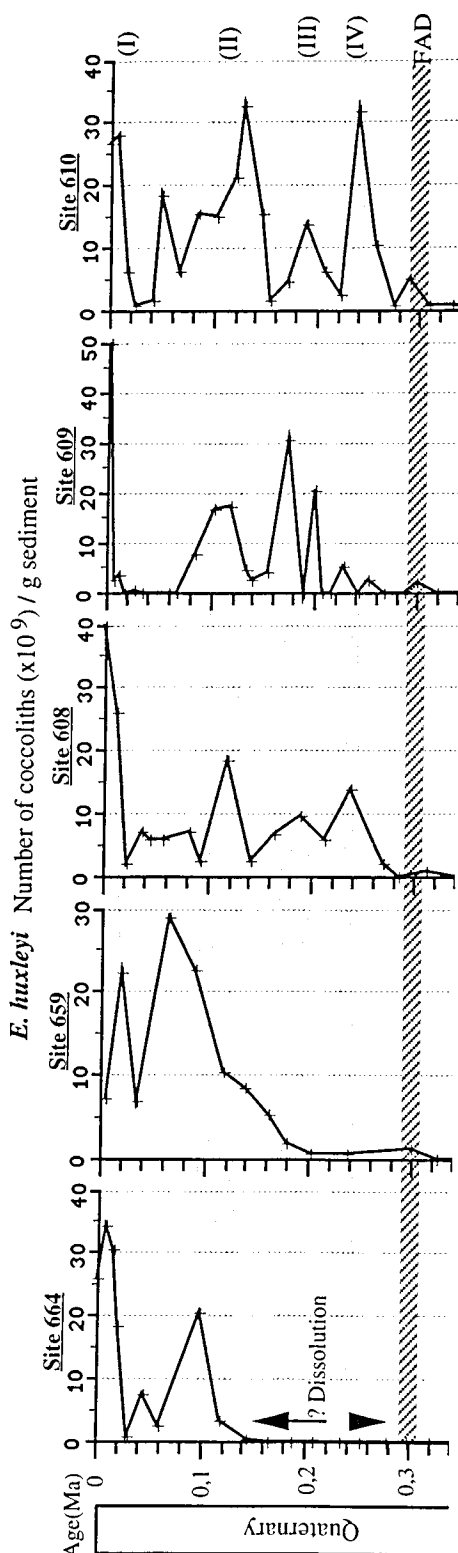
Figure 3.8 Absolute abundance plots of *E. huxleyi* at DSDP/ODP Sites 664, 659, 608, 609, 610.
Its FAD and main abundance peaks (I - IV) are marked with shaded areas.

G caribbeanica **and** *G. lumina* Number of coccoliths (x10⁹) / g sediment
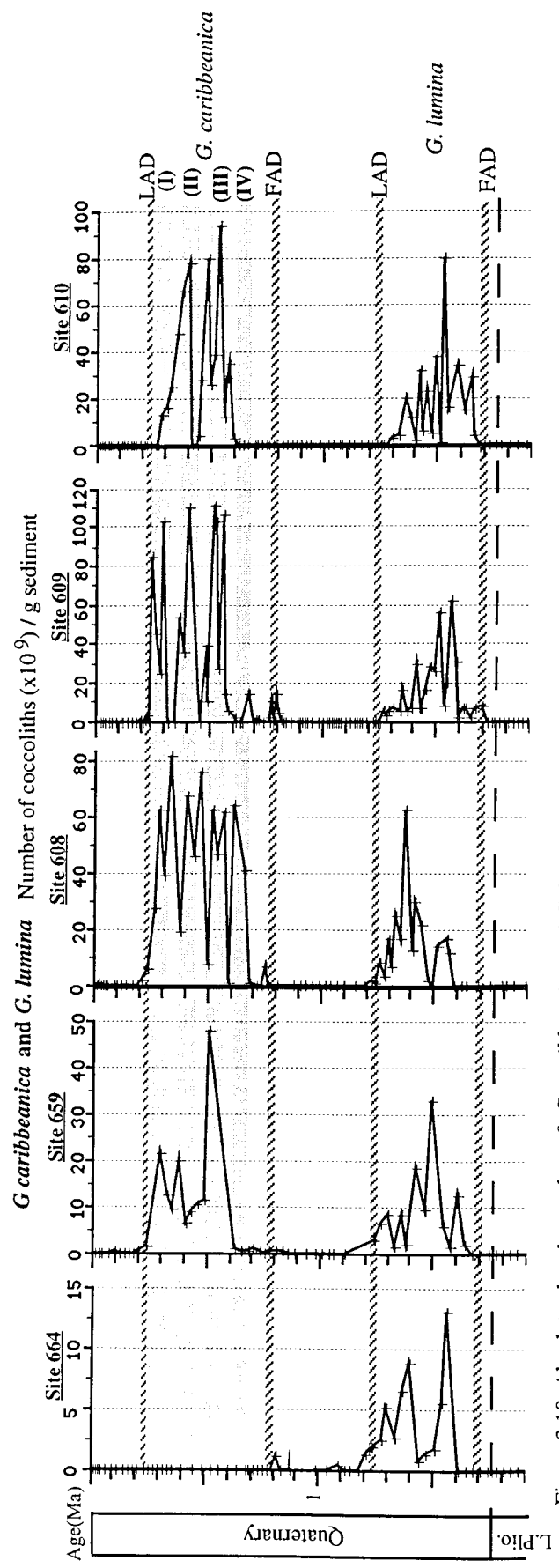
Figure 3.10 Absolute abundance plots of *G. caribbeanica* and *G. lumina* at DSDP/ODP Sites 664, 659, 608, 609, 610. Four abundance peaks of *G. caribbeanica* (namely I, II, III, IV) are shown by shaded areas.

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Biostratigraphy: The FAD of *E. huxleyi* marks the base of NN21 (Martini, 1971), dated at an age of 0.30 Ma (corr.) (Takayama, 1993).

Ecology: E. huxleyi is a cosmopolitan species and has a temperature range of 2 - 29°C in the North Atlantic (McIntyre and Bé, 1967). It occurs in all oceans from the tropics to the Arctic (or the Antarctic) regions (McIntyre and Bé, 1967; Okada and Honjo, 1975; Okada and McIntyre, 1977). Samtleben and Schröder (1992) showed that *E. huxleyi* represents the Atlantic-Arctic group in the Norwegian-Greenland Sea. Today *E. huxleyi* is the most abundant species and dominates the modern coccolithophorid communities, often producing large blooms (Holligan et al. 1983, 1993; Balch et al. 1991). It therefore plays an important role in ocean/atmosphere interactions and climate circulation (Westbroek et al., 1989, 1993; Robertson et al., 1993).

Occurrence: Common to dominant in upper Quaternary sediments of all sites (Figure 3.8). Four abundance peaks (I - IV) were recognized. The FAD of *E. huxleyi* is rather distinct in sites 659, 608, 609, 610, and was used in the stratigraphy of these sites (Table 2.4). In site 664 the FAD of this species appears to be too young (about 0.15 Ma). However, it is difficult to recognize this species in older samples of this site, with LM or with SEM, due to a strong dissolution in upper Quaternary sediment. Dissolution is also indicated by other poorly preserved fragile coccoliths, such as *Rhabdosphaera claviger* and *Umbellosphaera* spp. (see also Figure 3.23). Therefore, the event was not used for the stratigraphy of site 664.

Genus *Gephyrocapsa* Kamptner 1943

1943 *Gephyrocapsa* Kamptner: 45.
1980 *Gephyrocapsa* Kamptner, Samtleben: 99.

Description: Elliptical placolith with a central opening. On the distal side several elements elongate from the central tube to form a bridge over the opening. The form of the bridge varies greatly: it may be very thick and broad or very thin and narrow, very flat or highly arched perpendicular to the placolith. The bridge angle, measured between the bridge and the long axis, varies between different species. Hence, besides the features of coccolith size and form of the central opening, bridge angle is an important feature in the identification of *Gephyrocapsa* species.

The two rims of the coccoliths of *Gephyrocapsa* are composed of radially arranged tabular elements. Numbers of rim elements vary in close correlation with coccolith size. Proximally, the central opening is spanned by radially arranged laths to form a central grillwork. These features are similar to those of *Reticulofenestra*, indicating a close relationship between the two genera (Samtleben, 1980: 99).

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a) **Features in biometrical analyses**

b) **Species and species groups identified**

Bridge angle

Coccolith length
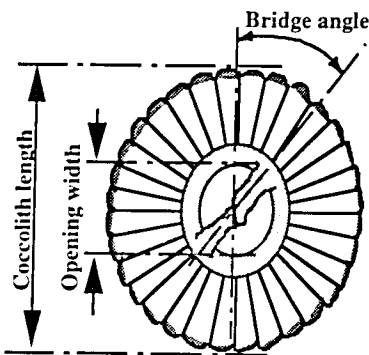
Opening width

$$\text{Opening width } (\%) = \frac{\text{Opening width}(\mu m)}{\text{Coccolith length } (\mu m)} \times 100\%$$

Ⓖ Variation of species or species groups

90°

Bridge angle

60°

30°

Gephyrocapsa spp.1

G. oceanica

G. car.

G. lumina

G.V

G. margereli-G. muellerae

Coccolith length (µm)

2   3   4   5   6

c) **Central area and rim**

Central area

Elements of rim

Closed central area

Small opening

Large opening

Slightly imbricate

Separate

d) **Bridge**

90°   45°   10°
Bridge angle

Narrow   Broad
Bridge width

Connected   Overlapped   Separate
Elements of bridge

Flat

Medium arched

Highly arched

Bridge height
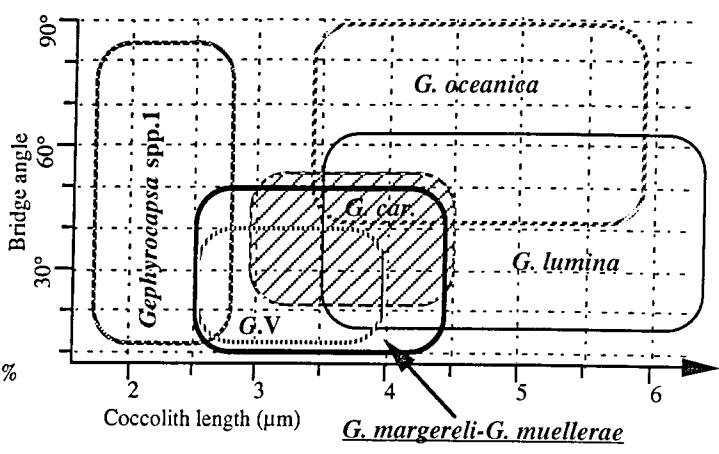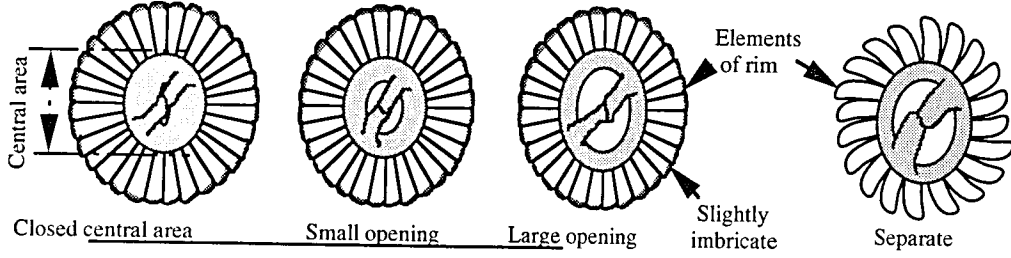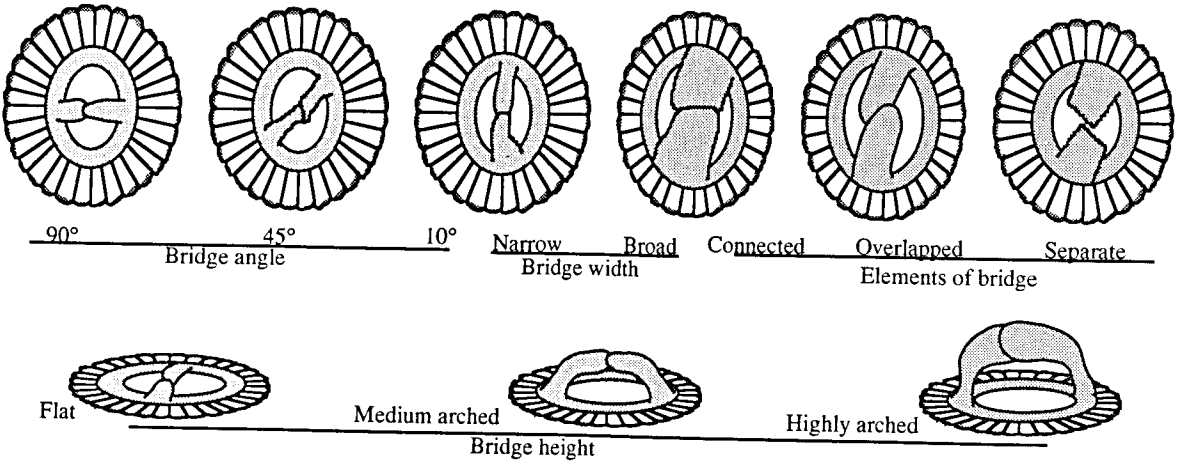
Figure 3.9a-d Characteristic features of *Gephyrocapsa* species and their variations. a) Coccolith length, bridge angle and opening width are the most important features for identification of species. b) Variations of species and species groups in coccolith length and bridge angle. Several species have similar variations in coccolith length and bridge angle, however, they are distinguished by differences in opening width and form of bridge etc. (figure c, d). For example, *G. caribbeanica* is separated from *G. margereli* by having a smaller opening or closed central area and a very flat bridge. Such differences are given in the remarks for each species and species group in detail.

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Remarks: Figures 3.9a-c show the characteristic features of *Gephyrocapsa*, namely coccolith length, opening width, bridge angle, forms of bridge etc. These features vary greatly, presenting various morphological intergradations between different species and showing a gradual change of morphological features through geological time. This makes identification, especially identification of individual coccoliths in a counting investigation with LM, very difficult. However, various species can be recognized and separated through biometrical analyses by means of SEM micrographs (Samtleben, 1980; Baumann, 1990). In connection with this investigation, a biometrical study of *Gephyrocapsa* is being carried out by C. Samtleben and K.-H. Baumann (see introduction). Results from that study, such as coccolith length, bridge angle etc., are used here to distinguish and to describe the species and species groups of *Gephyrocapsa* observed in the samples.

Species or groups in this study	Biometrical features			Correlation to species or form-groups
	Coccolith length (µm)	Bridge angle (°)	Opening width (%)	
G. oceanica	3.5 ~ 6	40 ~ 90	Large (40 ~ 50)	*G. oceanica* Kamptner 1943
G. caribbeanica	3 ~ 4.5	20 ~ 50	Small (20 ~ 40) or closed	*G. caribbeanica* Boudreaux and Hay 1967
G. lumina	3.5 ~ 6.5	10 ~ > 60	Small (20 ~ 40) or closed	*G. lumina* Bukry 1973
G. margereli - G. muellerae	2.5 ~ 4.5	10 ~ 50	Medium (40 ~ 60)	*G. margereli* Bréhéret 1978 *G. muellerae* Bréhéret 1978
"*G. margereli*"	2.5 ~ 4	10 ~ 40	Small to medium (25 ~ 50)	*G.* forma V
Gephyrocapsa spp.1 (Small forms)	<3	10 ~ 80	Small to large (20 ~ 70)	*G. aperta* Kamptner 1963 *G. ericsonii* McIntyre and Bé 1967 *G. sinuosa* Hay and Beaudry 1973 *G. rota* Samtleben 1980 *G.* formas D, F, H, P, Q

Table 3.2 Summary of species and form-groups of *Gephyrocapsa*.

In this investigation several large sized species were counted separately, since their features can be easily recognized under LM. Closely similar species which are difficult to separate, for example *G. margereli* and *G. muellerae*, were grouped together. Various small forms, *G. aperta*, *G. ericsonii*, *G. rota*, *G. sinuosa*, and newly separated form-groups which are marked with letters (D, F, H, P, and Q) at present time, were also united as "small species" or *Gephyrocapsa* spp.1, because they are too small to be safely distinguished. These species and groups are summarized in Table 3.2 and Figure 3.9.

Gephyrocapsa caribbeanica Boudreaux and Hay 1967

Plate 2, Figures 6,11, Plate 7, Figures 4-5

*1967 *Gephyrocapsa caribbeanica* Boudreaux and Hay, in Hay, Mohler, Roth, Schmidt and Boudreaux: 447, pls. 12-13, figs. 1-4.
1978 *Gephyrocapsa caribbeanica* Boudreaux and Hay; Bréhéret: 448-449, p. 2, fig. 5.
1980 *Gephyrocapsa caribbeanica* Boudreaux and Hay; Samtleben: 110-111, pl. 14, figs. 9-12.
 non 1980 *Gephyrocapsa caribbeanica* Boudreaux and Hay; Samtleben, pl. 14, figs. 13-14 (= *G. lumina*).

Description: Elliptical to subcircular placoliths sized 3 - 4.5 µm, having medium sized rims, small central openings (20 - 40 %) or closed central areas, and medium sized, very flat bridges and medium to small bridge angles (20 - 50 °).

Remarks: This species can be distinguished from the same sized *G. margereli* by having smaller openings or closed central areas and flat bridges; and from *G. lumina* by being smaller and having medium sized rims and smaller bridge angles. *G. caribbeanica* is considered to have evolved from *G. margereli* (Samtleben, 1980; S&B).

In some samples, variations of *G. caribbeanica*, e.g. those with closed central areas and very flat bridges, seem to be very similar to some types of *Reticulofenestra productella*, which have irregularly prominent central laths on closed central areas. In this study, the feature with a distinct bridge was used for separating *G. caribbeanica* from the latter.

Paleoecology: In the literature, *G. caribbeanica* has often been confused with *G. muellerae* (Bréhéret, 1978). Samtleben (1980) mistook *G. lumina* (Bukry 1973), in lower Quaternary sediments from the Sierra Leone, as *G. caribbeanica* (Boudreaux and Hay 1967) which is actually absent in the equatorial region. Geitzenauer (1972) observed *G. caribbeanica* to be a dominant species in upper Quaternary samples from Subantarctic areas.

Occurrence: In upper Quaternary sediments; very abundant at sites 608, 609, 610, common to abundant at site 659 and absent in the tropical site 664. This indicates that *G. caribbeanica* preferred cold waters. Four distinctive abundance peaks (I - IV) were recognized (Figure 3.10). *G. caribbeanica* is considered to be an extinct form. Its FAD was observed at 0.76 Ma and its LAD was at 0.24 Ma.

Gephyrocapsa lumina Bukry 1973
Plate 2, Figures 8-9, Plate 7, Figures 6-7

*1973 *Gephyrocapsa lumina* Bukry: 678, pl. 3, figs. 1-4.
1980 *Gephyrocapsa caribbeanica* Boudreaux and Hay; Samtleben, pl. 14, figs. 13-14.

Description: Large sized (3.5 - 6.5 µm) elliptical placoliths, composed of broad rims, broad central tubes, small central openings (20 - 40 %) or closed central areas, and with medium sized flat bridges which have variable bridge angles (10 - > 60°).

Remarks: This species differs from *G. oceanica* and *G. margereli* in having a wider rim with a smaller opening or with a closed central area. Its larger size and larger bridge angle make it distinguishable from *G. caribbeanica* and *Gephyrocapsa* forma V. *G. lumina* evolved from *Gephyrocapsa* forma V and is the ancestor of *G. oceanica* (S&B).

Occurrence: Very abundant in lower Quaternary sediments of all sites (Figure 3.10); its FAD was difficult to determine based on counting analysis, due to the morphological overlapping between this species, *G. margereli* and *Gephyrocapsa* forma V (Figure 3.9). However, based

on results from the biometrical study, its FAD was estimated to be at 1.68 Ma and its LAD was at 1.23 Ma.

Gephyrocapsa margereli-muellerae group

Remarks: *G. margereli* and *G. muellerae* were united into this group, because of the difficulty in separating them when using LM. However, these two forms are considered as separate species in this study, as described below.

Gephyrocapsa margereli Bréhéret 1978
Plate 2, Figures 7, 10

*1978 *Gephyrocapsa margereli* Bréhéret: 447, pl. 1, figs. 1-2.
1980 *Gephyrocapsa margereli* Bréhéret; Samtleben: 104, pl. 12, figs. 19, pl. 14, figs. 1-5.
 non 1980 *Gephyrocapsa margereli* Bréhéret; Samtleben, pl. 12, figs. 20-22 (= *G.* forma V).
1990 *Gephyrocapsa margereli* Bréhéret; Baumann: 122, pl. 6, figs. 9-11.

Description: Medium-sized (2.5 - 4.5 µm) placoliths with relatively large central openings (40 - 60 %), medium sized and arched bridges, and small to medium bridge angles (25 - 50°).
Remarks: This species has the same coccolith length range as *G. caribbeanica*, and differs from the latter by its relatively large central opening and smaller bridge angle. It is distinguished from *G. lumina* by its smaller size, larger central opening and smaller bridge angle. It is separated from *G. oceanica* by its smaller size and smaller bridge angle. *G. margereli* can be distinguished from its descendant *G. muellerae*, in having a somewhat larger bridge angle and central opening, and from its precursor, *Gephyrocapsa* forma V, by this form having a thick bridge which is formed by two broad and separate elements and a smaller central opening.
Occurrence: Common in the Quaternary of all sites (Figure 3.11). The variation in abundance (high values in sites 664, 659 and relatively low values in sites 608, 609, 610) indicates this species to be a eurythermal form, with a preference however for warm-waters. Its FAD was estimated to be at 1.70 Ma, and its LAD was at 0.285 Ma.

Gephyrocapsa muellerae Bréhéret 1978
Plate 2, Figures 4-5, Plate 7, Figure 3

*1978 *Gephyrocapsa muellerae* Bréhéret: 448, pls. 1-2, figs. 3-4.
1980 *Gephyrocapsa muellerae* Bréhéret; Samtleben: 106, pl. 14, figs. 6-8, pl. 15, figs. 1-4.
1990 *Gephyrocapsa muellerae* Bréhéret; Baumann: 123-124, pl. 5, figs. 1-6.

Description: Medium sized elliptical placoliths (2.5 - 4 µm), with medium sized central openings (40 - 60 %), and medium sized and arched bridges which have very small bridge angles (10 - 24°).

Remarks: This species is very similar to *G. margereli*, the differences between them have been given above. This species is considered to have evolved from *G. margereli* through a change in bridge angle (Samtleben, 1980).

G. muellerae is distinguished from *G. ericsonii* by the latter being smaller than 2.5 µm and having a very highly arched bridge, yielding a distinctive bright birefringence between crossed nicols. It differs from *G. caribbeanica* by having a smaller bridge angle and a relatively large central opening.

Ecology: *G. muellerae* is a eurythermal species, but prefers medium to lower temperatures; it occurs commonly in water masses above 5 °C (Samtleben et al., in press) and is dominant in sediments from the last interglacial period in the northern North Atlantic and common in the Würm-glacial sediments from the subtropical NE Atlantic (Samtleben, 1980; Baumann, 1990).

Occurrence: Around 0.36 to 0.27 Ma, a transition from *G. margereli* to *G. muellerae* occurs with a strong morphological overlap between them. The abundance peaks I and II in Figure 3.11 are due to *G. muellerae*, based on observations with SEM. An increase in abundance towards the northern areas (sparse at site 664, rare at site 659, common at site 608, abundant at sites 609 and 610, see Figure 3.11) suggests this species to have affinities with colder waters. *G. muellerae* is still extant today.

Gephyrocapsa forma V Samtleben and Baumann (in prep.)
Plate 2, Figures 1-2

1980 *Gephyrocapsa margereli* Bréhéret; Samtleben, pl. 12, figs. 20-22.

Description: Medium to small sized (2.5 - 4 µm) placoliths with medium sized central openings (25 - 50 %), thick and broad bridges which have small bridge angles (10 - 40°).

Remarks: This species is similar to *G. margereli* and *G. lumina*, hence, in this counting analysis this form was determined as a variant of *G. margereli*. However, the biometrical study (S&B) shows it to be a distinctive species, which differs from *G. margereli* by having a thicker and broader bridge, and from *G. lumina* by a smaller bridge angle and smaller placoliths.

Occurrence: Rare to common in the Upper Pliocene and lower Quaternary (Figure 3.11). Its earliest occurrence was observed at about 3.85 Ma in the tropical site 664. This species is seen as the precursor of *G. margereli* and *G. lumina*. *G. margereli* evolved from *Gephyrocapsa* forma V at around 1.9 Ma and *G. lumina* developed from it at around 1.7 Ma.

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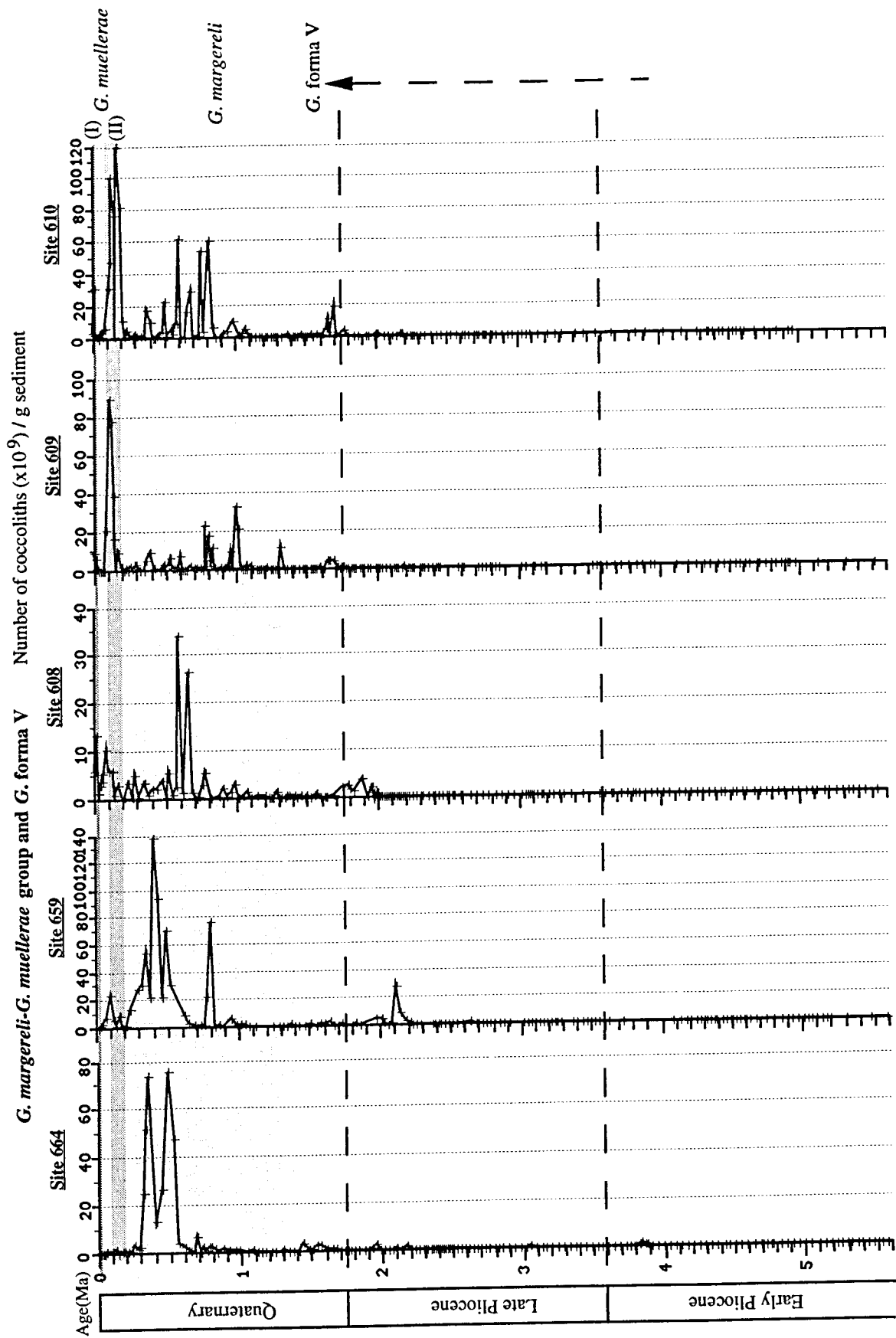
Figure 3.11 Absolute abundance plots of *Gephyrocapsa* forma V, *G. margereli* and *G. muellerae* at DSDP/ODP Sites 664, 659, 608, 609, 610. Here, an increase in abundance of *G. muellerae* towards the northern areas and its two abundance peaks (I, II) can be clearly seen.

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Gephyrocapsa oceanica Kamptner 1943

Plate 1, Figures 16-17, Plate 7, Figures 8-9

*1943 *Gephyrocapsa oceanica* Kamptner: 45.
1956 *Gephyrocapsa oceanica* var. *typica* Kamptner, figs. 4-5.
1973 *Gephyrocapsa parallela* Hay and Beaudry: 672, pl. 1, figs. 10-12.
1980 *Gephyrocapsa oceanica* Kamptner; Samtleben: 111-115, pl. 15, figs. 5-12.

Description: Large to medium-sized placoliths (3.5 - 6 µm) with medium to large central openings (40 - 50 %), medium broad rims, medium sized and arched bridges, and large bridge angles (40 - 90°).

Remarks: This species differs from *G. caribbeanica* and *G. margereli* by being larger and having a larger central opening and bridge angle. It is also distinguished from *G. lumina* by having a larger central opening and bridge angle.

Ecology: This species has a temperature range of 12 - 30°C (Okada and McIntyre, 1977) and is abundant in warm marginal seas (Okada and Honjo, 1975; Okada, 1984; Kleijne et al., 1989; Su, in Hao et al., 1989). Moreover, an increase in the abundance of *G. oceanica* towards coastal regions or upwelling areas has been observed (Wang and Samtleben, 1983; Kleijne, 1993).

G. oceanica   Number of coccoliths (x10^9) / g sediment
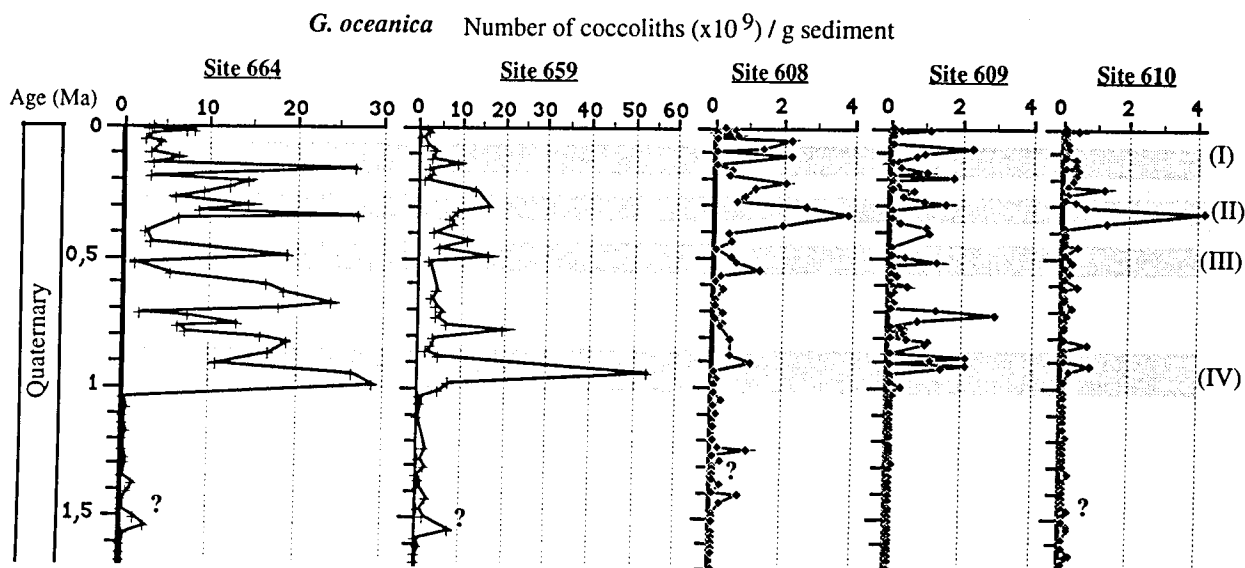
Figure 3.12 Absolute abundance plots of *G. oceanica* at DSDP/ODP Sites 664, 659, 608, 609, 610. Several main abundance peaks (I - IV) of this species are marked with shaded areas. Its "occurrences" marked with "?" are considered as being due to the presence of a variety of *G. lumina* with larger central openings (see also text).

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Occurrence: *G. oceanica* occurs from 1.26 Ma, and is abundant at sites 664 and 659 and rare at sites 608, 609, 610. This clearly indicates a decrease in abundance from the tropical areas to the transitional areas (Figure 3.12). Four abundance peaks (I - IV) were recognized. The FAD of this species is difficult to determine, because variants of *G. lumina*, its precursor, with large openings in the lower Quaternary, may be identified as *G. oceanica* in counting analyses. Around 1.26 Ma, a transition from *G. lumina* to *G. oceanica* occurs with a morphological overlap between them, and no distinctive boundary can be identified.

Gephyrocapsa spp.1 (small *Gephyrocapsa* species group)

Remarks: All small (<3 μm) species of *Gephyrocapsa*, *G. ericsonii*, *G. aperta*, *G. sinuosa*, and *G. rota*, were united here. However, they are separate species and are described below. Values of coccolith length, bridge angle and opening width, are from the biometrical study (S&B). Among these small forms, a number of new form-groups/species have been recognized by Samtleben and Baumann. Their descriptions of these species are cited briefly here.

Figure 3.13 shows the occurrence of *Gephyrocapsa* spp.1, several abundance zones were recognized, which are formed by the different species united in this group. Table 3.3 gives a brief summary of their distributions. However, it is necessary to point out that there are no strict correlations between sites, because these abundance zones are the sum of several species which have different ecological affinities.

Abundance zones in Figure 3.13	Main contributors
I	*G. ericsonii , G. aperta*
II	*G. aperta, G. sinuosa, G. ericsonii,*
III	*G. aperta*
IV	*G.* forma P
V	*G. aperta*
VI	*G. aperta, G. sinuosa, G.* forma F
VII	*G. sinuosa G. aperta, G.* formas F and D
VIII	*G. sinuosa*
IX	*G. sinuosa, G. aperta, G.* formas F and H
X	*G. aperta* and *G. sinuosa, G.* forma F

Table 3.3 Abundance zones of *Gephyrocapsa* spp.1 and their main contributors.

