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Late Eocene to Pleistocene Medium-Sized and Small-Sized "Reticulofenestrids"

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With 25 Figures and 3 Plates

Coccoliths
Cenozoic
Quaternary
Taxonomy
Stratigraphy
Evolution
Paleogeography

Contents

Zusammenfassung

Die „Reticulofenestriden" sind eine künstliche Gruppierung von rund-ovalen Coccolithen. Unsere Studie betrifft die kleinen und mittelgroßen Formen der *Reticulofenestra, Dictyococcites* und *Gephyrocapsa*, die wir hauptsächlich unter dem Lichtmikroskop beobachtet haben. So werden folgende Arten definiert: *minuta, minutula, doronicoides, productus, perplexus, gartneri, insignita, scrippsae, daviesi, hesslandii, pseudoumbilica, gelida*. Kriterien für eine Bestimmung sind: Größe der Coccolithen; Größe und Aspekt der Zentralfläche; Auslöschungsbilder im polarisierten Licht; eventuell Zahl der Elemente in den Platten. Diese Arten sind in verschiedenen Veröffentlichungen beschrieben worden und fanden sich in allen Ozeanen. Infolgedessen wurde es möglich, die räumliche und zeitliche Verbreitung der verschiedenen Arten hervorzuheben. Sie sind zu verschiedenen Zeiten erschienen und wieder verschwunden und zwar in Zusammenhang mit der geographischen Breite. Die Datums im strengsten Sinne sind selten zu finden. Die Verbreitung von *Reticulofenestra pseudoumbilica* und *R. minutula* ist besonders interessant: Der Einfluß der südlichen Vergletscherung im Miozän ist eindeutig. *Gephyrocapsa theyeri* n. sp. ist im pazifischen östlichen equatorialen Ozean schon seit dem Anfang des Obermiozäns zu finden. Schließlich war es möglich, gewisse entwicklungsfähige Verzweigungen hervorzuheben. Diese Entwicklung könnte einige zeitlich-räumliche Verbreitungen erklären.

Abstract

"Reticulofenestrids" are not a true taxonomical group of round-oval coccoliths. The present study concerns small- and medium-sized forms: *Reticulofenestra, Dictyococcites* and *Gephyrocapsa*, mainly studied with the aid of an optical microscope. Species were, in fact, defined on the basis of this method: *minuta, minutula, doronicoides, productus, perplexus, gartneri, insignita, scrippsae, daviesi, hesslandii, pseudoumbilica, gelida*. The measures of value are: coccolith size; the size and aspect of the central area; figure between crossed nicols; and eventually the number of shield elements. All these species were looked for in many publications corresponding to the sites distributed throughout the World Ocean. In this way, it was possible to evidence the spatial and temporal distribution of different taxa. It is apparent that they occurred and recurred at different ages, with respect to latitude. A few datums s. s. were noted. The *Reticulofenestra pseudoumbilica* and *R. minutula* distributions are worthy of particular mention; there is clear evidence of an im-

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pact of antarctic glaciation during the Miocene. *Gephyrocapsa theyeri* n. sp. was detected in the eastern equatorial Pacific from the base of the upper Miocene. Several evolutive ramifications were finally determined thereby accounting for the patial temporal distributions observed.

Résumé

Les „Reticulofenestridés" sont un groupement artificiel de coccolithes ronds-ovales. La présente étude porte sur les formes petites et moyennes des genres *Reticulofenestra, Dictyococcites* et *Gephyrocapsa* étudiés essentiellement au microscope optique. C'est ainsi que sont définies les espèces: *minuta, minutula, doronicoides, productus, perplexus, gartneri, insignita, scrippsae, daviesi, hesslandii, pseudoumbilica, gelida*. Les critères de détermination retenus sont: la taille des coccolithes; la taille et l'aspect de l'aire centrale; la figure d'extinction entre nicols croisés; éventuellement le nombre d'éléments des disques. Ces espèces ont été recherchées dans de nombreuses publications, correspondant à des sites répartis dans l'Océan Mondial. Il a ainsi été possible de mettre en évidence la distribution spatiale et temporelle des divers taxons. Il s'avère qu'ils sont apparus et ont disparu à des âges divers, en rapport avec la latitude. Rares sont les datums s. s. Les distributions de *Reticulofenestra pseudoumbilica* et *R. minutula* sont particulièrement intéressantes: l'influence de la glaciation antarctique miocène est évidente. *Gephyrocapsa theyeri* n. sp. a été trouvée dans le Pacifique équatorial oriental depuis la base du Miocène supérieur. Enfin, il a été possible de mettre en évidence certains rameaux évolutifs, l'évolution pouvant expliquer certaines distributions spatio-temporelles.

1. Introduction

The term "Reticulofenestrids" is currently used to denote a group of coccoliths that are simply built, with two oval or roughly round shields, and with or without a central structure. This morphology is characteristic when these coccoliths are observed with an optical microscope; all the details (visible only with a SEM) are erased between crossed nicols, and they have the same simple aspect of a bright lentil with a swastika. Thus, it is easy to group coccoliths with this morphology under the general term of "Reticulofenestrids". Nevertheless, although this term is widely used, it cannot be taken as a taxonomic one. There exist few nannofossil classifications; none of these uses a "Reticulofenestridae family" for example.

The genera I choose to study here are: *Reticulofenestra, Dictyococcites* and *Gephyrocapsa*. According to HAY (1977) and to TAPPAN (1980) they belong to the Gephyrocapsaceae family, while PERCH-NIELSEN (1985) put them in the Prinsiaceae family.

My purpose is not to study all the species of *Reticulofenestra, Dictyococcites* and *Gephyrocapsa*, but only those of them which were so abundant during the Tertiary and the Quaternary that they made up a constant background in most of the observed smear slides; they were present in many areas of the World Ocean, and they are easy to recognize with a light microscope.

2. Studied material

"Reticulofenestrids" are abundant in Tertiary and Quaternary samples where they compose a kind of background in most of the calcareous sediments. They are mentioned especially in studies of high latitude sediments where they are often the only nannofossils present. Several papers have been published with detailed descriptions and distributions of these forms found at northern and southern high latitudes (BACKMANN, 1980 and 1984; WISE, 1973, 1983). "Reticulofenestrids" are much less mentioned in sediments of middle and low latitudes, probably because these latitude seas were rich in "stratigraphical" nannofossils, such as *Sphenolithus, Discoaster, Helicopontosphaera,* large Reticulofenestrids. Medium and small-sized Reticulofenestrids either constitute a very small fraction of the assemblage or they are largely ignored.

On the contrary, in high latitude areas, it is impossible to make a stratigraphy based on nannofossils, because the rare nannofossils are small Reticulofenestrids which cannot be used for such a purpose, primarily because there exist not enough informations on these coccoliths. To try to obtain such informations, it is necessary to study the Reticulofenestrids in well-dated and calibrated sediments where they would be abundant and present at the same levels as nannofossil markers. Such sediments can be found in the equatorial Pacific (DSDP Leg 85).

2.1. The Central and Eastern Equatorial Pacific

Four sites were drilled in the high productivity area of the equatorial Pacific during the DSDP Leg 85. The samples span the period of time: latermost Eocene – Pleistocene. They are very rich in various microfossils, especially in diatoms (the study of which provides environmental observations: BARRON, 1985a and 1985b) and in nannofossils. Nannofossil assemblages have already been studied (PUJOS, 1985a and b) and they establish a regional stratigraphy based on preliminary observations of Reticulofenestrids.

The Reticulofenestrid assemblages of two sites are presented in detail:

❶ Site 573 can be considered as the "basic site" of the central equatorial Pacific; its sedimentation is almost always regular, with three main hiatuses or intervals with a very low sedimentary rate: at the Eocene – Oligocene boundary (38 to 35 Ma); in the earliest Miocene (24 to 21 Ma); and in the early Late Miocene (13 to 11 Ma). Several species of *Gephyrocapsa*, Reticulofenestrids and *Dictyococcites* were counted; in Figure 1 only the following coccoliths are taken into account for establishing percentages: medium and small-sized Reticulofenestrids and *R. hillae, R. umbilica, Pseudoemiliania lacunosa* and *Emiliania huxleyi*.

❷ Site 572 is the easternmost one of the DSDP Leg 85. BARRON (1985b) places this site in the "eastern equatorial Pacific area", where the environment is different from that of the central area being influenced by the Peru-Chile current. Site 572 reached the basement in early middle Miocene sediments at about 14,5 Ma. There was only one main period of low sedimentary rate: at the Middle – Late Miocene boundary (13 to 11 Ma). Nannofossil assemblages (Fig. 2) are very close to those of the upper part of Site 573, except for the extra presence of *Gephyrocapsa theyeri* (see taxonomy and stratigraphy of this new species below, in corresponding paragraphs).

All Leg 85 sites show almost the same variations in *Reticulofenestra* species during the same corresponding

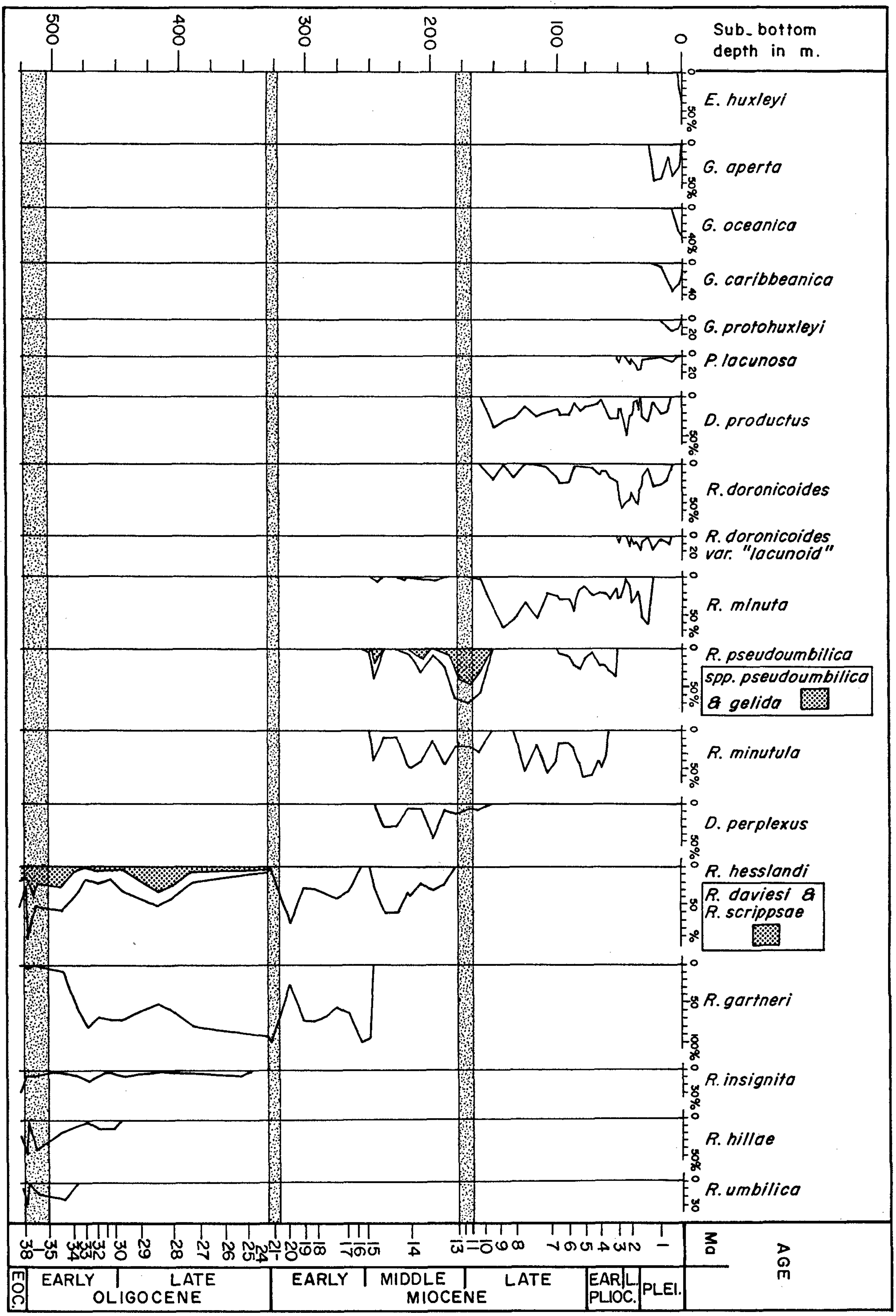

Fig. 1: Distribution of most of the Reticulofenestrids at Site 573, central equatorial Pacific (Leg 85).

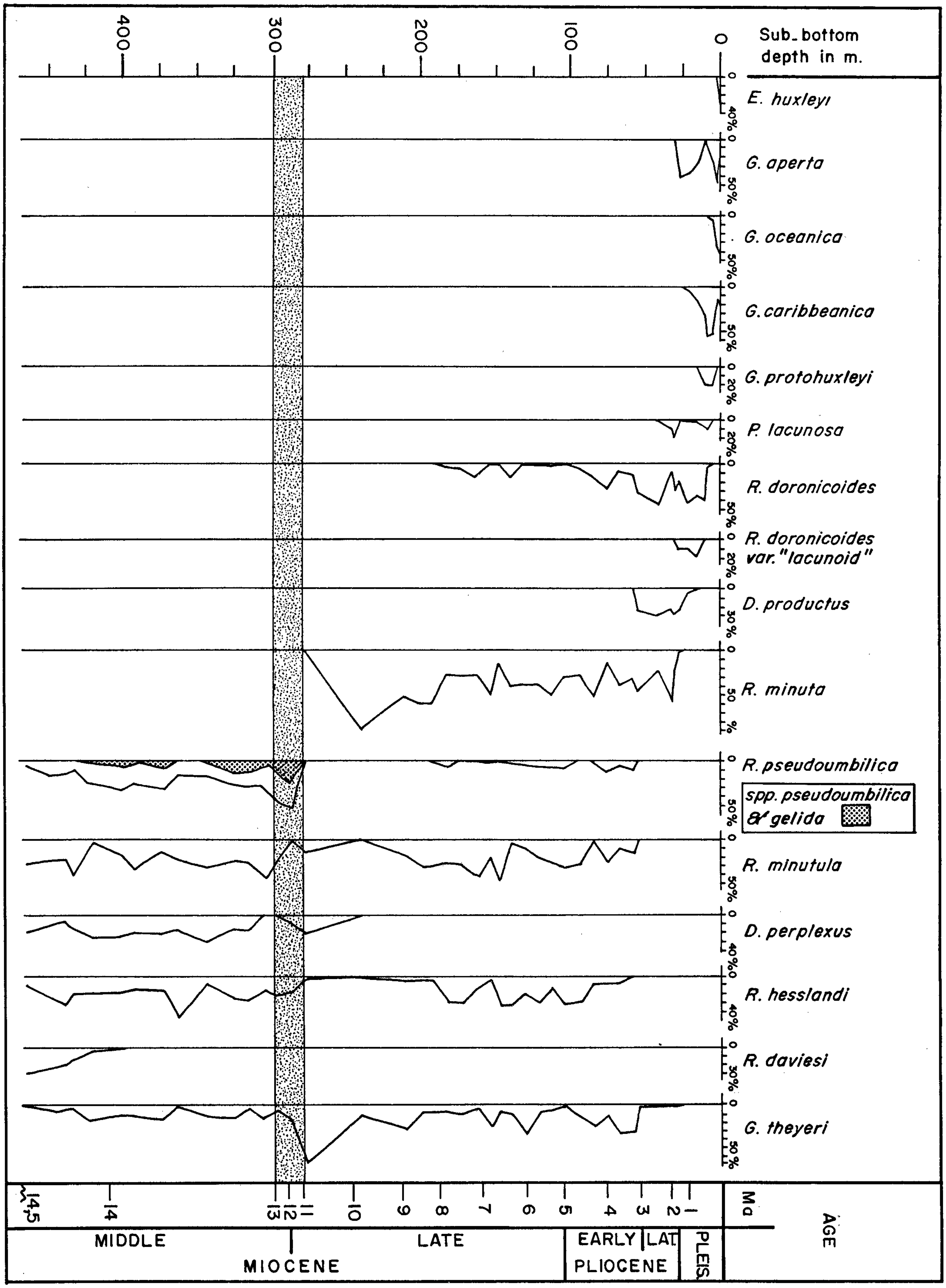

Fig. 2: Distribution of most of the Reticulofenestrids at Site 572, eastern equatorial Pacific (Leg 85).

periods: at about 15 Ma and at about 11 Ma. The former period corresponds with the beginning of the Antarctic glaciation which provided Antarctic bottom water and caused the steepening of latitudinal planktonic organism assemblages of the southern Pacific. The latter period corresponds to the intensification of the equatorial undercurrent which caused an increased upwelling in the eastern equatorial Pacific and the arrival of colder water in the area of Site 572 (BARRON, 1985b). These complex paleoenvironments have to be taken into account to explain the distribution of some species.

2.2. The Subantarctic Area

Several Kullenberg cores were drilled in the southern Indian Ocean, near the Antarctic convergence during a cruise named APSARA 2. Located in high latitudes, it provided Reticulofenestrid assemblages which are almost the only nannofossils present. One core is presented here: 84544 (Fig. 3). It penetrated Middle Miocene, Middle and Late Pliocene and Pleistocene sediments. The stratigraphy was established in using planktonic Foraminifera, radiolarians and paleomagnetic measurements (LABRACHERIE et al., in prep.).

Nannofossil distributions are presented as for DSDP Leg 85: percentages within all Reticulofenestrids used in the present study. As usual in southern high latitudes, Pleistocene and most of the Miocene sediments were rich in coccoliths. Nannofossils are notably absent in Pliocene sediments due to the presence of cold waters. The long gap (16 to 4.2 Ma) is due to the Antarctic ice-cap.

2.3. Bibliographic Data

DSDP Leg 85 and APSARA samples permitted the study of nannofossil assemblages representing different paleoenvironments. Between these two extreme latitudes, I had no material available. To try to correlate

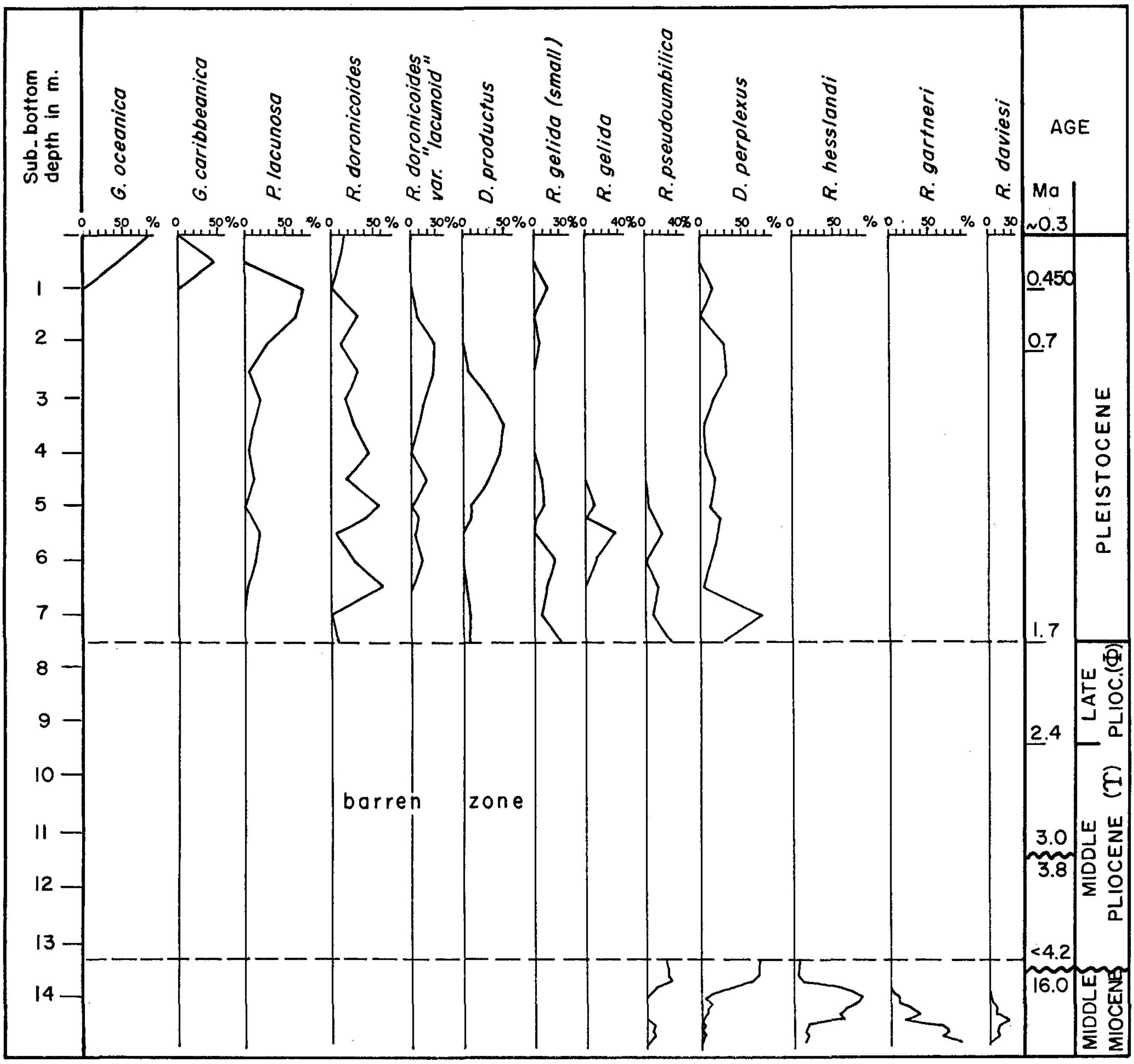

Fig. 3: Distribution of the Reticulofenestrids in Core 84544, southern Indian Ocean (APSARA 2).

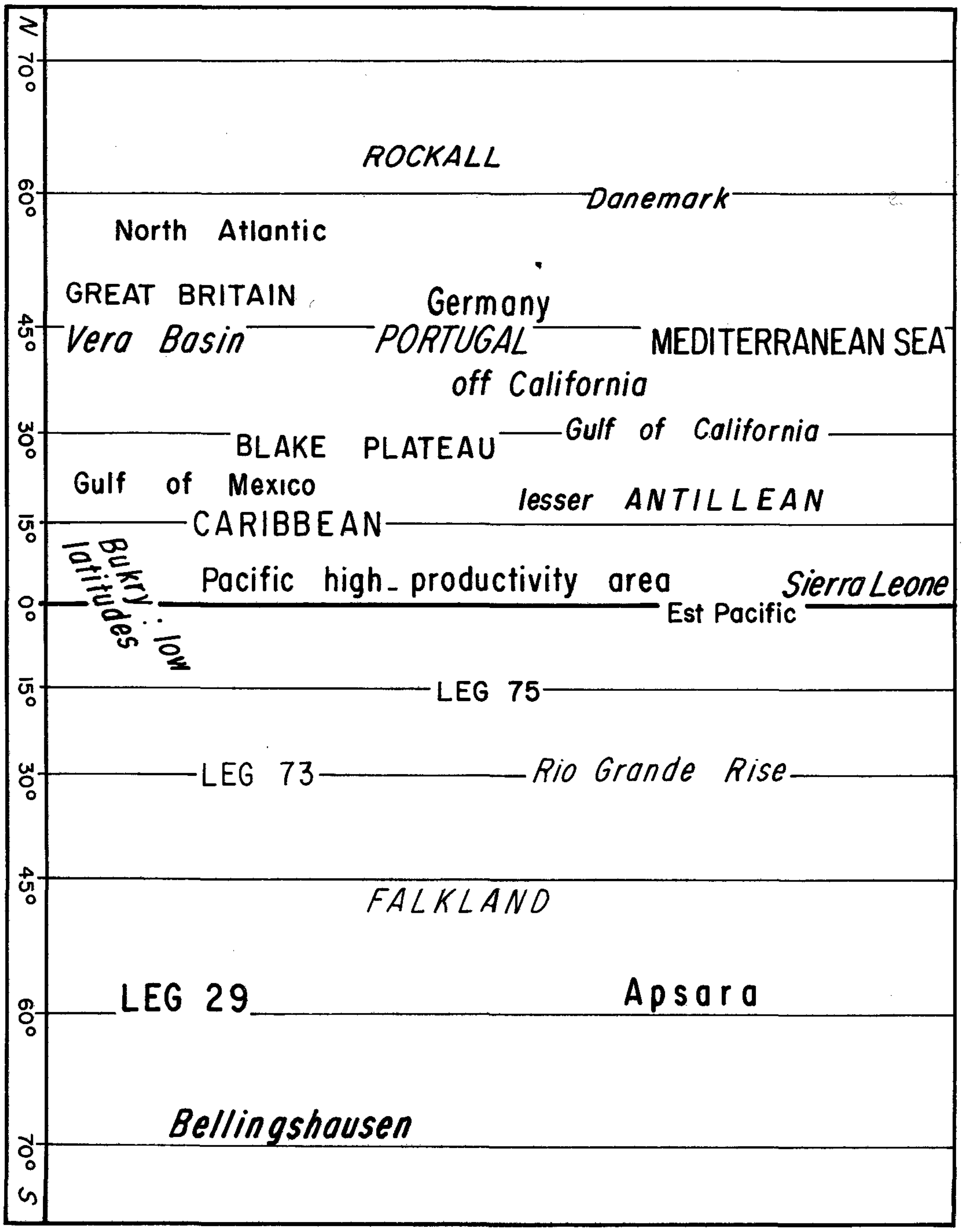

Fig. 4: Schematized latitudinal location of the main areas used in the present study.

my results, I had to use the numerous published papers on Tertiary and Quaternary nannofossils. This huge bibliographic work would provide the Reticulofenestrid distribution at various latitudes, in all the oceans because Reticulofenestrids have been encountered in all.

This bibliographic study provided detailed counts of nannofossil assemblages, mostly in DSDP specialized papers, and some large and often general synthesis (e. g. various papers from HAQ and others, which were very useful in the interpretation of several paleoenvironments).

Some remarks have to be made:

1) Although these papers are very numerous, the areas studied are not so; there are several references for the northern hemisphere (especially between 15 and 45°N) and for some parts of the Southern hemisphere (various DSDP Legs in the Falkland Sector and near Bellingshausen) while some latitudes are almost completely neglected (Fig. 4).
2) Few authors count Reticulofenestrids in detail, especially the smallest ones. Most of them use only one or two species, or they group them under the term of *Reticulofenestra* sp. or small *Reticulofenestra*. These studies can be used with difficulty, and only if authors give pictures of the corresponding coccoliths. An example of this problem is given in Figure 5 where I transferred the counts made by BACKMAN (1980) in the Rockall area. His work is one of the best published distributions, because the author gave good and numerous photos (SEM and optical microscope) as well as distribution tables. BACKMAN has to be considered as a pioneer for the study

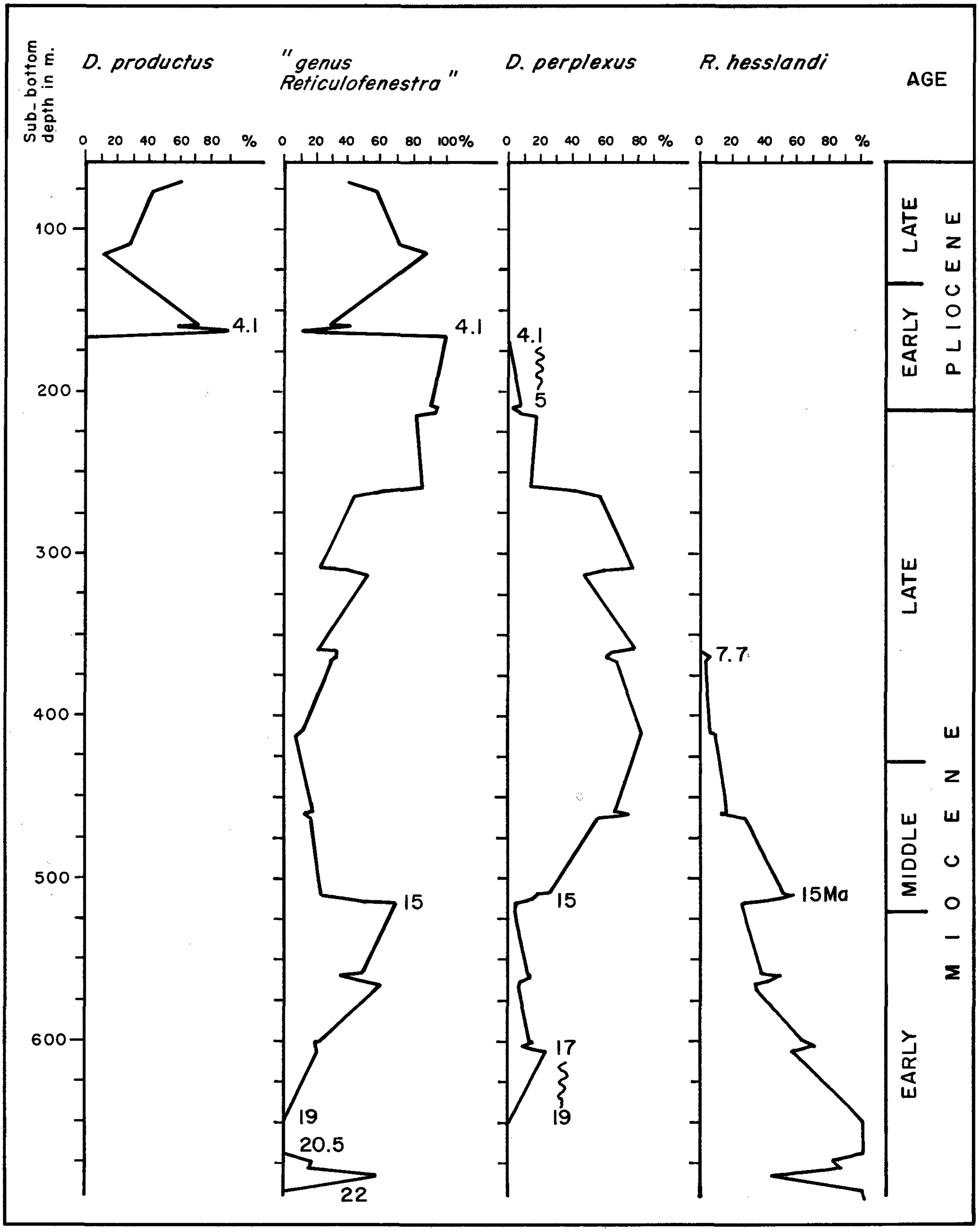

Fig. 5: Distribution of the Reticulofenestrids at Site 116, Rockall area (after BACKMAN, 1980).

of Reticulofenestrids. Nevertheless, Figure 5 shows that this abundant information is not precise because BACKMAN often grouped several taxa together in the figure summarizing all information used.

3) I have drawn on Figures 17 to 25 the chronological distributions of Reticulofenestrids according to several published works. Dates of LO and HO (= lowest and highest occurrence) are those given by the authors; either they use a nannofossil zonation (from

MARTINI or from BUKRY or their own local one) or they give dates or more rarely they correlate with magnetostratigraphy. Finally, some of them remain vague.

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In using my own results, as well as bibliographic information, I tried to establish a taxonomy and a spatial and latitudinal distribution of the studied group for the Late Eocene – Pleistocene period.

3. Taxonomy

"Medium-sized and small-sized Reticulofenestrids" are characterized by:

- their size which is medium to small (= length <10–12 µm);
- their aspect when observed with an optical microscope. Between crossed nicols, they give a very simple image corresponding to that of two oval or broadly round shields with a swastika extinction and with or without an open central area, sometimes closed with a grid.

A taxonomy restricted to such criteria is not very rigorous and does not correspond to the very detailed taxonomy usually reached with SEM observations. But one of my objectives is to try to establish a simple technique based on optical microscope observations. Indeed, it is necessary to establish a taxonomy in order to name the taxa used; but details allowing precise species and subspecies determinations are impossible to distinguish with an optical microscope; so they will be neglected to further the speed and the possible usefulness of the method.

The taxonomy I present below is established to facilitate the understanding of my work. Sometimes, I was led to place different taxa under the same specific name but all the coccoliths I put within the same "species" have the same appearance when observed between crossed nicols and the same size range.

Species are grouped within three genera, the distinction of which is based on observations between crossed nicols:

○ simple two-shield structure
  - with an apparent open central area: *Reticulofenestra*
  - with an apparent closed central area: *Dictyococcites*

○ presence of a cross-bar: *Gephyrocapsa*.

With such simple criteria the distinction between *Reticulofenestra* and *Dictyococcites* is not always easy: *Dictyococcites* with a dissolved central area can be mistaken as *Reticulofenestra*. LOEBLICH (1980) regards *Dictyococcites* as a synonym of *Reticulofenestra*. Nevertheless, I kept the two genera because for some species (*productus* and *perplexus*) coccoliths are always almost completely closed, even in dissolved samples and they are undoubtedly *Dictyococcites* s.s.

For each species I have drawn on the same figure and at the same magnification, the best published SEM pictures or drawings of the coccoliths I put under the same name. I have also drawn for each species a schematized characteristic image between crossed nicols. Finally, I have made a biometric graph of the species with my own measured specimens; I have also borrowed some published forms.

In the descriptions I have often grouped some species in the same paragraph because their morphologies look almost alike. Except for these groups, I arranged the species from the smallest to the largest; the *Gephyrocapsa* is apart. I have reduced the morphological remarks to a minimum because most of the characteristics are evident on the corresponding figures.

***Reticulofenestra minuta* ROTH 1970**

(Fig. 6; Pl. 1, Figs. 1–7)

= (?) *Prinsius minutus* HAQ 1971
= *Dictyococcites minutus* (HAQ) HAQ, LOHMANN & WISE, 1976

The species *minuta* and *minutus* were described almost at the same time, both from Oligocene sediments. Their morphologies and their sizes are very close, reason for which they are usually considered as synonyms.

It is certain that they look like each other, even with a scanning microscope. ROTH's specimens are nonetheless always clearly smaller than HAQ's types. My own specimens link these two stocks, and it is evident that *minuta-minutus* specimens come from a single population.

I add two other taxa to this species because they cannot be clearly distinguished from the *minuta-minutus* group, especially with an optical microscope:

- *Coccolithus taganus* FONSECA, 1976 resembles very much *R. minuta*, even if the central area is less open and its size very close to that of ROTH's type.
- "small *Dictyococcites* and *Reticulofenestra*" from the Pacific Late Miocene are taken in account by LOHMANN & CARLSON (1981). They also seem to be very close to ROTH's type.

Finally, *Gephyrocapsa* sp. 1 by SAMTLEBEN (1980) could be placed in the same taxonomic group by taking into consideration only the size of the coccoliths. The presence, however, of an evident cross-bar makes it a true *Gephyrocapsa* (see below corresponding paragraph).

***Reticulofenestra minutula* (GARTNER) HAQ & BERGGREN, 1978**

(Fig. 7)

R. minutula and *R. haqii* are grouped within this specific determination. The two taxa are often studied grouped together (BACKMAN, 1980; PUJOS, 1985b) or placed within the "small *Reticulofenestra*" (various studies published by HAQ et al.). I consider that as it was already done for *R. pseudoumbilica* s. l. (see below) these two taxa have to be taken as two ecotypes of the same species (for the relation with environment: see below the corresponding paragraph). Thus, I keep the specific term of *minutula* which is the older one and I transform the two species into two subspecies:

○ *Reticulofenestra minutula* (GARTNER) HAQ & BERGGREN 1978, ssp. *minutula* (GARTNER) HAQ & BERGGREN 1978. (pl. 1, fig. 8–11 & 12a)
  = *Coccolithus minutulus* GARTNER 1967
  = *Reticulofenestra minutula* (GARTNER) HAQ & BERGGREN 1978
  = *Reticulofenestra minutula*, in PUJOS 1985b

○ *Reticulofenestra minutula* (GARTNER) HAQ & BERGGREN 1978, ssp. *haqii* (BACKMAN) PUJOS, n. stat. (pl. 1, fig. 12b & 18–21)

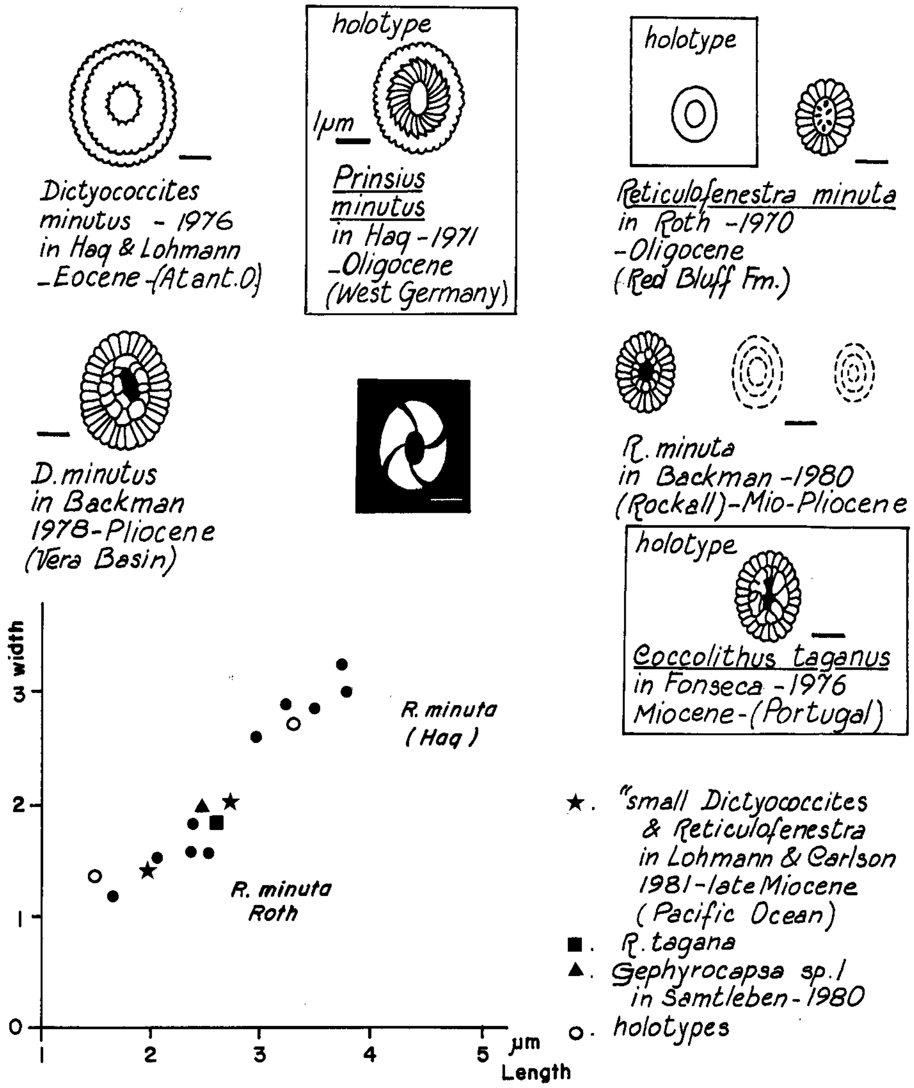


Fig. 6: *Reticulofenestra minuta*.

= *Reticulofenestra haqii* BACKMAN 1978
= *Reticulofenestra haqii* BACKMAN 1980
= *Reticulofenestra haqii* in PUJOS 1985b

R. minutula s. l. is a small form (length between 3,5 and 4 µm) with a very simple structure. The central opening is more or less open: almost closed for the ssp. *haqii*; widely open for the ssp. *minutula*. Such a differentiation was clearly demonstrated by BACKMAN (1980) in his biometrical study of the group; but he kept the two species. BACKMAN differentiated *R. minutula, R. haqii* and *R. minuta* according to their biometrical characteristics. His results can be summarized:

Total length	<3 µm	>3 µm	
Surface of the central area		<4.5 μm^2	>4.5 μm^2
	R. minuta	*R. minutula minutula*	*R. minutula haqii*

Some authors (ROTH, 1973; BACKMAN, 1980) take *R. doronicoides* as a synonym of *R. minutula* s. s., but the two taxa can be easily distinguished even with a light microscope: *R. doronicoides* is larger, rounder than *R. minutula*, and its central area is often closed. Their stratigraphic ranges are also different.