Gephyrocapsa aperta Kamptner 1963

Plate 1, Figures 5-6

*1963 *Gephyrocapsa aperta* Kamptner 1963: 173, pl. 6, figs. 32, 35.
1980 *Gephyrocapsa aperta* Kamptner; Samtleben: 103, pl. 13, figs. 7-9, figs. 11-18.
  non 1980 *Gephyrocapsa aperta* Kamptner; Samtleben, pl. 13, fig. 10 (= *G. ericsonii*).
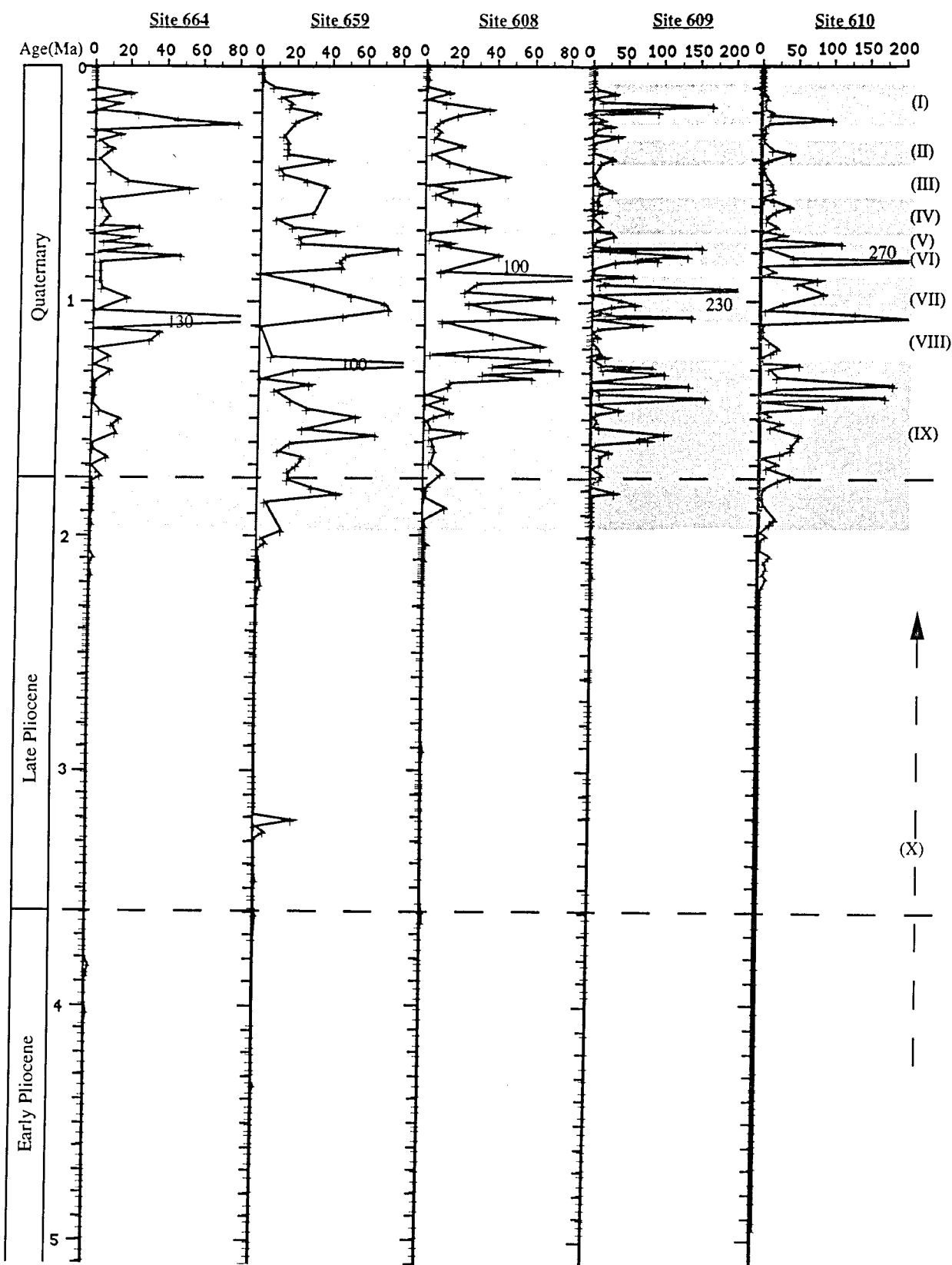
Figure 3.13 Absolute abundance plots of small *Gephyrocapsa* species group at DSDP/ODP Sites 664, 659, 608, 609, 610 (a few peaks are not plotted in total, the abundance values are printed next to them). Several abundance zones (I - X) are marked with shaded areas and are the product of different species of this group (see Table 3.3).

Description: Small sized (1.7 - 2.5 μm) elliptical placoliths with large open central pores (52 - 60 %), having flat and narrow bridges in which the two elements are usually separate, small bridge angles (23 - 32°), and narrow and denticulate rims.

Remarks: This species differs from *G. sinuosa* in having a smaller bridge angle and from *G. ericsonii* by its flat bridge and open central pore. It is distinguished from *G. margereli* by being smaller and having a flatter bridge, an exact separation can be made through biometrical analyses.

Occurrence: Rare in the Pliocene and abundant in the Quaternary of all sites (Table 3.3, Figure 3.13). Observations with SEM show this species to have a slightly affinity to warmer waters. The FAD of this species was observed at about 4.45 Ma, and the LAD of this species was at 0.13 Ma.

Gephyrocapsa ericsonii McIntyre and Bé 1967
Plate 1, Figure 4, Plate 7, Figure 2

1967 *Gephyrocapsa ericsonii* McIntyre and Bé: 571, pl. 10, pl. 12, fig. b.
1980 *Gephyrocapsa ericsonii* McIntyre and Bé; Samtleben: 107, pl. 13, figs. 1-6, 10, 25.

Description: Small sized (2.1 - 2.4 μm), subcircular to elliptical placoliths with relative broad rims, large to medium sized openings (45 - 55 %), narrow and very highly arched ("plank on edge") bridges perpendicular to rims, and small bridge angles (24 - 30°).

Remarks: This species differs from *G. aperta* in having a smaller central opening, and from *G. muellerae* by its highly arched bridge and smaller size.

Ecology: *G. ericsonii* has a temperature range of 14 - 25°C (McIntyre and Bé, 1967).

Occurrence: Abundant in the upper Quaternary of all sites (Table 3.3, Figure 3.13). Its rare occurrence in the top parts of the upper Quaternary and in the Holocene agrees with the study of Samtleben (1980), who suggested the suppression of this species by *E. huxleyi* in coccolith assemblages. *G. ericsonii* lives in modern oceans. Its FAD was not determined in this study, but an age of 0.34 Ma was suggested by the biometrical study (S&B).

Gephyrocapsa sinuosa Hay and Beaudry 1973
Plate 1, Figure 7

*1973 *Gephyrocapsa sinuosa* Hay and Beaudry: 672, pl. 1, figs. 13-14.
1980 *Gephyrocapsa sinuosa* Hay and Beaudry, Samtleben: 101, pl. 12, figs. 7-17.

Description: Small sized (1.75 - 2.3 μm) elliptical placoliths having denticulately edged narrow rims, relative large central openings (50 - 60 %), medium sized flat bridges and large bridge angles (45 - 60°).

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Remarks: Differences between this species and *G. aperta* and *G. ericsonii* have been given in the remarks for those species.

Occurrence: Rare in the Pliocene and abundant in the Quaternary of all sites (Table 3.3, Figure 3.13). Its FAD was observed at about 4.45 Ma, and the LAD was estimated to be at 0.24 Ma.

Gephyrocapsa rota Samtleben 1980
Plate 1, Figure 15

*1980 *Gephyrocapsa rota* Samtleben: 102, pl. 3, figs. 19-23.
 non 1980 *Gephyrocapsa rota* Samtleben, pl. 3, fig. 24 (= *Gephyrocapsa* forma D).

Description: Small to medium sized (2.4 - 3.4 μm) slender placoliths having strongly denticulate rims with slits between the radial elements, large central openings (42 - 61 %) and flat and narrow bridges which have medium to large bridge angles (38 - 75°).

Remarks: Having a medium sized coccolith and large central opening, this species is similar to larger variants of *G. sinuosa* and smaller variants of *G. oceanica*, but it differs from them in having strongly denticulate slit rims.

Occurrence: In the Quaternary of sites 664 and 659. It was also found in the Quaternary of tropical site 336, and its FAD is estimated to be at 1.22 Ma and its LAD at 0.48 Ma (S&B).

A number of new *Gephyrocapsa* form-groups or species are recognized by Samtleben and Baumann (in prep.):

Gephyrocapsa forma D
Plate 1, Figures 9-10

1980 *Gephyrocapsa rota* Samtleben, pl. 3, figs. 24.

Description: Small to medium sized (2.4 - 3.5 μm) elliptical placoliths having strongly denticulate rims, relatively small central openings (38 %), very broad and medium arched bridges, and medium bridge angles (32 - 40°).

Occurrence: In upper Quaternary sediments of sites 659 and 608. Its FAD is at 1.05 Ma and the LAD is at 0.70 Ma.

Gephyrocapsa forma F
Plate 1, Figures 12-13

1980 *Gephyrocapsa aperta/ margereli* Samtleben: pl. 12, figs. 18.
1980 *Gephyrocapsa* sp.1 Samtleben: pl. 12, fig. 23.

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Description: Small sized (1.9 - 2.3 µm) placoliths having narrow rims, large central openings (45 - 60 %), very small bridge angles (15 - 24°), and very highly arched broad bridges formed by two partly overlapping elements.

Remarks: Having high bridges with small bridge angles, this form is similar to *G. ericsonii*, however, its bridge is broader and much more massive than in *G. ericsonii*.

Occurrence: In the upper Pliocene and lower Quaternary of sites 659, 608. Its FAD is earlier than 2.0 Ma and the LAD is at 0.48 Ma. This species is probably the ancestor of *G. ericsonii*, however, a large time gap exists between them.

Gephyrocapsa forma H
Plate 1, Figure 11

Description: Small sized (2.1 - 2.5 µm) elliptical placoliths formed by narrow rims and medium sized central openings (45 - 50 %) which are mostly covered by large sized, medium arched broad bridges with medium to small bridge angles (27 - 35°).

Occurrence: In the upper Pliocene and lower Quaternary of sites 659 and 608. This form is probably a descendant of *Gephyrocapsa* forma F and the precursor of *Gephyrocapsa* forma D, having a morphological overlap with the latter. Its FAD is at 1.87 Ma and the LAD is at about 1.10 - 0.90 Ma.

Gephyrocapsa forma P
Plate 1, Figure 8

Description: Small sized (2.0 - 2.3 µm) and elliptical to irregularly rectangular placoliths, having relative broad rims and small central pores (40 %) with medium sized, very flat bridges and medium bridge angles (35 - 43°).

Remarks: This form differs from other small *Gephyrocapsa* forms by its very flat bridge and irregularly formed rim.

Occurrence: Common in the upper Quaternary of sites 659 and 608. Its FAD is at 0.76 Ma and the LAD varies with site: around 0.47 Ma at site 608 and around 0.43 Ma at site 659.

Gephyrocapsa forma Q
Plate 1, Figure 14

Description: Small sized (1.5 - 2.5 µm) elliptical to subcircular placoliths formed by broad denticulate rims, very small central openings and broad bridges with wide bridge angles (40 - 70°).

Occurrence: In lower Quaternary sediments of site 659. It was also found at site 552 and its FAD is at 1.45 Ma and its LAD at 1.06 Ma (S&B).

Genus *Pseudoemiliania* Gartner 1969

1969 *Pseudoemiliania* Gartner: 598.

Description: Elliptical to nearly circular placoliths. The shields may be solid, or perforated by a few or by numerous radial slits between adjacent shield elements. The centre may be open but is more commonly blocked by a lacy grillwork (after Gartner, 1969: 598).

Remarks: Most features of this genus are similar to those of *Reticulofenestra*, and morphologically transitional forms of *Pseudoemiliania* and *Reticulofenestra* exist, indicating *Pseudoemiliania* to be systematically related to *Reticulofenestra*. This leads to problems in separating several variants of *Pseudoemiliania* from the similar variants of *Reticulofenestra* (see Figure 3.14).
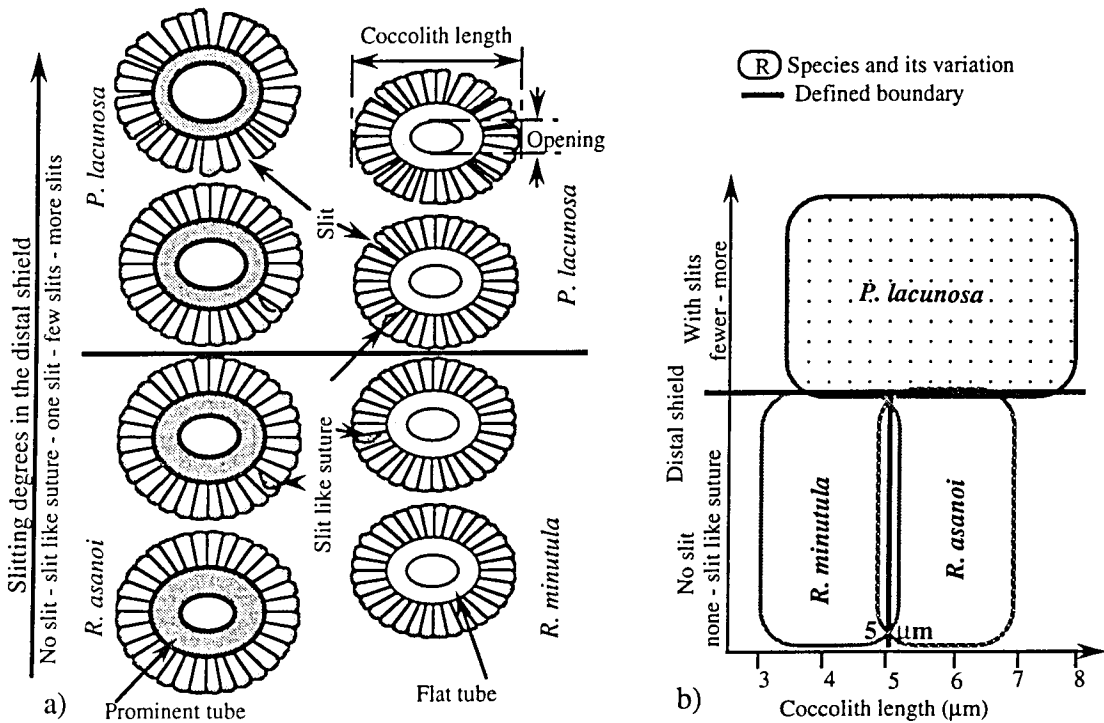

Figure 3.14 Morphological variations of *P. lacunosa, Reticulofenestra asanoi* and *R. minutula*. a)Slitting degree are seen in the distal shields of *R. asanoi* and *P. lacunosa,* and in the shields of *R. minutula* and *P. lacunosa.* b) Variations of coccolith length and slitting degree of the three species, and the morphological boundaries between these species from relevant literature.

Pseudoemiliania lacunosa (Kamptner 1963) Gartner 1969

Plate 3, Figures 7-12, Plate 4, Figures 7-8, Plate 7, Figures 17-21

*1963 *Ellipsoplacolithus lacunosus* Kamptner: 172; pl. 9, fig. 50.
1969 *Pseudoemiliania lacunosa* (Kamptner) Gartner: 598, pl. 2, figs. 9-10.
1971 *Emiliania annula* (Cohen); Bukry: 1514.
1973 *Emiliania ovata* Bukry: 678, pl. 2, figs. 10-12.
1979 *Reticulofenestra pacifica* Nishida: 106, pl. 1, Figs. 4-6.
1990 *Reticulofenestra lacunosa var. ovata* (Bukry) Young: 83.
1990 *Reticulofenestra lacunosa var. lacunosa* Young: 83.

Description: Gartner, 1969: 598.

Remarks: Although this species varies greatly in size (large to small) and in shape of coccoliths (circular to elliptical), and in number of slits, it is commonly accepted, that *P. lacunosa* are used both for circular and elliptical specimens, and that *Emiliania ovata* is a synonym of *P. lacunosa* (Backman, 1980; Perch-Nielsen, 1985). Young (1990) suggested a subdivision of this species: *R. lacunosa var. lacunosa* being larger (4 µm - 8 µm) with more than 12 slits, *R. lacunosa var. ovata* being smaller (3 µm - 5 µm) with fewer slits (1 - 11 slits). In agreement with these suggestions, both circular and elliptical forms are considered as one species: *P. lacunosa* in this study. The two variants: *var. lacunosa* and *var. ovata*, were counted separately in order to investigate their ecological differences. In many samples, however, they are indistinguishable. For example, the larger placoliths (> 4.5 µm - 8 µm) often bear fewer slits (1 - 11 slits), and the smaller ones (3 µm - 4.5 µm) may have more than 12 slits. Thus, the "*lacunosa* form" was separated from the "*ovata* form" only by being larger than 4.5 µm.

The occurrence of slits in the distal shield makes *P. lacunosa* different from *Reticulofenestra minutula/R. asanoi*. However, it is difficult to separate intergradations between *P. lacunosa* and *R. minutula/R. asanoi*. Figures 3.14a-b demonstrate the intergradations between shields without slits (*R. minutula/R. asanoi*) and shields with slits (*P. lacunosa*). When observed by SEM, the forms with one slit can be used to determine *P. lacunosa*, however, one or few indistinct slits in the placoliths are difficult to see with LM. Thus, only forms with recognizable slits were identified as *P. lacunosa*. This agrees with the observations of Samtleben (1978) who found also transitional forms between *P. lacunosa* and "*Crenalithus doronicoides*" (here = *R. minutula*). The existence of intergradations between *P. lacunosa* and *R. minutula* indicates *P. lacunosa* to have probably evolved from *R. minutula*. Moreover, a gradation in the form of the tube and opening between *R. asanoi* and *P. lacunosa* is observed (Figure 3.14a). Besides having slits in the distal shield, *P. lacunosa* differs from *R. asanoi* by its narrow and flat central tube and larger opening. However, variants of *P. lacunosa*, which have smaller openings with broader and highly prominent tubes, commonly occur together with *R. asanoi* in the Quaternary. So neither tube shape nor opening can be

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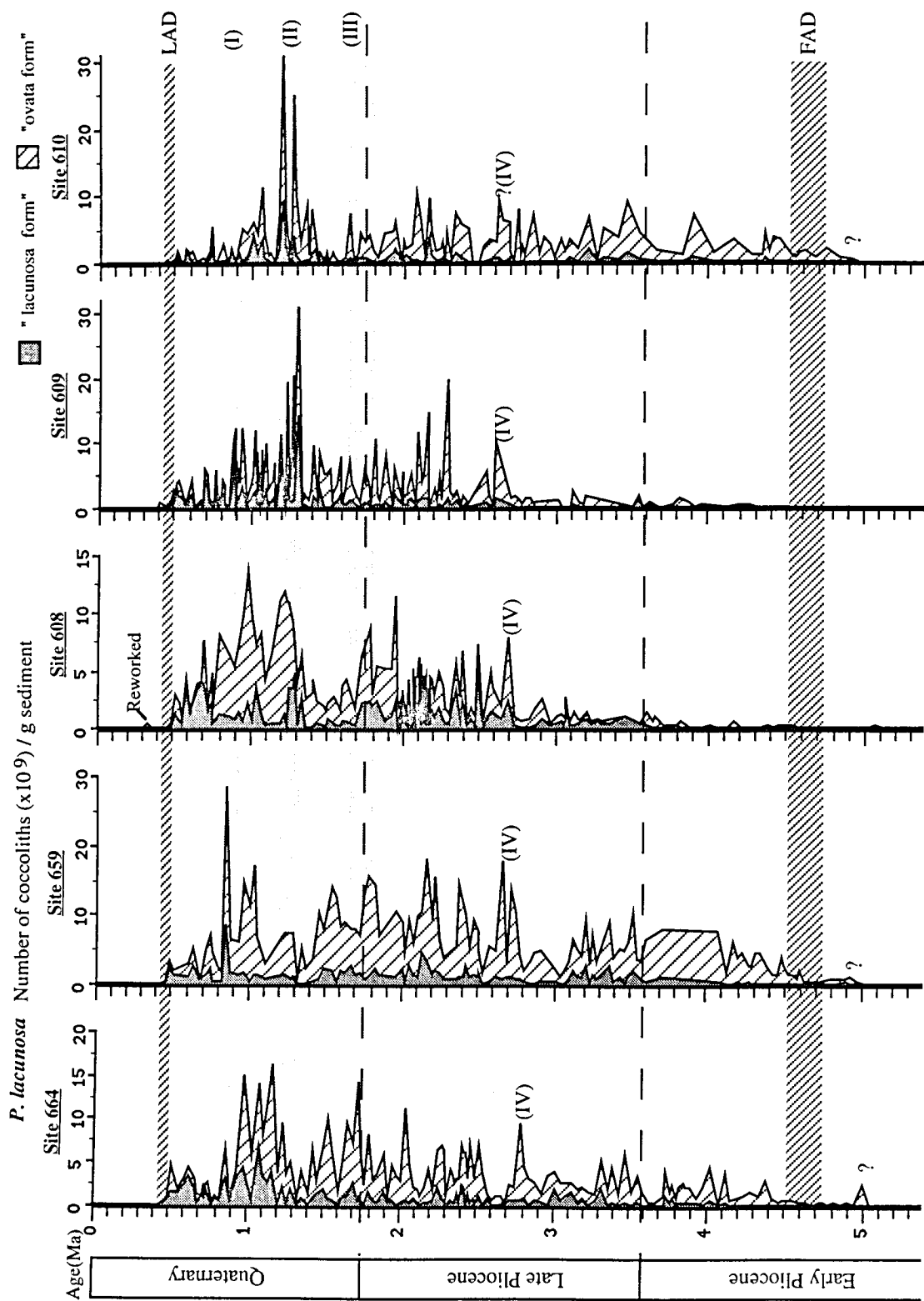Figure 3.15 Absolute abundance plots of *P. lacunosa* (for both the large "lacunosa form" and the small "ovata form") at DSDP/ODP Sites 664, 659, 608, 609, 610. The FAD, LAD of this species and its main abundance peaks (I - IV) are marked with shaded areas and numbers. Its "occurrences" marked with "?" are considered to show intergradations between *P. lacunosa* and *R. minutula* (see the text).

used to distinguish *P. lacunosa* from *R. asanoi* in these samples. They can only be separated by having or not having distinct slits. Therefore, species separated by such distinctions are just morphological species or species in term of palaeontology.

Biostratigraphy: The LAD of *P. lacunosa* defines the top of NN19 (Gartner, 1969, 1977). Takayama (1993) suggested an age of 0.49 Ma (corr.) for the LAD of *P. lacunosa.*

Paleoecology: The circular forms are found mainly in low latitudes and during temperature maxima, while the elliptical forms dominate in the higher latitudes and during temperature minima (Perch-Nielsen, 1985). In the NE Atlantic, the "*lacunosa* form" occurs more commonly in low latitudes (sites 664, 659, 608) than in high latitudes (sites 609, 610) and agrees generally with the paleoecology, as suggested by Perch-Nielsen (1985). However, as the "*ovata* form" also occurs commonly in the tropical areas this seems to disagree with previous observations of its paleoecology.

Occurrence: Common to dominant in Pliocene and Quaternary sediments of all sites (Figure 3.15). Several main abundance peaks (I - IV) were observed. Both the "*ovata* form" and the "*lacunosa* form" become extinct at the same time. The LAD of this species is rather distinct and synchronous at all sites and is used for stratigraphy in this study (see chapter 2.2).

Based on observations with SEM in this study, the FAD of this species was estimated to be at about 4.6 Ma (Figure 3.15). But the "*lacunosa* form" appears later (about 4.3 Ma) than the "*ovata* form" and the very distinct "*lacunosa* form" (> 5 μm and circular) first occurs at about 3.8 Ma. This indicates that this species probably evolved from *R. minutula* by developing slits on the elliptical distal shield.

Genus *Reticulofenestra* (Hay, Mohler and Wade 1966) emend. Gallagher 1987

1966 *Reticulofenestra* Hay, Mohler and Wade: 386.
1968 *Reticulofenestra* (Hay, Mohler and Wade) emend. Stradner: 19.
1973 *Reticulofenestra* (Hay, Mohler and Wade) emend. Edwards: 79.
1987 *Reticulofenestra* (Hay, Mohler and Wade) emend. Gallagher: 46.

Description: Circular to elliptical placoliths consisting of two shields and a central opening. A number of segments of the proximal shield are extended into the central opening to form the central grill and are projected distally to form the central tube. Projection of the tube can give the central area a closed appearance (Gallagher, 1987: 46).

Remarks: The species within *Reticulofenestra* are distinguished mainly by coccolith size, by the relative size of the central opening and by the relative width of the central tube. A group of medium to small sized forms of *Reticulofenestra* was found in the material from the NE Atlantic Ocean, namely *R. pseudoumbilicus, R. minutula, R. minuta, R. asanoi, R. perplexa,* and *R. productella.* However, these species show a great range of variation in coccolith size and central area, causing a number of problems in identification (Table 3.4). As discussed in

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section 2.4 (Figure 2.3), the various morphological intergradations of different species of *Reticulofenestra* are separated by defined features suggested from previous studies and biometrical measurements.

1)	Variation	coccolith length : small - medium - large
	Related species	*R. minuta : R. minutula : R. pseudoumbilicus*
		R. minuta : R. minutula : R. asanoi
		R. productella : R. perplexa
2)	Variation	**Central area: closed suture - slit - opening**
	Related species	*R. perplexa : R. pseudoumbilicus/R. minutula*
		R. productella : R. minutula/R. minuta
3)	Variation	**Central tube: narrow and flat - broad and prominent**
	Related species	*R. minutula : R. asanoi*
		R. pseudoumbilicus: R. asanoi
		P. lacunosa : R. asanoi

Table 3.4 Degrees of morphological variation in *Reticulofenestra*.

1) **Variation in coccolith length**   Figure 3.16c shows the size variations of different species and overlap in coccolith lengths of *R. minuta, R. minutula,* and *R. pseudoumbilicus* in Lower Pliocene samples and of *R. minuta, R. minutula,* and *R. asanoi* in Quaternary samples. Generally, the size variations of *R. minuta, R. minutula* and *R. pseudoumbilicus* observed in this study agree with the results of Backman (1980). Thus, separations of these three species were made after Backman (1980): *R. pseudoumbilicus* was used for forms larger than 5 μm, *R. minuta* for forms smaller than 3 μm, and *R. minutula* for forms sized 3 μm - 5 μm. In the same manner, *R. asanoi* was distinguished from *R. minutula* by being larger than 5 μm. Size variations of *R. productella* and *R. perplexa* are also observed. The forms smaller than 4.5 μm were determined to be *R. productella*, based on previous studies (Backman, 1980; Gallagher, 1989).

2) **Problem of an open or closed centre**   This is observed among *R. perplexa* and *R. pseudoumbilicus/R. minutula,* and among *R. productella* and *R. minutula/ R. minuta.* Usually, *R. productella* and *R. perplexa,* with closed central areas, are called "closed forms" whereas the other species with an open pore surrounded by a central tube are called "open forms" (Gallagher, 1987; Driever, 1988). A series of variants from closed sutures to large openings were found and are shown briefly in Figure 3.16b. Here, "closed forms" is used for forms without distinct central openings.

3) **Variation in the central tube**   A gradational change in the form of the central tube was noted between *R. asanoi* and *R. minutula,* as well as between *R. asanoi* and *R. pseudoumbilicus. R. asanoi* is a form sized 5 μm - 7 μm with a very broad and prominent central tube, whereas *R. minutula* and *R. pseudoumbilicus* have narrow and flat tubes. However, a gradual change in the tube form, narrow to broad and prominent to flat, exists (Figure 3.16a). Thus *R. asanoi* is distinguished from *R. minutula* only by being larger than 5

a) *R. asanoi*   b) *R. perplexa/R. productella*
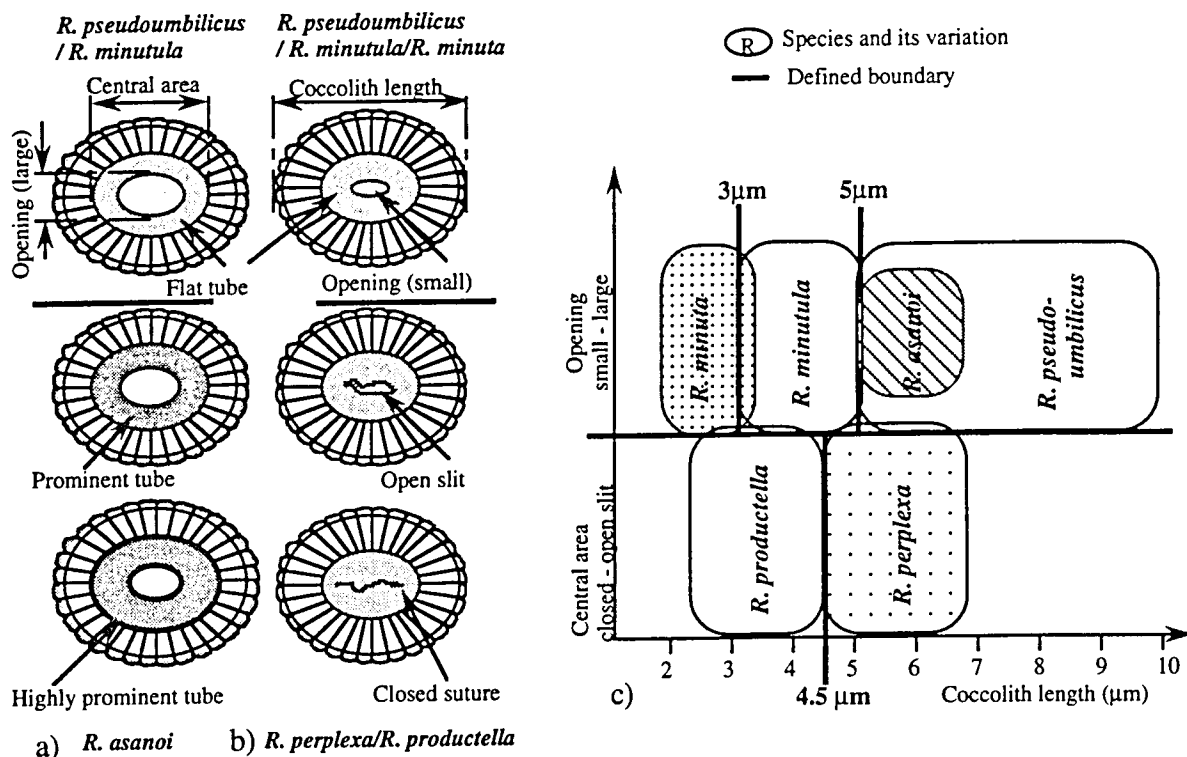
Figure 3.16 Generalized morphological variation of Late Cenozoic *Reticulofenestra*.   a) Variations of the central tube in *R. asanoi* and *R. pseudoumbilicus/R. minutula* . b) Gradations from central slit to opening between closed and open forms. c)Size variations of the closed and open forms, as well as the defined boundaries used for separating them; *R. pseudoumbilicus* differs from *R. asanoi* by its flatter tube and usually larger size.

µm in coccolith length, and from *R. pseudoumbilicus* mainly by having smaller (< 7 µm) and more circular shields.

As discussed above, the different forms of *Reticulofenestra* can be separated and identified only by using artificial boundaries, but they are still named as species in this study, according to previous studies of Neogene *Reticulofenestra* (Backman, 1980; Gallagher, 1987; Young, 1990; Gartner, 1992).

Reticulofenestra asanoi Sato and Takayama 1992

Plate 3, Figures 13-14, Plate 7, Figures 22-24

1987 *Reticulofenestra* sp. A Takayama and Sato: 692, pl. 3, figs. 3a-b.
1987 *Reticulofenestra* sp. B Takayama and Sato: 692.
1991 *Reticulofenestra asanoi* Sato and Takayama; Sato, Kameo and Takayama, pl. 1, figs. 7-10, pl. 2, figs.1-5.
*1992 *Reticulofenestra asanoi* Sato and Takayama: 458, 460, pl. 3, figs. 7-13.

Description: Sato and Takayama, 1992: 458, 460.

Figure 3.17 Absolute abundance plots of *R. asanoi* at DSDP/ODP Sites 664, 659, 608, 609, 610. Its FAD, LAD and an abundance peak (I) are marked with shaded areas. The form in the Late Pliocene is probably another form of *Reticulofenestra* (see the text).

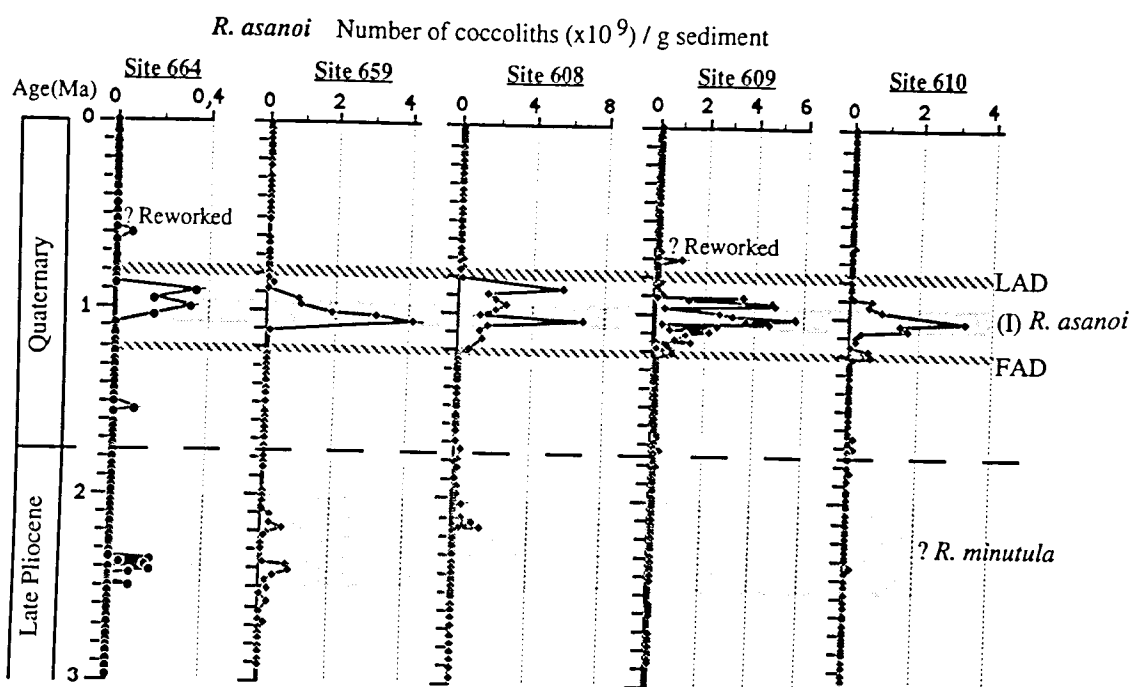*Remarks:* This species can be recognized by its medium size and broad, prominent central tube which is bright between crossed nicols. Problems in separating this species from *R. minutula*, *R. pseudoumbilicus* and *P. lacunosa*, have already been discussed above.

The morphological similarity of *R. asanoi* with *R. pseudoumbilicus* and *R. minutula*, as well as with *P. lacunosa*, indicates that this form is very closely related to the three species, and is probably a subspecies or an ecotype of one of them.

Occurrence: In middle Quaternary sediments: common at sites 659, 608, 609, 610; rare at site 664 (Figure 3.17), this indicates this species to be a eurythermal form but with a preference for temperate waters. Its FAD is distinctive and nearly synchronous at higher latitude sites (608, 609, 610), an age of 1.2 Ma was estimated for this event. Its LAD varies a little with sites in an age range of 0.86 ± 0.03 Ma. These two events are generally in agreement with the suggestion of Takayama (1993), who gave an age of 1.15 Ma (corr.) for the FAD and 0.90 Ma (corr.) for the LAD.