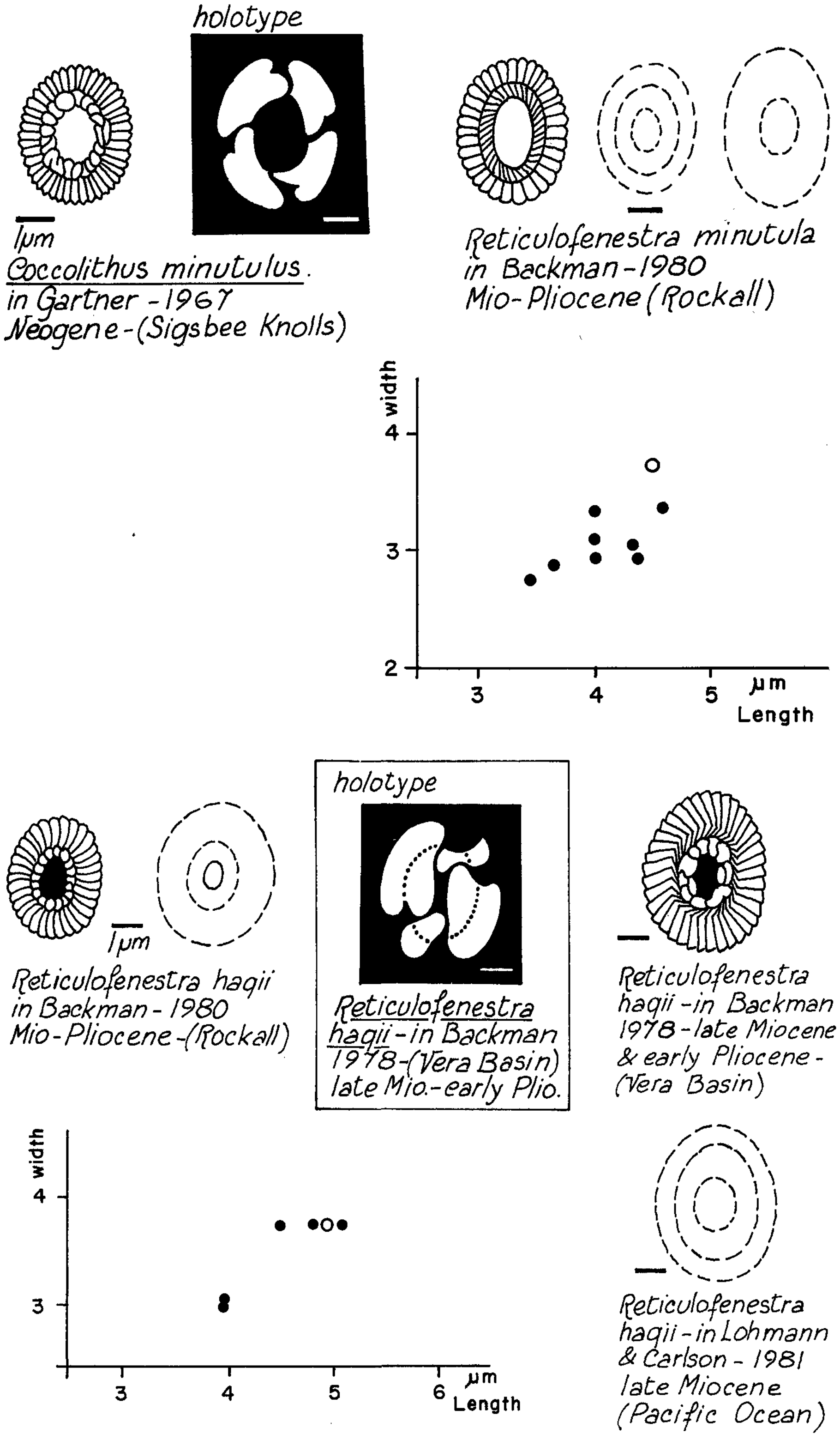
Reticulofenestra doronicoides **(BLACK & BARNES) PUJOS 1985**

(Fig. 8; Pl. 1, Figs. 13–17)

= *Coccolithus doronicoides* BLACK & BARNES 1961
= *Ellipsoplacolithus doronicoides* (BLACK & BARNES) BLACK 1971
= *Coccolithus doronicoides* BLACK & BARNES, in SACHS & SKINNER 1973
= *Crenalithus doronicoides* (BLACK & BARNES) ROTH 1973
= *Cyclicargolithus doronicoides* (BLACK & BARNES) WISE 1973
= *Reticulofenestra doronicoides* (BLACK & BARNES) PUJOS 1985b.

LOEBLICH & TAPPAN (1966) established that *Ellipsoplacolithus* was an illegitimate genus and BACKMAN (1980) stated that *Crenalithus* was a junior synonym of *Reticulofenestra*. Furthermore, the original diagnosis and pictures from BLACK & BARNES (1961) are not satisfying. BLACK himself (1971) thought that there were several species within the *doronicoides* concept. MC INTYRE and BÉ (1967) followed BLACK in giving three different pictures for the same species. After that, it is evident that the *doronicoides* concept is not simple!

For these reasons BACKMAN (1980) wrote that the species *doronicoides* was invalid and was synonym of *R. minutula* (see above); furthermore, he considered that *doronicoides* could not be distinguished from *Pseudoemiliania lacunosa*.



Coccolithus minutulus. in Gartner - 1967 Neogene - (Sigsbee Knolls)

Reticulofenestra minutula in Backman - 1980 Mio-Pliocene (Rockall)

Reticulofenestra hagii in Backman - 1980 Mio-Pliocene - (Rockall)

Reticulofenestra hagii - in Backman 1978 - (Vera Basin) late Mio. - early Plio.

Reticulofenestra hagii - in Backman 1978 - late Miocene & early Pliocene - (Vera Basin)

Reticulofenestra hagii - in Lohmann & Carlson - 1981 late Miocene (Pacific Ocean)

Fig. 7: *Reticulofenestra minutula minutula* and *Reticulofenestra minutula haqii*.

I do not agree with BACKMAN's position and I prefer to follow that of MC INTYRE & BÉ (1967) who suggested grouping the different types within the singular name of *doronicoides*. For my own, I already suggested (PUJOS, 1985a) that some variants could be distinguished in the *doronicoides* group, in Quaternary sediments; in such samples they have a stratigraphic usefulness, because they do not disappear at the same stratigraphic position. In Tertiary sediments, I used only the single specific name (PUJOS, 1985b).

The "*Dictyococcites productus-perplexus*" Group

● *Dictyococcites productus* (KAMPTNER) BACKMAN 1980

(Fig. 9; Pl. 1, Figs. 22–25)

= *Ellipsoplacolithus productus* KAMPTNER 1963
= *Coccolithus productus* (KAMPTNER) SACHS & SKINNER 1973
= *Coccolithus productellus* BUKRY 1975
= *Coccolithus* sp. HAQ & LIPPS 1971

D. productus has a nearly closed central area, with a slit along the long axis of the coccolith. The proximal

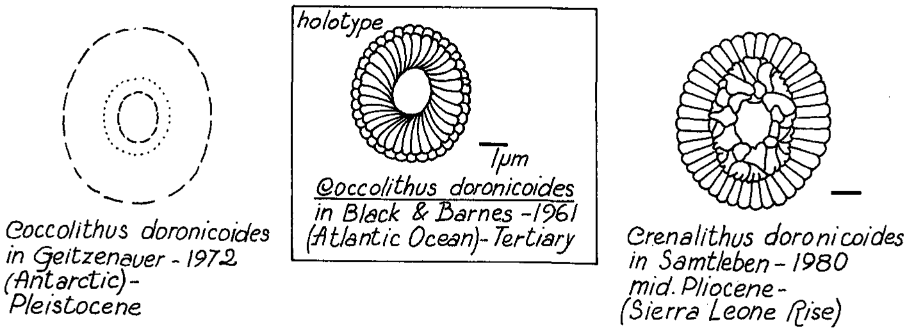
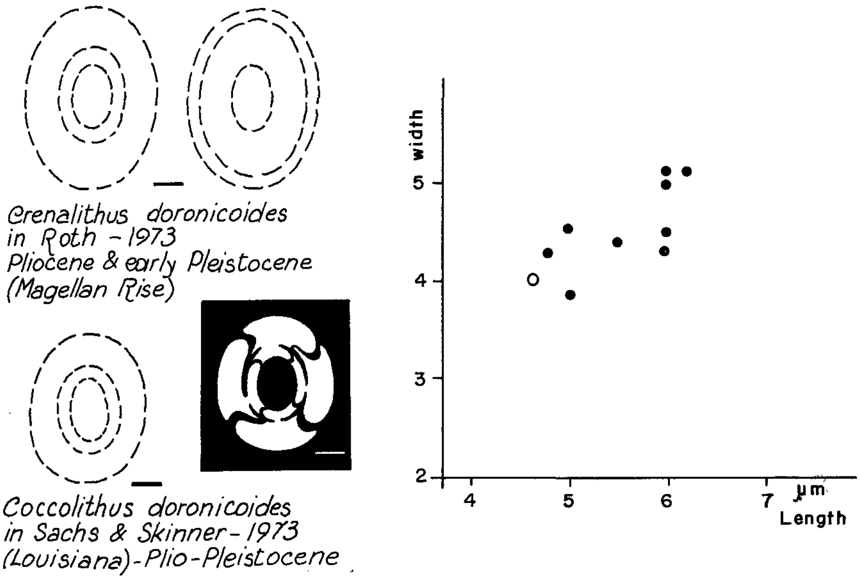


Fig. 8: *Reticulofenestra doronicoides.*



shield is composed of irregular elements, which sometimes seem to be formed by a calcite filling (i. e. on some pictures by BACKMAN, 1980). The figure between crossed nicols is very simple, a simple swastika cross.

This coccolith is always smaller than 4,5 µm in length. It is the smallest *Dictyococcites* I found. Its generic designation is not easy because, as I have written already (PUJOS, 1985a), a kind of crossbar appears in the central area of some *"Dictyococcites" productus* in the Early Pleistocene; the present study is limited to "non cross-barred" forms; *Gephyrocapsa* spp. will be discussed below.

● *Dictyococcites perplexus* BURNS 1975

(Fig. 10; Pl. 1, Figs. 26–29)

= *Dictyococcites perplexa* BURNS 1975
= *Dictyococcites antarcticus* HAQ 1976
= *Reticulofenestra perplexa* (BURNS) WISE 1983

Holotypes of *D. antarctica* are larger (length = 7 to 8 µm) than those of *"R." perplexa* (length = 4,5 to 6 µm) but this size difference does not seem to be significant for separating the two species. In some of my samples I found *D. perplexus* with a wide size variation.

The morphology of *D. perplexus* is very close to that of *D. productus*. The two shields of *D. perplexus* are more visible between crossed nicols because their differences are pronounced:

- The proximal shield is composed of numerous very irregular elements, which can hide the central slit.
- The distal shield is made of very numerous regular elements (60 to 80 elements).

HAQ (1976) separated *D. perplexa* from *D. scrippsae* (which is longer = 6 to 12 µm) and from *D. hesslandii* (which has less elements in its distal shield, and which has a subcircular central hole).

BACKMAN (1980) established that the morphologies of *D. perplexus* and *D. antarcticus* are very similar. He differentiated them by their size and their stratigraphic range (in the Rockall area):

Length	<4 µm	>4 µm
Stratigraphic Range	Early Pliocene – Recent	Miocene – Very Early Pliocene
	D. productus	*D. antarcticus*

Reticulofenestra gartneri ROTH & HAY 1967

(Fig. 11; Pl. 2, Figs. 1–3)

= *Reticulofenestra gartneri* ROTH & HAY 1967
= *Reticulofenestra gartneri* in PUJOS 1985b

This medium-sized coccolith has a broadly round periphery, which is very characteristic. According to HAY et al. (1967) its large central area has about 120

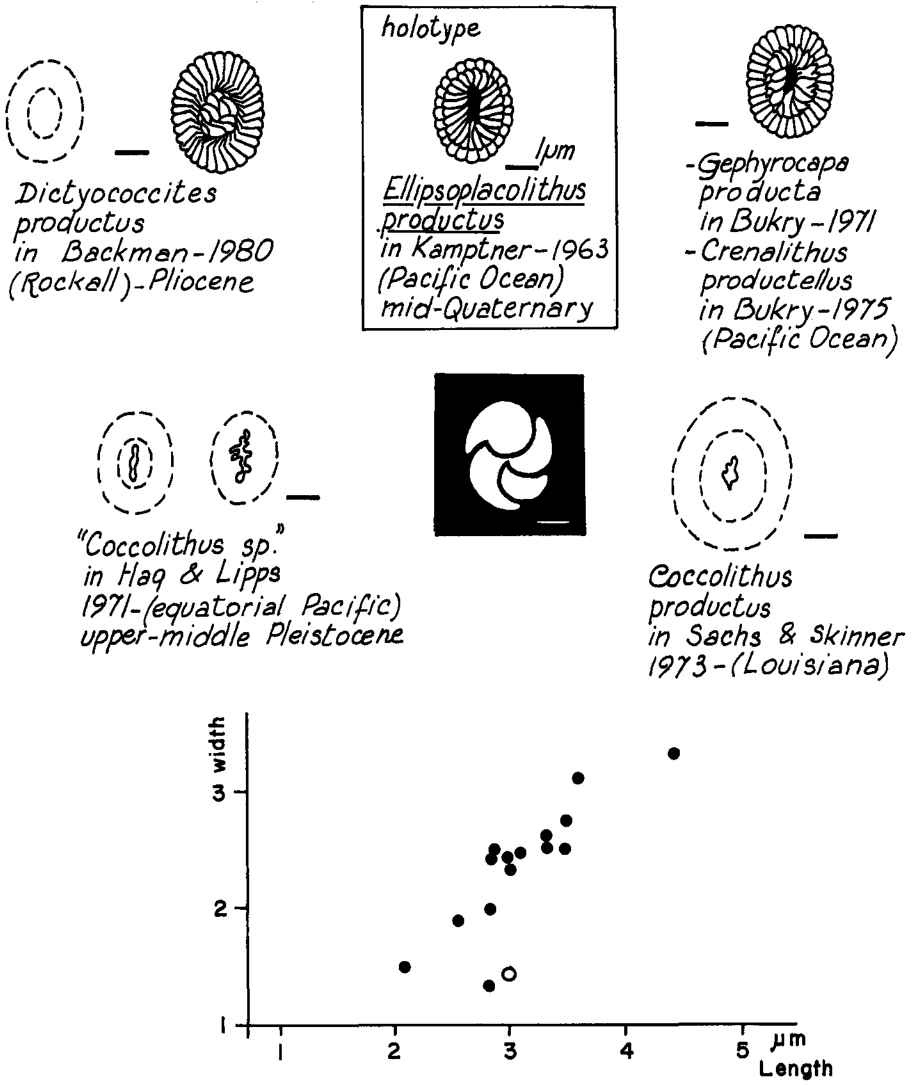


Fig. 9: *Dictyococcites productus.*

very small holes. The elements of the distal shield are numerous and very regular.

This species is very scarcely noted in published papers: only in the Blake Plateau and in the equatorial Pacific. This small number of publications is perhaps due to the species distribution restricted to the low latitudes or to a problem of taxonomy. It can be confused with *D. hesslandii*, but *D. hesslandii* has no central area, or with *R. pseudoumbilica* which has much less elements per shield.

The "*insignita-scrippsae-daviesi-hesslandii*" Group

Grouping these four species is a taxonomic problem because there is a true *Reticulofenestra (= R. insignita)* and three *Dictyococcites*, but it is very difficult to distinguish *R. insignita* from the smallest *Dictyococcites* of the group, for a study with an optical microscope.

Reticulofenestra insignita ROTH & HAY 1967

(Fig. 12; Pl. 2, Fig. 23)

R. insignita is a very small form (length = 3,5 to 4,2 µm) with a large central area closed by a grid pierced by 36 holes and 33 slits (from ROTH & HAY, 1967). This delicate grid is often missing and the resulting open central area gives a characteristic figure between crossed nicols.

In spite of its typical morphology *R. insignita* is very seldom mentioned. I think that several authors give other names to this coccolith. For example, the species I name *"insignita"* could be *"hesslandii"* by PERCH-NIELSEN (1972), some of the "small *hesslandii*" by WISE (1983), *"minuta"* by HAQ & LOHMANN (1976) and some *"minuta"* by BACKMAN (1984). I establish such equivalences either in comparing pictures given by the authors, or because some taxa could not have existed at the period when they were found (e. g. *"minuta"* could not have existed in the Paleogene).

These confusions are indicative of the problem of the specific name of *R. insignita*. It is true that they resemble small *hesslandii* when their central area is closed or calcified, and that their size is almost the same as that of *R. minuta* (HAQ type) which may explain some confusions.

Length Range	3.5–4.2 µm	3.2–4.0 µm	3.0–6.3 µm
Length of the central area	1.7–2.2 µm	0.5–1.0 µm	slit
	R. insignita	*R. minutula* (HAQ type)	*D. hesslandii*

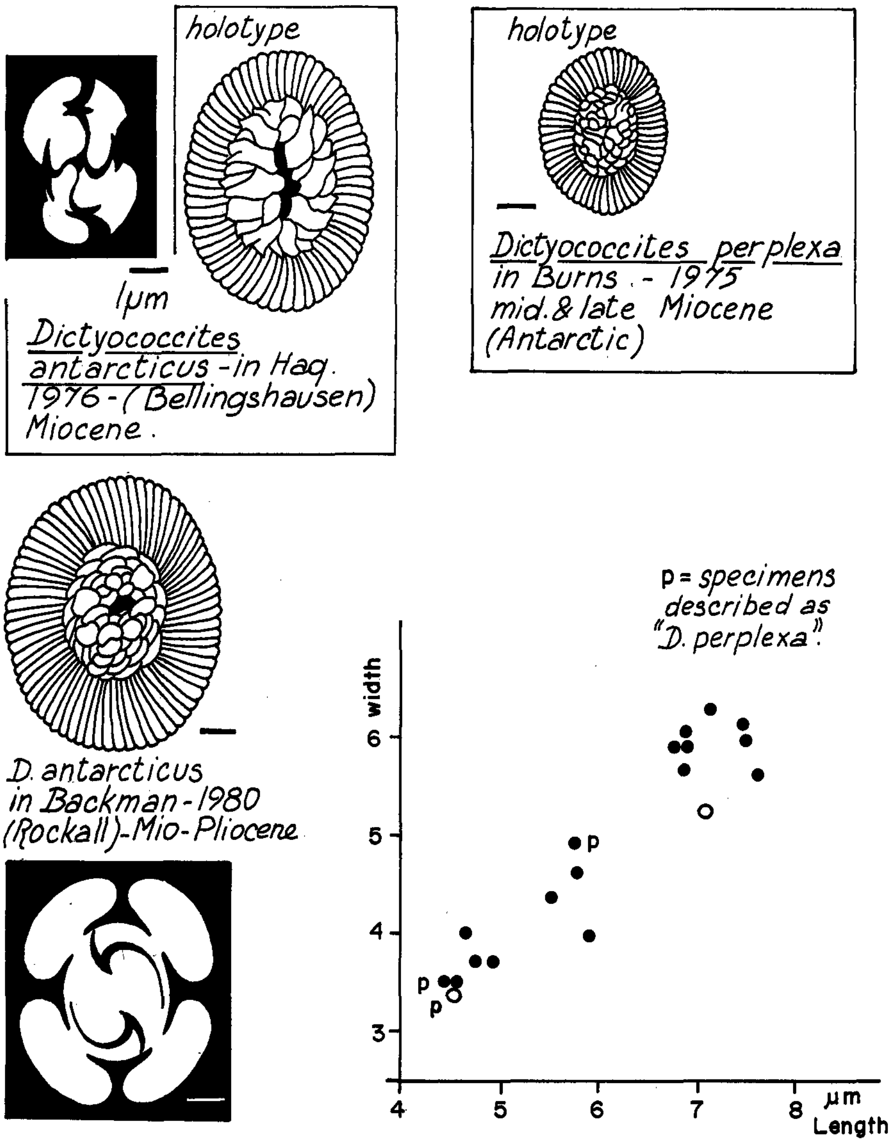


Fig. 10: *Dictyococcites perplexus.*

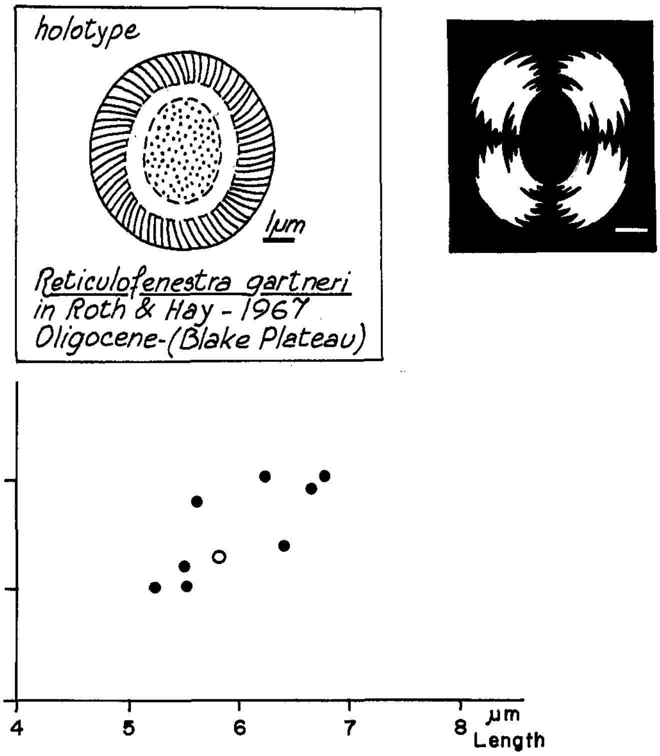


Fig. 11: *Reticulofenestra gartneri.*

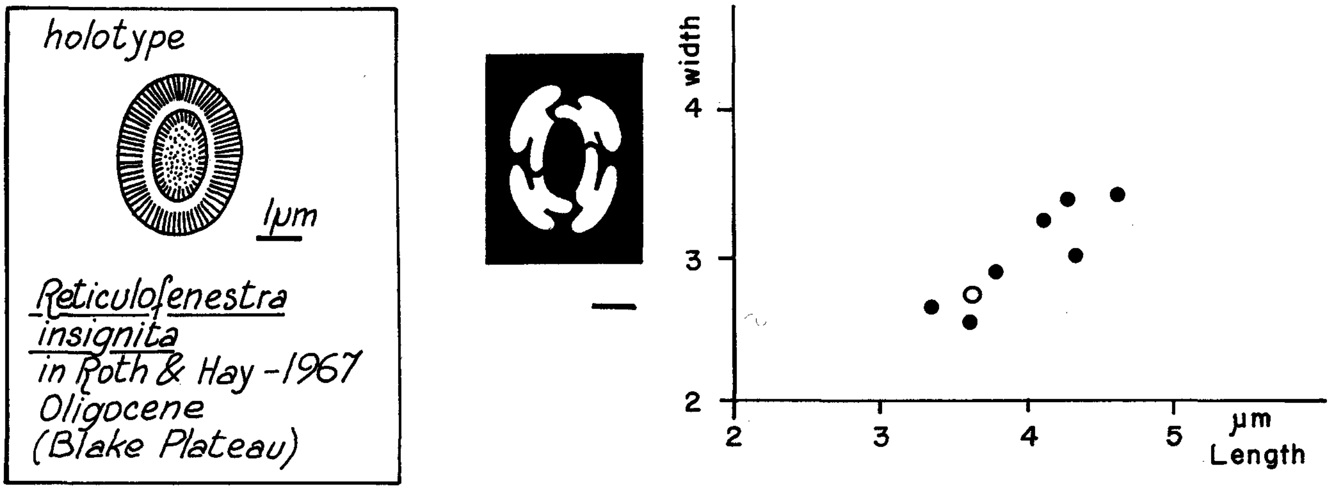


Fig. 12: *Reticulofenestra insignita.*

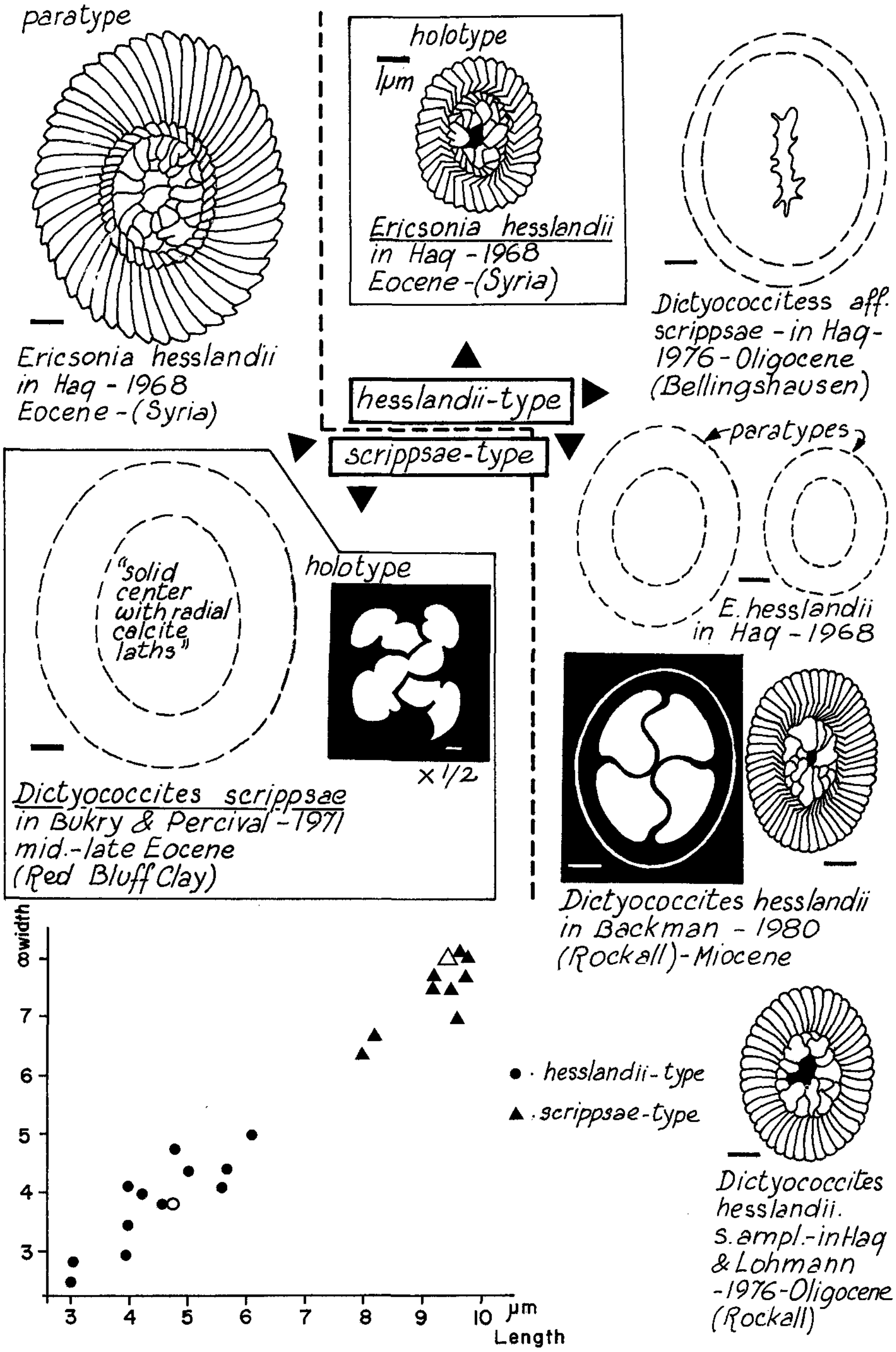


Fig. 13: *Reticulofenestra hesslandii* and *Reticulofenestra scrippsae.*

● *Dictyococcites scrippsae* and *D. hesslandii*

(Fig. 13; Pl. 2, Figs. 4–8)

D. hesslandii is one of the most mentioned *Dictyococcites*. In 1976 HAQ & LOHMANN compared *D. hesslandii* and *D. scrippsae* morphologies and figured them between crossed nicols; they concluded that *D. scrippsae* "may prove to be a junior synonym" of *D. hesslandii*. I do not agree; I develop my arguments in the discussion below, where I separate the two species.

Dictyococcites hesslandii (HAQ) HAQ & LOHMANN 1976

= *Ericsonia hesslandii* HAQ 1966
= *Reticulofenestra hesslandii* (HAQ) ROTH 1970
= *Prinsius hesslandii* (HAQ) HAQ 1971

D. hesslandii has small to medium-sized coccoliths (length = 2,8 to 6,3 µm). The various SEM pictures show a distal shield with numerous regular elements (40 to 60 elements) and a proximal shield with very irregular elements; the central area is completely closed or shows a very small slit. Between crossed nicols, *D. hesslandii* has a very simple swastika-like figure.

HAQ & LOHMANN (1976) tried to prove that *Prinsius martinii* (PERCH-NIELSEN) HAQ was a synonym of *D. hesslandii*. In my opinion such a subcircular form, with fewer elements on the distal shield, cannot be confused with the oval *D. hesslandii*. Furthermore, *P. martinii* has been described as a Paleocene coccolith; in our samples no "subcircular *hesslandii*" was found: if *P. martinii* and *D. hesslandii* have to be confused, it would be in sediments older than 38 Ma (which means in sediments older than those I study here).

Dictyococcites scrippsae BUKRY & PERCIVAL 1971

= *Dictyococcites scrippsae* BUKRY & PERCIVAL 1971
= *Dictyococcites* aff. *scrippsae*, in HAQ 1976
= *Ericsonia hesslandii*, in HAQ 1968

D. scrippsae is a medium-sized coccolith; BUKRY & PERCIVAL (1971) evaluated its length between 6 and 12µm, but the measurement taken from my own specimens and from published specimens (from BUKRY & PERCIVAL, 1971; HAQ, 1968; HAQ, 1976) are always larger than 7,6 µm. Thus, in comparing the length of *D. scrippsae* and *D. hesslandii*, it becomes evident that we have two different populations:

Length	2.8–6.3 µm	7.6–10 µm
	D. hesslandii	*D. scrippsae*

Furthermore, in its original diagnosis, the central area of *D. scrippsae* is described as a "solid center with radial calcite laths" which does not seem to correspond to the central area of *D. hesslandii*.

It is true that it is not always easy to distinguish the two species; in my study of the Cenozoic of the central equatorial Pacific, I put them together (PUJOS, 1985b); after further study I found that it was possible to separate them.

In published papers, *D. scrippsae* is scarcely used and sometimes I think that some especially big "*hesslandii*" can be considered as "*scrippsae*": this is why I put the *Ericsonia hesslandii* by HAQ (1968) as a synonym of *D. scrippsae*.

● *Reticulofenestra daviesi* (HAQ) HAQ 1971

(Fig. 14; Pl. 2, Figs. 9–12)

= *Stradnerius daviesi* HAQ 1969
= *Reticulofenestra daviesi* (HAQ) HAQ 1971
= *Dictyococcites daviesi* (HAQ) PERCH-NIELSEN 1971

BACKMAN (1980) described very well the alternation of names back and forth between *Reticulofenestra* and *Dictyococcites*, for the species *daviesi*. It is true that its generic attribution is difficult; it has a kind of pierced grid in its central area (characteristic of *Reticulofenestra*) but between crossed nicols it seems to be completely closed, with a complete thin swastika figure (as in the case of *Dictyococcites*).

Its size is medium (length = 5 to 8 µm) which places it between *D. scrippsae* and *D. hesslandii*. HAQ & LOHMANN (1976) named some specimens: *D.* aff. *daviesi* and they gave a picture of a large coccolith (length = 12 µm) with a wide empty central area. I suggest to place it within the *Reticulofenestra gelida* group (see below).

The "*pseudoumbilica-gelida*" Group

(Figs. 15,16)

Reticulofenestra pseudoumbilica is the largest coccolith of the present study and it presents a wide dimension range, as BACKMAN showed in his biometrical study (1980); BACKMAN also demonstrated that it was not possible to separate the two species *pseudoumbilica* and *gelida* with biometry. He concluded that *R. gelida* could be indicative of a cooler water and could represent winter forms of *R. pseudoumbilica*; thus he put the two forms as synonyms.

I personally prefer to keep a distinct *gelida*-type because in some parts of the ocean (i. e. subantarctic areas) it is predominant. I consider, as WISE did in 1983, that it would be useful to have two subspecies, as I did for the *haqii-minutula* group:

● *Reticulofenestra pseudoumbilica* (GARTNER) GARTNER 1969 subsp. *pseudoumbilica* (GARTNER) GARTNER

(Pl. 2, Figs. 13–17,18a)

= *Coccolithus pseudoumbilicus* GARTNER 1967
= *Reticulofenestra pseudoumbilica* (GARTNER) GARTNER 1969

Reticulofenestra pseudoumbilica (GARTNER) GARTNER 1969 subsp. *gelida* (GEITZENAUER) WISE 1983

(Pl. 2, Figs. 18b–c,19–22)

= *Coccolithus gelidus* GEITZENAUER 1972
= *Reticulofenestra gelidus* (GEITZENAUER) BACKMAN 1978

HAQ (1980) described three variants of *R. pseudoumbilica*; HAQ & BERGGREN (1978) figure one typical variety, one var. A and one var. B. In each of these papers the discrimination between variants was established according to the size of the coccolith and to the central area. BACKMAN (1980) proved that there was a single population composed of *pseudoumbilica* and *gelida*. Nevertheless, in most of the samples I studied, it was easy to differentiate a medium-sized *pseudoumbilica* with a large central opening (= ssp. *pseudoumbilica*) and a larger-sized one with a small central opening (= ssp. *gelida*). So I kept the two types.

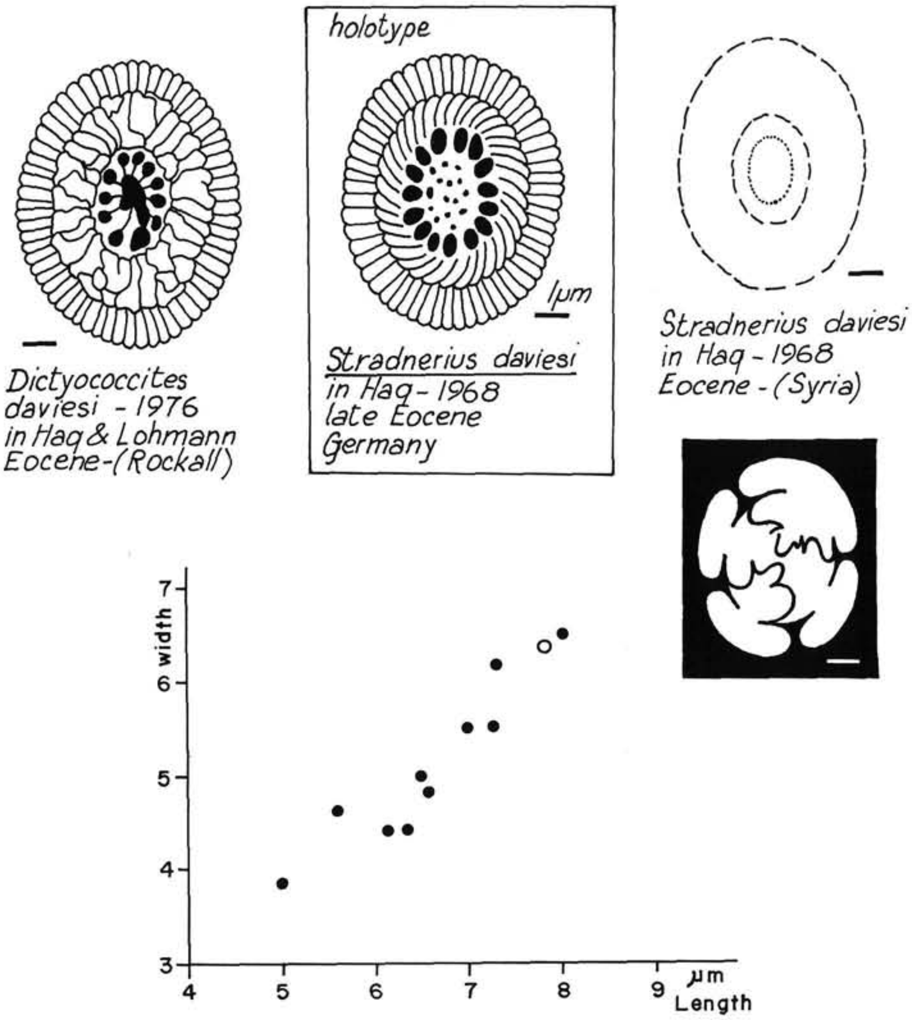
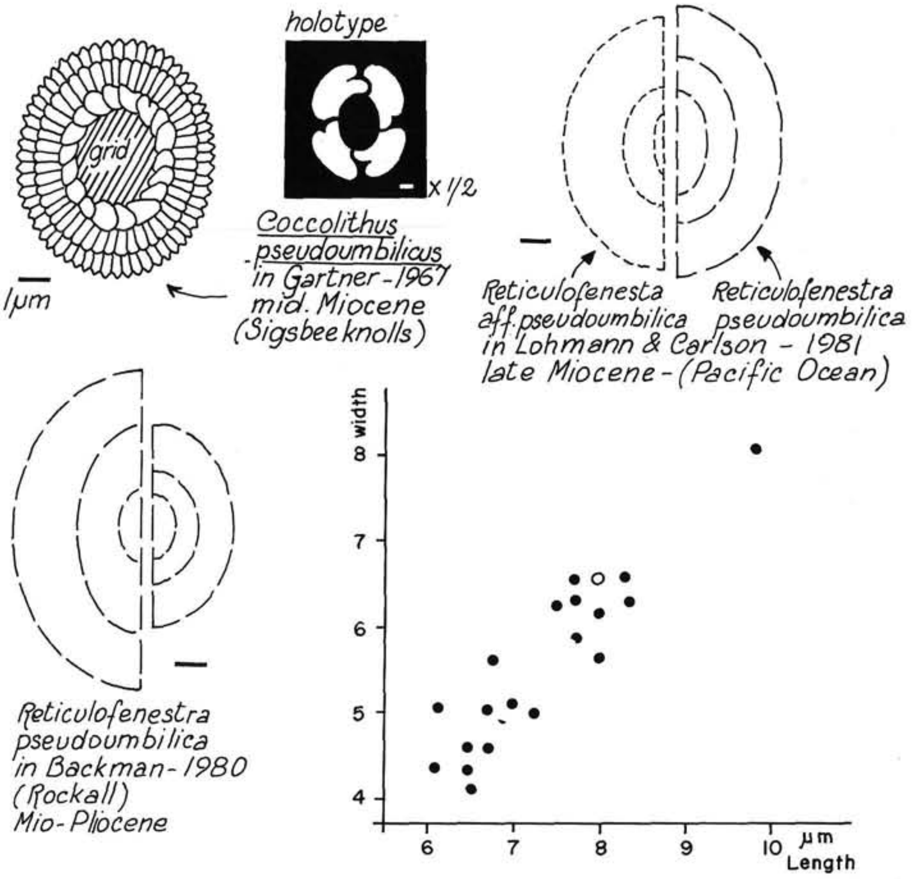


Fig. 14: *Reticulofenestra daviesi*.

Fig. 15: *Reticulofenestra pseudoumbilica pseudoumbilica*.