The forms in Upper Pliocene sediments occur irregularly. These forms are probably variants of *R. minutula* being somewhat larger and having prominent and broad tubes. However, it is impossible to distinguish these forms from *R. asanoi* in the present study, since no distinct boundary between them can be made. It is therefore likely that *R. asanoi* evolved from these forms.

Reticulofenestra minuta Roth 1970

Plate 3, Figures 1-2, Plate 7, Figures 12-13

*1970 *Reticulofenestra minuta* Roth: 850, pl. 5, figs. 3-4.
1971 *Prinsius minutus* Haq: 78, pl. 6, figs. 4-5.
1980 *Reticulofenestra minuta* Roth; Backman: 58, pl. 7, figs. 1-3.
1987 *Reticulofenestra minuta* Roth; Gallagher: 59.

Description: Gallagher, 1987: 59.

Remarks: This species is the smallest form of *Reticulofenestra*, but it varies greatly in coccolith size. The problem of size variation between *R. minuta* and *R. minutula* has been given in the remarks on the genus, and in this study *R. minuta* was used for forms being smaller than 3 µm (Figure 3.16c).

R. minuta differs from the same sized *R. productella* by its narrower tube and larger opening (ca 30% of total area of shield), while the latter has a very broad central tube and a closed central area. The problem of the gradation from closed to open forms has been shown (Figure 3.16b).

Occurrence: Common to dominant in Pliocene and lower Quaternary sediments of all sites (Figure 3.18). An age of about 1.6 Ma for its LAD is estimated.

Throughout the Pliocene its abundance patterns in low latitudes are different from those in high latitudes. In low latitudes (sites 664, 659), it shows a decreasing trend in abundance; whereas in high latitudes (sites 609, 610) its abundances increase during the middle Pliocene period and thereafter decrease in the late Pliocene. This increase at high latitudes may be related to the middle Pliocene warm interval in these areas, when water temperatures were warmer than the early or late Pliocene periods (Ruddiman et al., 1987, Dowsset et al., 1994; Chandler et al., 1994).

Reticulofenestra minutula (Gartner 1967) Haq and Berggren 1978

Plate 3, Figure 6, Plate 4, Figures 9-12, Plate 7, Figures 14-16

*1967 *Coccolithus minutulus* Gartner (part): 3, pl. 5, figs. 3-4.
1971 *Gephyrocapsa reticulata* Nishida: 150, pl. 17, figs. 1-7.
1973 *Crenalithus doronicoides* (Black and Barnes); Roth: 731, pl. 3, fig. 3.
1978 *Reticulofenestra minutula* (Gartner) Haq and Berggren: 1190
1978 *Reticulofenestra haqii* Backman: 110, pl. 1, figs. 1-4, pl. 2, fig. 10.
1980 *Reticulofenestra japonica* (Nishida) Nishida: 105, pl. 1, figs. 1,5,17.
1987 *Reticulofenestra minutula* (Gartner) Haq and Berggren; Gallagher: 60.
1991 *Reticulofenestra ampla* Sato, Kameo and Takayama: 50, pl. 1, figs. 4-6.

Description: Gallagher, 1987: 60.

Remarks: Backman (1978) suggested, that *R. haqii* differs from *R. minutula* by having an opening smaller than 1.5 µm. Since the variation of the opening size is gradual, a separation

Figure 3.18 Absolute abundance plots of *R. minuta* at DSDP/ODP Sites 664, 659, 608, 609, 610. Its LAD and main abundance peaks (I - VIII) are marked with shaded areas. Its abundances increase towards the northern areas during the mid Pliocene period, when this region was warmer than during the early or late Pliocene periods (see the explaination in the text).
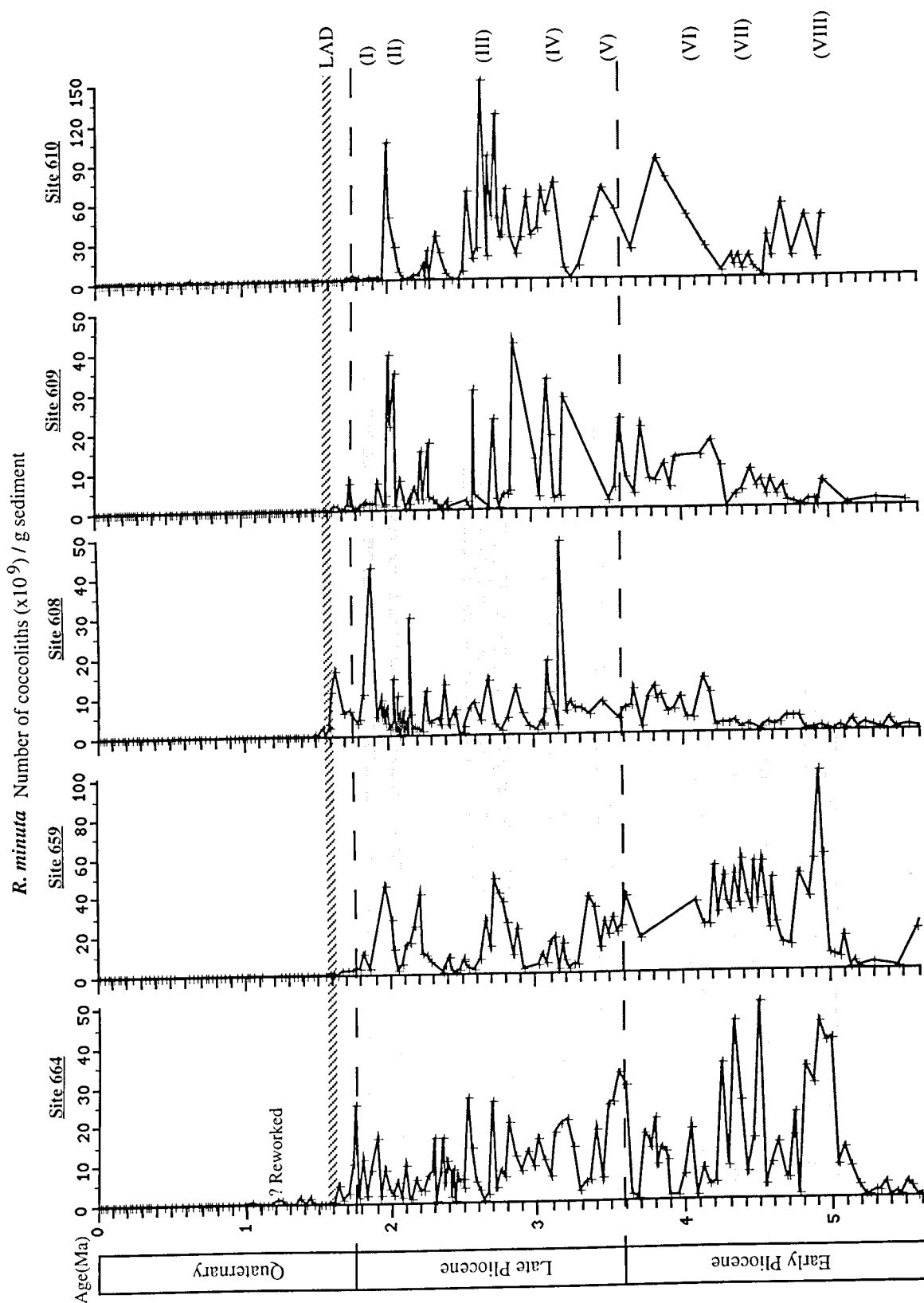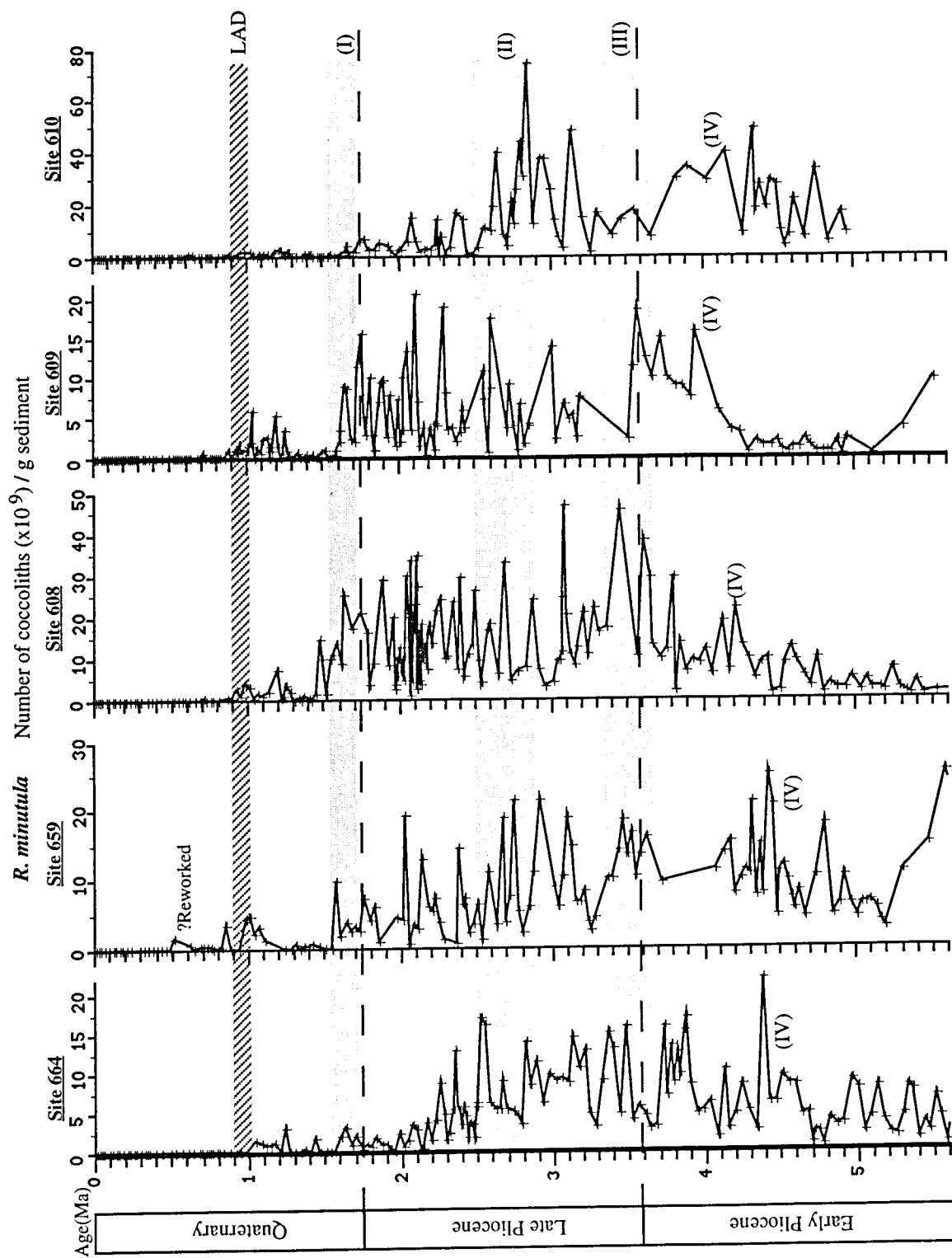
Figure 3.19 Absolute abundance plots of *R. minutula* at DSDP/ODP Sites 664, 659, 608, 609, 610. Its LAD and main abundance peaks (I - IV) are marked with shaded areas or numbers.

of these two forms can not be made. Therefore, differences in opening size is considered an intra-specific variation, and *R. haqii* is regarded as a junior synonym of *R. minutula* in this study. Sato et al. (1991) introduced *R. ampla*, a form sized ca. 5 μm with a narrow central tube. Based on observations in this study, *R. ampla* is very similar to *R minutula*; and a gradational variation in the width of the central tubes means there is no distinctive boundary between them. Thus, in this study, *R. ampla* was considered as a synonym of *R. minutula*.

Problems in separating this species from *R. minuta, R. pseudoumbilicus, R. asanoi, R. productella* and *R. perplexa*, as well as from *P. lacunosa* have been discussed in detail in the remarks on the genus.

Occurrence: At all studied sites: common to dominant in the Pliocene, rare to common in lower Quaternary sediments (Figure 3.19). Several abundance peaks (I - IV) were observed. The LAD of *R. minutula* occurs earlier in the tropical areas (about 1.0 Ma in site 664, 0.95 Ma in site 659) than in the northern areas (about 0.9 Ma in sites 608, 609, 610).

Reticulofenestra perplexa (Burns 1975) Wise 1983

Plate 4, Figures 5-6, Plate 7, Figure 29

*1976 *Dictyococcites antarcticus* Haq: 561, pl. 3, figs. 1-5, 7-8.
1987 *Reticulofenestra perplexa* (Burns) Wise; Gallagher: 62.

Description: Gallagher, 1987: 62.

Remarks: This species is distinguished from other medium-sized forms of *Reticulofenestra* by its closed central area with a slit. However, a series of variants are found, from closed slits to large openings between large *R. perplexa* (ca. 6 μm - 7 μm) and *R. pseudoumbilicus*; and between small *R. perplexa* (ca. 4.5 μm - 5 μm) and *R. minutula*. In this study, the slit in the central area is used to identify *R. perplexa* in the counting analyses (Figure 3.16b).

Occurrence: Rare or occasionally common in the Pliocene of all sites (Tables 3.6-3.10); it becomes extinct in upper Pliocene sediments, however, the level of its LAD is impossible to determine due to its sporadic occurrences.

Reticulofenestra productella (Bukry 1975) Gallagher 1987

Plate 3, Figures 3-6, Plate 7, Figures 10-11

*1963 *Ellipsoplacolithus productus* Kamptner: 172, pl. 8, figs. 42, 44.
1971 *Gephyrocapsa producta* (Kamptner) Bukry: 990, pl. 2, fig. 2.
1975 *Crenalithus productellus* Bukry: 688.
1980 *Dictyococcites productus* (Kamptner) Backman: 49, pl. 4, figs. 3, 6-7.
1987 *Reticulofenestra productella* (Bukry) Gallagher: 63.
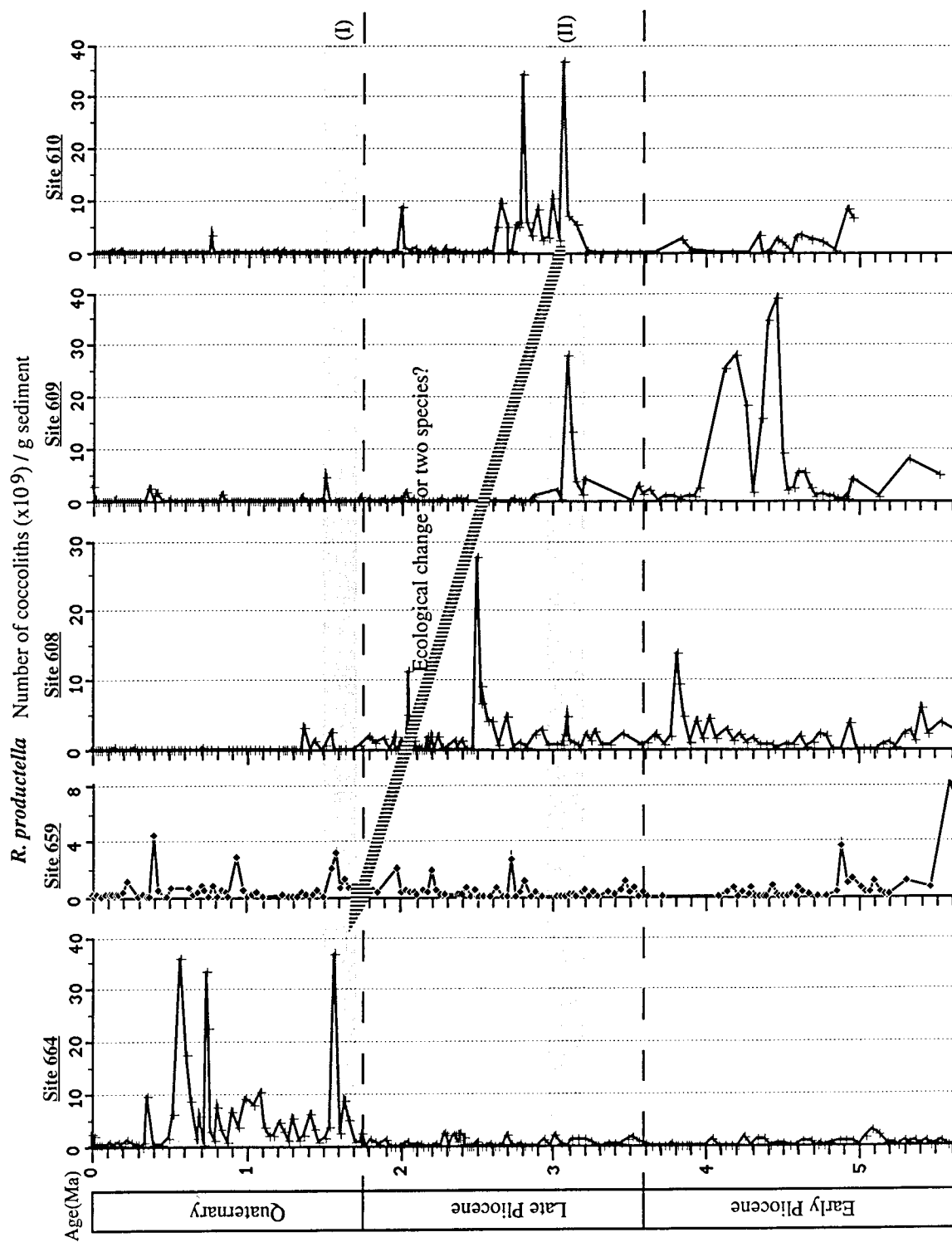

Description: Gallagher, 1987: 63.

Figure 3.20 Absolute abundance plots of *R. productella* at DSDP/ODP Sites 664, 659, 608, 609, 610. Two main abundance peaks (I - II) are marked with shaded areas, showing the quite different geographical distributions of this species in the Late Pliocene and in the Pleistocene (see the explanation in the text).

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Remarks: This species is characterized by its small size and closed central area. The problems in separating this species from *R. minutula /R. minuta* have already been discussed.

An overlap in coccolith size between *R. perplexa* and *R. productella* has been observed. According to Backman (1980) and Gallagher (1987), *R. productella* does not exceed a placolith length of 4.5 µm. In this study *R. productella* was used for forms smaller than 4.5 µm (Figure 3.16c).

Occurrence: In the Pliocene: rare at sites 664, 659; common to occasionally dominant at sites 608, 609, 610. In the Quaternary: common to dominant at sites 664, 659, rare at sites 608, 609, 610 (Figure 3.20).

The closed forms of *Reticulofenestra* are usually more abundant at higher latitudes. Its more abundant occurrence in the Pliocene sediments of sites 609, 610 agrees with such observations. By contrast, in the Quaternary it occurs rarely at high latitudes and abundantly at low latitudes. There are two possible reasons for this: 1) the form in the Quaternary of sites 664 and 659 is possibly a separate species, also with a closed central area, which is not recognized in the present investigation; 2) with the beginning of the Quaternary the ecology of this species may have changed, from a form living in colder waters to a form inhabiting the warm tropical regions, and through the change of ecological affinity this form survived into the Quaternary.

Reticulofenestra pseudoumbilicus (Gartner 1967) Gartner 1969

Plate 3, Figures 15-17, Plate 7, Figures 25-28

*1967 *Coccolithus pseudoumbilicus* Gartner: 4, pl. 6, figs. 1-4.
1969 *Reticulofenestra pseudoumbilicus* (Gartner) Gartner: 598, pl. 2, fig. 4.
1972 *Coccolithus gelidus* Geitzenauer: 407, pl. 1, figs. 1-2, 5-6.
1980 *Reticulofenestra pseudoumbilicus* (Gartner) Gartner; Backman: 59, pl. 5, figs. 1-8.
1987 *Reticulofenestra pseudoumbilicus* (Gartner) Gartner; Gallagher: 35, pl. 3.2, fig. 5.

Description: Gallagher, 1987: 35.

Remarks: *R. pseudoumbilicus* can be determined by its medium to large size and by its large central opening. However, it varies greatly in coccolith size as well as in size of the central area. The overlapping of size between this species and *R. minutula*, and the gradation of open to closed central area with *R. perplexa*, and its similarity to *R. asanoi* have been discussed in the remarks on the genus.

Here, the variation of larger to smaller opening between *R. pseudoumbilicus* and *R. gelidus* is regarded as an intra-specific variation, and so *R. gelidus* is considered as a synonym of *R. pseudoumbilicus*, based on the suggestions of Backman (1980) and the observations in this study.

Biostratigraphy: The LAD of *R. pseudoumbilicus* defines the top of NN15 and approximates the Lower/Upper Pliocene boundary (Gartner, 1969; Martini, 1971). Backman and Shackleton (1983) gave an age of 3.76 ± 0.02 Ma (corr.) for the LAD of *R. pseudoumbilicus.*

Occurrence: Common to dominant in the Lower Pliocene, rare in the Upper Pliocene of all sites studied (Figure 3.21). Several abundance peaks (I - IV) were recognized. This species is more abundant at mid latitude sites (659, 608, 609) than at site 664 or 610, this agrees with previous observations (Haq, 1980; Lohmann and Carlson, 1981) who also found it to have occurred mainly in mid-latitude areas. The LAD of *R. pseudoumbilicus* is not usable for the stratigraphy of the studied sites, because this species survived into the Upper Pliocene in this area and its LAD varies with sites, as discussed below.

In the investigated material, *R. pseudoumbilicus* occurs continuously from Lower Pliocene to Upper Pliocene sediments of all sites (Figure 3.21). This agrees with the study of these sites by Takayama and Sato (1987), who found identification of the LAD of *R. pseudoumbilicus* to be difficult, due to the occurrence of *R. pseudoumbilicus* in the Upper Pliocene of Leg 94 sites.

There are several possible explanations for the stratigraphical discrepancies in the LAD of *R. pseudoumbilicus.* They may result from: 1) differences in identification, 2) reworking and disturbances, 3) the extinction of this species is diachronous and in some area it survived into the Upper Pliocene.

1) **Differences in identification?** Is the identification of *R. pseudoumbilicus* in the study in agreement with the definition used by Gartner (1967) and Backman and Shackleton (1983)? Overlapping coccolith size between *R. pseudoumbilicus* and *R. minutula* may cause problems in the identification of *R. pseudoumbilicus.* For the discussion of this possibility, a brief comparison of the size definitions used by various authors is made (Table 3.5).

Authors	Gartner (1967:4)	Backman (1980:38)	Backman & Shackleton (1983:145)	Gallagher (1987:63)	Young (1990:82)	Young et al. (1994:22)	This study
Diagnoses of *R. pseudoumbilicus*	?(8 μm from the figures)	>5μm	> 5 - 10 μm	8μm (holotype)	>5μm	>5μm	> 5μm

Table 3.5 Comparison of the size definitions of *R. pseudoumbilicus* used by various authors.

Clearly, the identification of *R. pseudoumbilicus* in this study agrees well with those of Gartner (1967), Backman (1980) and Young (1990).

Morphological similarities between *R. pseudoumbilicus* and *R. asanoi* also create problems in recognition of the LAD of *R. pseudoumbilicus.* However, most variants of *R. pseudoumbilicus* differ from *R. asanoi* by being larger (>7 μm) and having a larger opening with a narrower and flatter tube, that can never confused with *R. asanoi.*
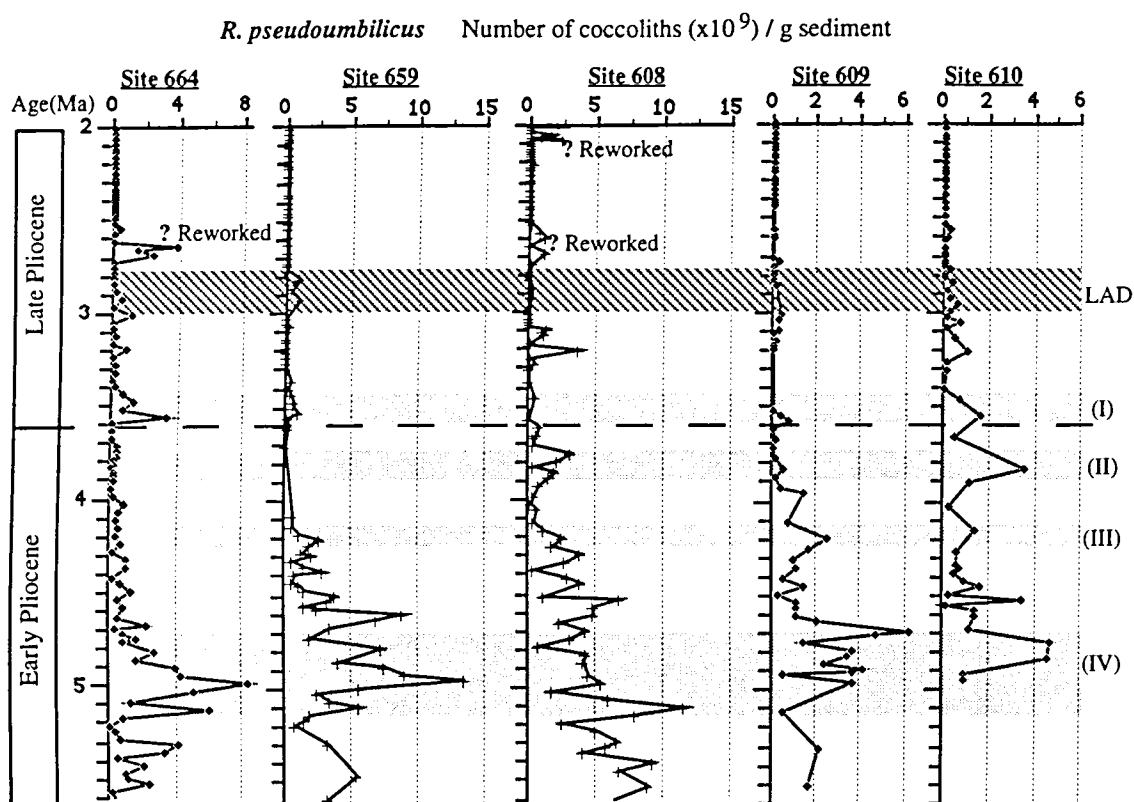
Figure 3.21 Absolute abundance plots of *R. pseudoumbilicus* at DSDP/ODP Sites 664, 659, 608, 609, 610. Its LAD and several main abundance peaks (I - IV) are marked with shaded areas and its occurrences marked with "?" are considered to be due to reworking (see also the text).

2) **Reworking?** The continuous occurrence of *R. pseudoumbilicus* in the lower parts of Upper Pliocene sediments do not support the idea of reworking (Figure 3.21). Moreover, *R. pseudoumbilicus* commonly occurs together with the *S. abies* group in the Lower Pliocene samples from all sites studied (see also Figure 3.26). The fact that *R. pseudoumbilicus* is found alone without the occurrence of the *S. abies* group in the lower parts of Upper Pliocene samples (from 3.6 to 2.8 Ma), indicates that the *R. pseudoumbilicus* found here is not reworked.

3) **Survival of *R. pseudoumbilicus* in the Upper Pliocene?** The possibility remains that in the NE Atlantic *R. pseudoumbilicus* survived into the Upper Pliocene. This is supported by several observations made in this study. Figure 3.21 shows the abundance patterns of this species around its extinction in all sites studied. Its absolute abundance decreases gradually in Lower Pliocene sediments. After a distinct minimum near the Lower/Upper Pliocene boundary, its abundances increase again and fluctuate with a decreasing tendency for an interval until disappearing in the Upper Pliocene. The LAD of *R. pseudoumbilicus* in the Upper Pliocene varies with sites. Such patterns are very similar to those of *Discoaster*

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asymmetricus around its extinction in V28-179 and DSDP Site 606, as described by Backman (1986), who considered the long tail of low abundances of *D. asymmetricus* to indicate the continued existence of *D. asymmetricus* with strongly reduced production levels. Therefore, in this study, the long survival of *R. pseudoumbilicus* may also be indicated by fluctuating low absolute abundances in the Upper Pliocene of the NE Atlantic.

The results of this study do not agree with the remarks of Backman and Shackleton (1983): the LAD of *R. pseudoumbilicus* being distinct world-wide and probably synchronous. The survival of *R. pseudoumbilicus* into the Upper Pliocene of the NE Atlantic seems to be reliable, and is in accordance with a short remark of Gallagher (1987, p. 63): the distribution of *R. pseudoumbilicus* : NN4-NN18.

Family Pontosphaeraceae Lemmermann 1908
Genus *Pontosphaera* Lohmann 1902

1902 *Pontosphaera* Lohmann: 129.

Description: Lohmann, 1902: 129.

Remarks: It is noted that coccospheres of *Scyphosphaera* have both coccoliths with low walls and coccoliths with high walls (Lohmann, 1902; Gaarder, 1970; Nishida, 1979). All fossil forms with low walls are called *Pontosphaera*, while those with high walls are called *Scyphosphaera*. Therefore, they are only palaeontological genera determined by morphology. However, the exact relationships between various forms of *Pontosphaera* and *Scyphosphaera* are not yet known. In this study, *Scyphosphaera* is still used for the forms with high walls, and *Pontosphaera* for those with low walls.

Only two species, *P. japonica* and *P syracusana*, were identified separately, while other forms were determined only at the genus level: *Pontosphaera* spp., due to their occasional occurrence and few applications for biostratigraphy or ecology.

Pontosphaera japonica (Takayama 1967) Nishida 1971
Plate 5, Figure 10

*1967 *Discolithina japonica* Takayama: 189-190, pl. 9, pl. 10, figs: 1, 2-d.
1985 *Pontosphaera japonica* (Takayama) Nishida, Perch-Nielsen: 543, fig. 53-10.

Description: Takayama, 1967: 189-190.

Remarks: This species is easily recognized by its broad rim without pores, and by numerous irregularly arranged small pores in the central area.

Occurrence: Sporadic in Pliocene and Quaternary sediments of all sites (Tables 3.6-3.10).

Pontosphaera syracusana Lohmann 1902

*1902 *Pontosphaera syracusana* Lohmann: 130, pl. 4, fig. 10.
1970 *Pontosphaera alboranensis* Bartolini: 148, pl. 6, figs. 6-7.
1977 *Pontosphaera syracusana* Lohmann; Okada and McIntyre: 15, pl. 5, fig. 7.

Description: Bartolini, 1970: 148.

Remarks: The "S"-shaped wall of cup-like coccoliths make this species distinguishable from other *Pontosphaera* species.

Occurrence: Sparse in the Pliocene and Quaternary of all sites.

Genus *Scyphosphaera* Lohmann 1902

1902 *Scyphosphaera* Lohmann: 132.
1942 *Scyphosphaera* Lohmann; Deflandre: 129.

Description: Lohmann, 1902: 132.

Remarks: As discussed in the remarks of the genus *Pontosphaera,* in this study, all large, high walled bell-like lopadoliths are referred to this genus and determined at the genus level only (*Scyphosphaera* spp.), because they occur too sparsely in the sediments studied.

Occurrence: Very sparse in the Pliocene at sites 664, 608, 609, 610 (Tables 3.6-3.10).

Family Rhabdosphaeraceae Ostenfeld 1899
Genus *Rhabdosphaera* Haeckel 1894

1894 *Rhabdosphaera* Haeckel: 111.
1992 *Rhabdosphaera* Haeckel; Kleijne: 39.

Description: Kleijne, 1992: 39.

Rhabdosphaera claviger Murray and Blackman 1898
Plate 4, Figure 4, Plate 7, Figure 40

*1898 *Rhabdosphaera claviger* Murray and Blackman: 438-439, pl. 15, fig. 13-15.
1902 *Rhabdosphaera stylifer* Lohmann: 148, pl. 5, fig. 65.
1992 *Rhabdosphaera claviger* Murray and Blackman; Kleijne: 39-40, pl. 8, figs. 3, 4, 6, 7.

Description: Kleijne, 1992: 39-40.

Remarks: *R. claviger* was described as a form without a spine at the top of its long appendix, whereas *R. stylifer* was used for forms with a spine on the top. However, coccospheres

bearing both of those rhabdolith forms have been found, and *R. stylifer* is regarded as a synonym of *R. claviger* (Kleijne, 1992).

Ecology: McIntyre and Bé (1967) observed this species to have a temperature range of 15 - 28°C (optimum 17 - 27°C) in the North Atlantic. Kleijne (1992) showed it to be a tropical and transitional water species, occurring frequently in the NE Atlantic and very frequently in the Mediterranean Sea.

Occurrence: In the Pliocene and Quaternary; rare to common at sites 664, 659, 608, 609; rare at site 610 (Tables 3.6-3.10). This agrees with its ecology as suggested by McIntyre and Bé (1967), and Kleijne (1992).

Family Syracosphaeraceae Lemmermann 1908
Genus *Syracosphaera* Lohmann 1902

1902 *Syracosphaera* Lohmann: 133.
1991 *Syracosphaera* Lohmann; Kleijne: 21.

Description: Kleijne, 1991: 21.

Remarks: Most of the coccospheres of this genus are dimorphic, having differently shaped coccoliths, however, only isolated coccoliths of the genus are found in sediments. Furthermore, this genus has very small coccoliths with a fragile central structure that is usually etched. It is impossible to identify them exactly at the species level by using LM. Therefore, only the larger sized form, *S. pulchra*, is identified separately, and the other species are placed into the group *Syracosphaera* spp.

Syracosphaera species live in the modern oceans and display a high diversity within the living communities of the Atlantic (about 20 species, based on Winter and Siesser, 1994). However, they are strongly underrepresented in sediment samples, due to their fragile coccolith structure and selective dissolution in sediments. Therefore, they are of little stratigraphical or ecological value.

Syracosphaera pulchra Lohmann 1902
Plate 5, Figure 6, Plate 7, Figure 33

*1902 *Syracosphaera pulchra* Lohmann: 134, pl. 4, figs. 33, 36-37.
1992 *Syracosphaera pulchra* Lohmann; Kleijne: 241, pl. 5, fig. 10.

Description: Kleijne, 1992: 241.

Remarks: This form is usually larger than 4 µm and easily recognized between crossed nicols.

Ecology: This species was found commonly from the tropical to the subarctic North Atlantic by Okada and McIntyre (1979). Kleijne (1992) also showed the extant *S. pulchra* to be widely distributed in the Red Sea, Mediterranean Sea and NE Atlantic.

Occurrence: Common to rare in the Pliocene and Quaternary of all sites (Figure 3.22), this indicates its paleoecology to be in agreement with its present day ecology, as suggested by Okada and McIntyre (1979) and Kleijne (1992).

GENERA INCERTAE SEDIS

Genus *Umbellosphaera* Paasche, in Markali and Paasche, 1955

emend. Gaarder, in Heimdal and Gaarder, 1981

Plate 2, Figure 3

1955   *Umbellosphaera* Paasche, in Markarli and Paasche: 96.
1981   *Umbellosphaera* Paasche emend. Gaarder, in Heimdal and Gaarder: 62.
1993   *Umbellosphaera* Paasche, Kleijne: 201.

Description: Kleijne, 1993: 201.

Remarks: Coccospheres of this genus are dimorphic, having both smaller and larger umbelloliths. Only two species, *U. irregularis* and *U. tenuis,* are included in this genus. *U. tenuis* differs from *U. irregularis* by its larger umbelloliths with strongly bent shields and its smaller umbelloliths with coarser and more irregular stripes on the distal side. However, only isolated smaller coccoliths of *Umbellosphaera* are found in sediments (Perch-Nielsen, 1985; this study); and differences in stripes on the distal sides between these two species can only be observed with SEM. Thus, umbelloliths are determined only at the genus level in this study (*Umbellosphaera* spp.). SEM observations shows that most of the *Umbellosphaera* coccoliths found in this study are the smaller umbelloliths of *U. tenuis* with coarse and irregular stripes on the distal shield.