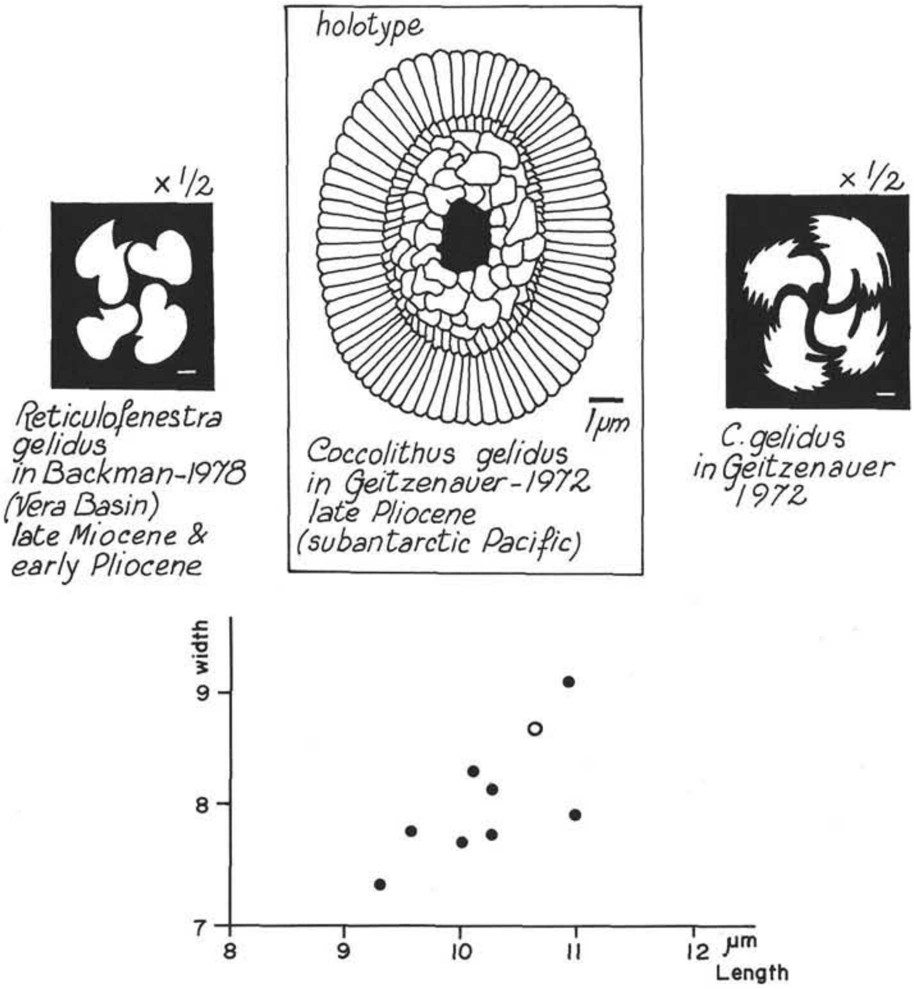


Fig. 16: *Reticulofenestra pseudoumbilica gelida.*

The Genus *Gephyrocapsa*

(Fig. 16)

Although *Gephyrocapsa* is usually taken as a Pleistocene genus, several authors have found it in Pliocene sediments (PERCH-NIELSEN, 1972; BERGEN, 1984; SAMTLEBEN, 1980). I personally observed many *Gephyrocapsa* specimens in Pliocene and also Miocene samples (Leg 85). These Tertiary *Gephyrocapsa* are usually named "small *Gephyrocapsa*". Except for SAMTLEBEN (1980) there have been no pictures representing them. The *Gephyrocapsa* sp. 1 by SAMTLEBEN is very similar to mine and I think it is necessery now to create a species:

Gephyrocapsa theyeri n. sp.

(Pl. 3, Figs. 1–4)

= *Gephyrocapsa* sp. 1 SAMTLEBEN, pl. 12, figs. 23, 26, 27.

Diagnosis: very small species belonging to the *Gephyrocapsa* genus, with a broad and clearly elevated cross-bar.

Description: it is a very small *Gephyrocapsa* (length = 1,65 μm; width = 1,125 μm) with a wide open central area (length = 1,3 μm; width = 0,65 μm). The distal shield has 30 regular elements and the proximal one has about 24 elements. The most characteristic feature is a heavy cross-bar which covers most of the central area; it is 0,925 μm wide at its base and 0,375 μm wide in its middle part; each half-bar is made of 4 elongated elements stemming from 6 elements of the proximal shield. This cross-bar is elevated above the plane of the shields like a bridge; there is a kind of break in the bridge roundness, like a plane face of calcite crystal on each half part of the bridge just at the place where they meet. The bar makes an angle of 34° with the long axis of the coccolith. With an optical microscope, *G. theyeri* gives a Z figure, like *G. sinuosa* does occasionally.

I name this species *theyeri* in honour of FRITZ THEYER who was a chief scientist of DSDP Leg 85.

Differences: *G. theyeri* resembles many small Pleistocene *Gephyrocapsa*. It can be distinguished by its dimension (in μm) and morphological details:

Gephyrocapsa species	Total length	Total width	Shield thickness	Bar thickness	Bar angle	No. of distal elements
sinuosa⁺)	2.4	2.0	?	0.75	43°	?
aperta f. 1*)	1.55	1.10	0.30	0.15	32°	26
aperta f. 2*)	2.10	1.35	0.45	0.15	32°	26
*ericsonii**)	2.20	1.70	0.55	0.275	30°	32
sp. 1°)	2.10	1.6	0.40	1.0–0.425	40°	24–34
theyeri	1.65	1.125	0.30	0.925– 0.375	34°	30

*) in PUJOS-LAMY (1976); ⁺) in HAY & BEAUDRY (1973); °) in SAMTLEBEN (1980).

Except for *G. aperta* f. 1, *G. theyeri* is the smallest of these *Gephyrocapsa*. It resembles *G. ericsonii*, because they both have an elevated bridge, but the bridge of *G. theyeri* is much wider at its base. The general appearance of *G. sinuosa* is similar to that of *G. theyeri*, but the original diagnosis of *G. sinuosa* HAY & BEAUDRY (1973) gives only an optical microscope picture which does not show enough detail.

Type level: early Late Miocene to Late Pliocene.

Type locality: central equatorial Pacific Ocean, DSDP Leg 85, Site 572.

Depository: Département de Géologie et Océanographie – Université de Bordeaux I, Talence, France.

*

G. theyeri is often frequent in abundance at Site 572. Another *Gephyrocapsa* is also present in the same samples. Their coccoliths are slightly longer than those of *G. theyeri* (L = 2 µm) and their appearance is really different: they are very close to some *"G. sinuosa"* by SAMTLEBEN (1980). I have very few photos of this type, so I name it *G.cf. sinuosa*.

4. Stratigraphy and Paleogeography

The stratigraphy of the chosen species is transferred to the nannofossil zonation from OKADA & BUKRY (1980) and to ages in Ma. Magnetostratigraphy could not be used because many published distributions are not enough precise. I found few paleoecological remarks; usually ecology is given for some groups of coccoliths (cf. various papers by HAQ and coll.) and cannot be applied to species. When it is possible, specific ecology is given. I put all the stratigraphical and paleoecological results on graphs; latitudinal and chronological scales were used to follow the spatial and temporal distributions of the species or genera.

4.1. *Reticulofenestra minuta*

(Fig. 17)

R. minuta is a "tropical element" according to HAQ & LOHMANN (1976) who considered it as a biogeographi-

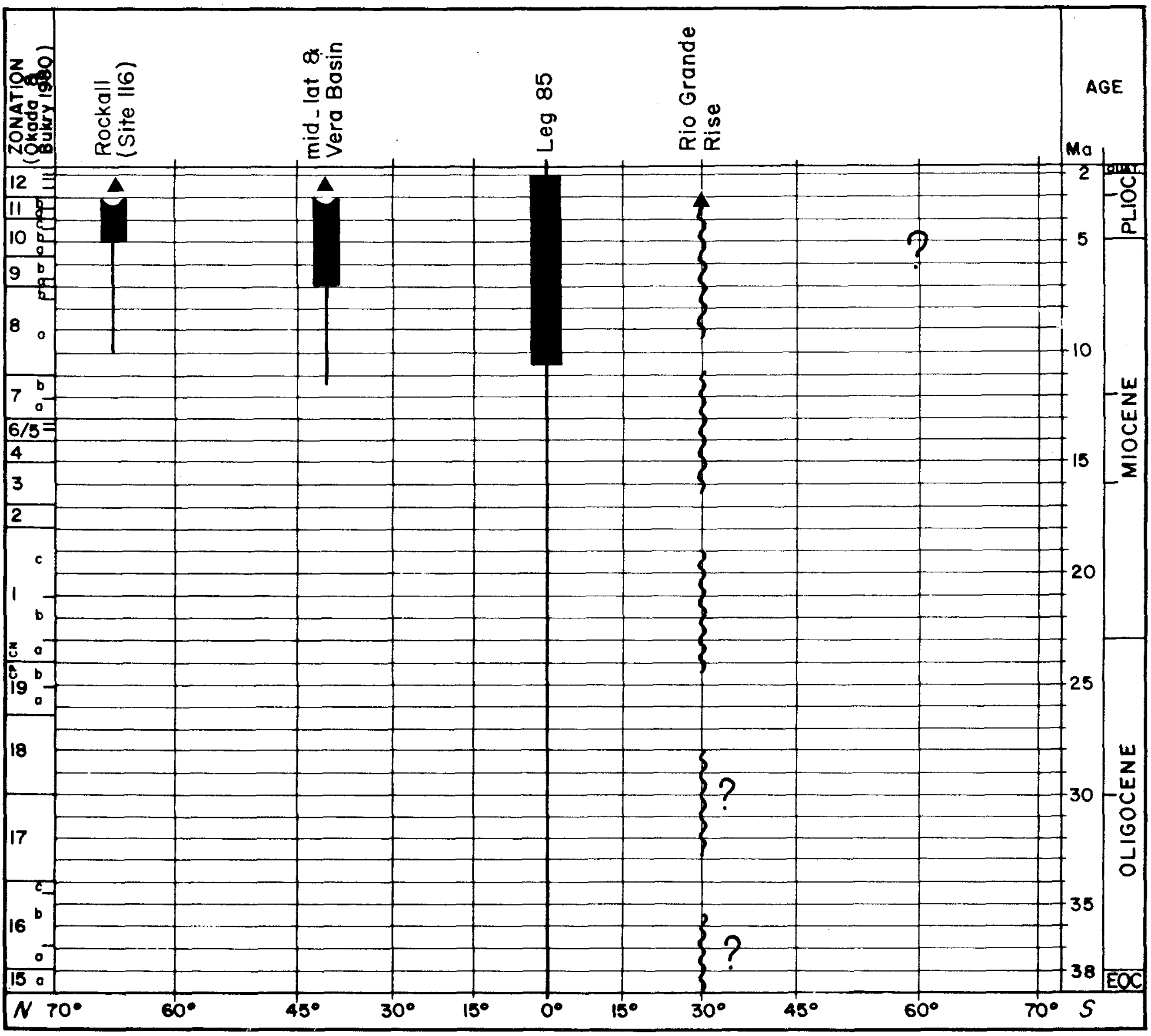


Fig. 17: Spatial and temporal distribution of *Reticulofenestra minuta*.

cally important taxon. These authors thought that the *R. minuta* association appeared during zone CN 4 at low latitutes and invaded mid and high latitudes in two waves: the first one during zones CN 5–6 and the second one during zones CN 9b–10b. This complex distribution is at odds with several authors and it is perhaps due to a confusion with some other small Reticulofenestrids.

LOHMANN & CARLSON (1981) considered *R. minuta* to be a cosmopolitan nannofossil "that was relatively more prominent in the Late Miocene than earlier". It is true that *R. minuta* is often present in Mio-Pliocene sediments at mid and high latitudes. I think that in older sediments, it can be confused with small *D. hesslandii* (Oligocene and Miocene) and with *R. insignita* (Eocene and Oligocene).

According to HAQ & BERGGREN (1978), *R. minuta* existed continuously from Eocene to Pliocene in the area of the Rio Grande Rise. This distribution can be interpreted

1) either as the evidence of a continuous evolution from the Eocene – Oligocene *R. insignita* to the Miocene *R. minuta*,
2) or as the first appearance of *R. minuta* s. s. at Southern high latitudes in the Eocene; later it colonized equatorial areas (in the Early Miocene) and northern mid and high latitudes (at the Mio-Pliocene boundary). This second hypothesis is schematized in Figure 17.

R. minuta has never been found South of the Rio Grande Rise (about 30° S).

4.2. *Reticulofenestra minutula minutula* and *R. minutula haqii*

(Fig. 18)

The two subspecies *minutula* and *haqii* are usually mentioned as a group; it is not necessary to study them

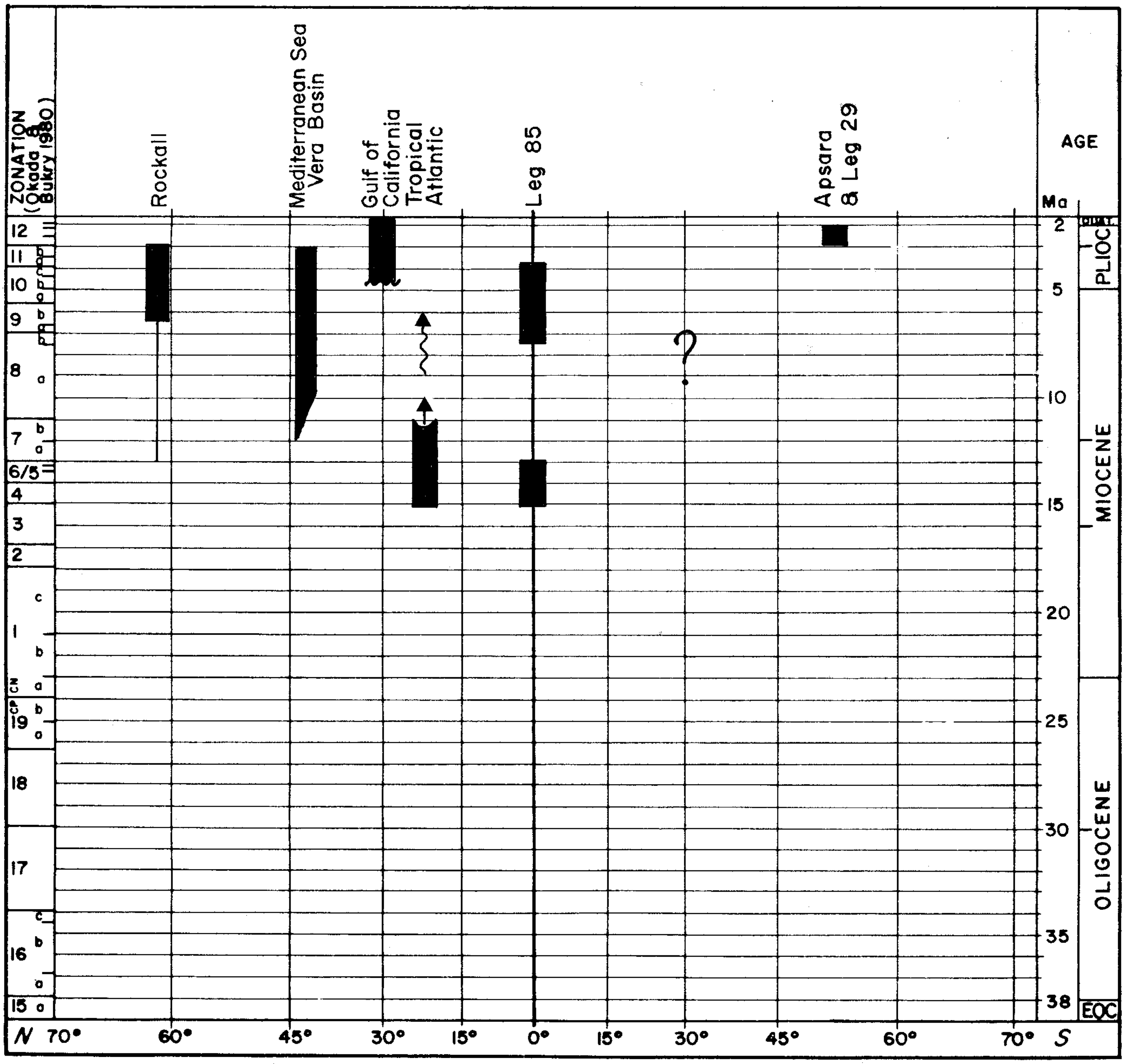


Fig. 18: Spatial and temporal distribution of *Reticulofenestra minutula minutula* and *Reticulofenestra minutula haqii*.

separately, because their distribution is almost similar. In the Northern hemisphere, from Equator to high latitudes, they are present from the Middle Miocene till the earliest Quaternary; but at low and mid latitudes, they are already abundant since the Middle Miocene, while at the same time they are episodic at high latitudes.

In the equatorial Leg 85, they are abundant from the Middle Miocene to the Early Pliocene; but from 10,8 Ma to 9,5 Ma they are rare or absent. The same phenomenon was observed for *R. pseudoumbilica*; a tentative paleoecological explanation will be given in the corresponding paragraph.

In the Southern hemisphere there is no *R. minutula* s. l. cited in any paper, except at Leg 29, where EDWARDS & PERCH-NIELSEN (1975) found it only in Late Pliocene sediments. I found also *R. minutula* in the same age sediments of APSARA. Inspite of the small number of studies in the Southern hemisphere, it is possible that the distribution of *R. minutula* in the Southern hemisphere is symmetrical to that of the Northern hemisphere. It would have reached high latitudes very late, only in the Pliocene.

The two subspecies are not dissociated. Nevertheless, it might be possible to interpret them in the same way as for the *pseudoumbilica* group (see corresponding paragraph), i. e. the subspecies *minutula* (characterized by a small central opening) could be the winter type or the cold type of the species *minutula*; this is emphasized by the presence of this subspecies only in the Pliocene of Leg 29 (= *"Coccolithus" minutulus*, EDWARDS & PERCH-NIELSEN, 1975) and of APSARA.

4.3. *Reticulofenestra doronicoides*

(Fig. 19)

R. doronicoides has an almost synchronous HO: everywhere it disappeared in the CN 14 Zone of OKADA & BUKRY (1980). Its LO is not always given with precision and, according to BLACK (1971), BACKMAN (1980), BUKRY (1973b), BERGEN (1984) it usually did not occur before the Middle Pliocene. Other authors found this species in older sediments (STRADNER, 1973; BERGEN, 1984; ROTH, 1974). BACKMAN (1980) stated that "the FAD of *C. doronicoides* is vaguely determined ... the specific epithet *doronicoides* should be rejected"; to support his conclusions, BACKMAN listed the *doronicoides* distributions given by several authors; nevertheless, the same distributions illustrated in Figure 19 with respect to the latitude can be easily interpreted as follows.

The oldest LO is given by ROTH & THIERSTEIN (1972) at the Middle – Late Miocene boundary in the Falkland sector. The earlier appearance of *R. doronicoides* occurred progressively from Southern high latitudes to Northern high latitudes: this phenomenon is evident on Figure 19, in spite of some approximate distributions and various ages estimated by different authors in the same area (i. e. in the Mediterranean Sea, BUKRY [1973a]

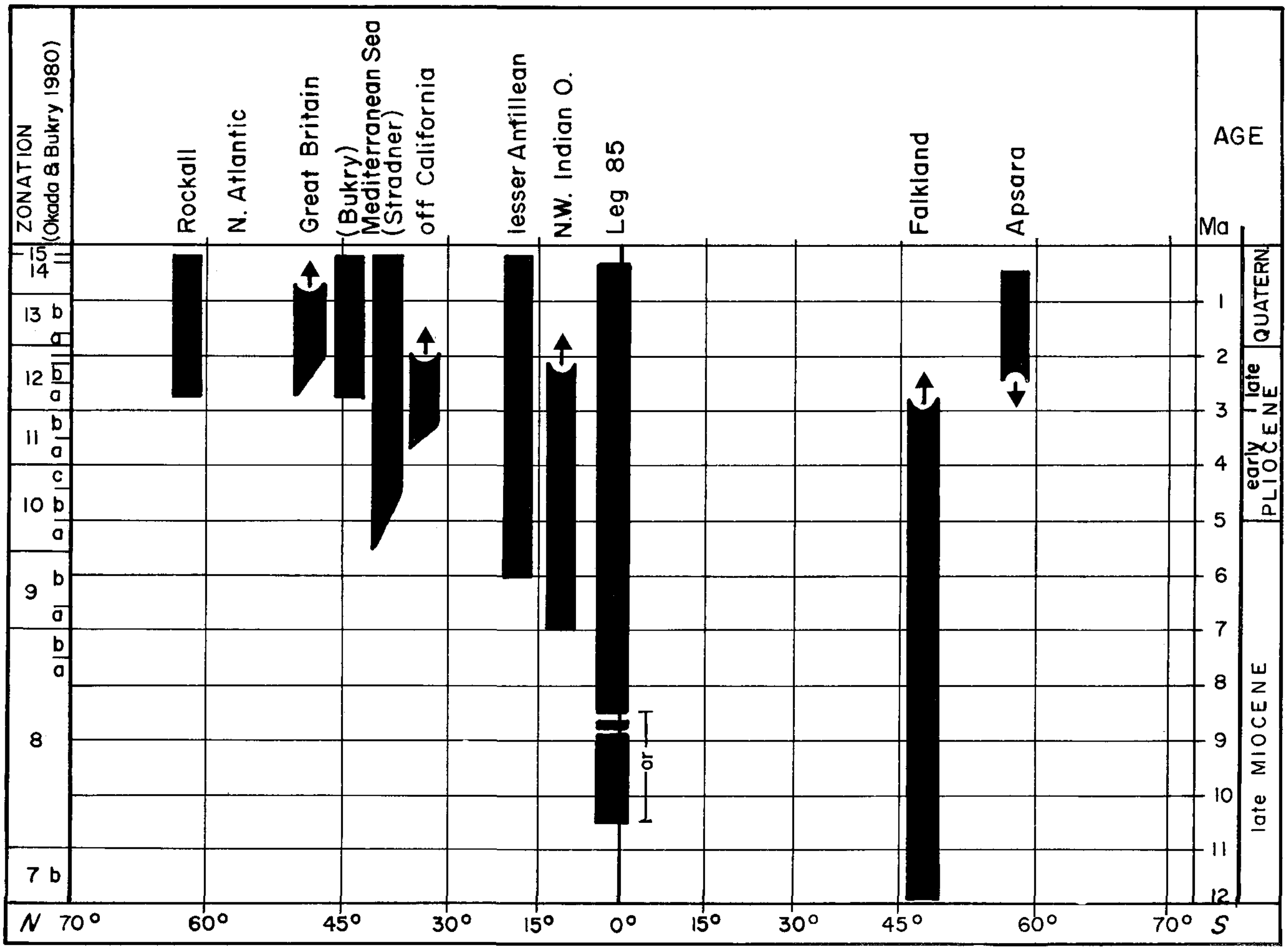


Fig. 19: Spatial and temporal distribution of *Reticulofenestra doronicoides*.

mentioned the LO of *R. doronicoides* in the middle of the CN 12a Subzone, and STRADNER [1973] at the Mio-Pliocene boundary, in the NN 12 Zone).