Ecology: McIntyre and Bé (1967) suggested a temperature range of 21 - 30°C for *U. irregularis,* and a range of 15 - 28°C for *U. tenuis.* They found the two species to be the dominant or common species in the tropical/subtropical floral assemblages, with *U. tenuis* existing only rarely in transitional assemblages of the North Atlantic. Kleijne (1993) also indicated, that *U. irregularis* prefers tropical to subtropical (up to 40° latitude) regions, while *U. tenuis* extends into colder waters, with maximum frequencies at somewhat higher latitudes (up to 50° N) in the North Atlantic.

Occurrence: In Pliocene and Quaternary sediments; common at site 664; rare at sites 659, 608; and sparse at sites 609, 610 (Figure 3.23).These observations indicate the paleoecology of *Umbellosphaera* spp. to be in agreement with their recent ecology. However, they are generally found in lower abundances in sediments than in the modern oceans, due to the selective dissolution within sediments.
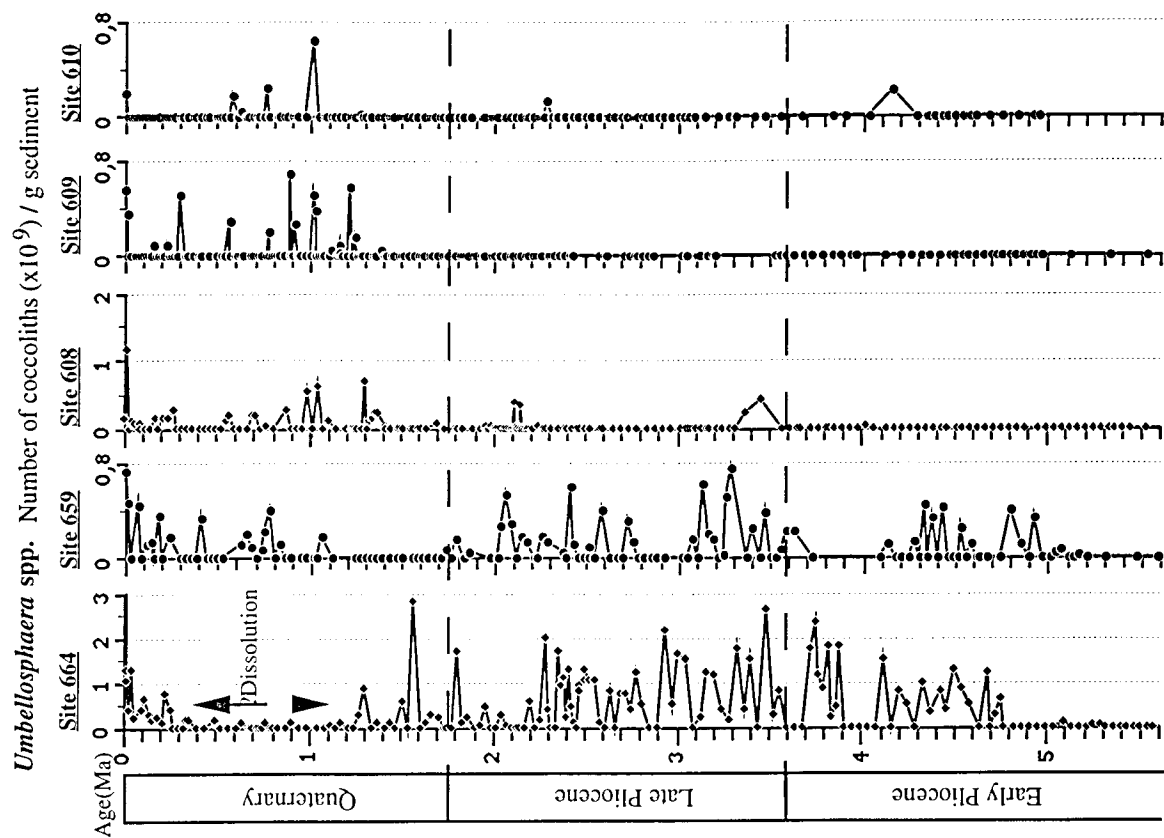
Umbellosphaera spp. Number of coccoliths (x10⁹) / g sediment

Figure 3.23 Absolute abundance plots of *Umbellosphaera* spp. at DSDP/ODP Sites 664, 659, 608, 609, 610.

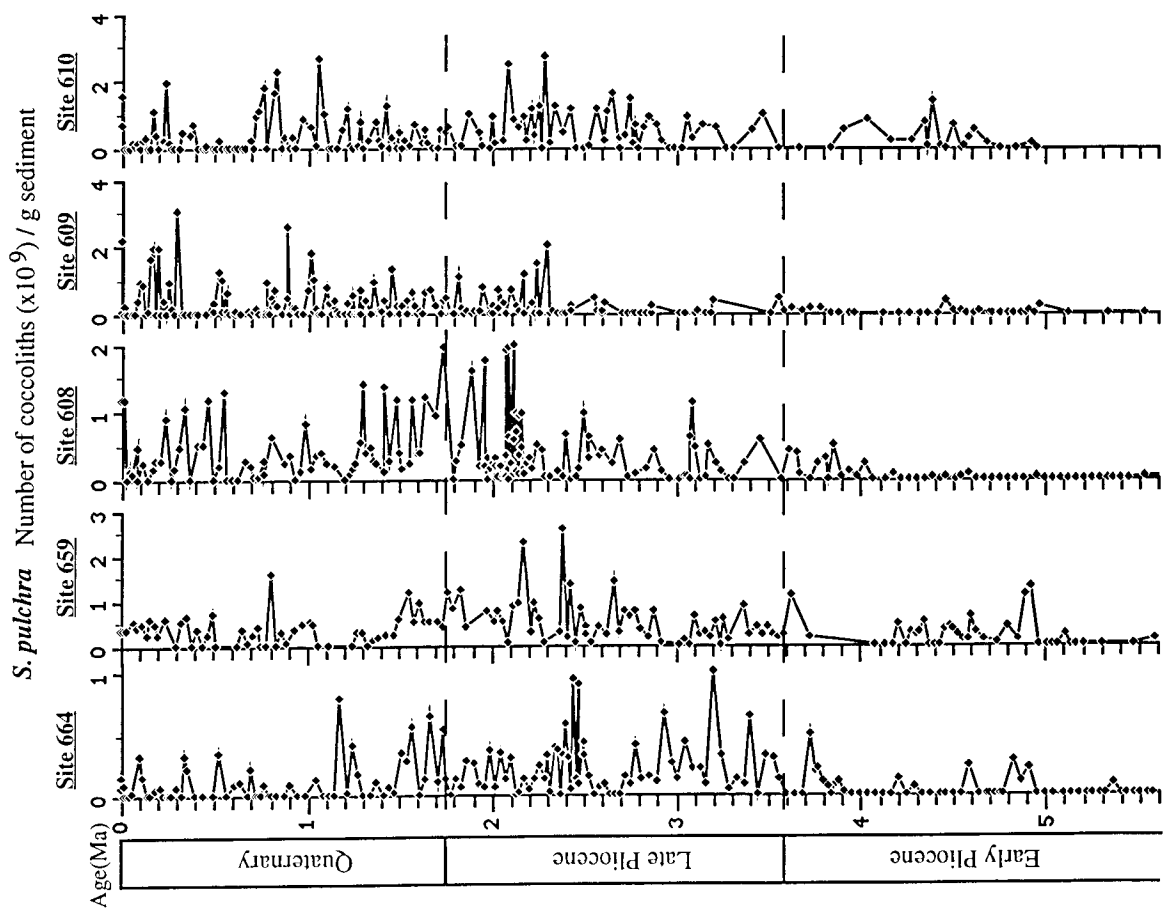
S. pulchra Number of coccoliths (x10⁹) / g sediment

Figure 3.22 Absolute abundance plots of *S. pulchra* at DSDP/ODP Sites 664, 659, 608, 609, 610.

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Family Discoasterceae Tan Sin Hok 1927

Genus *Discoaster* Tan Sin Hok 1927

Description: Tan Sin Hok, 1927: 415.

Remarks: Only species or forms of the genus, which are significant for stratigraphy, were identified separately, while others were united into one group: *Discoaster* spp., since they occur sporadically.

Paleoecology: Discoasters occurred commonly in low-latitude sediments and therefore probably favoured warm-water masses (Bukry, 1975, 1978; Haq and Lohmann, 1976).

Discoaster brouweri (Tan 1927) Bramlette and Riedel 1954

Plate 6, Figure 1

*1927 *Discoaster brouweri* Tan: 120, figs. 8a-b.
1954 *Discoaster brouweri* (Tan) Bramlette and Riedel: 402, pl. 39, fig. 12.
1967 *Discoaster tamalis* Kamptner: 166, pl. 24, fig. 131.
1969 *Discoaster asymmetricus* Gartner: 598, pl. 1, fig. 1-3.
1985 *Discoaster triradiatus* Tan; Perch-Nielsen: 479, fig. 32-7.

Description: Bramlette and Riedel, 1954: 402.

Remarks: This species usually has six rays and differs from other six-rayed forms by its non-bifurcated, elongate and bent rays. The number of rays of *D. brouweri* varies from 3 to 6; however, the 3 to 5 rayed variants with stratigraphical significance are determined separately as three to five rayed morphotypes, following the suggestions of Theodoridis (1984).

Biostratigraphy: The LAD of *D. brouweri* defines the top of NN18 (Martini, 1971). An age of 1.96 Ma (corr.) for the of LAD of *D. brouweri* was suggested by Takayama (1993).

Occurrence: In Pliocene sediments; showing an increase in abundance towards the tropical areas: absent at site 610, rare at sites 609 and 608, common at sites 659 and 664 (Figure 3.24). This species disappears earlier from the northern areas (site 609), therefore, the LAD of this species has only been used for the stratigraphy of sites 664, 659, 608.

Discoaster asymmetricus morphotype

Plate 6, Figure 7

Description: Asymmetrical five-armed discoasters with pointed terminations.

Remarks: In agreement with the suggestion of Theodoridis (1984), in this study these forms are considered as a morphotype of *D. brouweri* .

Biostratigraphy: An age of 2.3 Ma (corr.) for the LAD of *D. asymmetricus* was given by Backman and Shackleton (1983).
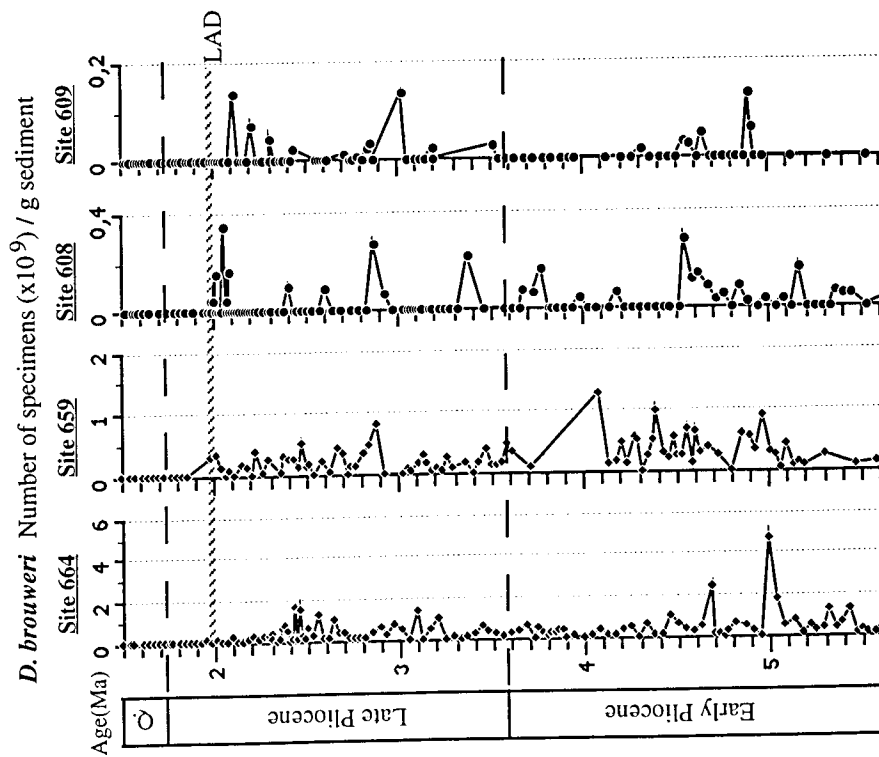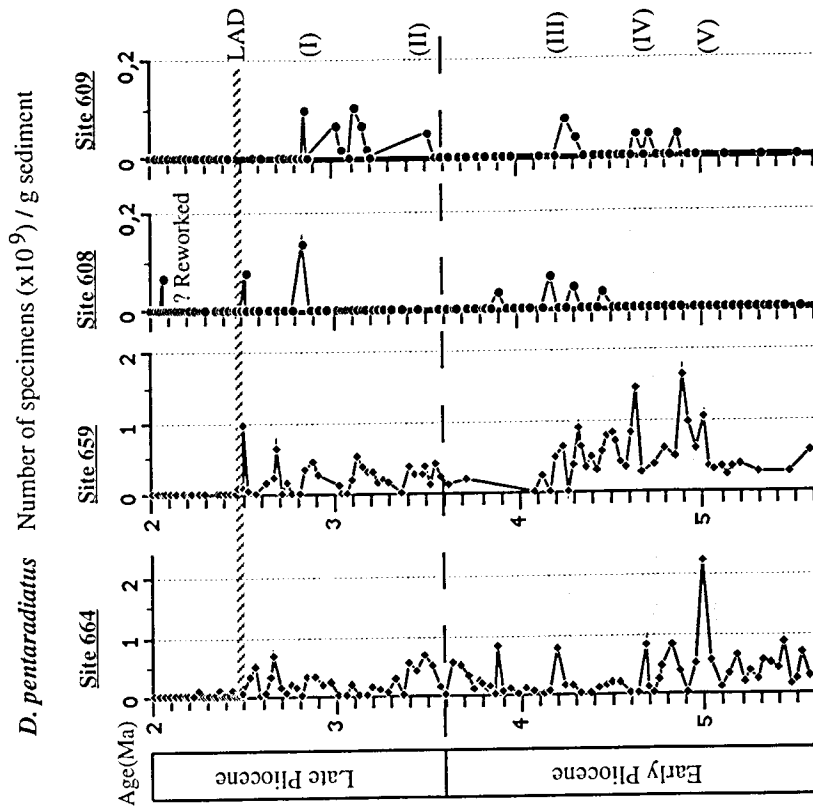
Figure 3.25 Absolute abundance plots of *D. pentaradiatus* at DSDP/ODP Sites 664, 659, 608, 609. Its LAD and several main abundance peaks (I - V) are marked with shaded areas.

Figure 3.24 Absolute abundance plots of *D. brouweri* at DSDP/ODP Sites 664, 659, 608, 609. Its LAD is marked by the shaded area.

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Occurrence: Rare in the Pliocene of sites 664, 659, 608 (Tables 3.6-3.8), this makes the determination of its LAD difficult, therefore it was not used for stratigraphy in this study.

<div align="center">

Discoaster tamalis morphotype

Plate 6, Figure 6

</div>

Description: Discoasters with four slender rays meeting at 90°.

Remarks: This form is a morphotype of *D. brouweri,* according to Theodoridis (1984).

Biostratigraphy: An age of 2.83 Ma for the LAD of *D. tamalis* was estimated by Tiedemann et al. (1994).

Occurrence: Rare in the Pliocene of sites 664, 659, 608, 609 (Tables 3.6-3.9). It is not easy to determine the LAD of this species even in the tropical sites, due to its rare occurrences. However, based on results of several counts, the event was still used for the stratigraphy of sites 664, 659, 608, since no chronostratigraphical data are available in those sample intervals.

<div align="center">

Discoaster triradiatus morphotype

Plate 6, Figure 4

</div>

Description: Discoasters with three slender rays meeting at 120°.

Remarks: Theodoridis (1984) suggested, that these three-armed forms are variants of the species *D. brouweri.* Hence, these forms were regarded as a morphotype of *D. brouweri.*

Biostratigraphy: An age of 1.96 Ma (corr.) for the LAD of *D. triradiatus* was suggested by Backman and Shackleton (1983).

Occurrence: Rare in the Pliocene of sites 664, 659, 608 (Tables 3.6-3.10). Its rare occurrences in these three sites make a use of its LAD difficult, so it was not used for stratigraphy in this study.

<div align="center">

Discoaster pentaradiatus (Tan 1927) Bramlette and Riedel 1954

Plate 6, Figure 5

</div>

1927 Discoaster pentaradiatus var. (r)Tan: 120, fig. 2 .
1954 *Discoaster pentaradiatus* (Tan) Bramlette and Riedel: 401-402, pl. 39, fig. 11.

Description: Bramlette and Riedel, 1954: 401.

Remarks: This species always has five rays and differs from other five-rayed forms by its bifurcations and slight birefringence between crossed nicols.

Biostratigraphy: Its LAD defines the top of NN17 (Martini, 1971). An age of 2.50 Ma for the LAD of *D. pentaradiatus* is recalculated, based on the suggestion of Takayama (1993).

Occurrence: In the Pliocene; common at sites 664, 659; sparse at sites 608, 609; absent at site 610 (Figure 3.25). Several abundance peaks (I - V) were recognized. Its LAD is relatively distinct in the lower latitude sites (664, 659), and was used in the stratigraphy of these two sites. In the higher latitude sites the sparse occurrence of this species leads its LAD unusable.

<div align="center">

Discoaster quinqueramus Gartner 1969
Plate 6, Figure 3

</div>

*1969 *Discoaster quinqueramus* Gartner: 589, pl. 1, figs. 6.

Description: Gartner, 1969: 589.

Remarks: This species always has five rays and a five-sided central knob, which makes it different from *D. brouweri*. It differs from the *D. asymmetricus* morphotype by its symmetrically arranged arms.

Biostratigraphy: The LAD of *D. quinqueramus* defines the top of NN11 (Martini, 1971). Backman et al. (1990) gave an age of 5.47 Ma (corr.) for the LAD of *D. quinqueramus*.

Occurrence: In Upper Miocene and Lower Pliocene sediments; common at sites 664 and 659, sparse at site 608 (Tables 3.6-3.8). Its LAD is similar to that of *D. pentaradiatus*, and is only suitable for the stratigraphy of sites 664, 659. However, besides this datum there is no available chronostratigraphical data for the very lower Pliocene samples of site 608. So its LAD in site 608 was determined by further observations and used for stratigraphy.

<div align="center">

Discoaster surculus Martini and Bramlette 1963
Plate 6, Figure 2

</div>

*1963 *Discoaster surculus* Martini and Bramlette: 854, pl. 104, figs. 10-12.

Description: Martini and Bramlette, 1963: 854.

Remarks: This species is easily distinguished from other six rayed forms by its trifurcations.

Biostratigraphy: The LAD of *D. surculus* marks the top of NN16 (Martini, 1971). An age of 2.53 Ma (corr.) for the LAD of *D. surculus* has been suggested (Takayama, 1993).

Occurrence: In the Pliocene; rare at sites 664, 659, 608, and sparse at site 609 (Tables 3.6-3.9). Observations in this study show that its LAD and the LAD of *D. pentaradiatus* occur almost simultaneously. In addition, *D. surculus* is rarer than *D. pentaradiatus*, this makes the determination of its LAD difficult. Therefore, the LAD of *D. surculus* is not used for stratigraphy in this study.

Discoaster variabilis group

Plate 6, Figure 8

1954 *Discoaster deflandrei* Bramlette and Riedle: 399, pl. 39, fig. 6.
1954 *Discoaster challengeri* Bramlette and Riedle: 401, pl. 39, fig. 10.
1963 *Discoaster variabilis* Martini and Bramlette : 854, pl. 104, figs. 4-8.
1971 *Discoaster variabilis decorus* Bukry: 48, pl. 3, figs. 5-6.

Description: Discoasters with six broad bifurcated rays.

Remarks: The species given above are united together, because diagenetically they are heavily overgrown and cannot be separated correctly. However, they can be easily distinguished from other six rayed forms by their broad bifurcated rays. The species in this group agree well with those in the *D. variabilis* group used by Backman and Shackleton (1983).

Biostratigraphy: An age of 3.02 Ma (corr.) for the of LAD of the *D. variabilis* group has been given by Backman and Shackleton (1983).

Occurrence: In the Lower Pliocene; rare at sites 664, 659, 608, sporadic at site 609 (Tables 3.6-3.9). In this study, the LAD of the group was not used for stratigraphy, due to its rare occurrences in the sites studied.

Family Sphenolithaceae Deflandre 1952

Genus *Sphenolithus* Deflandre 1952

1952 *Sphenolithus* Deflandre: 466.

Description: Deflandre, 1952: 466.

Remarks: A number of *Sphenolithus* forms were found in the material studied. Morphologically, they vary greatly both in size and in shape. The problems in separating *S. abies* and *S. neoabies* were studied by Backman (1980). Since an exact separation of them is impossible, they were united as the *S. abies* group in this study. Other forms of *Sphenolithus* were identified only as: *Sphenolithus* spp., due to their sparse occurrence in the sites studied.

Paleoecology: Sphenoliths were found in low latitude areas, and they are assumed to be warm-water nannoplankton (Perch-Nielsen, 1985).

Sphenolithus abies group

Plate 5, Figures 2-4, Plate 7, Figures 30-31

1954 *Sphenolithus abies* Deflandre, in Deflandre and Fert: 164, pl. 10, figs. 1-4.
1969 *Sphenolithus neoabies* Bukry and Bramlette: 140, pl. 3, figs. 9-11.

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Description: Small sphenoliths, sized about 2 - 5 µm, having shapes ranging from smoothly rounded to cone-shaped.

Remarks: Species given above are grouped here, since it is impossible to separate them safely in counting analyses. Forms of this group differ from other sphenoliths by their smaller size.

Biostratigraphy: An age of 3.62 Ma (corr.) for the LAD of *Sphenolithus abies* and *S. neoabies* was suggested by Takayama (1993).

Occurrence: In Lower Pliocene sediments; common to abundant at sites 664, 659, rare to common at sites 608, 609; rare at site 610 (Figure 3.26). The LAD of this species was used only in the tropical sites 664, 659, because it disappears earlier from the northern areas.
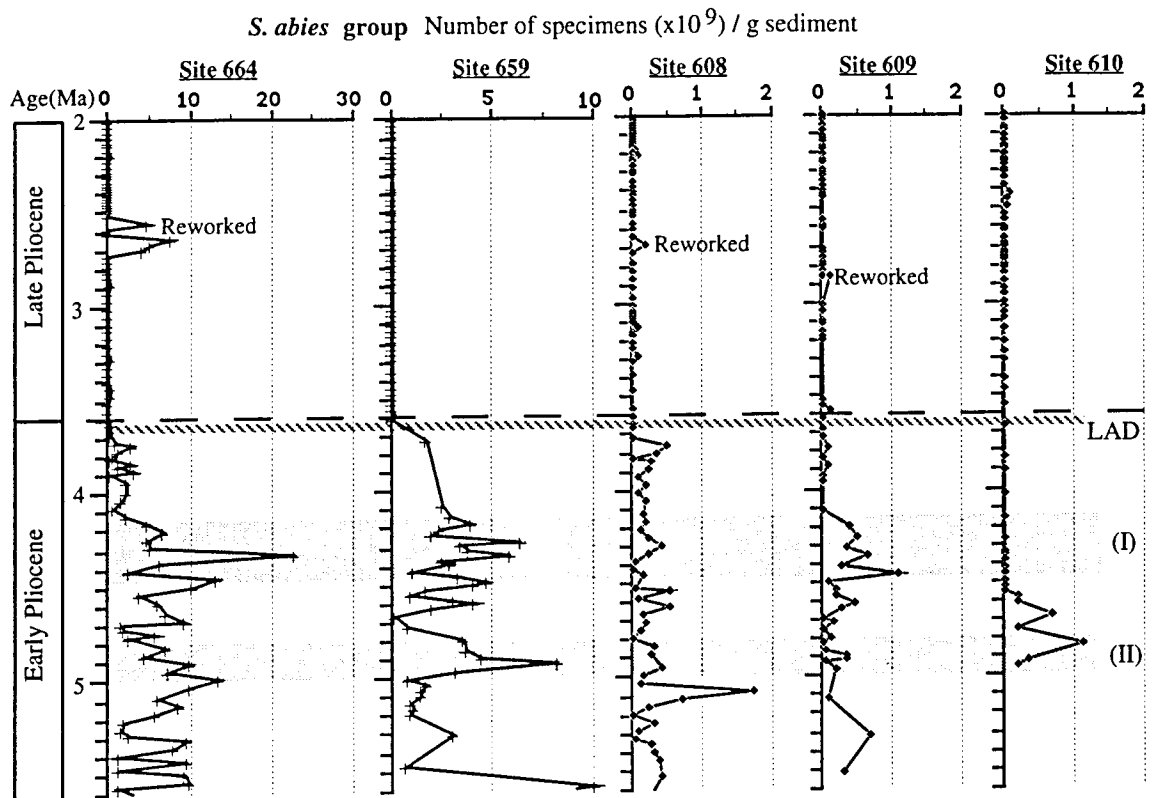
Figure 3.26 Absolute abundance plots of the *S. abies* group at DSDP/ODP Sites 664, 659, 608, 609, 610. Its LAD and main abundance peaks (I - II) are marked with shaded areas. Its occasional occurrences in the Late Pliocene are considered to be due to reworking.

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CHAPTER 4   OBSERVATIONS AND RESULTS

4.1   Coccolith species and their record

In chapter 3, stratigraphical and ecological variations of investigated coccolith species have been discussed with illustrations of 26 species or species groups. Detailed data of absolute abundances of these species from the five studied sites are given in Tables 3.6-3.10 (in appendix).

According to the occurrences of these species, they are divided into three categories.

1) **Abundant to common species**: species of *Reticulofenestra* and *Gephyrocapsa*, *Pseudoemiliania lacunosa* and *Emiliania huxleyi*. Most of these species are biostratigraphical markers; several of them have been used for the stratigraphy in this study (chapter 2). As species groups, *Discoaster* spp. and *Sphenolithus* spp. occur commonly in Pliocene sediments from the tropical to transitional regions. A number of species from these two genera were employed in construction of age-models (chapter 2).

2) **Less common species**: *Calcidiscus leptoporus, C. macintyrei, Coccolithus pelagicus, Helicosphaera carteri, H. sellii,* and *Syracosphaera pulchra.* Only the LAD of *C. macintyrei* was selected as a biostratigraphical marker in this study. *Umbilicosphaera sibogae, Rhabdosphaera claviger, Neosphaera coccolithomorpha,* and *Umbellosphaera* spp., representative of Quaternary warm-water forms, also fall into this category.

3) **Rare forms**: various species of the genera *Pontosphaera, Scyphosphaera, Coronocyclus, Oolithus, Ceratolithus,* and *Amaurolithus,* and *Helicosphaera* spp. and *Syracosphaera* spp. Only the LAD of *Ceratolithus rugosus* was used for stratigraphy in this study (chapter 2).

Since the abundant to common species are essential components of Pliocene and Quaternary coccolith assemblages, their appearances and disappearances, increases and decreases in abundance and their major evolutionary changes, result in fundamental changes of the coccolith assemblages.

In addition, the time ranges of most investigated species and the evolutionary lineages of several genera which are described in chapter 3, are summarized in Figure 4.1. These species are called "Miocene species", "Pliocene species" and "Quaternary species", according to their time of origin.

4.2   Major evolutionary changes of the abundant species

Accumulation rates of the abundant species from the studied sites are plotted to show their changes through time in detail (Figures 4.2a-e). The accumulation patterns of these
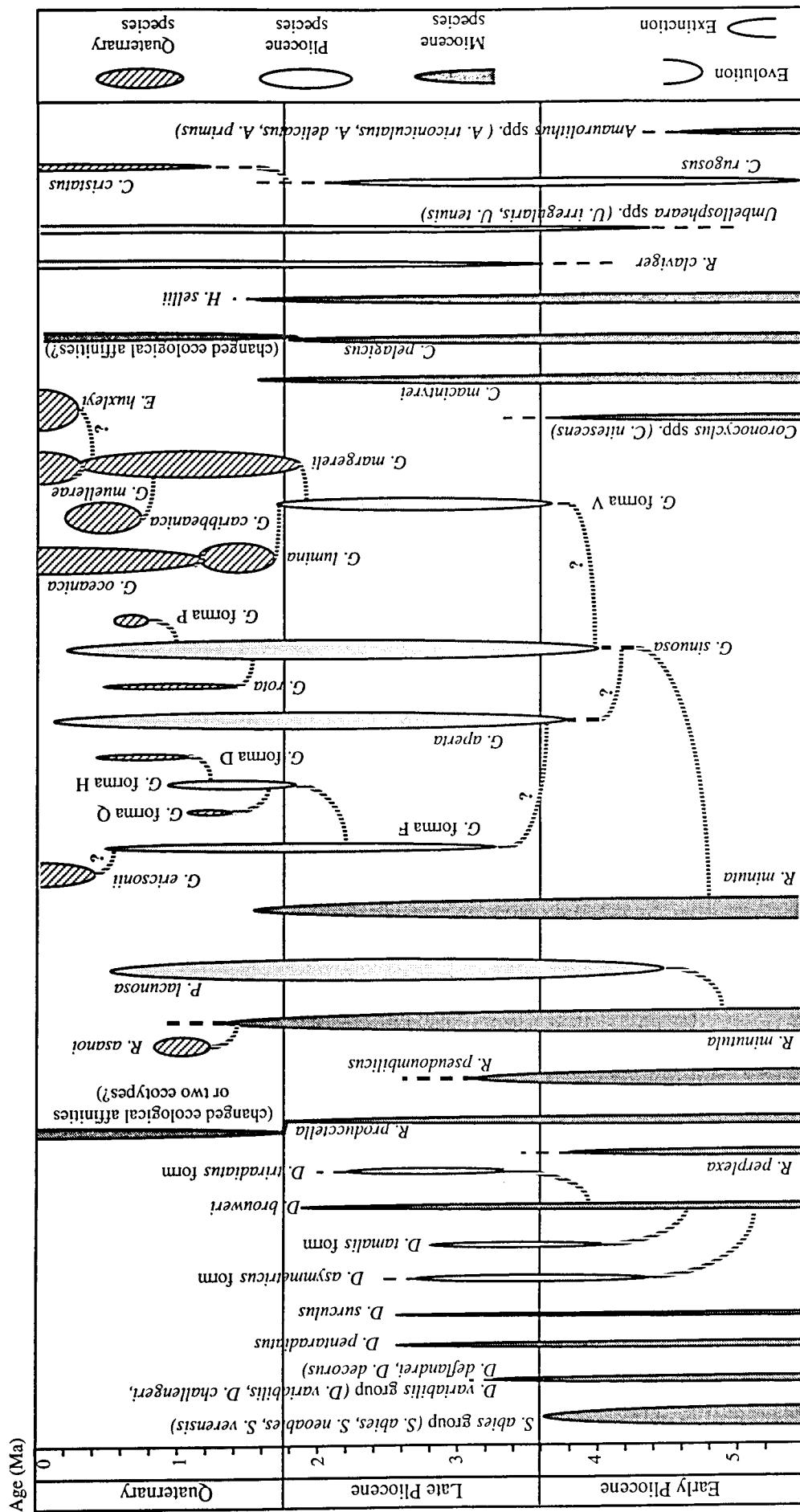
Figure 4.1 Summary of the major evolutionary changes described in this study and phylogenetic relationships in several genera. The phylogenetic lineage of the genus *Gephyrocapsa* is after Samtleben and Baumann (unpubl.), the lineage of *Discoaster* is based on Prins (1971) and that of *Ceratolithus* is from Gartner and Bukry (1975).

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species are not significantly different to their absolute abundance patterns illustrated in chapter 3.

Based on variations in accumulation rates the major evolutionary changes in these abundant species are seen as: 1) the gradual decline of "Miocene species" in the Pliocene and their extinction, 2) the appearance and gradual rise of "Pliocene species" in the Pliocene, 3) the rapid and frequent evolutionary changes of "Quaternary species".

4.2.1 Decline and extinction of "Miocene species"

Sphenolithus spp., *Discoaster* spp., and *Reticulofenestra* spp. (except for *R. asanoi*) are known as "Miocene species" since they carry over from the Miocene into the Pliocene.

Sphenolithus and *Discoaster* gradually decline in abundance and become extinct. The decline of *Sphenolithus* spp. (mainly *S. abies* and *S. neoabies*), begins at about 4.9 Ma, after an abundance maximum at 5.0 Ma (peak II in Figure 3.29). They show a gradual decrease until disappearing near the end of the Early Pliocene. Several new morphotypes of the species *Discoaster brouweri*: *D. asymmetricus, D. tamalis,* and *D.triradiatus,* evolve in the Early Pliocene, however, these new forms bring about no significant change in the general decline of the genus; the last existing *Discoaster* species and forms become extinct within the Pliocene.

Most *Reticulofenestra* species decline also gradually.

a) The last abundance maximum of *R. pseudoumbilicus* at about 4.9 Ma marks the begin of its decline (Figure 3.21). However, with low abundances this species survives into the Late Pliocene and dies out at 2.5 Ma (chapter 3).

b) *R. minuta* shows differences in abundance patterns between the low latitude sites and the high latitude sites (Figure 3.18). In low latitudes (sites 664, 659), at around 5.0 Ma an abrupt flowering of this species produces an outstanding abundance maximum (peak VIII in Figure 3.18); soon after the species declines gradually throughout the middle and late Pliocene. In high latitudes (609, 610), this species increase during the middle Pliocene when water temperatures in this region were warmer than the early and late Pliocene (chapter 3), and it declines in the late Pliocene. The extinction of *R. minuta* is found in the early Quaternary.

c) *R. minutula* increases in abundance in the Early Pliocene (Figures 3.19, 4.2a-e) after the sharp decrease of *R. pseudoumbilicus*. This implies that the decline of *R. pseudoumbilicus* probably provided an ecological space for the rise of *R. minutula* in the plankton coccolithophore assemblages (peaks III and IV in Figure 3.19). In this period *R. minutula* not only increases in abundance but also changes its morphology; the slit-like structure on the rim of the distal shields appears. From such new forms *P. lacunosa* evolves (chapter 3). Around

2.6 Ma *R. minutula* begins to decline, except in mid latitudes where its decline occurs later. After a sudden and critical drop in abundance around 1.5 to 1.6 Ma (peak I in Figure 3.19), *R. minutula* survives for a time with strongly reduced abundances and then becomes extinct in the middle Quaternary.

d) The history of *R. productella* is difficult to explain, owing to its irregular occurrences at the five sites (Figure 3.20). In general, this species decreases in the Late Pliocene and its abundances remain low during the Quaternary at most sites. Exceptionally, this species occurs abundantly in the lower to middle part of the Quaternary at site 664, this may be explained by two possible causes: 1) divergence of a new ecological variety from this species, i.e. a new species with the same morphological appearance (a case of parallelism that cannot be detected by morphological investigations); 2) the ecological affinities of this species change (chapter 3). Due to one or the other of these two causes, *R. productella* ranges until the present day. This range agrees with the study of Gallagher (1987).