4.4. *Dictyococcites productus* and *D. perplexus*

(Fig. 20)

D. perplexus

According to HAQ & LOHMANN (1976), *D. perplexus* was a dominant species during the Middle and Late Miocene. But they said also that it is a species restricted to the Southern high latitudes and that the true *D. perplexus* has not been observed elsewhere. It is evident that the appearance of this species coincides with the beginning of the development of "an extensive ice-cap on Antarctica and the marked climatic deterioration at 15 Ma" (HAQ & MALMGREN, 1981/1982).

HAQ (1976) found an assemblage dominated by *D. perplexus*, during "Oligocene and Middle Miocene" in the Bellingshausen area; thus *D. perplexus* appeared during Oligocene in Southern high latitiudes; it invaded Subantarctic waters (APSARA and Falkland) at about 16 Ma, low latitudes (Leg 85) at 15 Ma, and Northern high latitudes at 14 Ma. *D. perplexus* could have followed the progression of the Antarctic waters, which it can typify.

D. productus

D. productus is often cited, but its boundaries are not well established. It disappeared during the Quaternary (PUJOS, 1985b at about 0,4 Ma) and it appeared approximately when *D. antarcticus* disappeared. According to BACKMAN (1980), *D. productus* could have evolved from *D. perplexus*, during the earliest Pliocene in the Rockall area; this evolution occurred during the Middle Miocene elsewhere.

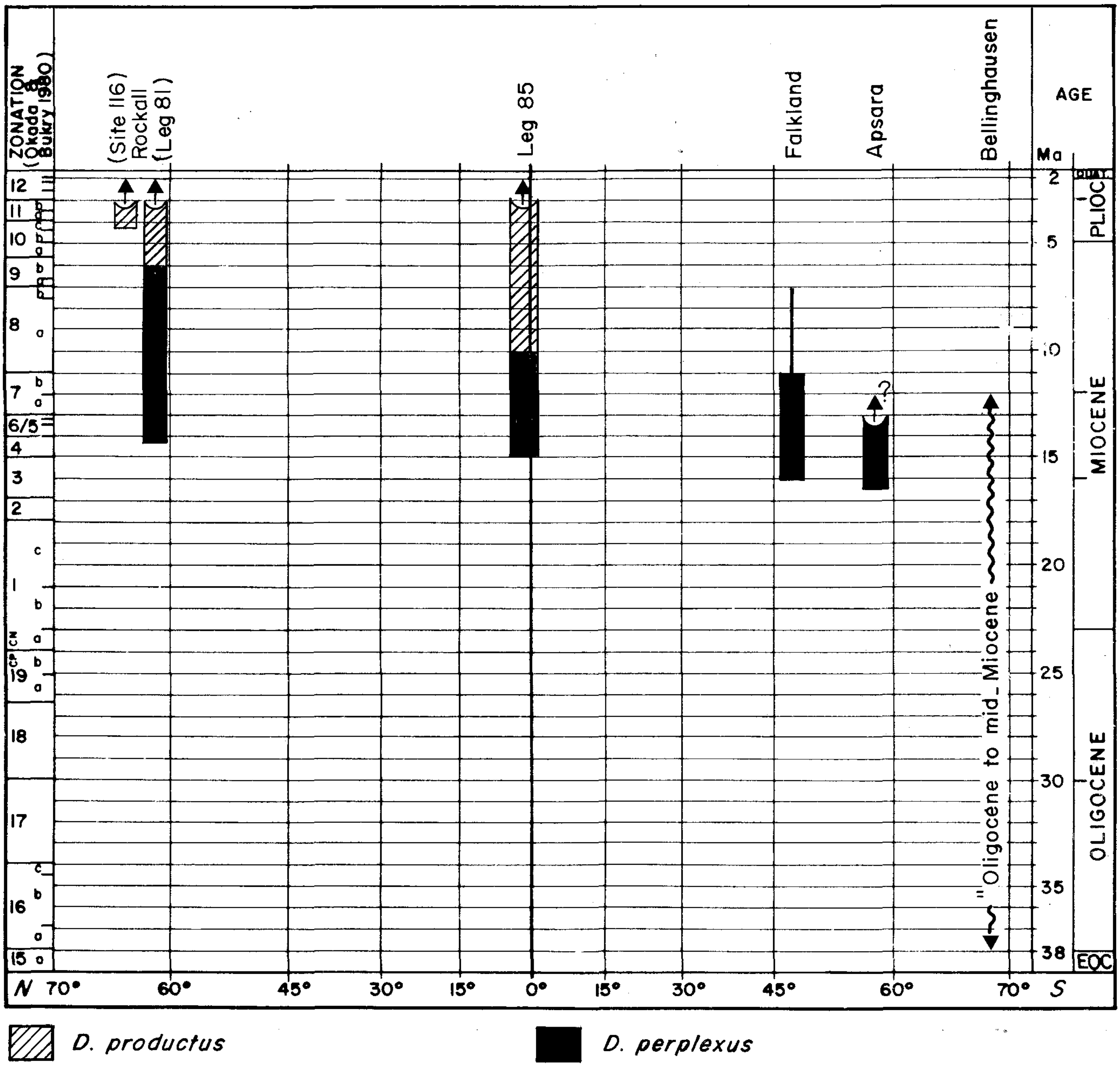


Fig. 20: Spatial and temporal distribution of *Dictyococcites productus* and *Dictyococcites perplexus*.

4.5. *Reticulofenestra gartneri*

(Fig. 21)

This species is scarcely used. It was created by ROTH & HAY in HAY et al. (1967) who described it in the Oligocene of the Blake Plateau. At low latitudes (BUKRY, 1973b; PUJOS, 1985b) it was present during most of the Oligocene and until the early Middle Miocene. In the Southern high latitudes, it disappeared at the top of the Early Miocene.

In spite of the small number of published references, *R. gartneri* was an important element of the nannofossil populations, from the earliest Oligocene to the late Early Miocene, at least in the Southern hemisphere and in the Northern low latitudes. It is not possible to draw conclusions from the assumed presence of the species for the Northern middle and high latitudes.

4.6. *Reticulofenestra insignita*

(Fig. 22)

According to my position on the taxonomy of *R. insignita* (see taxonomical paragraph above) I group the stratigraphical distributions of several different taxa which I put within my "*insignita*" concept. It follows that *R. insignita* was already present at the Eocene – Oligocene boundary and that it disappeared at this period at the high latitudes (from BACKMAN, 1984: "*R. minuta*", pars; HAQ & LOHMANN, 1976: "*R. minuta*"; PERCH-NIELSEN, 1972: "*R. hesslandi*"; WISE, 1983: "*R.* cf. *hesslandi* [small]", pars). In the sediments from the Blake Plateau, it was found throughout the Early Oligocene (HAY et al., 1967). At the lowermost latitudes, it was present but not abundant up to 25 Ma.

This latitudinal distribution is consistent enough to

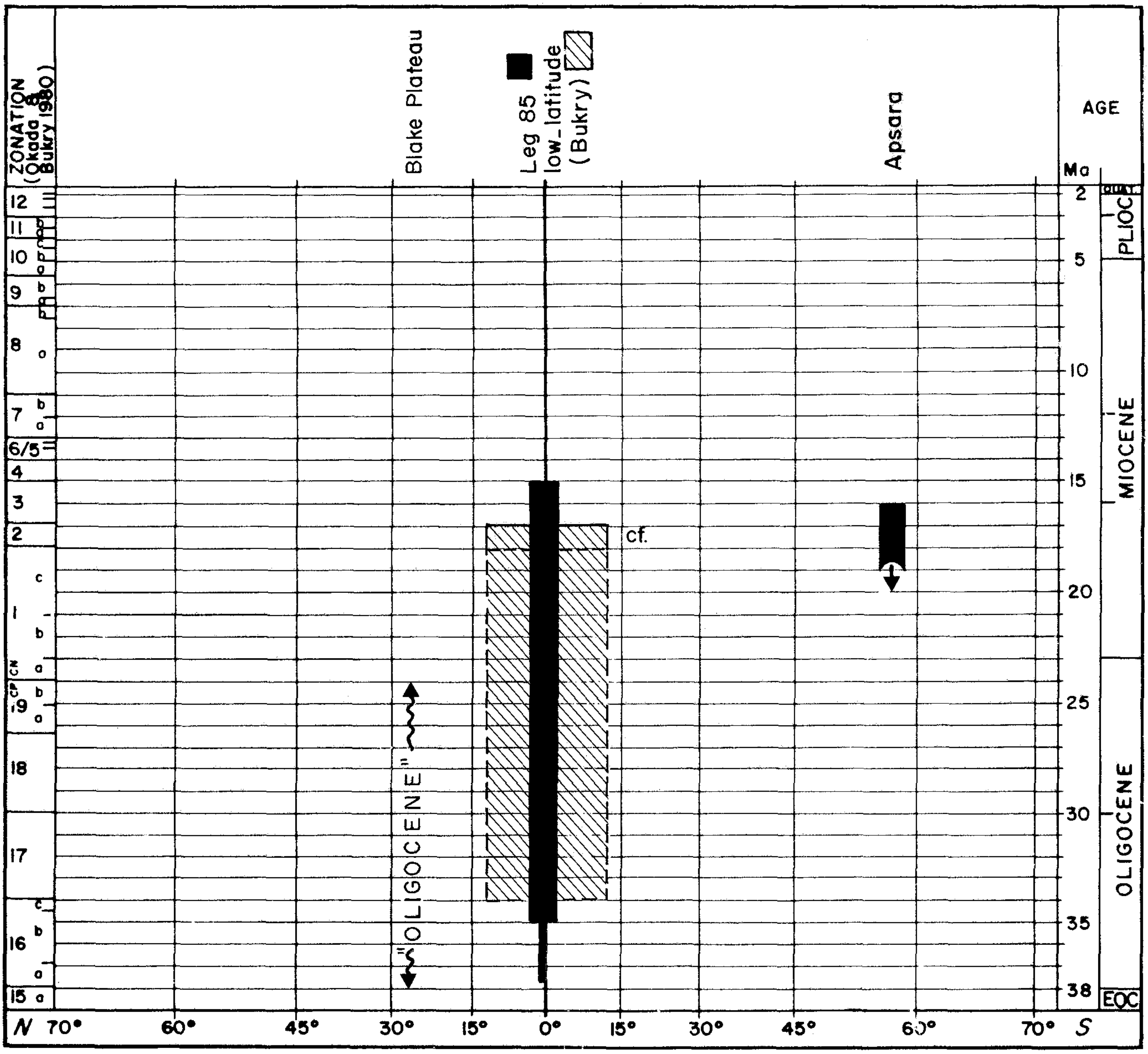


Fig. 21: Spatial and temporal distribution of *Reticulofenestra gartneri*.

substantiate my taxonomical interpretation of various published papers.

4.7. *Reticulofenestra daviesi* and *R. scrippsae*

(Fig. 23)

As for the previous species, there are some taxonomic problems with *R. daviesi* and *R. scrippsae* (see taxonomical paragraph above). It follows that I kept the distributions of coccoliths which correspond well with my concept of the group *daviesi-scrippsae*.

The two species were already present in the latest Eocene. *R. scrippsae* disappeared between 24 and 26 Ma (24 Ma for BUKRY, 1973b; 26 Ma for PUJOS, 1985b) at the lowermost latitudes; it was not found in most of the Northern latitudes. *R. daviesi* remained common during almost the entire Oligocene; its abundance was very reduced at the Oligo-Miocene boundary near the Equator; it disappeared during the Early Miocene•at middle latitudes, and during the Middle Miocene at high latitudes. This distribution of *R. daviesi* is partly in contradiction with the assertions by HAQ & MALMGREN (1981/1982) and HAQ & LOHMANN (1976) who concluded that this species was dominant everywhere (in the Atlantic Ocean) during the CN 2/3 Zone, and was strongly reduced later. In my opinion, *R. daviesi* was dominant at all the latitudes up to the latest Oligocene (with *R. scrippsae*); it disappeared completely during the Middle Miocene, after a latitudinally progressive disappearance during the Early Miocene.

4.8. *Reticulofenestra hesslandii*

(Fig. 24)

The specific name of *"hesslandii"* is one of the most used in the study of Cenozoic nannofossils. But it is often taken as "cf." or as a part of a group and these approximations can hide an ambiguity in the taxonomy. Thus, I kept only three "reliable" *hesslandii* and their corresponding distributions.

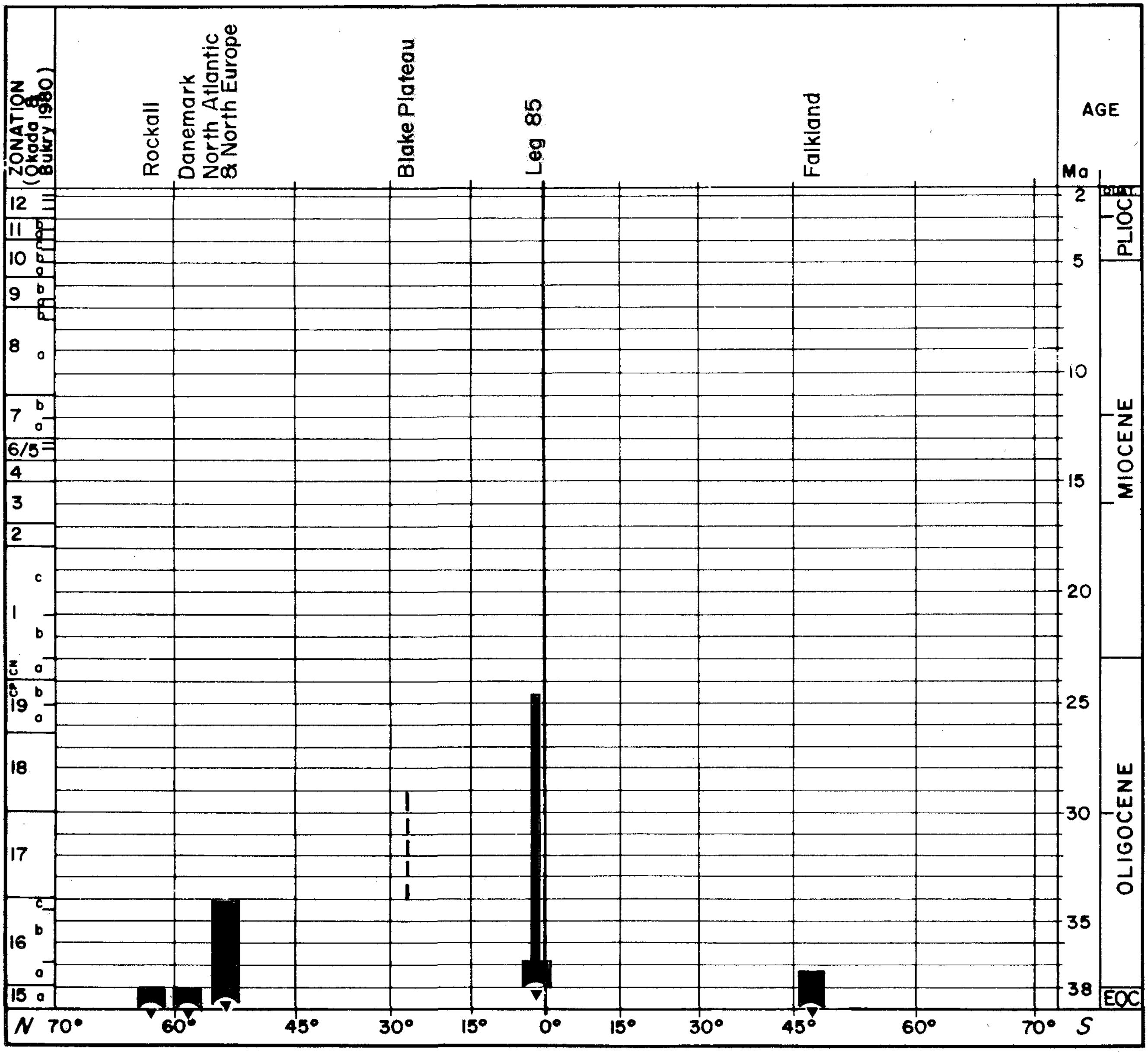


Fig. 22: Spatial and temporal distribution of *Reticulofenestra insignita*.

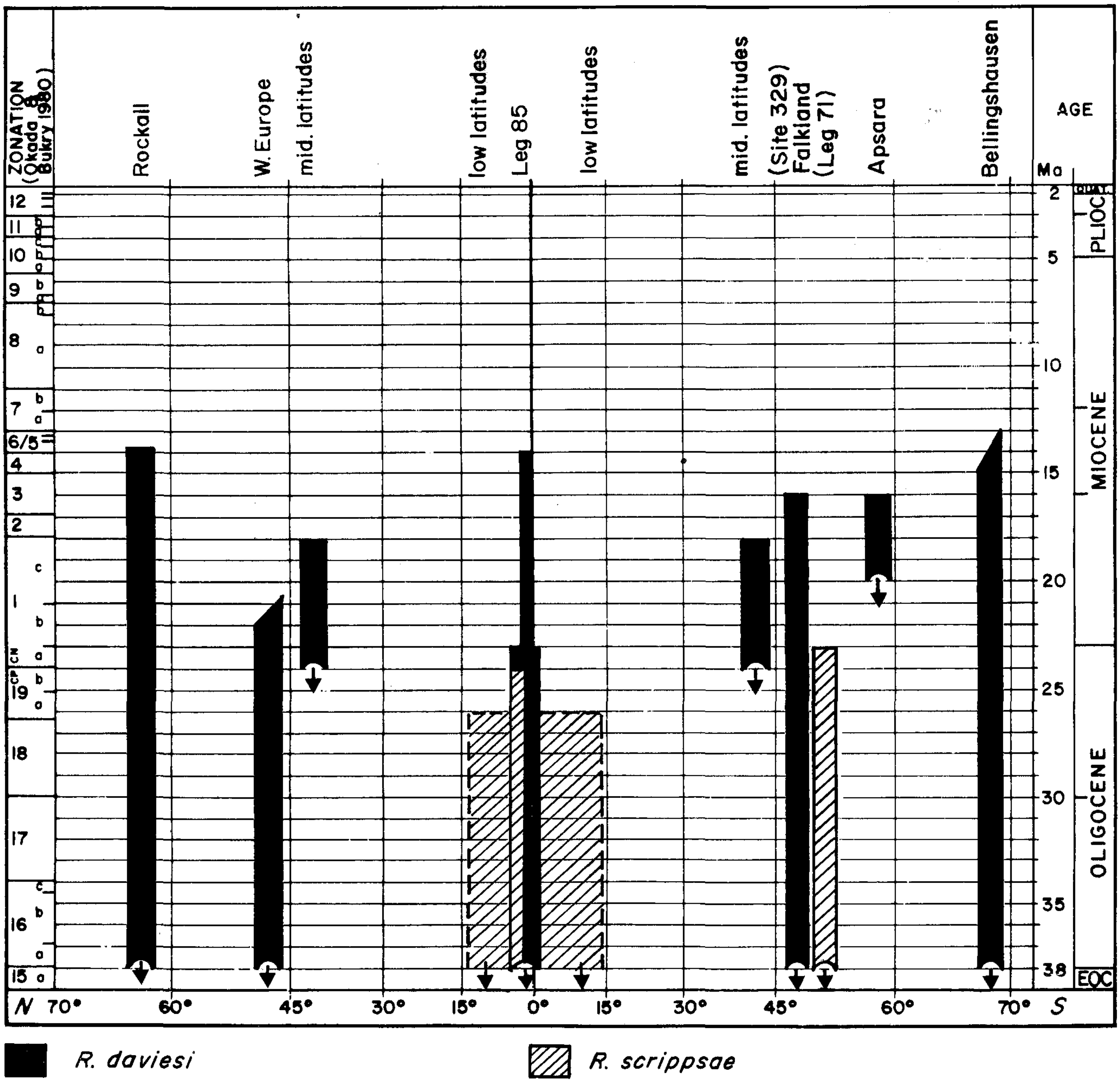


Fig. 23: Spatial and temporal distribution of *Reticulofenestra daviesi* and *Reticulofenestra scrippsae*.

At high and low latitudes, it appeared at the Oligo-Miocene boundary, perhaps first at the Equator. It disappeared (or rather it was the end of the acme) at the Early-Middle Miocene boundary at high latitudes, and slightly later near the Equator. This diachronism for the LO and HO of *R. hesslandii* was already noted by HAQ & LOHMANN (1976). For them, it was a dominant species at the low and middle latitudes during the NN 1 Zone, but it was less dominant in the Northern high latitudes. During the NN 2–4 Zones, there was a general reduction at all the latitudes.

In the Rockall area (BACKMAN, 1984) as in the equatorial Pacific (PUJOS, 1985b) the acme of *R. hesslandii* was followed by the presence of few specimens of the same species, sometimes up into the Pliocene. This continuous presence cannot be explained only by reworking and makes this taxon difficult to separate from the other Late Miocene *Reticulofenestra*.

BUKRY (1976) considered *R. hesslandii* an indicator of cold water, as *Coccolithus pelagicus* s. ampl. and *D. bisectus* could be. This opinion is difficult to defend for a species which is present mostly at the Equator. I prefer to follow HAQ & LOHMANN (1976) who concluded that it was a cosmopolitan form (but in the same paper they used it as an indication of "warm climate"!).

4.9. *Reticulofenestra pseudoumbilica pseudoumbilica* and *R. pseudoumibilica gelida*

(Fig. 25)

R. pseudoumbilica pseudoumbilica is the best known of the medium-sized *Reticulofenestra* and many reliable references can be taken in account, mostly for its HO: it is an irrefutable datum s. s. (dated at 3,56 Ma, according to BACKMAN & SHACKLETON, 1983, at the top of the Gil-

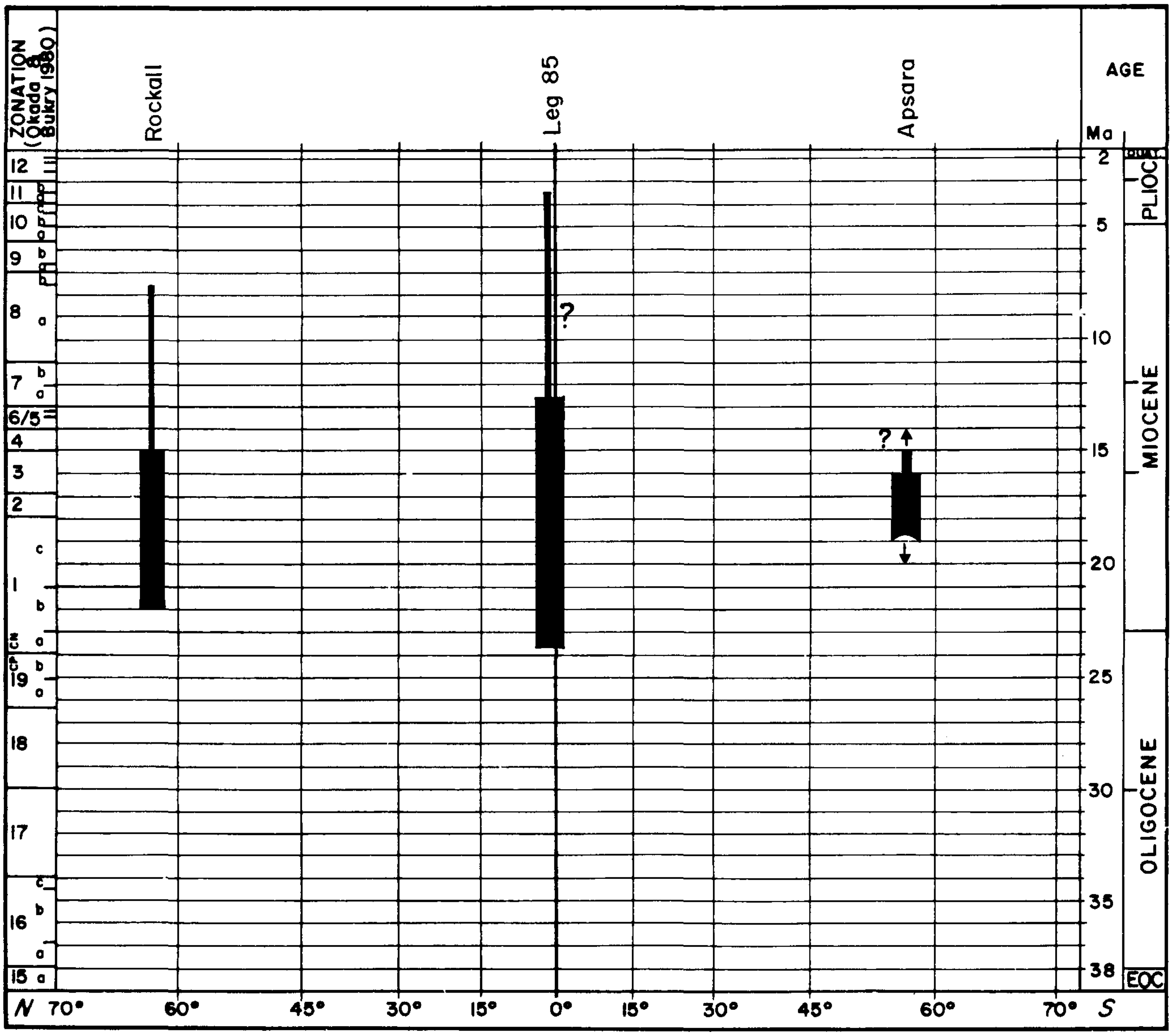


Fig. 24: Spatial and temporal distribution of *Reticulofenestra hesslandii*.

bert paleomagnetic event). Nevertheless, in the North Atlantic, PERCH-NIELSEN (1972) stated that this HO occurred "possibly somewhat earlier than in lower latitudes", i. e. 3 Ma, which is the age of the beginning of the North Atlantic glaciation. The LO of *R. pseudoumbilica pseudoumbilica* is less often cited than its HO, but it was also virtually synchronous: about 15–16 Ma for all the latitudes.

R. pseudoumbilica gelida is taken by BACKMAN (1980) as a winter ecotype of *R. pseudoumbilica* s. s., and he did not differentiate each in his study. WISE (1983) studied *gelida* in the Falkland sector and made it a subspecies of *R. pseudoumbilica*; for him, "these are subspecies which predominate in different water masses", but he did not indicate what kind of water masses. Whatever the exact significance of *gelida* (winter ecotype or water mass marker) it has to be taken as a cold coccolith. The "species" *gelida* was described first in the Southern high latitudes (GEITZENAUER, 1972) and some authors think that it is restricted to them. But several references prove that it is a cosmopolitan species. It seems to be distributred almost as *R. pseudoumbilica* s. s., except in APSARA where it is represented by 2 forms in the Pleistocene sediments (*gelida* s. s.: HO at about 1,2 Ma and small *gelida* HO at about 0,450 Ma) and in the equatorial Pacific (where it was restricted to the Middle Miocene). Thus it had a much longer presence at high latitudes than at low latitudes.

4.10. The Genus *Gephyrocapsa*

(Fig. 26)

This genus is often considered as restricted to the Quaternary, but several authors pointed the LO of "small *Gephyrocapsa*" in the Late Pliocene (BERGEN, 1984, PERCH-NIELSEN, 1972) and in the Early Pliocene (SAMTLEBEN, 1980, at Site 366, in the Sierra Leone Rise; PIRINI-RADRIZZINI & VALLERI, 1977, at Site 132, in the Tyrrhenian Sea). In the eastern equatorial Pacific, some sporadic *G. theyeri* were found since about 14,5 Ma; they became abundant at 11 Ma, at the Middle – Late Miocene boundary.

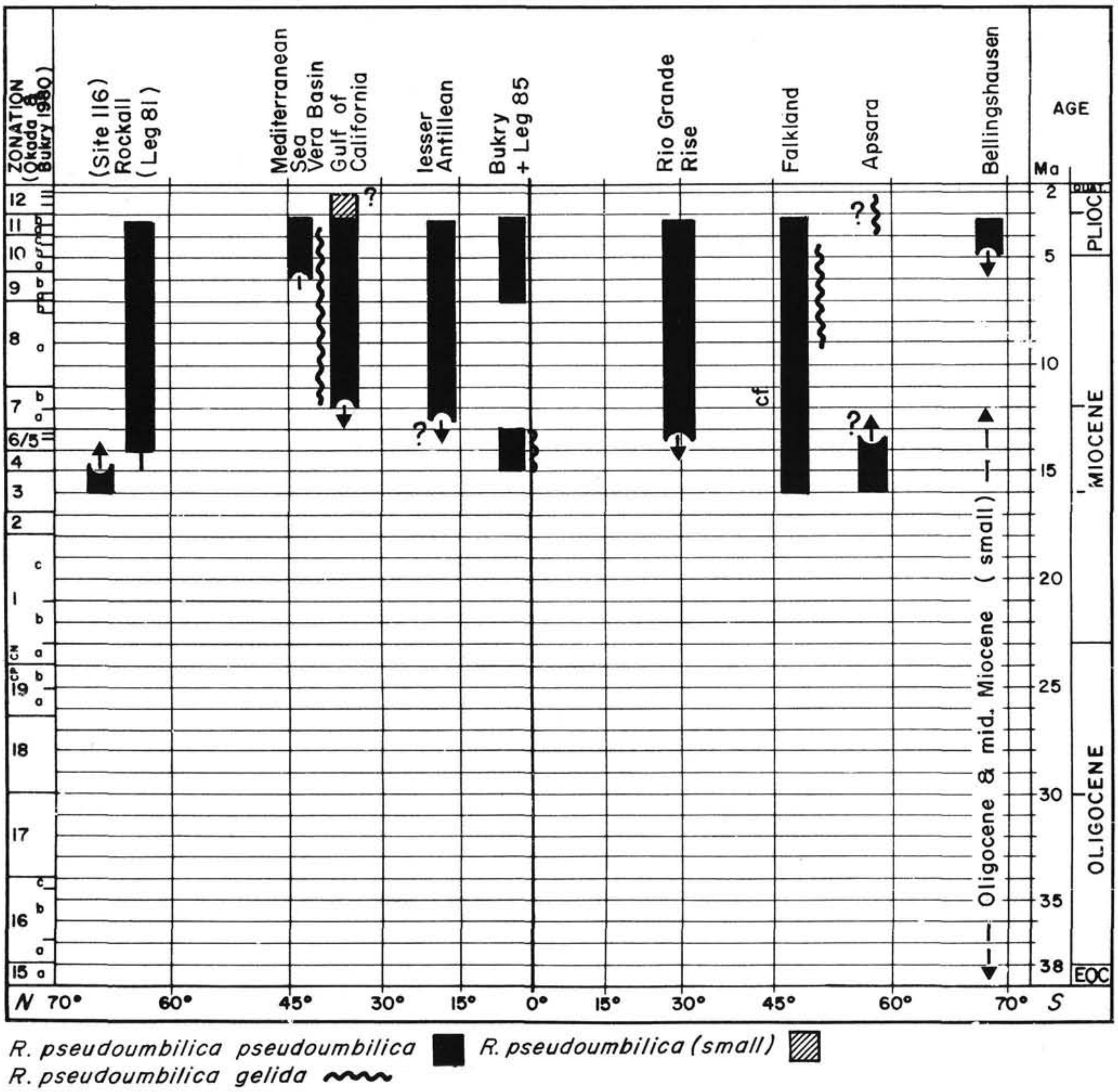


Fig. 25: Spatial and temporal distribution of *Reticulofenestra pseudoumbilica pseudoumbilica* and *Reticulofenestra pseudoumbilica gelida*.

It is possible to link these various appearances of small *Gephyrocapsa* with climatic events:

1) In the Sierra Leone Rise, the small *Gephyrocapsa* were already present at 4 Ma, but they were well differentiated at about 3 Ma (SAMTLEBEN, 1980). At this period (= 3 Ma), there occurred the "onset of enhanced circulation and a progressive climatic deterioriation" ... and consequently "a number of environmental changes started simultaneously ... near 3.2 Ma" (SARNTHEIN et al., 1982); thus "there was a marked decrease of equatorial surface-water temperatures at Site 366" (PFLAUMANN, in SARNTHEIN et al., 1982). All these environmental changes have to be related to the beginning of the northern glaciation which began at about 3.2 Ma.
2) In the Tyrrhenian Sea, PIRINI-RADRIZZINI & VALLERI (1977) found "small *Gephyrocapsa*" in the late Early Pliocene, more precisely just above the paleomagnetic Gilbert event, at about 3,5 Ma. At the same period, the "Acquatraversal phase" is described in the same area; this phase is a cold period "which is considered to reflect the onset of high latitude glaciation in the North Atlantic" (CITA & RYAN, 1973; LAWRENCE, 1973). Thus, it seems that a relation existed between the appearance of *Gephyrocapsa* and the beginning of the northern glaciation.
3) At Site 572 of the eastern equatorial Pacific, *G. theyeri* appeared at 14,5 Ma, during the first period of major polar cooling induced by the Antarctic ice-cap (dated between 14,5 and 13,5 Ma). It was present sporadically between 13,5 and 11 Ma: during this period, there were three short phases of polar cooling. *G. theyeri* became much more abundant after

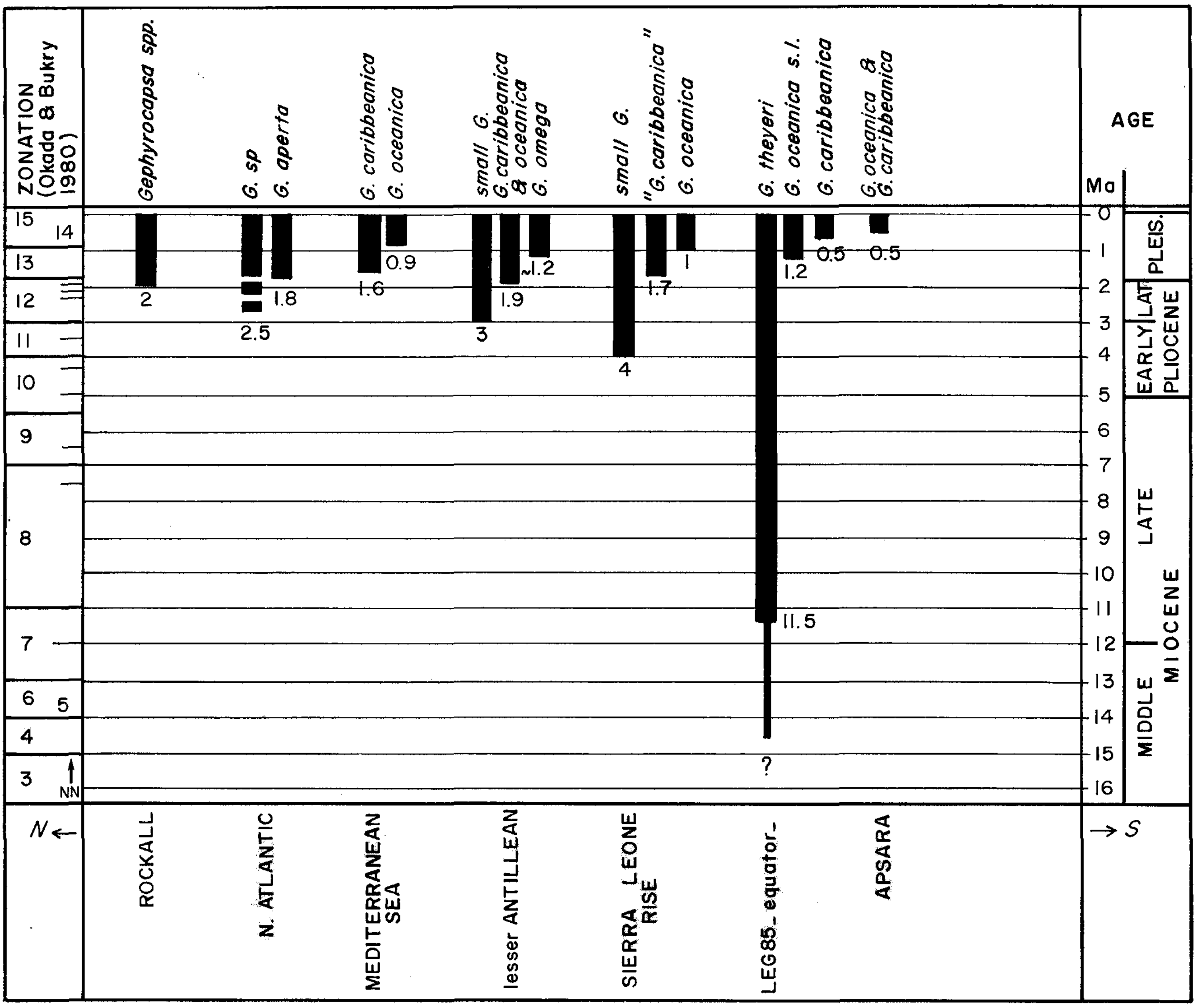


Fig. 26: Spatial and temporal distribution of *Gephyrocapsa* div. sp..

11 Ma, which corresponds with the beginning of the expansion of the Antarctic glaciation. *G. theyeri* was found only at Site 572, which is the easternmost site of the Leg 85. BARRON (1985b) put this site in the "eastern equatorial Pacific" area, in opposition with the other Leg 85 sites, which are in the "central equatorial Pacific" area. The eastern equatorial Pacific is influenced by the equatorial undercurrent and by the Peru – Chile current. These currents bring cold waters into the eastern part of the area (Site 572), while the central area (Sites 573, 574 and 575) is cut off from southern influences. This circulation began at about 11,3 Ma (BARRON, 1985b). As for the two previous examples, the appearance of small *Gephyrocapsa* can be linked to the onset of (Antarctic) glaciation.

These small *Gephyrocapsa* are abundant up to the Late Pliocene where they are diversified into several larger species. Most of them continue to exist in present-day oceans (see PUJOS, 1985a, for the detailed HO of *Gephyrocapsa* div. sp.).

5. The Impact of the Middle Miocene Paleoenvironment on *Reticulofenestra pseudoumbilica* and *R. minutula*

(Fig. 27)

The very unusual distribution of *R. pseudoumbilica* and *R. minutula* in the high productivity area has to be examined in detail in middle Miocene sediments. One of the most important hiatuses occurred at about 13–10 Ma, and an unusual distribution of the two species seems to be linked to this sedimentary phenomenon.