4.2.2   Increase of "Pliocene species"

P. lacunosa probably arose from *R. minutula* at about 4.5 Ma (chapter 3). It increases steadily in abundance and becomes a dominant species in the Late Pliocene (peak IV in Figure 3.15). The dominance of *P. lacunosa* continues into the Quaternary. This species is more abundant in low latitudes than in high latitudes. However, around 1.3 to 1.2 Ma its abundance increases in the northern sites (peak II in Figure 3.15), indicating a better adaptation to the ecological conditions in high latitudes than before. Its decline begins after about 1.2 Ma, which probably provides an ecological space for the rise of some new forms. For example soon after this, *G. oceanica* increases in importance in the tropical areas and *R. asanoi* increases in the northern regions.

Early Pliocene *Gephyrocapsa* species are *G. sinuosa*, *G. aperta*, and *Gephyrocapsa* forma V. *Gephyrocapsa* forma F appears in the early Late Pliocene (Figure 3.13, Table 3.3). These species at first increase only gradually and are still very rare during this time. Near the end of the Pliocene they have distinctly increased accumulation rates. With the beginning of the Quaternary, they increase rapidly, diverge into different species and the flowering of the genus *Gephyrocapsa* begins.

4.2.3   Evolutionary changes of "Quaternary species"

In the Quaternary the genus *Gephyrocapsa* flourishes and shows a variety of evolutionary changes.

1) Changes of **medium to large sized** *Gephyrocapsa* species These species are *G. margereli/G. muellerae, G. caribbeanica, G. lumina,* and *G. oceanica.* According to the biometrical study (S &B), all these species are the descendants of *Gephyrocapsa* forma V. Most of them have short ranges characterized by a very rapid increase and decline, except for *G. oceanica* which still lives today. All these species have different ecological preferences.

a) Having increased near the end of the Pliocene, *Gephyrocapsa* **forma** V gave arise of *G. margereli* firstly and then it evolved into *G. lumina* in the early Quaternary at 1.67 Ma. *G. lumina* and *G. margereli* are the ancestors of two further lineages (Figure 4.1).

b) *G. lumina* increases rapidly, this occurs at the same time as the sudden decline of *R. minutula* in the mid latitudes (Figures 4.2c-d). *G. lumina* is the first *Gephyrocapsa* species to achieve dominance in the Quaternary. It increases rapidly to an accumulation maximum and then immediately starts to decline (Figure 3.10). In correspondence with the decline of *G. lumina, P. lacunosa* and the small *Gephyrocapsa* species increase. *G. lumina* also undergoes morphological changes during its range: an increase in coccolith length and in bridge angle, showing it to be a transitional form of *Gephyrocapsa* forma V to *G. oceanica.* Through gradual changes *G. lumina* evolves into *G. oceanica* at around 1.25 Ma (chapter 3).

c) Ecologically, *G. oceanica* differs from its eurythermal ancestor, *G. lumina,* by favouring warmer waters. This species becomes abundant in the tropical and subtropical areas where it rapidly achieves dominance at around 0.9 Ma. Since then, *G. oceanica* continues to show high accumulation levels in these areas. In the modern oceans *G. oceanica* occurs abundantly not only in the tropical to subtropical regions but also in warm marginal seas and upwelling areas (Okada and Honjo, 1975; Wang and Samtleben, 1983; Kleijne, 1993).

d) *G. margereli* is another descendant of *Gephyrocapsa* forma V (Figure 4.1). Initially this species increases slowly, a rapid increase happens around 0.8 Ma, after the decline of the small *Gephyrocapsa* species (Figures 4.2a-e). Apparently, *G. margereli* preferred warm waters and was abundant in the tropical and subtropical areas. In the northern regions *G. caribbeanica,* a cold-water form with a closed central area or small central opening, split off from *G. margereli.* After a decline, *G. margereli* passed through a gradual morphological change into *G. muellerae* at around 0.36 to 0.27 Ma (Samtleben, 1980).

e) As an ecologically separate descendant of *G. margereli, G. caribbeanica* first arose in the northern regions. A sudden and large increase occurs around 0.7 Ma, after the extinction of *R. asanoi* (Figure 4.2). *G. caribbeanica* favours temperate to colder waters and has more complete records in the mid latitudes, where it has longer time ranges and more abundance peaks, than in the southern and northern areas, and is missing in the tropical areas, e.g. at sites 664 and 366 (Figure 3.10). Four distinct abundance peaks at sites 608, 609 are recognized, which probably reflect climatic fluctuations or the shifting fronts of different water masses in this region. This species suffered an abrupt decline at 0.24 Ma and survived only in the mid

latitudes for only a very short time. This seems to leave an ecological space for the rise of *G. muellerae* in this area.

f) *G. muellerae*, the last descendant of *G. margereli*, is different from its ancestor in two ways: having a smaller bridge angle and preferring cold waters. Soon after its appearance, *G. muellerae* increases very rapidly in the northern regions and is the dominant species in the north NE Atlantic until the rapid increase of *E. huxleyi* (0.09 Ma). In comparison with *G. caribbeanica*, *G. muellerae* prefers colder waters and has highest accumulation rates and more detailed records at the most northerly site 610 (Figure 3.11). Today, this species occurs commonly in the northern North Atlantic (Samtleben et al. 1992).

2) The group *Gephyrocapsa* spp.1 includes a variety of small sized species with different ecological affinities (chapter 3). They increase in abundance near the end of the Pliocene (Figure 3.13), and with the beginning of the Quaternary they increase also in species diversity.

During the Quaternary a number of abundance peak zones of these small species (zones I - IX in Figure 3.13) are recognized. However, these peak zones are not strictly comparable between sites, due to the different ecological preferences of these species. For example zone VII can be correlated with the small *Gephyrocapsa* acme zone ranged from 1.22 to 1.05 Ma (corr.) (Gartner, 1977; Berggren et al, 1980). But from Figure 3.13 it can be seen that the range of zone VII decreases towards the south: from 1.1 to 0.9 Ma at site 610 to 1.1 to 1.05 Ma at site 664. Thus, the small *Gephyrocapsa* acme zone is not synchronous in the NE Atlantic. After this acme, these small *Gephyrocapsa* species show a gradual decline and most of them die out. At about 0.35 Ma *G. ericsonii* appears and increases very rapidly to form a large abundance peak (peak I in Figure 3.13). Since 0.2 Ma this species has declined, but it still lives in the modern oceans.

3) In the late Quaternary, *E. huxleyi* evolves from *Gephyrocapsa*, most probably from *G. margereli*, at about 0.30 Ma. *E. huxleyi* dominates the modern coccolithophorid communities from the tropics to the polar regions, and its large blooms play an important role in the oceanic biomass and in the ocean/atmosphere circulation (Westbroek et al., 1989, 1993).

Apart from the *Gephyrocapsa* species, *R. asanoi* rises and declines rapidly in the middle Quaternary. The extinction of this species represents the last disappearance of the medium to large sized *Reticulofenestra* forms.

To sum up, the decline of *Reticulofenestra* in the Pliocene and the florescence of the genus *Gephyrocapsa* with a variety of evolutionary changes in the Quaternary, are main processes which alter the essential components of the assemblages and promote the development of the assemblages.
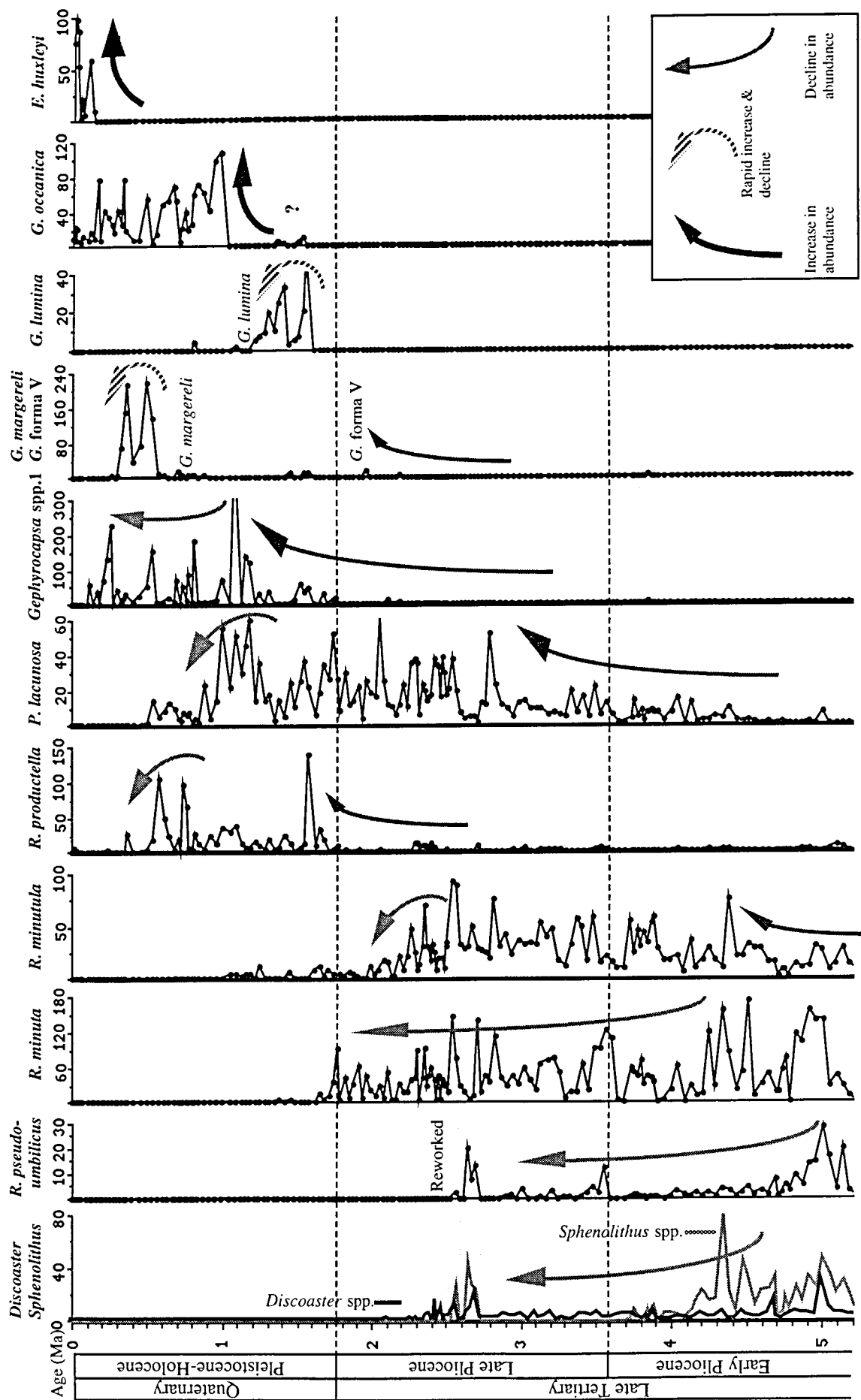
Figure 4.2a Development of Late Tertiary-Quaternary coccolith assemblages in the NE Atlantic demonstrated by variations in coccolith accumulation rates of the dominant species from site 664. *R. asanoi, G. caribbeanica,* and *G. muellerae* are not ploted here due to their absenceor too rare occurrences at this site; The "occurrences" of *G. oceanica* marked with "?" are considered as being due to the presence of a variety of *G. lumina* with larger central openings.
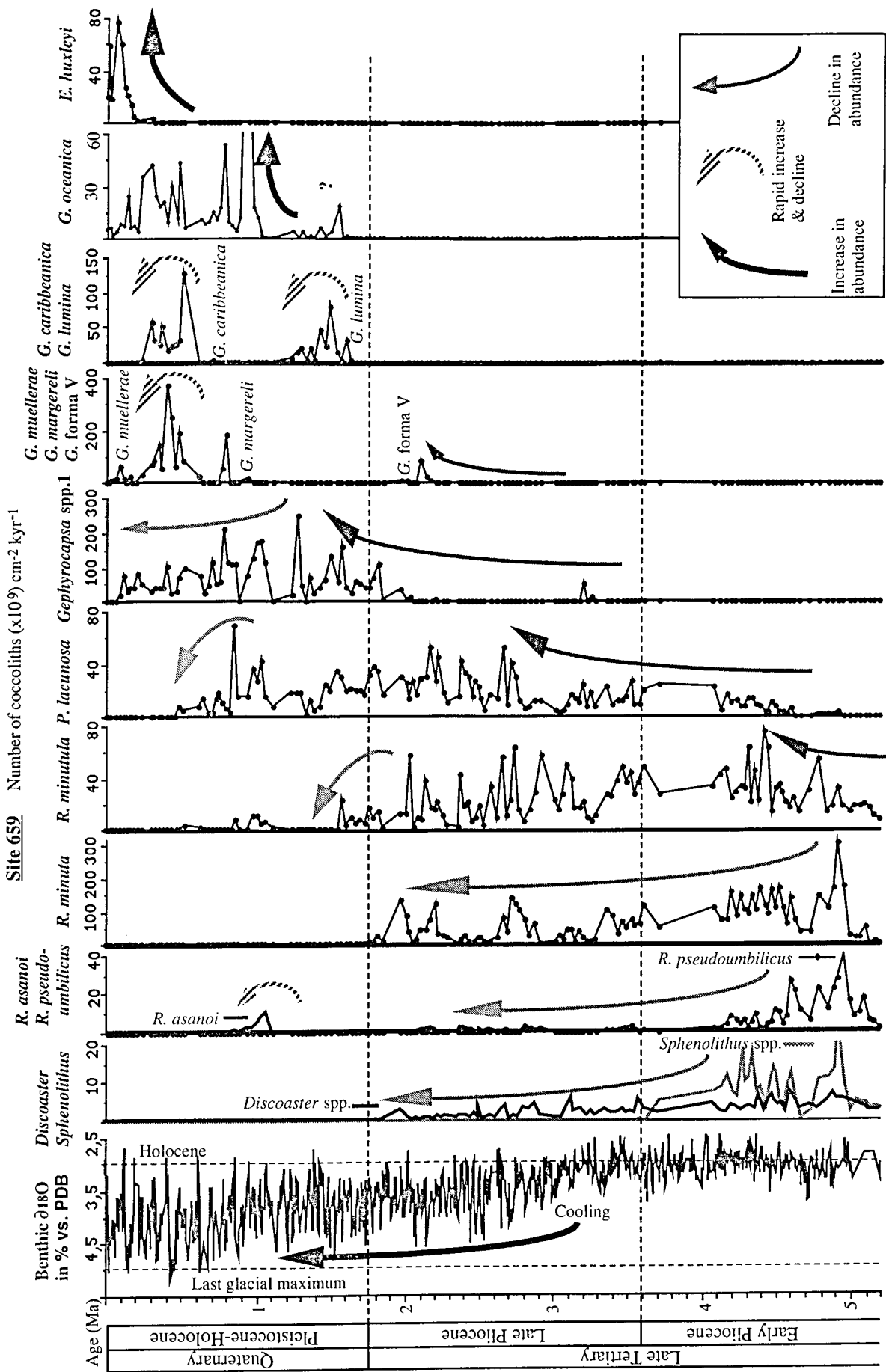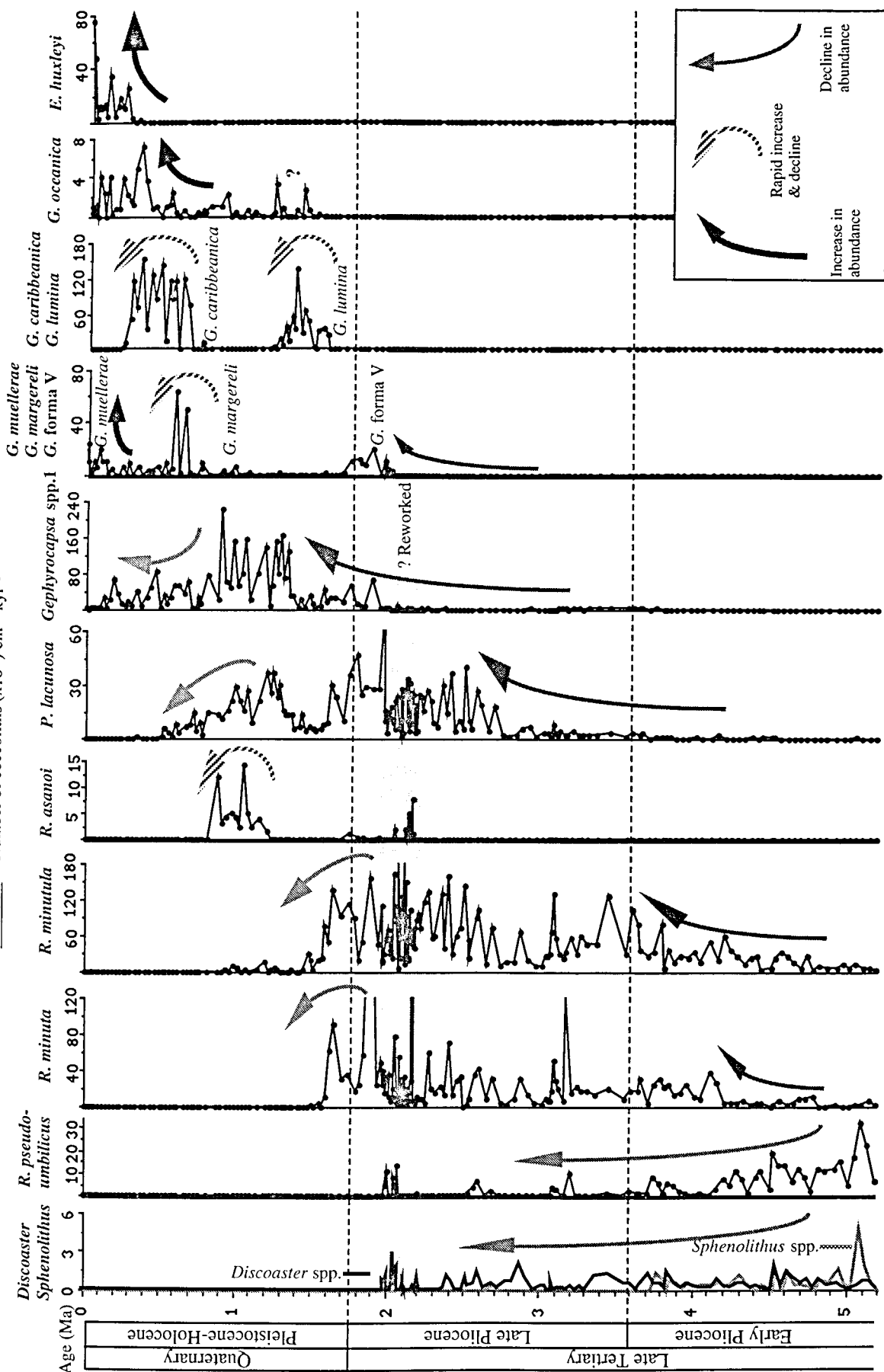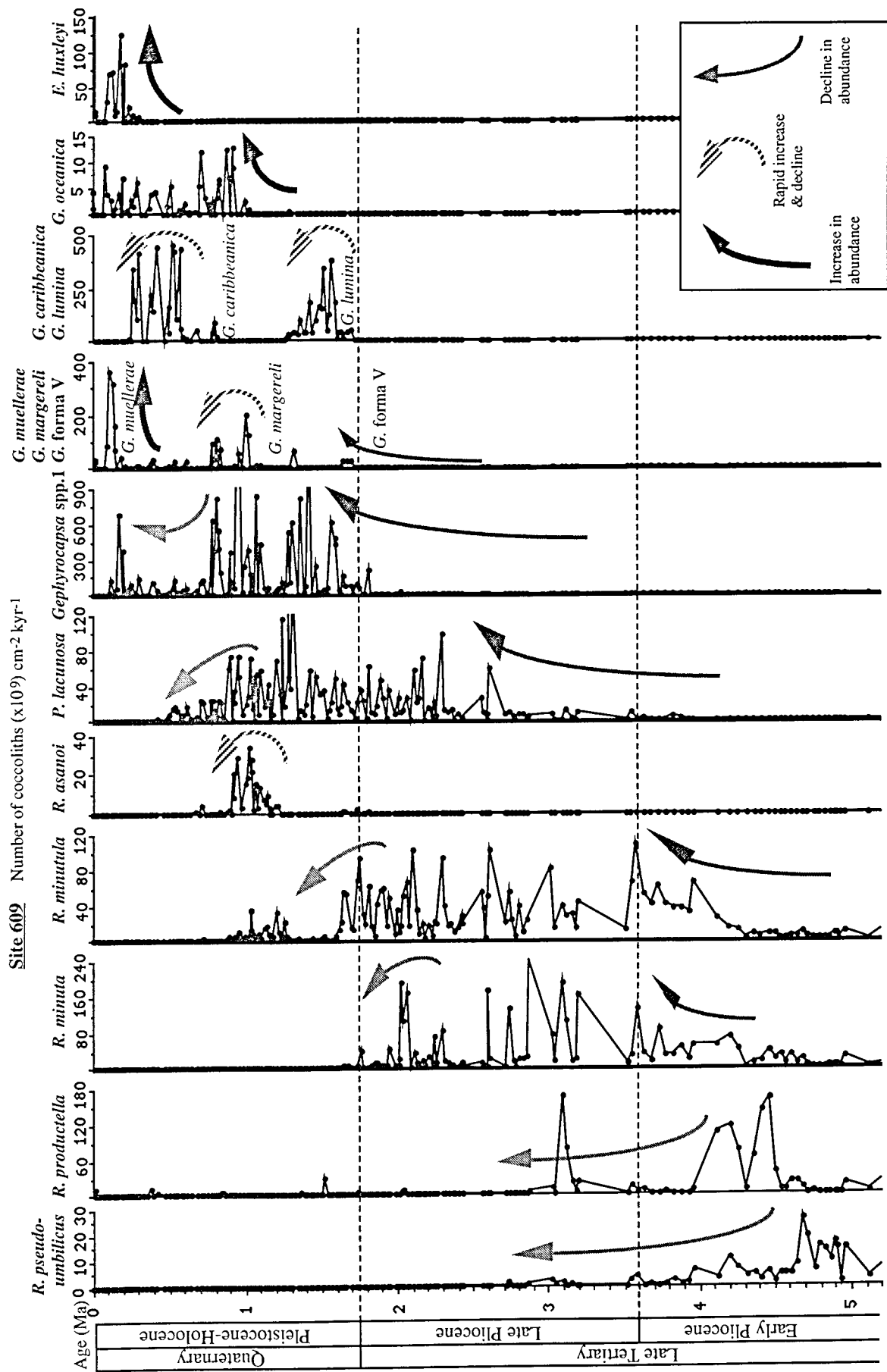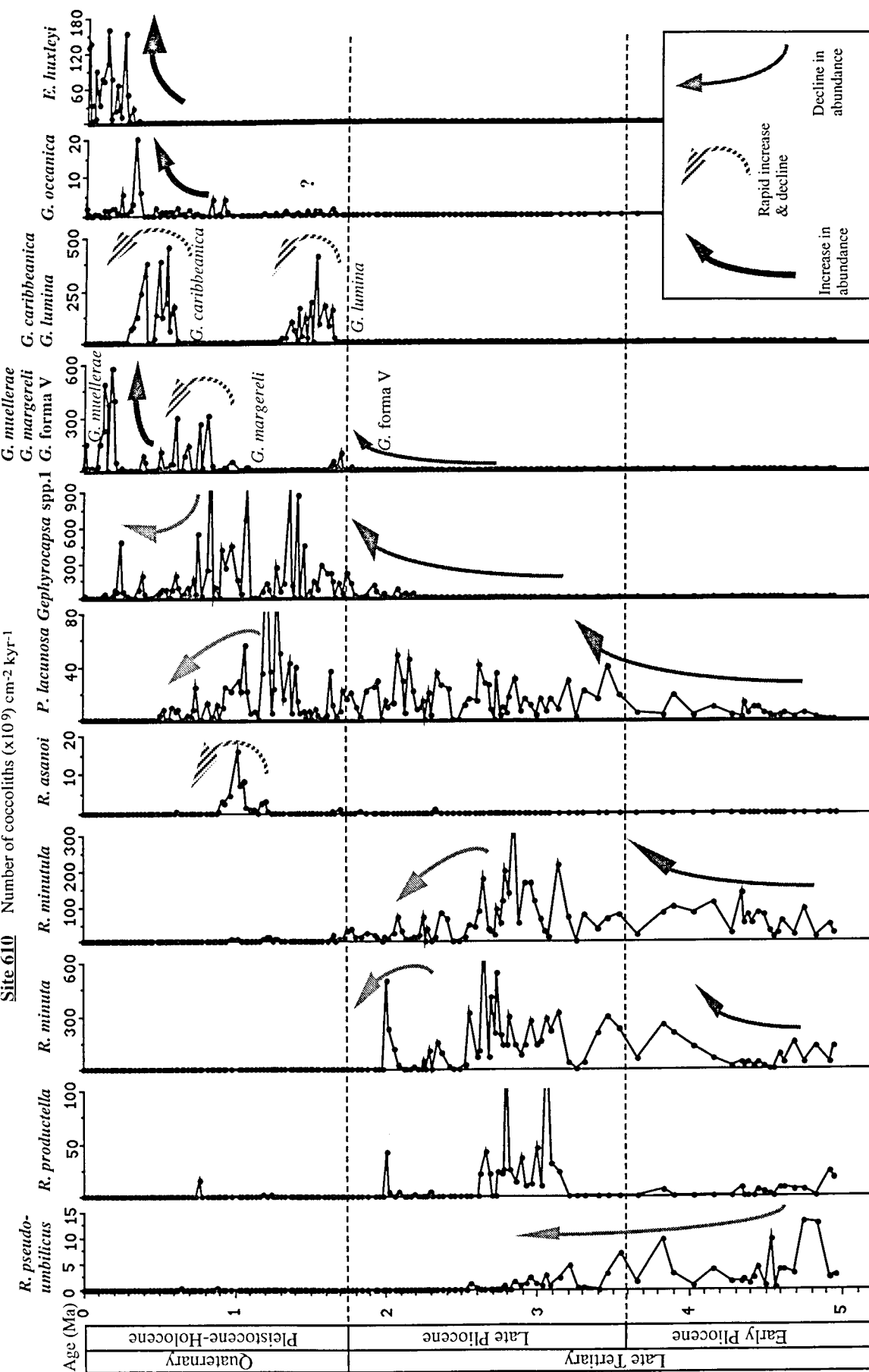
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Figure 4.2b Development of Late Tertiary-Quaternary coccolith assemblages in the NE Atlantic demonstrated by variations in coccolith accumulation rates of the dominant species from site 659, compared to variations in $\partial^{18}O$ of $C.$ $wuellerstorfi$ from site 659 (Tiedemann et al., 1994). The "occurrences" of $G.$ $oceanica$ marked with "?" are considered as being due to the presence of a variety of $G.$ $lumina$ with larger central openings.

Site 608 Number of coccoliths (x10⁹) cm⁻² kyr⁻¹

Figure 4.2c Development of Late Tertiary-Quaternary coccolith assemblages in the NE Atlantic demonstrated by variations in cocolith accumulation rates of the dominant species from site 608. The "occurrences" of *G. oceanica* marked with "?" are considered as being due to the presence of a variety of *G. lumina* with larger central openings.

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Figure 4.2d Development of Late Tertiary-Quaternary coccolith assemblages in the NE Atlantic demonstrated by variations in coccolith accumulation rates of the dominant species from site 609.

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Figure 4.2e Development of Late Tertiary-Quaternary coccolith assemblages in the NE Atlantic demonstrated by variations in coccolith accumulation rates of the dominant species from site 610. The "occurrences" of *G.oceanica* marked with "?" are considered as being due to the presence of a variety of *G. lumina* with larger central openings.

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4.3 Late Tertiary and Quaternary coccolith assemblages in the NE Atlantic

4.3.1 Determination of coccolith assemblages

The main objective of this study is to determine the temporal and spatial structures of Late Tertiary and Quaternary coccolith assemblages in the NE Atlantic and to obtain insights into their developmental processes. This study focuses attention on the main compositional features of the coccolith assemblages and their fundamental changes through time.

Relative abundances of coccoliths have been utilized to delineate the constituents of coccolith assemblages. Various species of *Reticulofenestra* and *Gephyrocapsa*, *P. lacunosa* and *E. huxleyi*, plus species of *Discoaster* and *Sphenolithus*, are the primary components of the coccolith assemblages. According to significant variations in abundances (accumulation rates and relative abundances), eight time slices, two from the Pliocene and six from the Quaternary, were distinguished (Figures 4.3a-h). The main characteristics of the assemblages in the five sites are plotted using mean relative abundances of coccolith species or species groups through each time slice. The abundant to common species are presented separately and the less common to rare taxa (mean relative abundance < 3%) are shown in groups. For example, *U. sibogae, N. coccolithomorpha, R. claviger*, and *Umbellosphaera* spp. are united as the group of warm-water forms, since they prefer warm waters (chapter 3). *C. leptoporus* and *C. macintyrei* are also grouped due to their similar ecological occurrences. As a typical cold-water form in the Quaternary, *C. pelagicus* is plotted separately when its abundance is greater than 3%. "Rare species" is used for all rare taxa, e.g. *Syracosphaera, Helicosphaera*, and *Pontosphaera* etc., indepentend of their ecology. Abundant to common species may fall into "rare species" when they occur rarely. For example, in the time slice 0.70-0.25 Ma (Figure 4.3e), *G. oceanica* is presented separately at sites 664, 659, but it falls into "rare species" at sites 608, 609, 610, owing to its scarcity in the northern regions.

4.3.2 Spatial and temporal variations of the coccolith assemblages

1) **The Early Pliocene (5.2 - 3.59 Ma, Figure 4.3a):** the coccolith assemblage is dominated by *R. minuta*, and *R. minutula*, which make up about 60% of the assemblage. However, *R. minuta* occurs more abundantly at the southern sites 664, and 659 than at the northern sites 608, 609, 610; whereas *R. minutula* is more abundant at sites 608, and 610. *R. pseudoumbilicus* is also a dominant species in the period 5.2 to 4.5 Ma, thereafter it is only a common form due to its decreased abundances. This species occurs more abundantly at sites 659, 608, 609 than at sites 664, or 610. *Discoaster* spp. and *Sphenolithus* spp. are abundant in low latitudes, whereas *R. productella, R. perplexa*, and *C. pelagicus* occur abundantly in high

latitudes. These differences are seen as ecological variations in the Early Pliocene coccolith assemblage. Most species of *Reticulofenestra*, and species of *Discoaster* and *Sphenolithus* are Miocene species that continued into the Pliocene. Thus, the dominant part of this assemblage is a remnant of a late Miocene coccolith assemblage. *Sphenolithus* spp. become extinct at the end of the Early Pliocene; however, they disappear earlier in the northern areas. A newly evolved Pliocene form, *P. lacunosa*, becomes a common species in low latitudes. Small species of *Gephyrocapsa* (*G. sinuosa*, *G. aperta*) also evolved in the Early Pliocene but were still very rare.

2) **The Late Pliocene (3.59 - 1.75 Ma, Figure 4.3b):** the coccolith assemblage is characterized by the dominance of *R. minutula*, *R. minuta*, and *P. lacunosa*, which account for 60% of the assemblage. The dominance of *P. lacunosa* makes this assemblage significantly different from the Early Pliocene one. *P. lacunosa* is more abundant in the tropical than in the northern areas. *R. minutula* occurs abundantly at site 608 and becomes rarer towards the north and the south, while *R. minuta* remains dominant at all sites. Common species are various warm-water forms, *U. sibogae*, *N. coccolithomorpha*, *R. claviger*, and *Umbellosphaera* spp., in low latitudes and *C. pelagicus* in high latitudes. Two new *Gephyrocapsa* species, *Gephyrocapsa* forma F and forma V, evolved at this time but were still rare, although, as a united group "*Gephyrocapsa* spp." (*G. aperta*, *G. sinuosa*, *Gephyrocapsa* forma F and forma V), they are common at sites 659, 609, 610, additionally, at around 2 Ma *G. margereli* splits off from *Gephyrocapsa* forma V. *R. pseudoumbilicus* dies out in the middle Pliocene and the last species of *Discoaster* become extinct towards the end of the Late Pliocene.

The main characteristic of the Quaternary coccolith assemblages (since 1.75 Ma, Figures 4.3c-h) is the predominance of various species of *Gephyrocapsa* together with *P. lacunosa*. A series of rapid replacements of old dominant species by new ones resulted in a number of fundamental changes in the coccolith assemblages, as summarized in Table 4.1.

Age	Time intervals	Dominant species
Early Pliocene	5.20 - 3.59 Ma	*R. minuta, R. minutula*
Late Pliocene	3.59 - 1.75 Ma	*R. minutula, R. minuta, P. lacunosa*
Quaternary	1.75 - 1.65 Ma	*P. lacunosa/R. minutula, Gephyrocapsa* spp.1
	1.65 - 1.25 Ma	*G. lumina, Gephyrocapsa* spp.1, *P. lacunosa*
	1.25 - 0.70 Ma	*Gephyrocapsa* spp.1, *P. lacunosa, G. oceanica*
	0..70 - 0. 25 Ma	*G. caribbeanica/G. margereli and G. oceanica*
	0.25 - 0. 09 Ma	*G. oceanica/G. muellerae, E. huxleyi*
	since 0.09 Ma	*E. huxleyi , G. muellerae*

Table 4.1 Summary of the dominant species in the eight time slices of the Pliocene and the Quaternary.

3) **Time slice 1.75 - 1.65 Ma (Figure 4.3c):** In this time slice, the coccolith assemblage is dominated by *P. lacunosa* and *R. minutula* together with the small *Gephyrocapsa* species group.
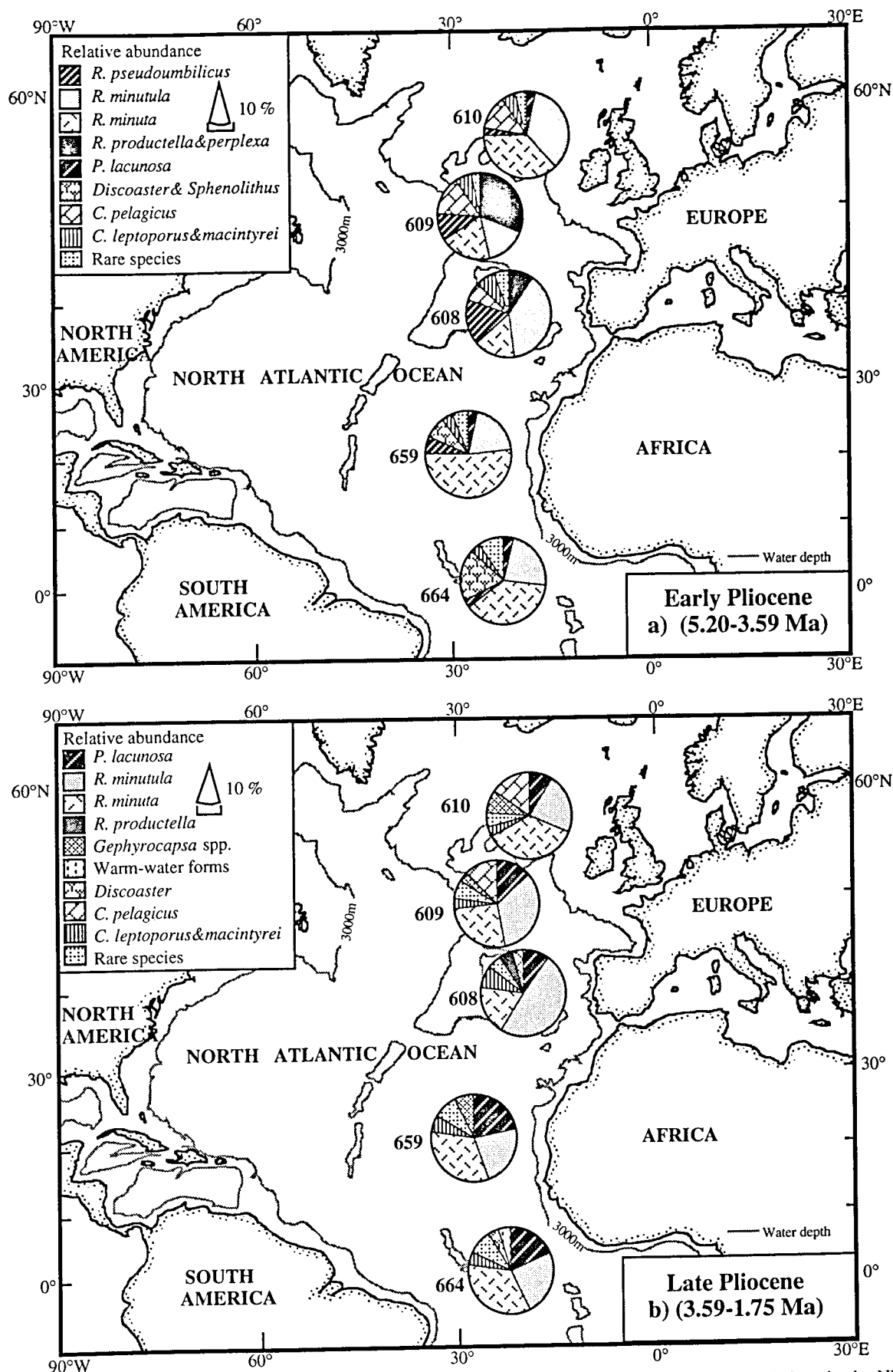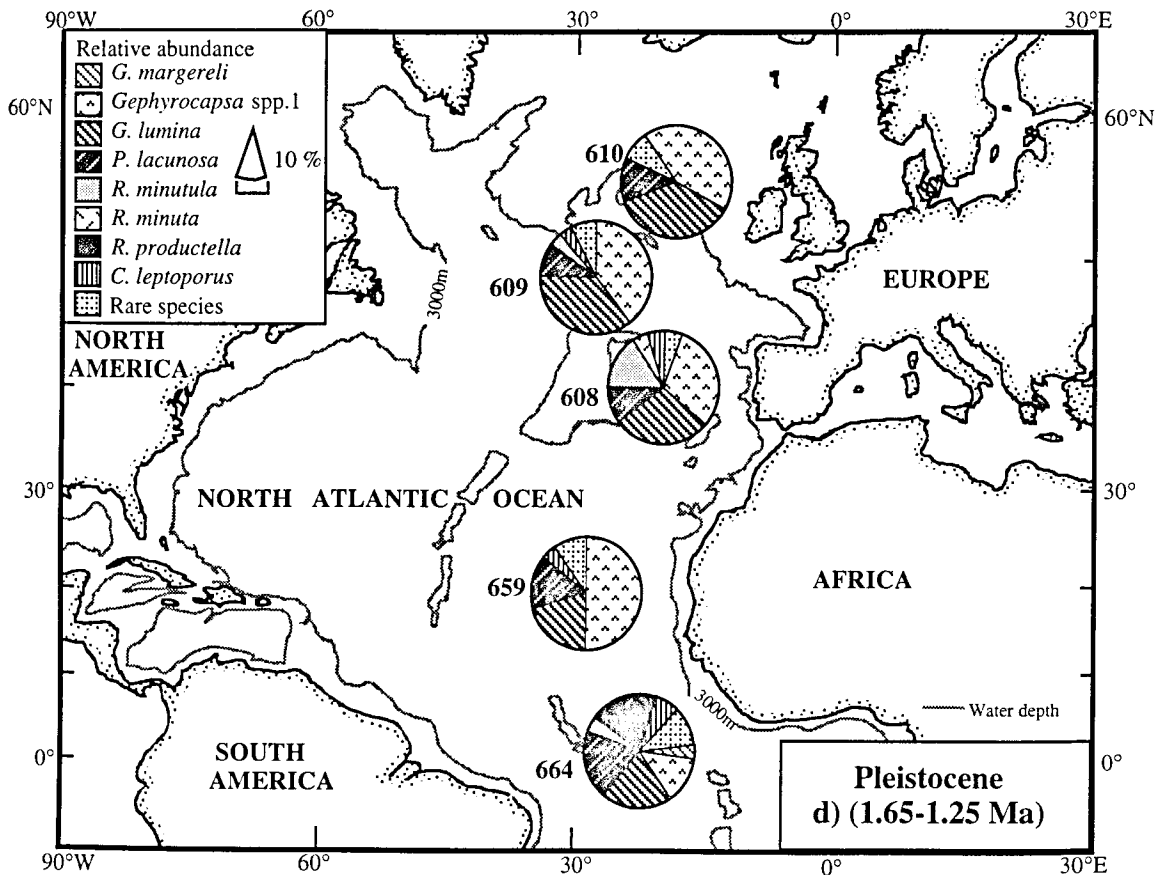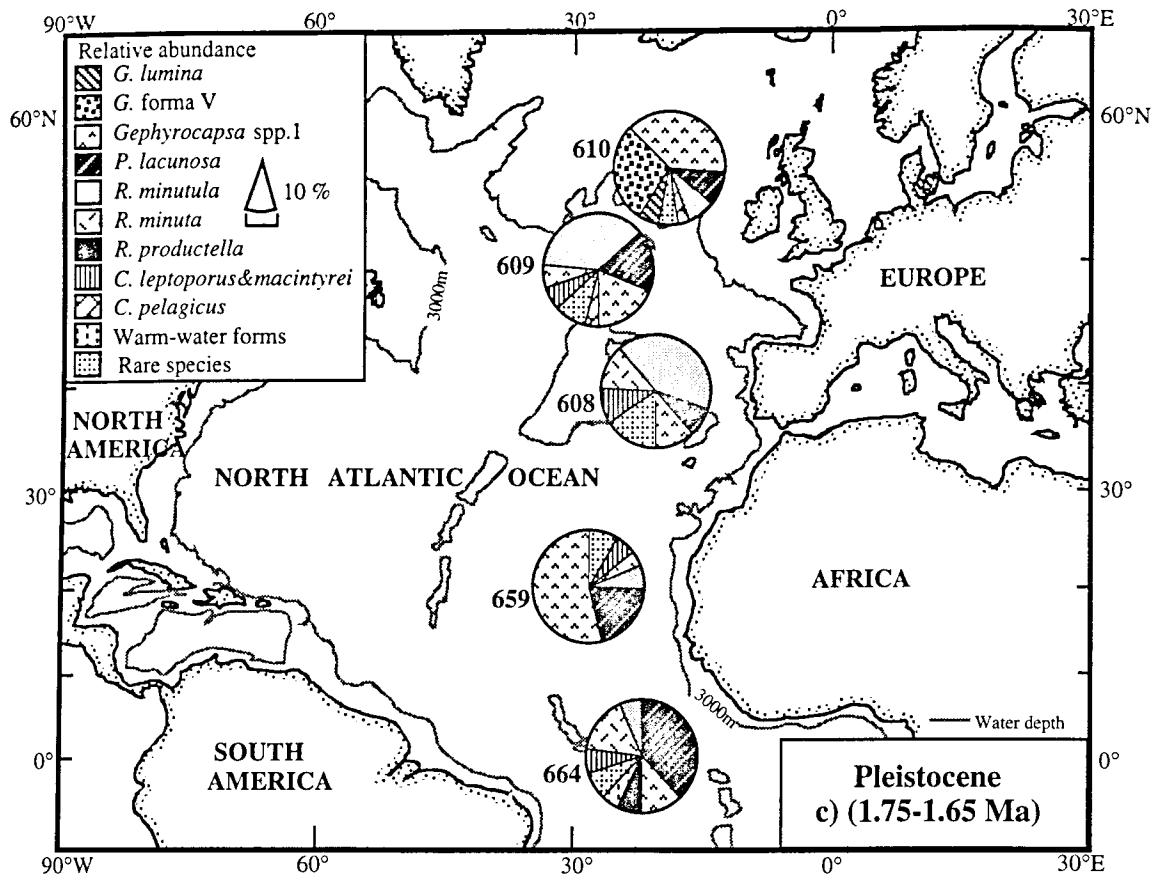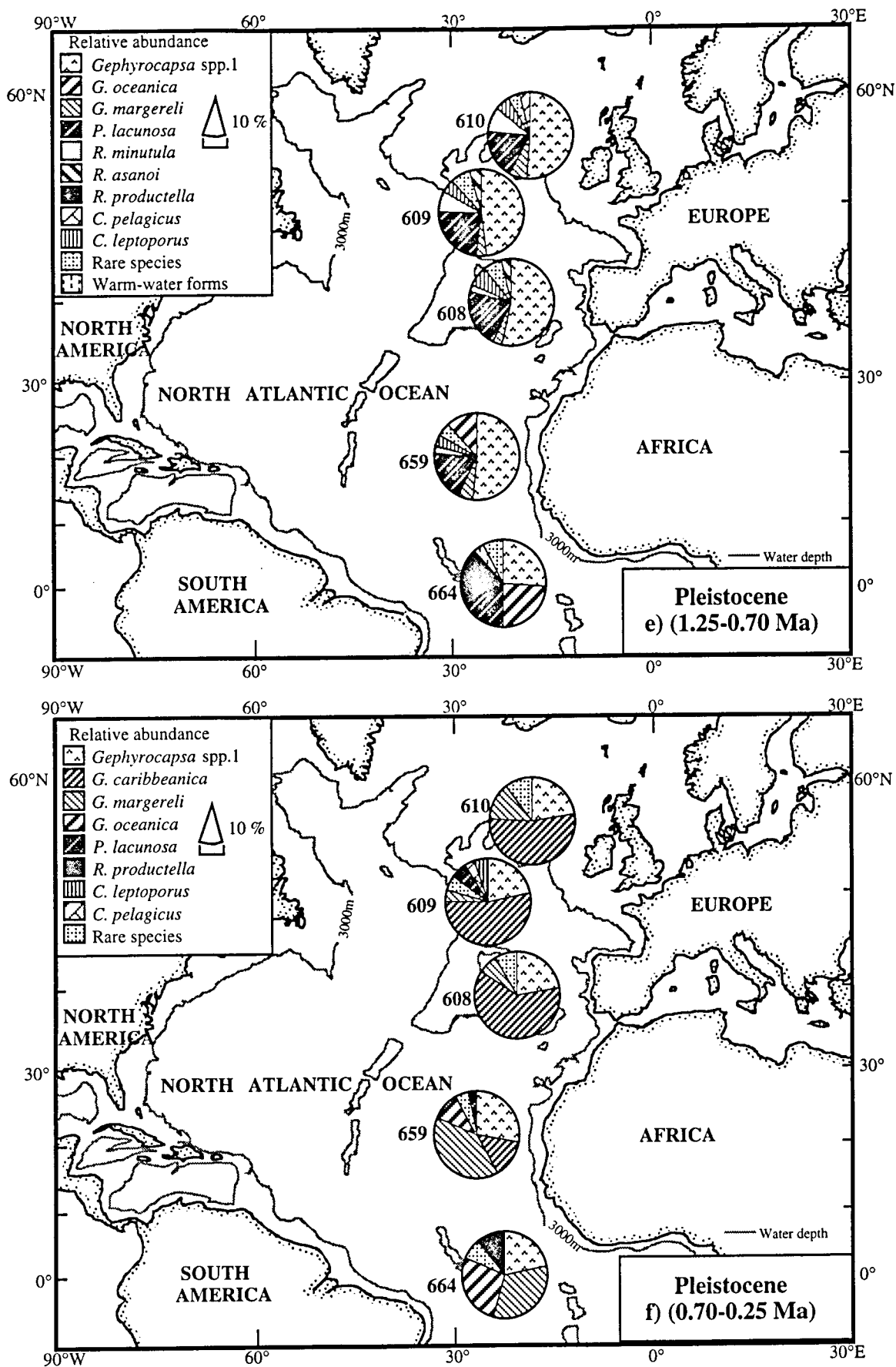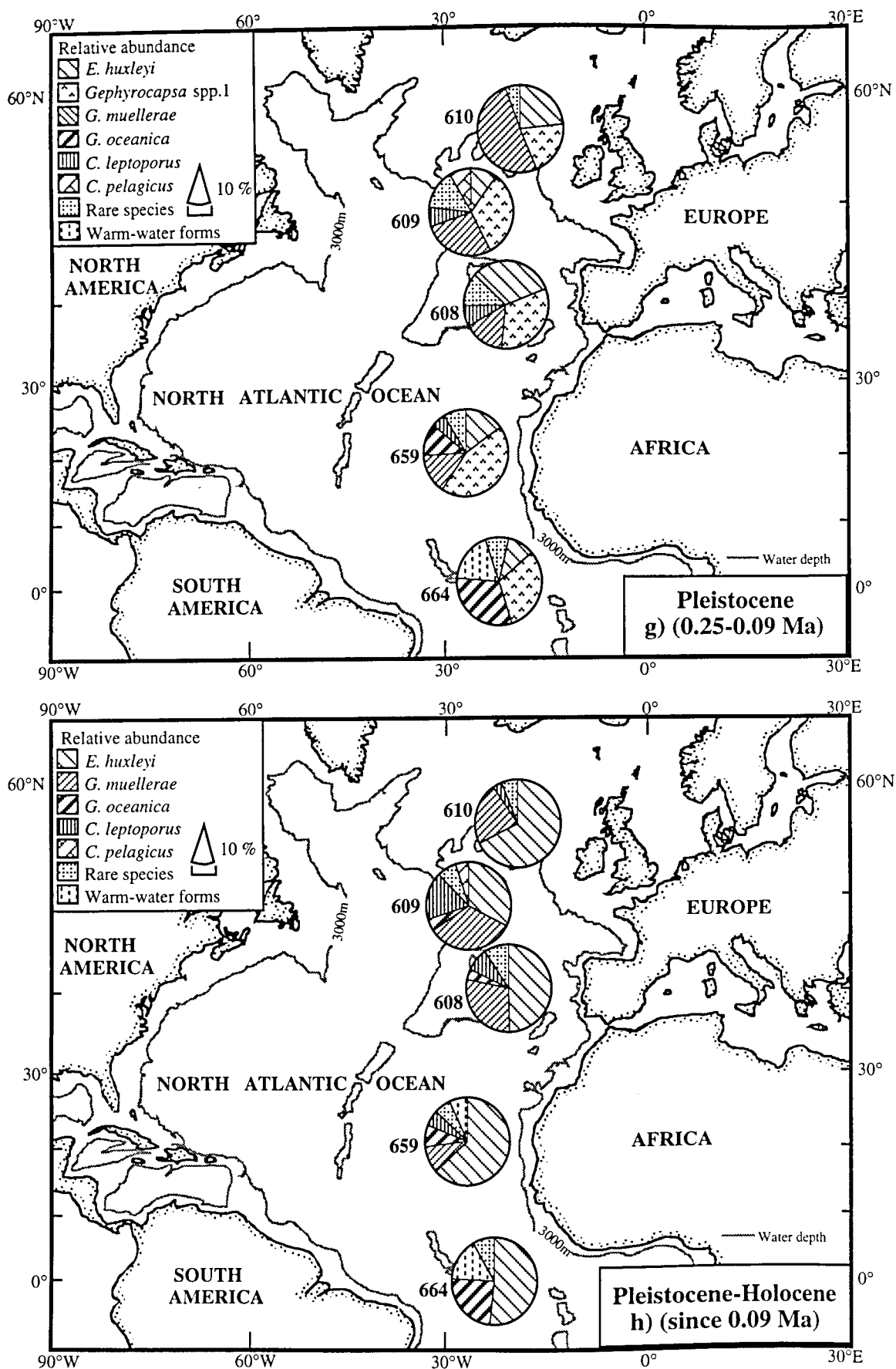
Figure 4.3a-h Evolution of late Tertiary-Quaternary coccolith assemblages with geographical variations in the NE Atlantic, demonstrated by variations in relative abundance of the abundant to common species. a) The Early Pliocene assemblage is dominated by *R. minuta* and *R. minutula* with abundant *Discoaster&Sphenolithus* in low latitudes, abundant *R. pseudoumbilicus* in mid latitudes and prominent *R. productella* in high latitudes. b) The Late Pliocene assemblage is dominated by *R. minutula, R. minuta,* and *P. lacunosa,* the latter decreases in abundance to the north.

Figure 4.3a-h Evolution of late Tertiary-Quaternary coccolith assemblages with geographical variations in the NE Atlantic, demonstrated by variations in relative abundance of the abundant to common species. c) At the begining the Pleistocene assemblages are dominated by *P. lacunosa* with *R. minutula* in high latitudes together with *Gephyrocapsa* spp.1 in low latitudes. d) In this time slice *G. lumina* and *Gephyrocapsa* spp.1 are prominent in the assemblage and *P. lacunosa* decreases to the north.

Figure 4.3a-h Evolution of late Tertiary-Quaternary coccolith assemblages with geographical variations in the NE Atlantic, demonstrated by variations in relative abundance of the abundant to common species. e) In this time slice *Gephyrocapsa* spp.1 and *P. lacunosa* are the dominant species with more *R. asanoi* in high latitudes and with abundant *G. oceanica* in low latitudes; note: *P. lacunosa* occurs abundantly from north to south. f) In this time slice *G. caribbeanica* is dominant in high latitudes whereas *G. margereli* and *G. oceanica* are prominent in low latitudes.

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Figure 4.3a-h Evolution of late Tertiary-Quaternary coccolith assemblages with geographical variations in the NE
Atlantic, demonstrated by variations in relative abundance of the abundant to common species. g) In this time slice
G. muellerae is prominent in high latitudes with decreased abundance to the south whereas G. oceanica is abundant
only in low latitudes; E. huxleyi is prominent at a few sites. h) E. huxleyi dominates the Recent assemblages from low
latitudes to high latitudes with abundant G. muellerae in high latitudes and abundant G. oceanica in low latitudes.

However, abundances of these dominant species vary greatly between the studied sites. At the tropical sites *P. lacunosa* accounts for 40 - 20 % but it is rarer at the northern sites. *R. minutula* is prominent at sites 608 and 609, but occurs only rarely towards the south and the north. In this period, small *Gephyrocapsa* species, mainly *G. aperta, G. sinuosa, Gephyrocapsa* forma F and forma H, are most abundant at sites 659 or 610. Around 1.68 Ma, *G. lumina* evolves from *Gephyrocapsa* forma V and soon after is a common species at site 610.

4) **Time slice 1.65 - 1.25 Ma (Figure 4.3d):** The dominance of *G. lumina* and the small *Gephyrocapsa* species group together with *P. lacunosa* is characteristic of the assemblage in this interval. *G. lumina* and various small *Gephyrocapsa* species (mainly *G. aperta, G. sinuosa, Gephyrocapsa* forma F and forma H) make up 60 - 70% of the coccolith assemblage at most sites, except site 664 where they account for 35%. *R. productella* is very abundant at site 664, but rare in the northern regions, which is distinctly different from its occurrences in Pliocene sediments (chapter 3). *R. minutula* remains a common species at sites 664, 608, and especially 609. The extinctions of *R. minuta, C. macintyrei* and *H. sellii* occur in this time slice.

5) **Time slice 1.25 - 0.70 Ma (Figure 4.3e):** During this period, *P. lacunosa* and various small *Gephyrocapsa* species are prominent in the assemblage. The small *Gephyrocapsa* species (mainly *G. sinuosa, G. aperta, Gephyrocapsa* forma F and forma D) make up 50% of the assemblage at most sites. *P. lacunosa* occurs at all sites with similar percentages (about 20%), showing increased abundances in the northern areas. *G. margereli* is also common at most sites. *R. productella* remains abundant only at site 664. Around 1.25 Ma *G. oceanica* arises from *G. lumina* but is abundant in low latitudes and rare in high latitudes. In contrast, another new species, *R. asanoi* (which evolved at about 1.2 Ma), increases rapidly in high latitudes and decreases in abundance to the south. In the transition to the next time slice, *R. minutula* and *R. asanoi* die out and *G. caribbeanica* evolves at 0.76 Ma.

6) **Time slice 0.70 - 0.25 Ma (Figure 4.3f):** In this time period, the coccolith assemblage in low latitudes (sites 664, 659) is quite different from that in high latitudes. At low latitudes *G. margereli* and *G. oceanica* make up more than 50% of the assemblage, whereas *G. caribbeanica* is overwhelmingly dominant in high latitudes with more than 50% of the assemblage. The abundance of *G. caribbeanica* decreases southwards and it is absent at site 664. In contrast, in the northern areas *G. margereli* occurs only in low percentages and *G. oceanica* is very rare. The small *Gephyrocapsa* species, including mainly *G. aperta, G. sinuosa*, and *Gephyrocapsa* forma P, and after 0.34 Ma *G. ericsonii*, remain abundant during this time. *P. lacunosa* becomes extinct at 0.49 Ma. From 0.36 to 0.27 Ma *G. margereli* changes into *G. muellerae* which replaces *G. caribbeanica* in the northern regions. At 0.30 Ma *E. huxleyi* evolves, probably from *G. margereli*, but is still rare in this period.

7) **Time slice 0.25 - 0.09 Ma (Figure 4.3g):** The dominance of *G. muellerae* and *E. huxleyi* makes the coccolith assemblage in this time slice significantly different from the one before. *G. muellerae* increases rapidly and accounts for about 50% of the assemblage at site 610, but its abundance decreases to the south and it is absent at site 664, indicating its preference for colder waters (chapter 3). *E. huxleyi* also occurs more abundantly in high latitudes than in low latitudes and rises very rapidly to dominance. The reversal in the dominance between *G. muellerae* and *E. huxleyi* happens at about 0.14 Ma in the subtropical areas (site 659) and at about 0.09 Ma in the northern regions (site 610); this is obviously earlier than the date of 0.073 to 0.085 Ma given by Thierstein et al. (1977) and Berggren et al. (1980). In their studies *G. muellerae* was named as "*G. caribbeanica*" (chapter 3). In the early period of this time slice *G. caribbeanica* remains common only at sites 608, and 609 and dies out at about 0.20 Ma. The dominance of *G. oceanica* remain restricted to the tropical area where the group of warm-water forms, *U. sibogae, N. coccolithomorpha, R. claviger,* and *Umbellosphaera* spp., is also very abundant. Among the small *Gephyrocapsa* species, *G. ericsonii* now occurs abundantly, *G. sinuosa* becomes extinct at 0.24 Ma and G. *aperta* disappears at 0.17 Ma.

8) **The time slice since 0.09 (Figure 4.3h):** *E. huxleyi* is overwhelmingly dominant species making up more than 50% of the assemblage at most sites. *G. muellerae* remains abundant in the northern areas. *G. oceanica*, together with the group of warm-water forms, occurs abundantly only in the tropical regions. The components of the coccolith assemblages in this time slice correspond to those of modern coccolith assemblages from surface sediments in the North Atlantic (McIntyre and Bé, 1967).

CHAPTER 5 CLIMATIC IMPACT ON COCCOLITH DEVELOPMENT

5.1 Linkage of climatic changes and coccolith development

To evaluate the climatic impact on coccolith development, variations in benthic $\partial^{18}O$ values and variations in accumulation rates of coccolith species are compared.

As a parameter for the climatic record the benthic $\partial^{18}O$ data from site 659 (Tiedemann et al., 1994) are chosen, because they provide a detailed record of the time and magnitude of Pliocene and Quaternary changes in temperature or ice-volume.

The accumulation rates of coccolith species in sediments are mainly controlled by the abundances or production levels of the species in the former coccolithophorid flora. Variations in production levels of a species through time are the response of this species to a altered marine ecosystem or to climatic changes (chapter 1). Furthermore, variation in abundances of a species through time documents the evolutionary history of this species. For example, the history of *P. lacunosa*, from its appearance and increase to decline and extinction, is indicated by variations in accumulation rates (chapter 4, Figures 4.2a-e).

It is expected that the variations in accumulation rates of a species should show a certain correlation with variations in $\partial^{18}O$ values. This correlation may indicate the response of coccolith species in production levels to varied ecological conditions induced by climatic changes. Such a simplified link is possible for the reasons below.

Firstly, production levels of coccolith species are controlled by various ecological factors in the marine ecosystem, including physico-chemical and biological factors (chapter 1). However, we are unable to distinguish the exact effects of various ecological parameters and that of genetic variation on the production levels. Secondly, climatic changes involve complex interactions of external forcings, including orbital cycles, and internal forcings (chapter 1). It is impossible to obtain a complete record of various physico-chemical parameters and a comprehensive understanding of the complex changes of the climate system. On the other hand, changes in temperature/global ice-volume are the result of the interactions of the components of the climate system. Therefore, it is reasonable to take temperature change as an indicator of climatic change and to evaluate the response of coccolith species to climatic change by analysing variations in their accumulation rates.

5.2 Evidence from ODP Site 659

Both the coccolith accumulation rates (ARcoccoliths) of the dominant species from site 659 and the benthic $\partial^{18}O$ values from site 659, are plotted (Figure 4.2b) for comparison.

From Figure 4.2b it can be seen that it is difficult to make a detailed correlation between peaks of the $\partial^{18}O$ curve and peaks of ARcoccoliths curves of various species, since the time resolution in the $\partial^{18}O$ analyses is about 3 kyr and that in the coccolith analyses is 30 kyr. However, several general correlations can be made:

1) The $\partial^{18}O$ curve shows a trend of decreasing temperatures or increasing ice-volumes since the middle Pliocene and indicates lowest temperatures and the largest ice-volumes in the Quaternary. ARcoccoliths curves show a significant change of the coccolith assemblages and a trend of the coccolith development: Miocene taxa (*Discoaster, Sphenolithus,* and *R. pseudoumbilicus*) decline and become extinct within the Pliocene, and the genus *Gephyrocapsa* flourishes in the Quaternary. *Gephyrocapsa* replaces *Reticulofenestra* as the dominant genus. The continuously decreasing temperatures may be the main cause of the decline and extinction of Miocene species; whereas Pliocene and Quaternary species adapted to the altered conditions, therefore increasing in the Quaternary.

2) The amplitude variation of $\partial^{18}O$ values is small in the Early Pliocene, however it increases continuously through the Late Pliocene and Quaternary and has the largest amplitude in the late Quaternary. This indicates that in the Early Pliocene the variability of temperature/ice-volume is small in gentle climatic fluctuations. From the Late Pliocene the climatic variability increases and is largest in the Quaternary, due to frequent and large-amplitude glacial-interglacial climatic alternations. Within the coccolith assemblages, gradual and long-term changes in abundances of Miocene/Pliocene species occur in the Pliocene; whereas abrupt and frequent changes happen in the Quaternary. The gradual changes of species in the Pliocene seem to be related to the relatively stable climatic conditions at that time; while the rapid and abrupt changes in Quaternary coccolith assemblages are their response to the large climatic instability.

3) Very commonly, small-amplitude fluctuations of $\partial^{18}O$ values and small-amplitude variations in ARcoccoliths are observed in the same time interval; while distinct large variations in $\partial^{18}O$ values are paralleled by a sharp change of ARcoccoliths. For example, in the time interval of 4.6 to 4.2 Ma both variation amplitudes of $\partial^{18}O$ values and of *R. minuta* ARcoccoliths are small (Figure 4.2b); whereas distinct large variations of $\partial^{18}O$ values in the time intervals from 4.9 to 4.8 Ma and from 4.1 to 3.8 Ma are accompanied by remarkable decreases in ARcoccoliths of this species. The same correlations are observed between $\partial^{18}O$ values and the ARcoccoliths of other species. These facts support the correlation given above (2), that is, steady production levels correspond to stable climatic conditions and large variability of production is related to unstable climatic conditions.

These evidences suggest that the changes in production of coccolith species are caused not only by variations in single ecological parameter, such as temperature, but also by the paleoclimatically induced complex changes within the complete ecosystem, e.g. variations in

insolation, light, water masses, water circulation and stratification, and nutrients. Thus, the change of $\partial^{18}O$ values and the change of ARcoccoliths of species are not directly correlated, but the amplitude of variations that indicate climatic or ecological instability correspond to each other.

On the basis of such a correlation, a detailed examination of the link between variations in $\partial^{18}O$ values and variations in ARcoccoliths of species can help to produce more information about the response of coccolith species to climatic changes.

5.3   Statistical determinations

5.3.1   Application of fluctuation rates

A statistical method, determination of coefficent of variation, is employed to analyse and depict amplitudes of variation of the $\partial^{18}O$ values and of the ARcoccoliths values. In statistics, a coefficent of variation is primarily used to measure the variance of a sample population. A high coefficent is derived from a large variance of individual samples and indicates an unstable sample population; whereas a low one is derived from a small variance of individual samples and indicates a stable sample population (chapter 2).

In this study, a low $\partial^{18}O$ coefficent ($\partial^{18}O$ fluctuation rate), derived from small-amplitude $\partial^{18}O$ variations, is used to describe a relative stable climatic condition; whereas a high $\partial^{18}O$ fluctuation rate, derived from large-amplitude $\partial^{18}O$ variations, indicates an unstable climatic and ecological condition. A low ARcoccoliths coefficent (coccolith fluctuation rate) indicates a small variability of the production within a certain time interval; and a high coccolith fluctuation rate indicates a large variation in production. Variations in $\partial^{18}O$ amplitudes and in ARcoccoliths amplitudes can be correlated.

Only the $\partial^{18}O$ data from site 659 were statistically analysed and used for comparison with coccolith fluctuation rates from the five studied sites, for the following reasons: 1) The $\partial^{18}O$ record from site 659 is the only complete Pliocene and Quaternary $\partial^{18}O$ record (including plankton $\partial^{18}O$ data) available from the five sites. 2) According to the study of Tiedemann et al. (1994), long- and short-term variations in the isotope record from site 659 during the last 2.5 m.y. are similar to those from site 607 in high latitudes (Ruddiman et al., 1989; Raymo et al., 1989). Furthermore, the $\partial^{18}O$ amplitudes observed at site 552A are similar to those observed at sites 607 and 606 (Keigwin, 1986; Curry and Miller, 1989; Raymo et al., 1989). So the $\partial^{18}O$ amplitudes and trends observed in low latitudes are similar to those in high latitudes. 3) The stratigraphical results of site 659 in this study agree with the results of Tiedemann et al. (1994), and the stratigraphical correlations between the five sites

are good. Therefore, coccolith fluctuation rates from the five sites can be compared with the $\partial^{18}O$ fluctuation rates from site 659.

5.3.2   Correlations and interpretations

a) Variations in $\partial^{18}O$ rates

The $\partial^{18}O$ fluctuation rates (FR$\partial^{18}O$) from site 659 are plotted as a background curve for illustrating the climatic variability from the last 5.2 m.y. (Figures 5.1a-f).

Initially it is necessary to examine the sensitivity and reliability of the FR$\partial^{18}O$ by comparing them with the results of a number of paleoclimatic studies.

In the Early Pliocene the FR$\partial^{18}O$ are low and show little variance with a slight increase near the end of the Early Pliocene (around 3.8 Ma). This reflects a relatively stable ecosystem due to gradual and slight climatic variations, which agrees well with the study of Tiedemann et al. (1994), who found long-term gradual variations in temperature/global ice volume in the Early Pliocene.

From the Late Pliocene, the FR$\partial^{18}O$ show an increasing trend up to the Holocene and have the highest values in the last 0.25 m.y. Several variations in the fluctuation rates are distinguished.

1) In the Late Pliocene, after a slight increase around 3.8 Ma, the FR$\partial^{18}O$ distinctly increase up to around 2.7 Ma and then decrease until 2.0 Ma after which they increase again, indicating differences of the climatic variability with times.

The first slight increase (around 3.8 Ma) is derived by means of a series of short-term and large-amplitude isotope fluctuations. The fluctuations at that time indicate deep water cooling or increasing ice volume and are paralleled by large-amplitude variations in orbital obliquity (Tiedemann et al., 1994). Later, a strong increase in the FR$\partial^{18}O$ indicates the major phase of Pliocene northern hemisphere ice growth between 3.15 and 2.5 Ma (Shackleton and Hall, 1984; Raymo et al., 1989; Jansen and Sjøholm, 1991; Tiedemann et al., 1994).

Lower FR$\partial^{18}O$ between 2.4 and 2 Ma are associated with small-amplitude variations in $\partial^{18}O$ values. Small-amplitude variations were also observed at sites 552A (Shackleton and Hall, 1984), 606 (Keigwin, 1986), 607 (Raymo et al., 1989), and 665 (Curry and Miller, 1989) and are believed to indicate a climatic interval which had smaller polar ice sheets between the large ice-rafting events at 2.5 Ma and at 2.1 Ma (Raymo et al., 1989).

Therefore, the increased FR$\partial^{18}O$ in the early period of the Late Pliocene imply an increased ecological instability corresponding to the beginning of ice growth in the northern Hemisphere and indicate large-amplitude variations in orbital obliquity; the later decreased FR$\partial^{18}O$ reflect a relatively stable climatic period between two large ice rafting periods.
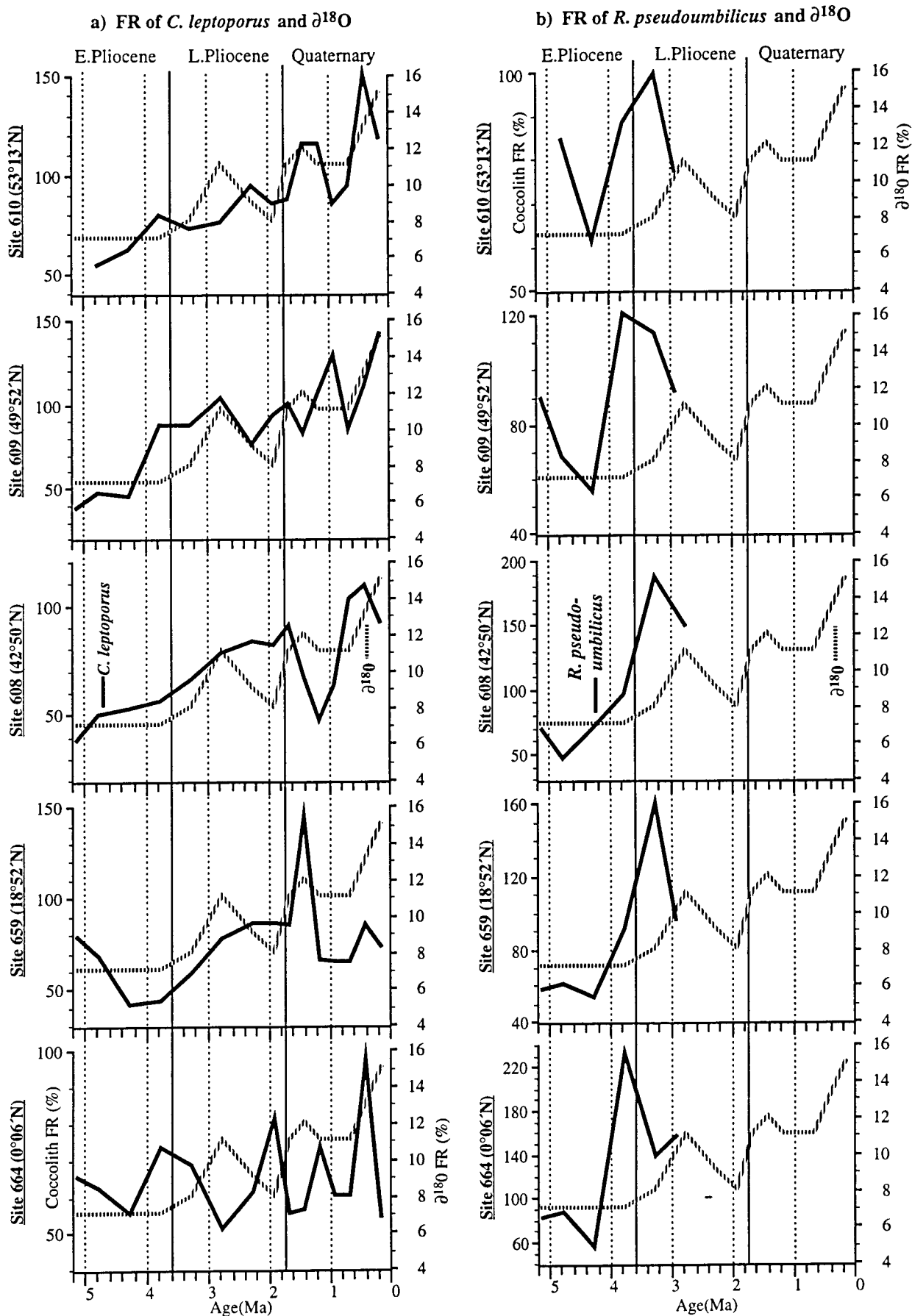
Figure 5.1a-f   Coccolith fluctuation rate (FR) curves of coccolith species at the five studied sites in comparison with the $\partial^{18}O$ fluctuation rate (FR) curve from site 659.

c) FR of *R. minuta* and ∂¹⁸O
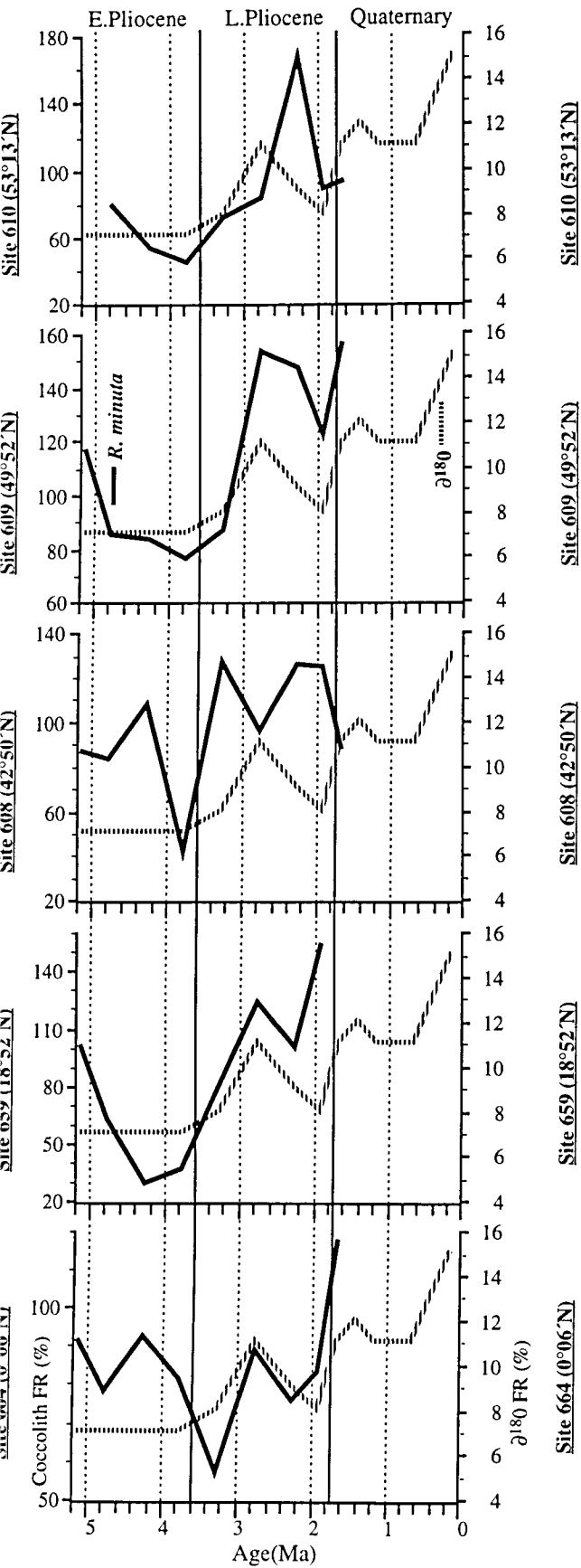
d) FR of *R. minutula* and ∂¹⁸O

Figure 5.1a-f (continued).

100
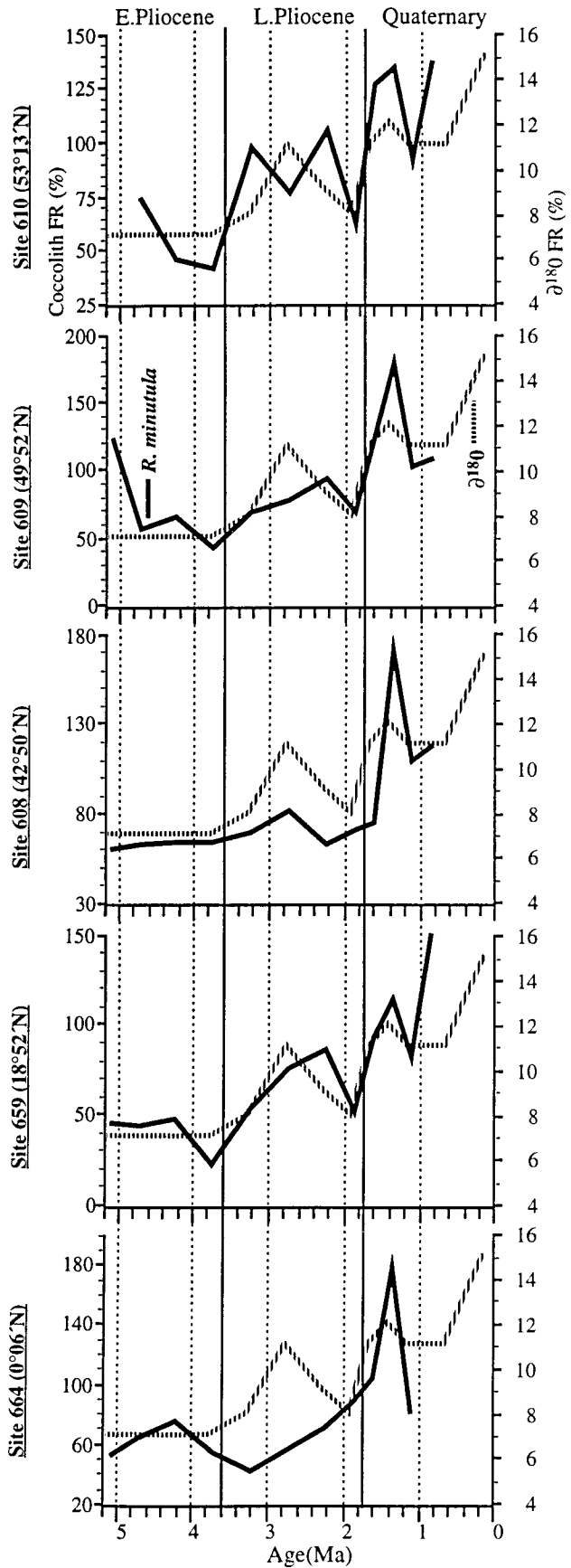
e) FR of *P. lacunosa* and $\partial^{18}O$
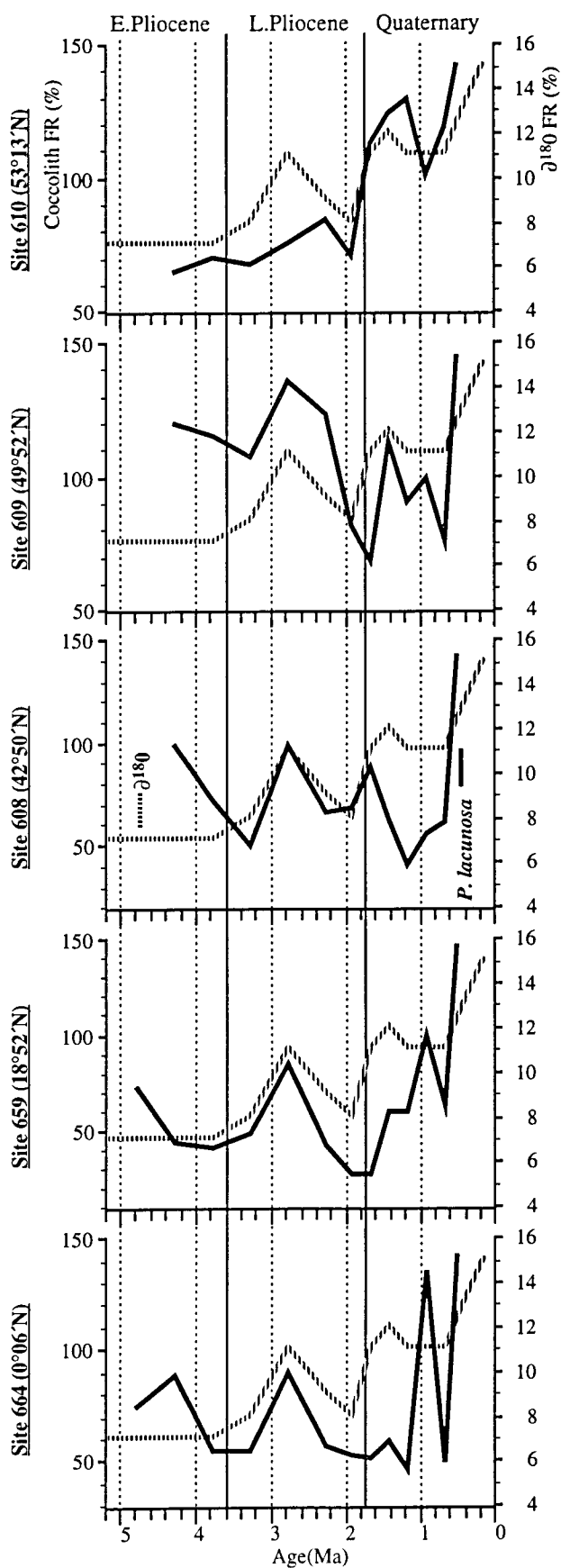
f) FR of *G. oceanica* and $\partial^{18}O$
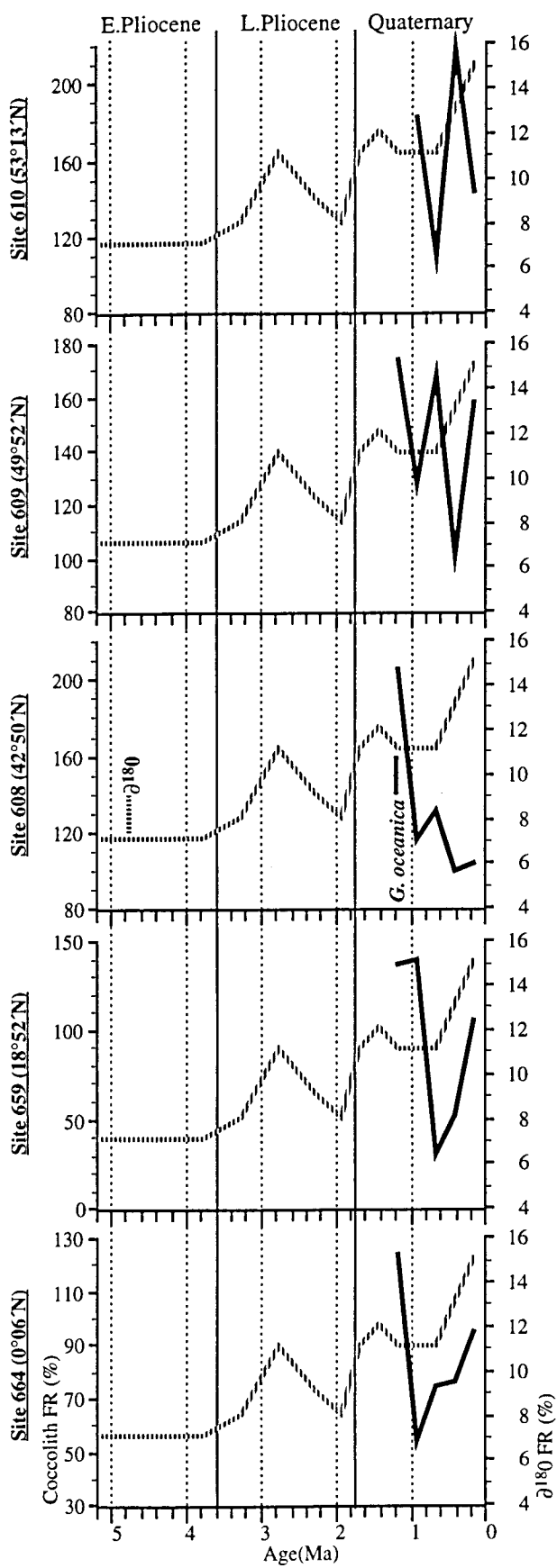
Figure 5.1a-f (continued).

2) In the Quaternary, the $FR\partial^{18}O$ are high and continue to increase with time. Such high variability is related to the large and frequent glacial-interglacial fluctuations known from numerous isotopic records from the Quaternary, and hence indicates the very unstable climatic conditions in this time. The maximum in the late Quaternary indicates much more instability than in the early Quaternary. This agrees with the results of Ruddiman et al. (1987) who suggested higher-amplitude climatic fluctuations in the northern Hemisphere during the Brunhes epoch than in the earlier Quaternary. A slight decrease in the $FR\partial^{18}O$ during the middle Quaternary (between 1.1 and 0.7 Ma) perhaps reflects a reduced climatic variability before the large fluctuations and the strongest glaciations from about 0.60 m.y. (Ruddiman et al., 1989).

In conclusion, variation amplitudes indicated by the $FR\partial^{18}O$ are sensitive to the significant climatic changes which have occurred during the last 5.2 m.y.

b) Correlation of coccolith fluctuation rates to the $\partial^{18}O$ variations

Six coccolith species, *C. leptoporus, R. pseudoumbilicus, R. minuta, R. minutula, P. lacunosa,* and *G. oceanica,* were statistically analysed. Their coccolith fluctuation rates (FRcoccoliths) from each studied site are plotted over the $\partial^{18}O$ fluctuation curve from site 659 in one diagram (Figures 5.1a-f).

1) *C. leptoporus* ranges from the Miocene to Recent and is a less common species in Late Tertiary and Quaternary coccolith assemblages. In most time intervals, its FRcoccoliths from the five sites show an increasing trend and are parallel to the $\partial^{18}O$ fluctuation curve (Figure 5.1a). Furthermore, the FRcoccoliths in the northern sites are larger than those in the tropical sites; e.g. in the Quaternary its FRcoccoliths are larger than 100% at sites 610 and 609, whereas they are less than 100% at site 664. This implies that in high latitudes *C. leptoporus* has undergone more ecological stress than in low latitudes due to stronger climatic instability in high latitudes, possible causes being ice rafting extending to 40°N in the North Atlantic or the stronger influence of orbital variations on the surface of the Atlantic Ocean from 40°N to 63°N (Ruddiman and McIntyre, 1984; Ruddiman et al., 1989; Raymo et al., 1989). However, in a few time intervals, the *C. leptoporus* fluctuation curves do not parallel the $\partial^{18}O$ fluctuation curve. For example, from 0.25 Ma, the *C. leptoporus* fluctuation rates decrease in contrast to the strongly increased $FR\partial^{18}O$, indicating reduced variations in productivity. This may be explained in two ways: 1) large ecological tolerances, 2) changes in its ecological affinity derived by biological evolution; both of these are largely independent of climatic conditions. Due to this independence, this species still lives today.

2) *R. pseudoumbilicus* ranges from the Miocene to the Pliocene and occurs abundantly in very early Pliocene sediments. This species shows high FRcoccoliths in response to slightly

increased FR∂¹⁸O around 3.8 Ma (Figure 5.1b). This suggests that *R. pseudoumbilicus* probably had a small tolerance to the increased ecological stress in the Pliocene. *R. pseudoumbilicus* is unable to survive the first severe climatic instability in the Late Pliocene (around 2.8 Ma) and dies out.

3) *R. minuta* ranges from the Eocene to the early Quaternary and is a dominant species in the Pliocene. Generally, the coccolith fluctuation curves of this species at the five sites parallel the ∂¹⁸O fluctuation curve, except for a few intervals at site 664 and 608 in the Early Pliocene (Figure 5.1c). In comparison with *R. pseudoumbilicus*, *R. minuta* shows smaller variation amplitudes in response to the increased climatic instability in the middle Pliocene, indicating it to have a large tolerance to the climatic changes in the Late Pliocene. Its fluctuation rates increase towards the north in the Late Pliocene, showing larger variation amplitudes in response to the larger climatic variations there. *R. minuta* becomes extinct at around 1.6 Ma, when the extreme Quaternary climatic variability begins.

4) *R. minutula* ranges from the Miocene to the early Quaternary and also dominates the Pliocene coccolith assemblages. The coccolith fluctuation curves of this species are nearly parallel to the ∂¹⁸O fluctuation curve (Figure 5.1d). In response to the first intensified climatic instability, its maximum FRcoccoliths in the Late Pliocene is less than 100%, thus showing smaller variations in production levels than *R. minuta*. This implies that *R. minutula* was better adapted to the Pliocene oceanographic conditions. In the early Quaternary its high FRcoccoliths (larger than 100%) indicate its limited tolerance to further increased climatic instability and it dies out in the middle Quaternary.

5) *P. lacunosa* ranges from the Pliocene to the Quaternary and occurs abundantly in the Late Pliocene and early Quaternary coccolith assemblages. In the Early Pliocene, its rather low FRcoccoliths are not parallel to the ∂¹⁸O fluctuation curve. This is seen as a result of biological evolution, because at this time the species had just developed from *R. minutula* and successfully adapted to Early Pliocene oceanographic conditions. In the Late Pliocene, its fluctuation curves correspond to the ∂¹⁸O fluctuation curve. However, the maximum is less than 100% at most sites, showing small variations in productivity. This implies that this species was well adapted to the Late Pliocene oceanographic and ecological conditions. In the Quaternary, the FRcoccoliths of this species increase in correlation with increased FR∂¹⁸O. Additionally, the differences in its FRcoccoliths between the southern sites and the northern ones in the middle Quaternary are probably caused by biological variations, as during the middle Pliocene this species occurs more abundantly in the northern sites than before (chapter 4). However, *P. lacunosa* was unable to adapt to the strongest climatic oscillations of the late Quaternary and became extinct at around 0.49 Ma.

6) *G. oceanica* ranges from the middle Quaternary to Recent and shows distinctly decreased FRcoccoliths around 1.0 Ma after its origin, in contrast to high FR∂¹⁸O. This

suggests that this newly evolved species adapted successfully to the ecological conditions at this time, as seen with *P. lacunosa* in the Early Pliocene. Later, its increased fluctuation curves parallel the $\partial^{18}O$ fluctuation curve but the variation amplitudes are still small, indicating that this species is still able to adapt to the changing climate in the late Quaternary. *G. oceanica* lives in the modern oceans and occurs abundantly from tropical to subtropical regions and in warm marginal seas and upwelling areas (Okada and Honjo, 1975; Wang and Samtleben, 1983; Mitchell-Innes and Winter, 1987; Su, in Hao et al., 1989; Kleijne, 1993; Roth, 1994).

The analyses of these six species confirm the correlations between variation amplitude of $\partial^{18}O$ values and of ARcoccoliths, in most cases: low FRcoccoliths are parallel to low FR$\partial^{18}O$ and *vice versa*. Thus, variations in ARcoccoliths or production of a coccolith species through time mainly reflect its response to paleoclimatically induced complex changes within the complete marine ecosystem. The statistical examinations show that coccolith species have small variations in production levels in relatively stable climatic and ecological conditions; and *vice versa*. Furthermore, these results suggest that those variations in species which are driven by biological evolution are not directly correlated to climatic changes.

Variations in FRcoccoliths of different species indicate a variety of potential tolerances to changing ecological conditions: 1) species with large tolerances; 2) species with limited tolerances; 3) species with changing tolerances.

1) Species with large tolerances, e.g. *C. leptoporus*, live under both stable or unstable ecological conditions. They are probably ecologically independent of climatic changes and can survives in changing climate or ecological environments without undergoing distinct biological evolution. Variations in abundances may not be directly correlated to variations in ecological factors.

2) Species with limited tolerances, e.g. *R. pseudoumbilicus*, are largely dependent on climatic or ecological factors. As they do not evolve in response to ecological changes, they are unable to adapt to increasing ecological instability, thus they decline and become extinct.

3) Species with changing tolerances, e.g. *R. minuta, R. minutula, P. lacunosa*, and most species of *Gephyrocapsa*, mostly have primarily small tolerances and are largely dependent on ecological factors. However, they do show evolution in response to ecological changes, probably as the results of natural selection (Darwin, 1859; Levinton, 1989), which may help to obtain a new ecological adaptation, or to change the limited tolerances. Therefore they are able to survive increased ecological instability. However, at a later time they may fail to adapt to further changing ecological instability and their tolerances may become limited again which may lead to their decline and extinction.

5.4 Climatic impact on the development of Late Tertiary and Quaternary coccolith assemblages from the NE Atlantic

Based on the correlations between the $\partial^{18}O$ fluctuation curve from site 659 and the various coccolith fluctuation rate curves, the impact of climatic changes on the development of Late Tertiary and Quaternary coccolith assemblages can be discussed:

1) **Impact on the fundamental changes in coccolith assemblages**: the alterations of dominant species. Pliocene dominant species, such as *R. minuta, R. minutula*, fail to adapt to the increased climatic instability of the Quaternary and decline and become extinct, leaving a free ecological space in the coccolithophorid ecosystem. On the other hand, newly evolved species, such as *P. lacunosa, Gephyrocapsa* species and *E. huxleyi*, adapt to the Quaternary conditions and also have the space to develop. Therefore, they become the dominant species.

2) **The impact on less common species**: less common species are *C. leptoporus, C. pelagicus, U. sibogae*, and *H. carteri*, and they originated before the Pliocene. *C. leptoporus* may be well preadapted to the different climatic and ecological conditions of Miocene to Quaternary times, indicating that it is probably an ecologically rather independent species. However, other species seem to adapt to the changed climatic and ecological conditions and to survive as extant species through genetic variations but which bring about no distinct morphological variations. Successful adaptations are indicated by, e.g. altered ecological affinities of *C. pelagicus* (chapter 3) and increased abundances of *U. sibogae* and *H. carteri* in the Quaternary (Figures 3.5, 3.6). Furthermore, the extinctions of *C. macintyrei* and *H. sellii* (Figure 3.3, 3.7) are similar to the extinction of *R. minuta*. Presumably, these species have been habituated to the Pliocene environmental conditions and fail to adapt to the intensified climatic instability in the earlier Quaternary.

3) **Effects of latitudinal differences of climatic variability on variations of the coccolith assemblages**: Quaternary FRcoccoliths of *C. leptoporus* and *R. minuta* are higher in the northern sites than in the southern sites, indicating more ecological instability (Figures 5.1a, c). Generally, more direct correlations between FRcoccoliths and FR$\partial^{18}O$ are observable in high latitudes (Figures 5.1a-d). For the same reason, in the Quaternary more distinct changes in the coccolith assemblages from high latitudes are observed than in those from low latitudes (chapter 4, Figures 4.2a-e). These changes in coccolith species and abundances suggest that coccolithophorid floras in high latitudes are directly under the control of temperatures of climatic fluctuations throughout glacial-interglacial periods; whereas the floras in low latitudes are affected mainly by the changes in the complete ecological system caused by glacial-interglacial fluctuations in high latitudes, that means, they are under a relatively indirect control of climatic changes.

4) **Impact on evolutionary rates of species:** from Figure 5.2 it can be seen that the $FR\partial^{18}O$ are paralleled by extinction rates of coccolith species. This suggests that the increased climatic instability in the Quaternary results in the extinction of more species than in the Early Pliocene and in the Late Pliocene. However, the appearance rates of species are not parallel to the $\partial^{18}O$ fluctuation curve, since newly evolved species are the result of biological evolution which deals with very complex processes and can not be directly correlated with climatic changes.

5) **Impact on coccolith development:** increased climatic instability in the Quaternary results in the extinction of dominant species. On the other hand, it may also cause the origin and increase of new dominant species. For example in the early Quaternary the abrupt decline of *R. minutula* probably supplies an ecological niche for the strong increase of *G. lumina*. Similarly, the rapid decline and extinction of *G. caribbeanica* provides ecological space for the intensified rise of *G. muellerae* in the northern areas. Furthermore, the high species diversity of *Gephyrocapsa* in the Quaternary is probably related to the large climatic variability in this time. For these reasons, rapid coccolith development in the Quaternary can be seen as the response of the coccolith assemblages to the increased ecological stress produced by intensified climatic instability.
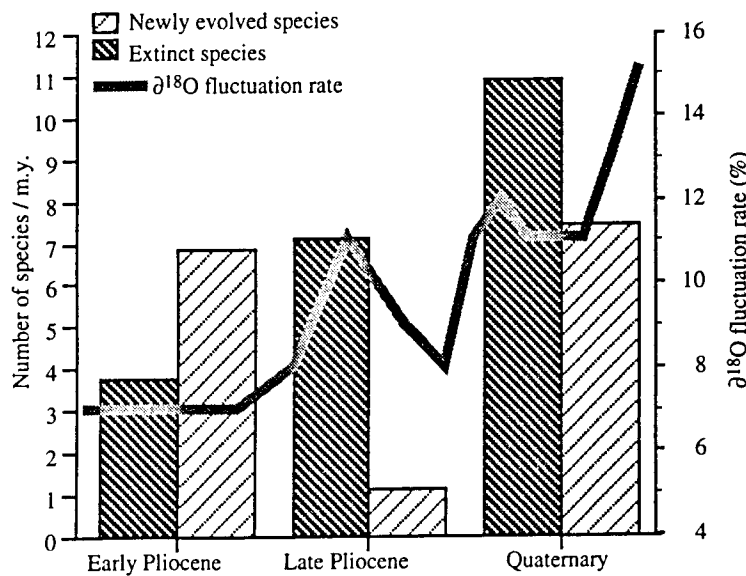
Figure 5.2 Coccolith appearance and extinction rates (number of extinct/newly evolved species per million years) in comparison with the $\partial^{18}O$ fluctuation rate curve from site 659. The evolutionary rates were calculated based on the coccolith evolutionary events in chapter 4, figure 4.1.

Conclusions

1. A detailed history of late Tertiary and Quaternary coccolith development with geographical variations in the Northeast Atlantic is demonstrated in eight developmental stages.

Since the last 5.2 m.y., the main constituents of the coccolith assemblages have been fundamentally changed through a series of replacements of old dominant species by new ones. The dominance of *Reticulofenestra* in the Pliocene is replaced by *Gephyrocapsa* in the Quaternary.

2. The changes in coccolith development are seen as results of major evolutionary changes in the dominant species or within the members of the family Noehaerbdaceae. *Reticulofenestra* species found in this study originated mainly in the Miocene and are the oldest forms of this family during the Pliocene and Quaternary. Their decline in the Pliocene provided a free ecological space for the increase of the newly evolved *P. lacunosa* and *Gephyrocapsa* species. The Quaternary assemblages are characterized by rapid evolutionary changes in *Gephyrocapsa*. Lastly, *E. huxleyi* evolved from *Gephyrocapsa* and dominates the Recent coccolithophorid flora.

3. Geographical variations of the coccolith assemblages in the studied area are due to various ecological preferences of these abundant species and indicate paleoceanographic variations in the Northeast Atlantic. Small latitudinal variations of the assemblages are related to small paleoceanographic variations from the low to high latitudes; whereas large differences between the studied sites, found in several time slices of the Quaternary and caused by the different ecological affinities of the various *Gephyrocapsa* species, reflect different paleoceanographic conditions between the north and the south.

4. General comparisons of variations in accumulation rates of coccolith species with variations in benthic $\partial^{18}O$ data at site 659 (Tiedemann et al., 1994) indicate that coccolith flora show variability in production levels in response to climatic changes.

5. Correlations between the coccolith fluctuation rates of six species and the $\partial^{18}O$ fluctuation rates indicate that in the Pliocene, under stable climatic conditions, the coccolith species showed small variations in accumulation rates, whereas during the Quaternary large-amplitude variations of coccolith accumulations in response to increased climatic instability were seen.

During the Quaternary, more abrupt changes in the assemblages are observed at the northern sites. Furthermore, during this period, coccolith fluctuation rates increase to the north and indicate stronger ecological stresses.

Therefore, increased climatic instability during the Quaternary resulted in high-amplitude variations in the marine ecosystem and produced large ecological stresses for the

coccolithophores which lived in this ecosystem. This is the main cause of the rapid and abrupt changes in the Quaternary coccolith assemblages.

6. It is observed that various genera and/or species show different tolerances and responses to climatic changes and increased ecological stress.

A few coccolith species, as *Calcidiscus leptoporus*, show small variations in abundance, indicating a large tolerance to the strong ecological variability during the Quaternary. Such species may be relatively independent of climatic changes.

The extinction of most *Reticulofenestra* species are possibly due to their small ecological tolerance and their failure to adapt to the increased climatic instability. This is also the main reason for increased coccolith species extinction rates in the Quaternary.

Through certain genetic variations within species, the ecological affinities of a few species have changed, e.g. *Coccolithus pelagicus*; or ecological tolerances of several species increased, e.g. *Helicosphaera carteri*. Such changes helped them to adapt to varied ecological conditions.

The high species diversity of *Gephyrocapsa* with large ecological divergence indicates a successful adaptation of this genus to the increased climatic and ecological instability and to the large latitudinal differences during the Quaternary.

7. The analyses also indicate that during a few time intervals coccolith fluctuation rates do not correspond to the $\partial^{18}O$ fluctuation rates due to biological variations, and that appearance rates of coccolith species are not parallel to variations of the $\partial^{18}O$ fluctuation rates. This suggests that biologically derived variation in abundances cannot be directly correlated with global climatic changes.

Acknowledgements

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Appendix:

1) Photographic plates (Plates 1 - 7).

2) Tables of Coccolith absolute abundance data from DSDP/ODP
   sites 664D, 659, 608, 609, 610A (the data can be obtained from the original doctoral
   thesis (Su, 1995) in the library of GEOMAR).

Plate 1

Figure 1,2   *Emiliania huxleyi* (Lohmann) Hay and Mohler, DSDP Site 608 (0.03 m).

Figure 3   *Calcidiscus leptoporus* (Murray and Blackman) Loeblich and Tappan, a small
and elliptical variety, DSDP Site 608 (70.12 m).

Figure 4   *Gephyrocapsa ericsonii* McIntyre and Bé, ODP Site 664D (6.32 m).

Figure 5,6   *Gephyrocapsa aperta* Kamptner,
5) DSDP Site 608 (20.12 m),   6) DSDP Site 608 (6.04 m).

Figure 7   *Gephyrocapsa sinuosa* Hay and Beaudry, DSDP Site 608 (17.14 m).

Figure 8   *Gephyrocapsa* forma P*, DSDP Site 608 (6.04 m).

Figure 9,10   *Gephyrocapsa* forma D*, DSDP Site 608 (17.14 m).

Figure 11   *Gephyrocapsa* forma H*, DSDP Site 608 (33.22 m).

Figure 12,13   *Gephyrocapsa* forma F*,
12) DSDP Site 608 (17.14 m),   13) DSDP Site 608 (33.22 m).

Figure 14   *Gephyrocapsa* forma Q*, ODP Site 659A (40.31 m).

Figure 15   *Gephyrocapsa rota* Samtleben
DSDP Site 366A (8.19 m), x 95000 (provided by C. Samtleben).

Figure 16,17   *Gephyrocapsa oceanica* Kamptner, ODP Site 664D (6.32 m).

Except for figure 15, all figures x 12000

(*Note: *Gephyrocapsa* formas D, H, F, P, Q, and V are new species or form-groups
recognized by Samtleben and Baumann (pers. commun.) and
named only in letters at the present time).

1 2 3

1 μm

4 5 6 7

8 9 10 11

12 13 14 15

1 μm 1 μm

16 17

Plate 2

Figure 1.2   *Gephyrocapsa* forma V*, DSDP Site 608 (40.33 m).

Figure 3   *Umbellosphaera* spp., DSDP Site 608 (0.03 m).

Figure 4,5   *Gephyrocapsa muellerae* Bréhéret, DSDP Site 608 (0.03 m).

Figure 6,11   *Gephyrocapsa caribbeanica* Boudreaux and Hay, DSDP Site 608 (6.04 m).

Figure 7,10   *Gephyrocapsa margereli* Bréhéret, DSDP Site 608 (13.03 m).

Figure 8,9   *Gephyrocapsa lumina* Bukry, DSDP Site 608 (33.22 m).
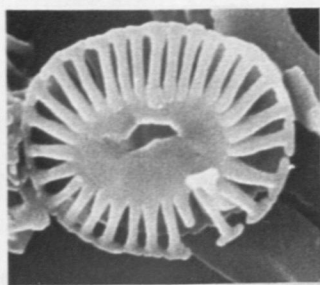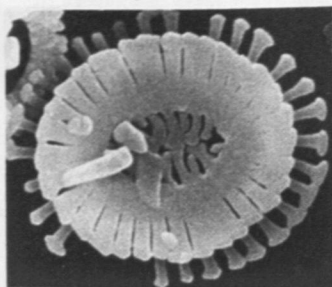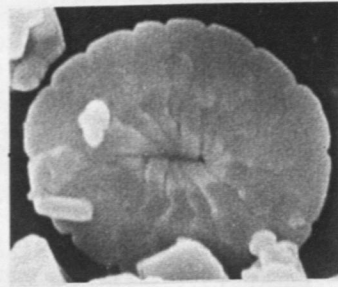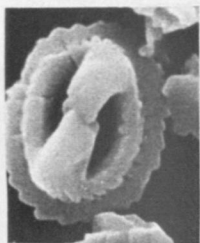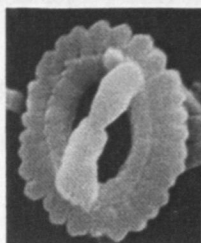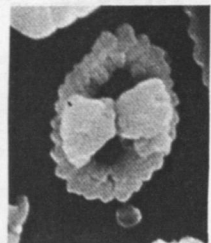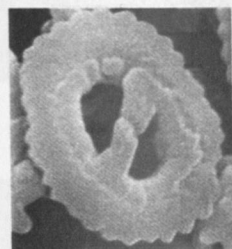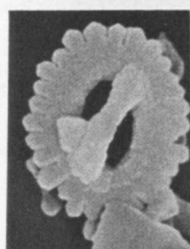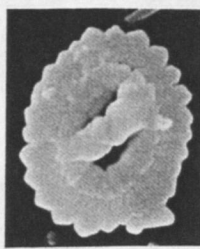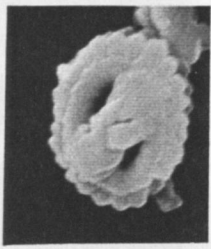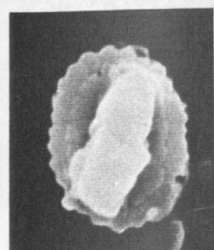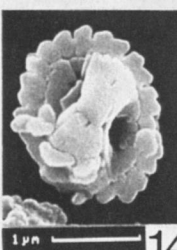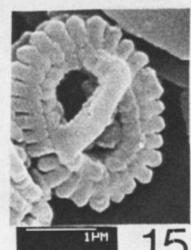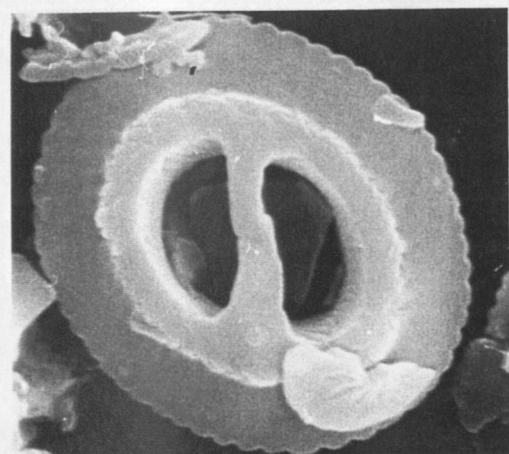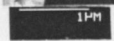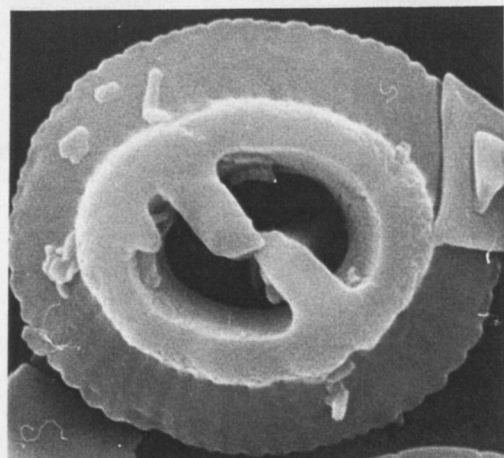
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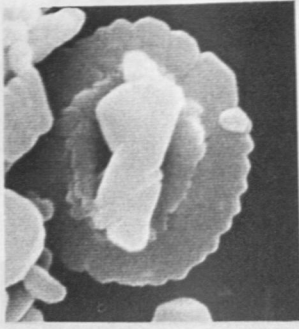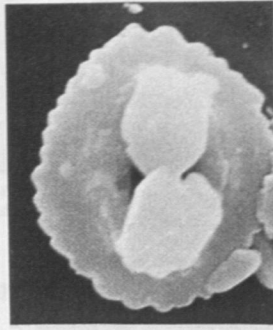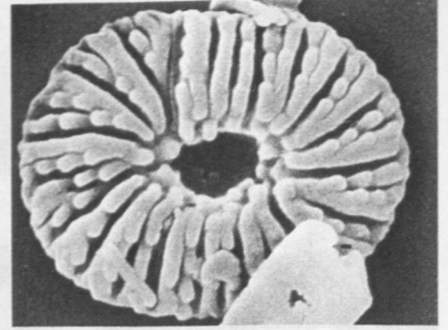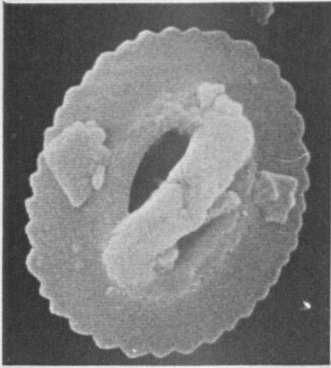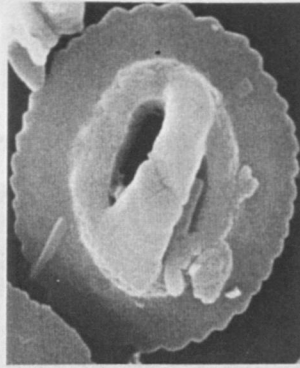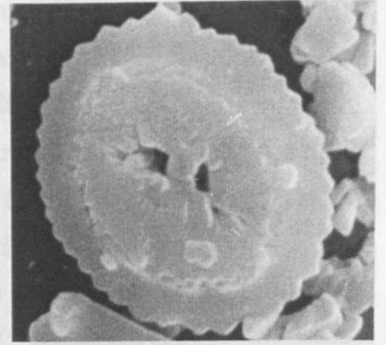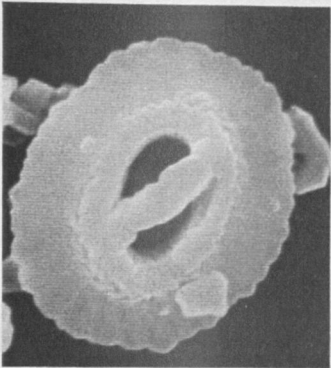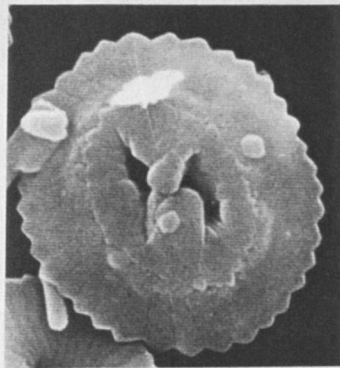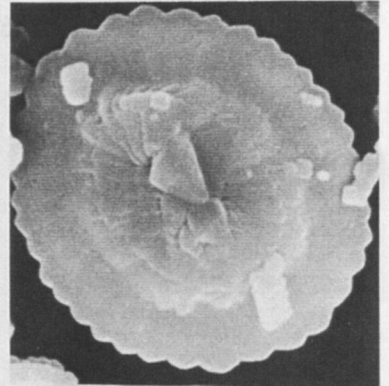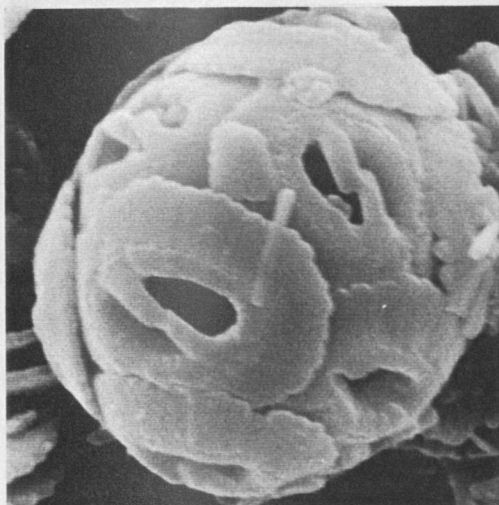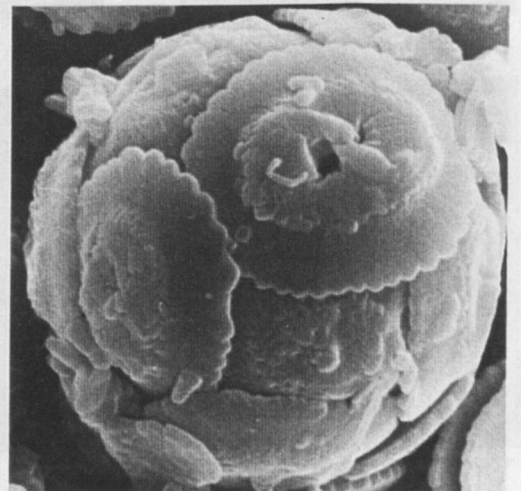
PLATE 2

Plate 3

Figure 1,2   *Reticulofenestra minuta* Roth,
1) DSDP Site 608 (100.92 m),   2) ODP Site 659A (151.21 m).

Figure 3-5   *Reticulofenestra productella* (Bukry) Gallagher, with variations in central areas,
3) DSDP Site 608 (40.33 m),   4 - 5) DSDP Site 608 (100.92 m).

Figure 6   *Reticulofenestra productella* (Bukry) Gallagher (left),
Reticulofenestra minutula (Gartner) Haq and Berggren (right),
DSDP Site 608 (20.12 m).

Figure 7-12   *Pseudoemiliania lacunosa* (Kamptner) Gartner, with variations in size of
coccoliths and of central pores, in form of central tubes and in number of slits
on the distal shields.
7) DSDP Site 608 (33.22 m),   8) DSDP Site 608 (70.12 m),
9 - 10) DSDP Site 608 (17.14 m).

Figure 13,14   *Reticulofenestra asanoi* Sato and Takayama, DSDP Site 608 (17.14 m).

Figure 15-17   *Reticulofenestra pseudoumbilicus* (Gartner) Gartner,
15) ODP Site 659A (119.95 m),   16, 17) ODP Site 659A (151.21 m).

All figures x 6000

PLATE 3

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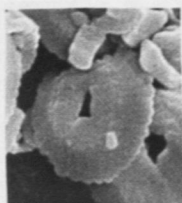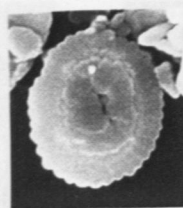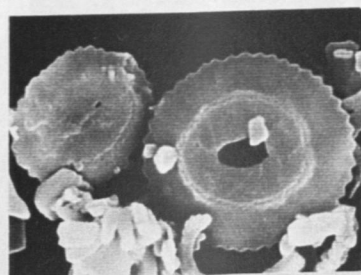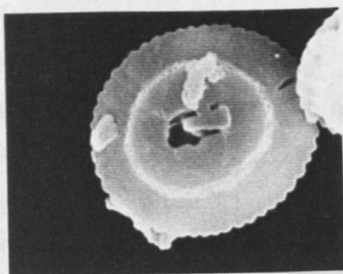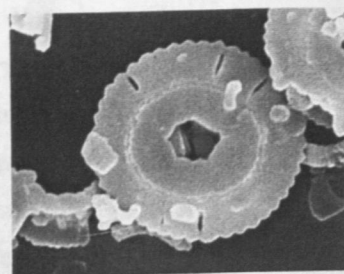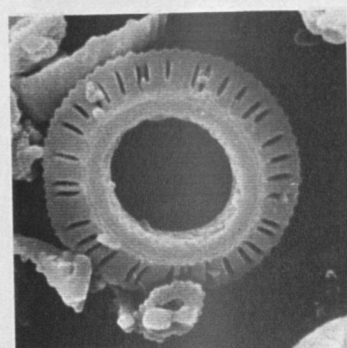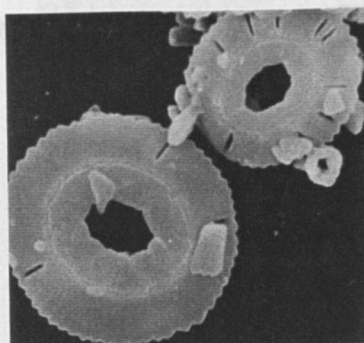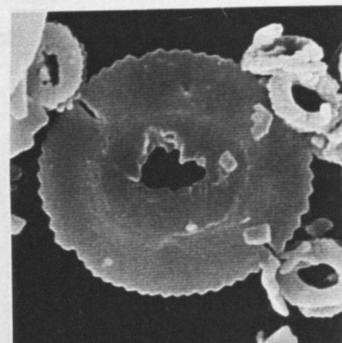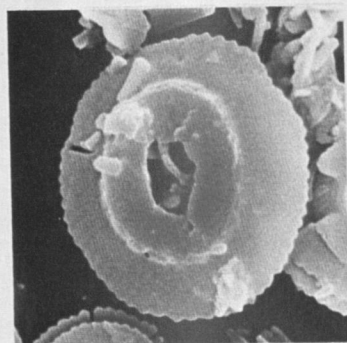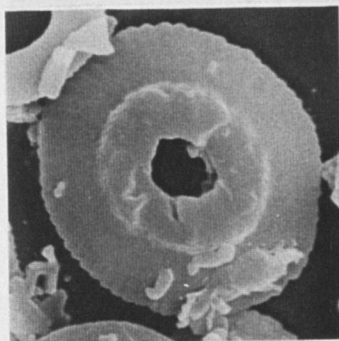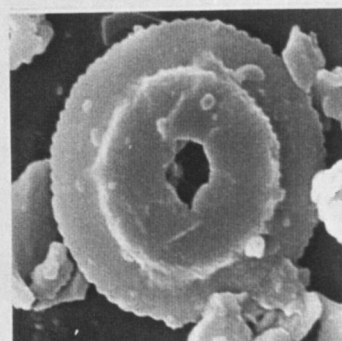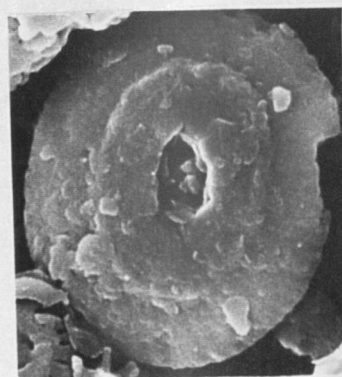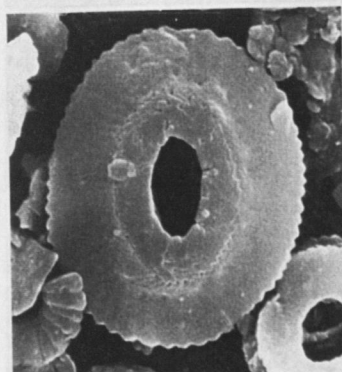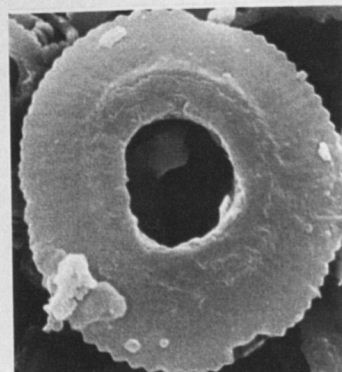
Plate 4

Figure 1,2   *H. carteri* (Wallich) Kamptner, DSDP Site 608 (13.03 m).

Figure 3   *H. sellii* Bukry and Bramlette, DSDP Site 608 (33.22 m).

Figure 4   *Rhabdosphaera claviger* Murray and Blackman, DSDP Site 608 (17.14 m).

Figure 5,6   *Reticulofenestra perplexa* (Burns) Wise, ODP Site 659A (151.21 m).

Figure 7,8   *Pseudoemiliania lacunosa* (Kamptner) Gartner,

    7) DSDP Site 608 (70.12 m),   8) DSDP Site 608 (17.14 m).

Figure 9-12   *Reticulofenestra minutula* (Gartner) Haq and Berggren, with variations in size of coccoliths and of central pores and in form of central tubes,

    9) DSDP Site 608 (100.92 m),   10 - 12) DSDP Site 608 (70.12 m).

All figures x 6000

PLATE 4

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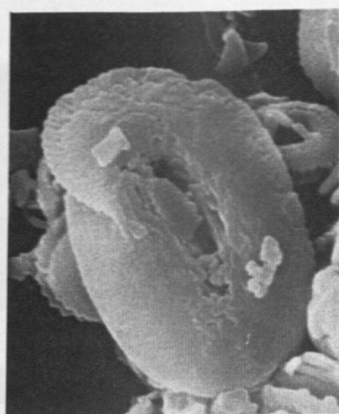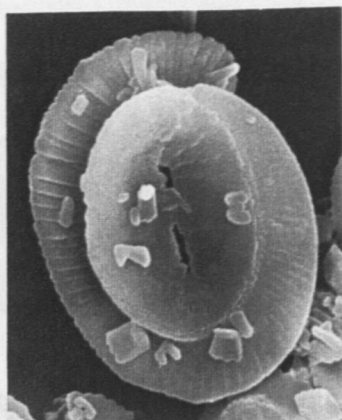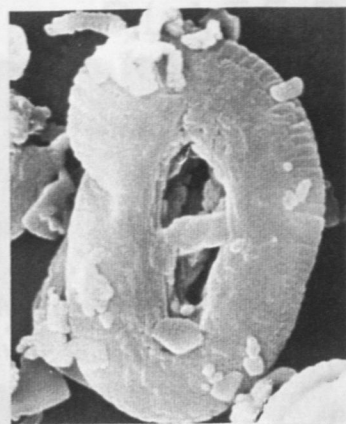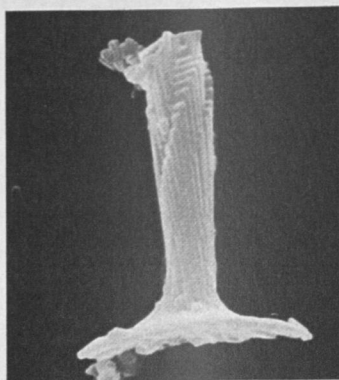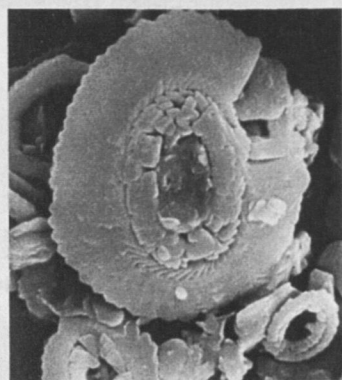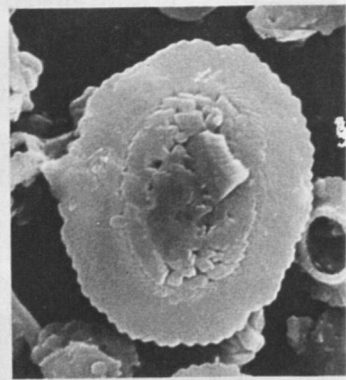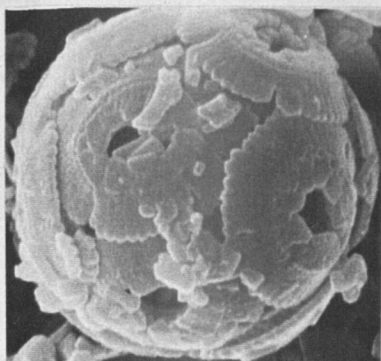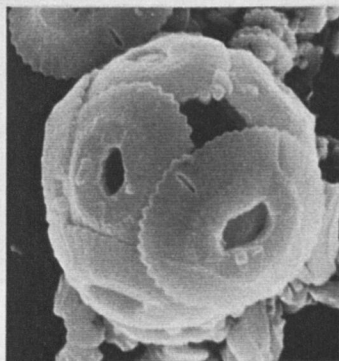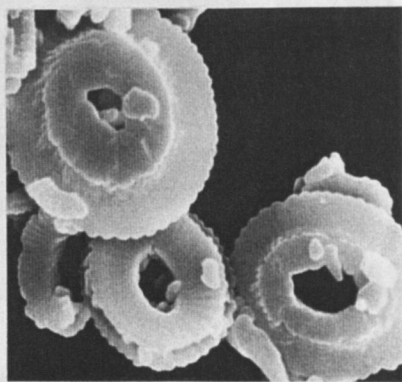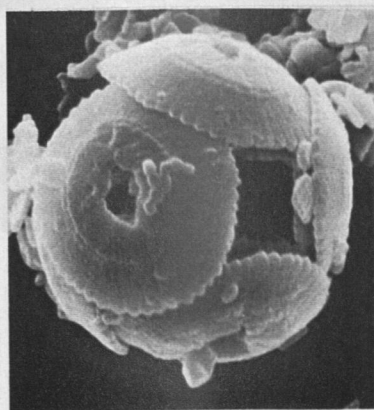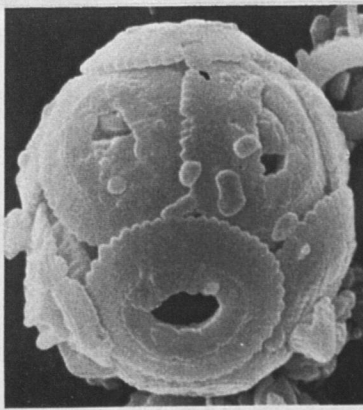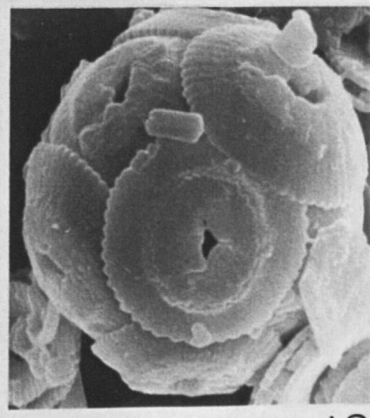
Plate 5

Figure 1   *Umbilicosphaera sibogae* (Werbe-van Bosse) Gaarder,
            DSDP Site 608 (17.14 m).

Figure 2   *Coronocyclus* spp. ODP Site 659A (100.08 m).

Figure 3,4 *Sphenolithus abies* group, ODP Site 659A (151.21 m).

Figure 5   *Calcidiscus leptoporus* (Murray and Blackman) Loeblich and Tappan,
            DSDP Site 608 (0.03 m).

Figure 6   *Syracosphaera pulchra* Lohmann, DSDP Site 608 (0.03 m).

Figure 7   *Oolithotus fragilis* (Lohmann) Martini and Müller, DSDP Site 608 (17.14 m).

Figure 8   *Calcidiscus macintyrei* (Bukry and Bramlette) Loeblich and Tappan,
            DSDP Site 608 (100.92 m).

Figure 9   *Neosphaera coccolithomorpha* Lecal-Schlauder, ODP Site 659A (151.21 m).

Figure 10   *Pontosphaera japonica* (Takayama) Nishida, DSDP Site 608 (0.03 m).

Figure 11   *Coccolithus pelagicus* (Wallich) Schiller, DSDP Site 608 (13.03 m).

All figures x 6000

PLATE 5

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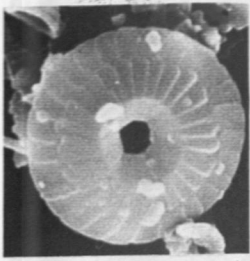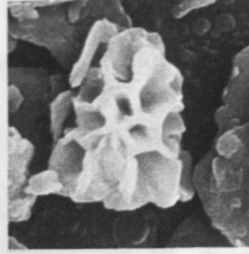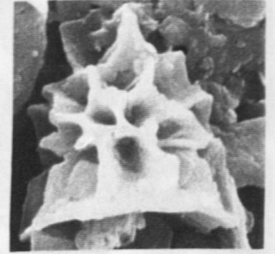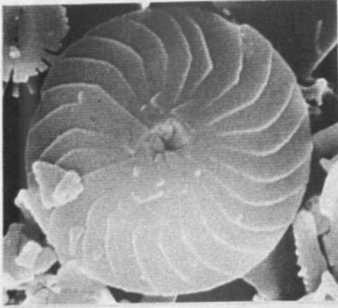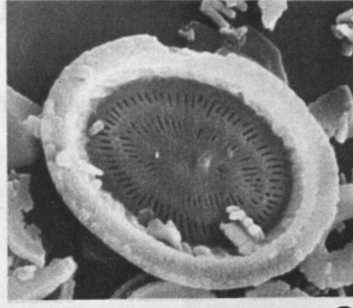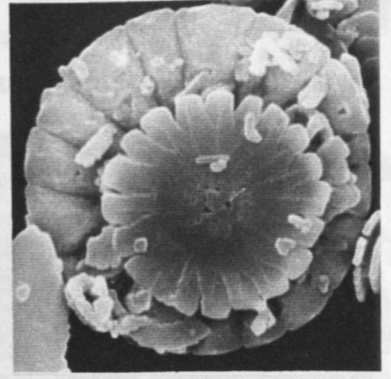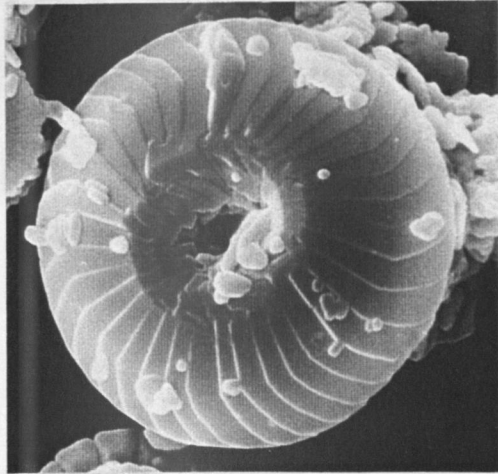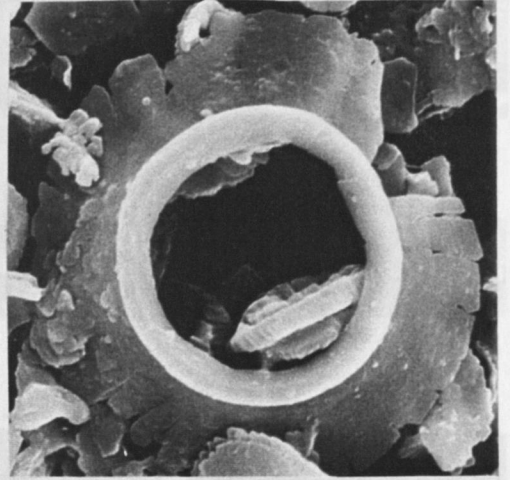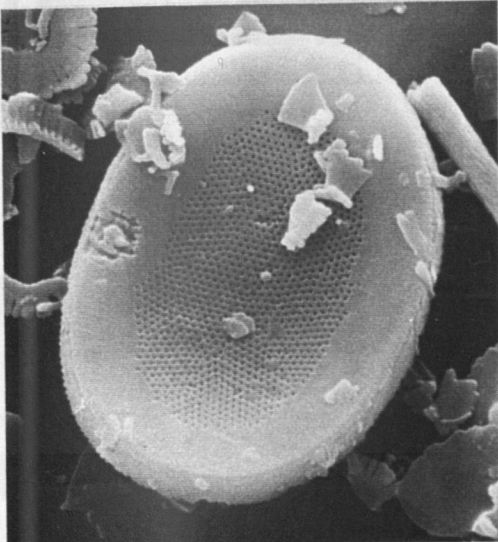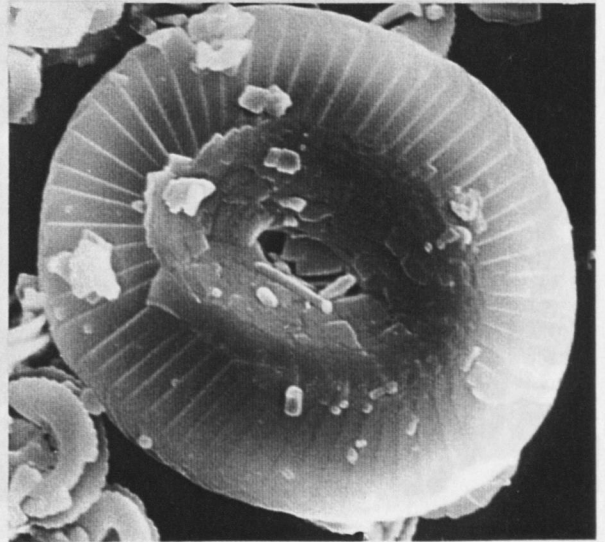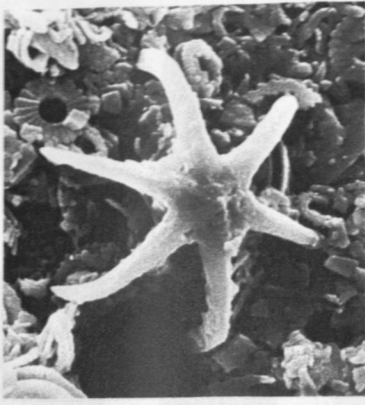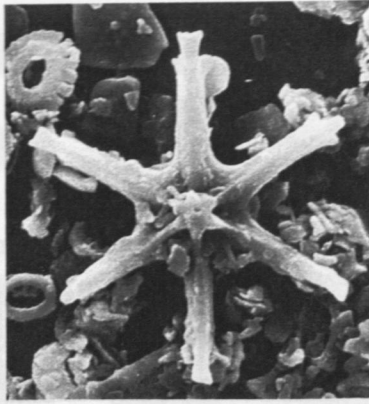
Plate 6

Figure 1   *Discoaster brouweri* (Tan) Bramlette and Riedel, ODP Site 659A (100.08 m).

Figure 2   *Discoaster surculus* Martini and Bramlette, ODP Site 659A (151.21 m).

Figure 3   *Discoaster quinqueramus* Gartner, ODP Site 659A (151.21 m).

Figure 4   *Discoaster triradiatus* morphotype, ODP Site 659A (55.31 m).

Figure 5   *Discoaster pentaradiatus* (Tan) Bramlette and Riedel, ODP Site 659A (151.21 m).

Figure 6   *Discoaster tamalis* morphotype, ODP Site 659A (100.08 m).

Figure 7   *Discoaster asymmetricus* morphotype, ODP Site 659A (100.08 m).

Figure 8   *Discoaster variabilis* group, ODP Site 659A (151.21 m).
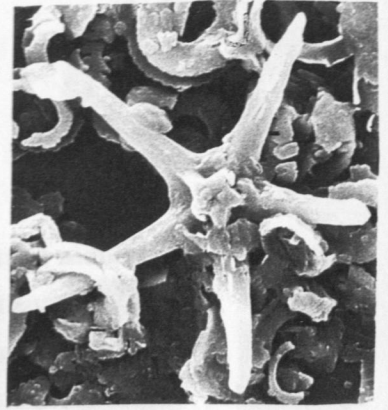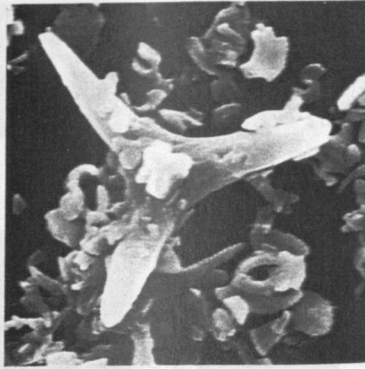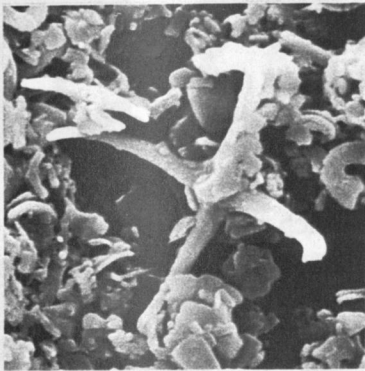
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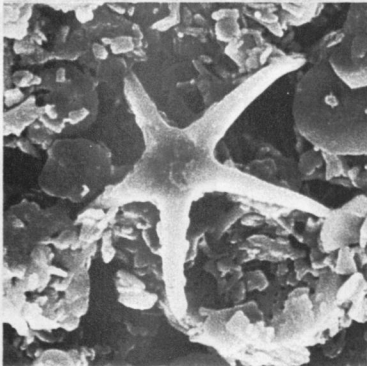PLATE 6
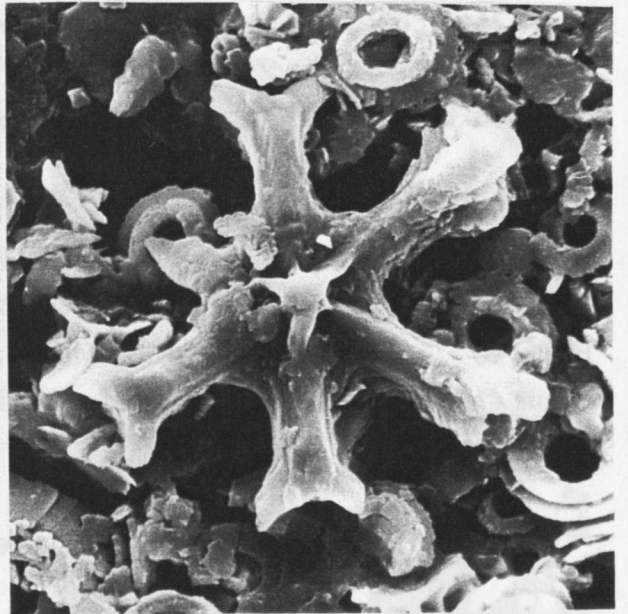

3 μm

Plate 7

Figure 1   *Emiliania huxleyi* (Lohmann) Hay and Mohler, ODP Site 659A (4.01 m).

Figure 2   *Gephyrocapsa ericsonii* McIntyre and Bé, ODP Site 659A (4.01 m).

Figure 3   *Gephyrocapsa muellerae* Bréhéret, ODP Site 659A (4.01 m).

Figure 4,5   *Gephyrocapsa caribbeanica* Boudreaux and Hay, DSDP Site 608 (8.02 m).

Figure 6,7   *Gephyrocapsa lumina* Bukry, DSDP Site 608 (28.22 m).

Figure 8,9   *Gephyrocapsa oceanica* Kamptner, ODP Site 659A (4.01 m).

Figure 10,11   *Reticulofenestra productella* (Bukry) Gallagher,
                 10) ODP Site 659A (154.06 m),   11) DSDP Site 608 (152.52 m).

Figure 12,13   *Reticulofenestra minuta* Roth, ODP Site 659A (55.31 m).

Figure 14-16   *Reticulofenestra minutula* (Gartner) Haq and Berggren,
                 14) DSDP Site 608 (42.32 m),   15 - 16) DSDP Site 608 (42.32 m).

Figure 17-21   *Pseudoemiliania lacunosa* (Kamptner) Gartner,
                 17) DSDP Site 608 (42.32 m),   18 - 21) DSDP Site 608 (20.12 m).

Figure 22-24   *Reticulofenestra asanoi* Sato and Takayama, DSDP Site 608 (20.12 m).

Figure 25-28   *Reticulofenestra pseudoumbilicus* (Gartner) Gartner,
                 25) ODP Site 659A (154.06 m),   26 - 28) DSDP Site 608 (152.52 m).

Figure 29   *Reticulofenestra perplexa* (Burns) Wise, DSDP Site 608 (152.52 m).

Figure 30-31   *Sphenolithus abies* group,
                 30) ODP Site 659A (154.06 m),   31) DSDP Site 608 (152.52 m).

Figure 32   *Umbilicosphaera sibogae* (Werbe-van Bosse) Gaarder, ODP Site 659A (4.01m).

Figure 33   *Syracosphaera pulchra* Lohmann, ODP Site 659A (4.01 m).

Figure 34   *Calcidiscus macintyrei* (Bukry and Bramlette) Loeblich and Tappan,
                 ODP Site 659A (55.31 m).

Figure 35-36   *Calcidiscus leptoporus* (Murray and Blackman) Loeblich and Tappan
                 ODP Site 659A (4.01 m).

Figure 37   *Coccolithus pelagicus* (Wallich) Schiller, DSDP Site 608 (28.22 m).

Figure 38   *Helicosphaera carteri* (Wallich) Kamptner, ODP Site 659A (4.01 m).

Figure 39   *Helicosphaera sellii* Bukry and Bramlette, ODP Site 659A (55.31 m).

Figure 40   *Rhabdosphaera claviger* Murray and Blackman, ODP Site 659A (4.01 m).

Figure 41   *Ceratolithus rugosus* Bukry and Bramlette, ODP Site 659A (100.08 m).

All figures x 2500

PLATE 7