R. pseudoumbilica s. l. and *R. minutula* s. l. both appeared at about 15 Ma. *R. pseudoumbilica* disappeared everywhere at about 3,5 Ma and *R. minutula* between 6.5 and 3.5 Ma. But it is well known (BUKRY, 1973b) that in the equatorial Pacific area, *R. pseudoumbilica* – and *R. minutula* too – are almost totally absent from the sediments corresponding to the period: 13 to 9–7 Ma

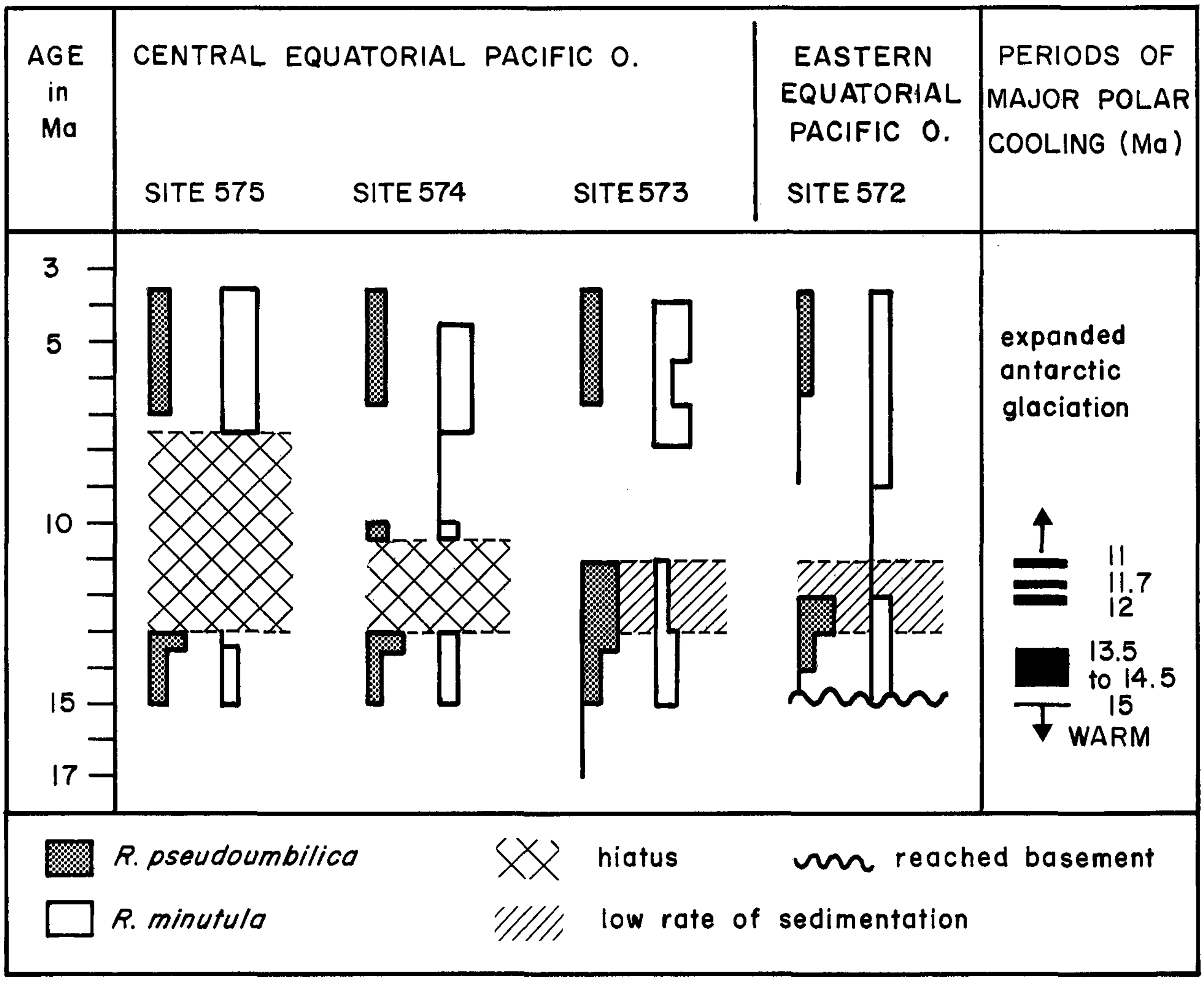


Fig. 27: Distribution of *Reticulofenestra pseudoumbilica* s. l. and of *Reticulofenestra minutula* s. l. in the central equatorial Pacific, between 15 and 5 Ma.

(fig. 27). There were two stages of sedimentation during this period:

1) Between 13 and 7,5 Ma, there exists a gap (= complete hiatus or a very low rate of sedimentation).
2) Between 11 and 7,5 Ma the rate of sedimentation is normal for the area and continuous, but *R. pseudoumbilica* and *R. minutula* are absent, except in the eastern area, where they are rare. They appear, normally abundant, everywhere at about 7,5 Ma.

The distribution of both species can be tentatively explained with the paleoenvironmental history of the Pacific Ocean in the late Middle Miocene and in the early Late Miocene. At about 13 Ma, there was a global deterioration of the climate, in relation to the onset of Antarctic glaciation. BARRON (1985b and in press), LOHMANN & CARLSON (1981) and BERGER (1970) worked on the hydrology of the Pacific Ocean for this period; I try to piece together their results for reconstructing the environment of the Middle – Late Miocene in the equatorial Pacific and its possible impact on *R. pseudoumbilica* and *R. minutula*.

○ After the onset of the Antarctic ice cap, Antarctic bottom waters invaded most of the Pacific. Between 13 and 11 Ma, the ABW (Antarctic Bottom Water) production increased and the ABW reached the central equatorial area; they were strong enough to erode sediments and prevent their deposition, which can explain the hiatus and the low rate of sedimentation. The erosive impact of the ABW seems to have been much stronger and more continuous in the westernmost part of the area (Sites 574 and 575); at Sites 573 and 572 (and at one level at Site 574), there were a few episodes of sedimentation which recorded the presence of both *R. pseudoumbilica* and *R. minutula* during this period; they were even abundant at Site 573. Thus, nannofossil assemblages were „normal" between 13 and 11 Ma in the whole equatorial area, which attests to "a free exchange of surface water masses between middle and low latitudes", as suggested by BARRON, 1985b.

○ At about 11,3 Ma, there occurred an increase of polar cooling which induced "a steepening of latitudinal thermal gradients by altering circulation patterns" and "a latitudinal provincialism" (BARRON, 1985b) in the southern Pacific. Hydrology is different in the eastern and western parts of the area; the two cannot be studied together:

a) in the central equatorial Pacific: the ABW was always erosive at Site 575: the hiatus lasts until 7,5 Ma. At the other sites, sedimentation resumed. *R. pseudoumbilica* and *R. minutula* were almost totally absent in the central part of the area

(Sites 573 and 574): it could be explained by the latitudinal provincialism. The environment might be unfavourable for the two species, due to the consequences of the strongest phase of the Antarctic glaciation. The two species disappeared from this part of the ocean, but they stayed in the vicinity, in southern tropical latitudes where the environment was favourable. This agrees well with the observations of HAQ & MALMGREN (1981/82) who found *R. pseudoumbilica* s. l. as a dominant species in the southern hemisphere, mostly during 15 to 10 Ma.

b) in the eastern equatorial Pacific: during the same period the Peru – Chile current (PCC) surfacing with the EUC (Equatorial undercurrent) brought southern cooler waters into the eastern equatorial area (WYRTKI, 1966); this was enough to "create an effective barrier" which prevented most of the dispersal of *R. pseudoumbilica* and *R. minutula*. Thus, some specimens of both species stayed at Site 574.

○ Between 10,5 and 8 Ma, the strength of the ABW diminished and sedimentation could start again everywhere. But henceforth the surface water circulation had changed in the Pacific:

a) "deep waters are produced in the Atlantic and Southern oceans and old deep waters upwell in North Pacific. This pattern was most intense 8–10 Ma ago" (BERGER, 1970).

b) "equatorial Pacific surface water circulation is the same as modern-day. They are warmer: it is presumably due to reorganisation of equatorial surface water masses in response to polar cooling" (BARRON, 1985b). Thus, during this period, the environment seemed to become favourable to nannoplankton at the Equator. Nevertheless, *R. pseudoumbilica* and *R. minutula* were still absent from the central equatorial Pacific.

It may be due to:

a) the instability of water temperature; according to LOHMANN & CARLSON (1981), there was still a temporary water cooling at 7 Ma;

and

b) the consequences of the previous latitudinal provincialism which was still predominant. For HAQ & MALMGREN (1981/1982) *R. pseudoumbilica* s. l was always dominant in the southern hemisphere, as a stock for a future expansion.

At the end of Late Miocene and up to Pliocene, modern-day surface water circulation was well established and upwelling phenomena expanded into the equatorial Pacific; the latitudinal provincialism disappeared. *R. pseudoumbilica* and *R. minutula* returned everywhere.

The appearance of *R. pseudoumbilica* was almost synchronous at all sites of Leg 85 (= 6,5 to 7 Ma) while *R. minutula* reappeared earlier (9 Ma) in the eastern area than in the central area (7,5 Ma). Thus, distributions of these two species (or specific groups) show some similarities and seem to react in the same manner to environmental changes. Nevertheless, *R. minutula* seemed to break the latitudinal provincialism slightly before *R. pseudoumbilica* i. e., its earlier appearance at the end of the Late Miocene could be explained in this way.

6. Results

The complexity of the medium and small-sized Reticulofenestrids is evident. To distinguish the various species with an optical microscope is difficult and it is necessary to have a lot of experience to do so. It is not easy to plot stratigraphical distributions from various papers on a latitudinal graph, but results are very encouraging and can be interpreted in a stratigraphical and ecological way.

6.1. Time-related Biogeographic Distributions

(Fig. 28)

The distributions of all the studied taxa can be interpreted logically, often in relation with a time-related thermal gradient. It is not possible to differentiate the oceans, but the latitudinal influence is evident in considering the whole World Ocean. There are five kinds of distributions:

1) Synchronous events
are the least numerous but the most important. They have to be taken as datums s. s.:

- LO of *R. pseudoumbilica* at 15–16 Ma
- HO of *R. pseudoumbilica* at 3,56 Ma (from BACKMAN & SHACKLETON, 1983)
- HO of *R. gartneri* at 15–16 Ma.

2) Some species have
almost synchronous HO;
their LOs present a latitudinal gradient: they appeared first in southern high-latitudes; then they colonized low latitudes and at last the northern high-latitudes.

- *R. doronicoides*:
  HO at about 0,5 Ma (PUJOS, in press)
  LO from 12 (in the South) to 2,5 Ma (in the North)
- *D. perplexus*:
  LO from the "Oligocene" in the South, via 15 Ma at the Equator, to 14 Ma in the North.
- *D. productus*:
  HO at about 1 Ma (PUJOS, in press)
  LO ..?.. (not found) in the South; from 11 Ma at the Equator, to 4–6 Ma in the North.
- *R. minuta*:
  HO at the Plio-Pleistocene boundary
  LO from at least the Early Oligocene in the southern mid latitudes, via 16 Ma at the Equator, to 10 Ma in the North.

2) Two groups have
an almost synchronous HO;
they appeared first at low latitudes and they colonized high latitudes later:

- *R. minutula*:
  HO at about 2–4 Ma
  LO from 10 Ma at the Equator to 6 Ma in the North; unknown in the South.
- the small *Gephyrocapsa*:
  HO at about 0,050 Ma (PUJOS, in press)
  LO from 11,5 Ma in some sites at the Equator to 0,5 Ma (in the South) and 2 Ma (in the North).

NB: The appearance of the small *Gephyrocapsa* cannot be interpreted as a consequence of the latitudinal thermal gradient but of some special local environment: the sudden arrival of surface cooler waters, for example.

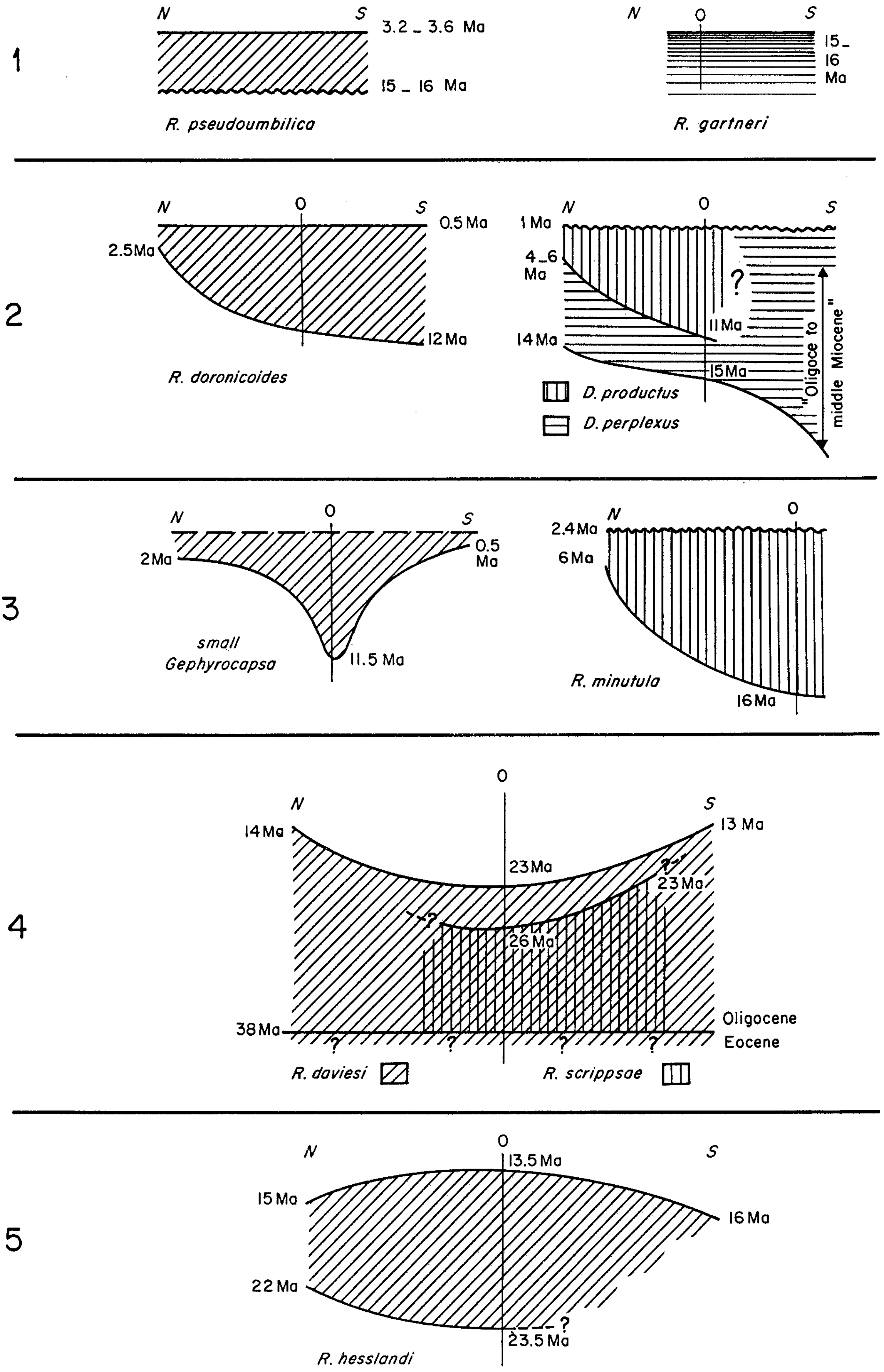


Fig. 28: Time-related latitude of the small- and medium-sized Reticulofenestrids (*R. hesslandi* must read *R. hesslandii*).

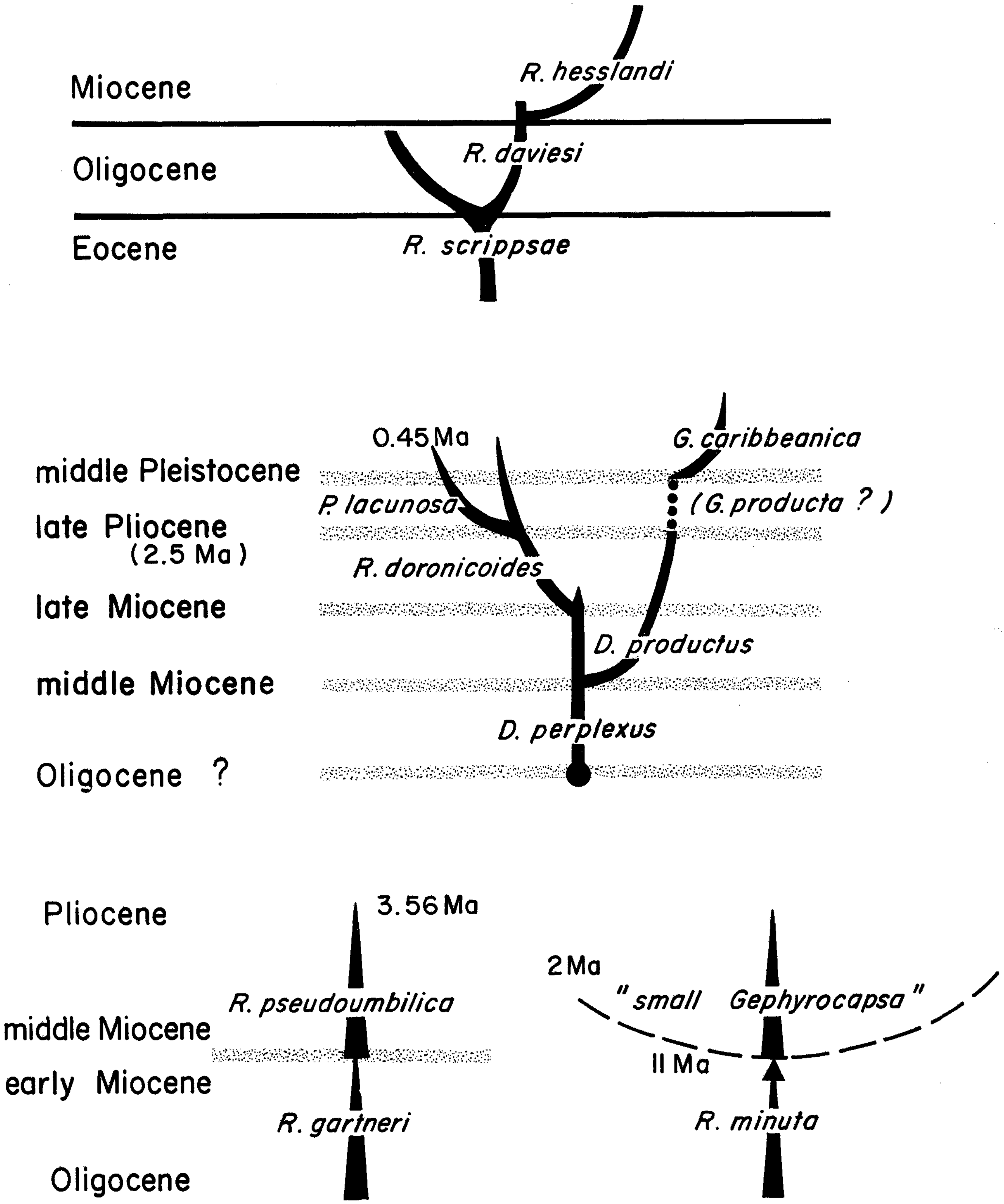


Fig. 29: Evolutionary trends (*R. hesslandi* must read *R. hesslandii*).

4) The *R. daviesi-scrippsae* group

is already present in the latest Eocene. It disappeared first at the Equator and later at middle and high latitudes:

- *R. scrippsae*:
  HO from 26 Ma at the Equator to 23 Ma at southern middle latitudes.
- *R. daviesi*:
  HO from 23 Ma at the Equator to 13–14 Ma at northern and southern high latitudes.

5) The spatio-temporal distribution of *R. hesslandii*

shows a longer presence of the species at the Equator (between 23,5 and 13,5 Ma) than at high latitudes (between 22 and 15–16 Ma).

These different spatio-temporal distributions can be interpreted in terms of thermal markers. *D. perplexus* is taken as a marker of southern cool waters; but it is also the case for *R. doronicoides, D. productus* and *R. minuta*, which show the same distribution trends. *R. pseudoumbilica* has synchronous LO and HO: is it enough to consider it as a cosmopolitan species? I showed that in the equatorial Pacific, this species disappeared between about 13 and 7,5 Ma, when the Antarctic glaciation expanded, which is the proof of the influence of an environmental parameter on this "cosmopolitan" taxon. Thus I think that there is not enough information to try to use the presence-absence of Cenozoic nannofossils as paleoenvironmental markers, with precision.

6.2. Evolutionary trends

(Fig. 29)

Some family trees can be attempted to establish among the Reticulofenestrids. They are drawn on Figure 29. The evolution *scrippsae* → *daviesi* → *hesslandii* is established in a group where it is not easy to separate the different species, because of their very close morphology. The tree which starts from *D. perplexus* and ends either with *G. caribbeanica* or with *P. lacunosa* confirms the results of several authors, such as SACHS & SKINNER (1973), PIRINI-RADRIZZINI & VALLERI (1977). The evolution from *R. minuta* to the "small *Gephyrocapsa*" is questionable: *R. minuta* has the same size range as the small *Gephyrocapsa*, and they relate well to each other. The transition between the two taxa may be due to the influence of sudden special environmental factors, which might occur at various ages, depending on the area. A possible lineage between *R. gartneri* and *R. pseudoumbilica* was already suggested by BUKRY (1973): "There may be a gradation from *R.* sp. cf. *gartneri* of lower zones to larger more oval *R. pseudoumbilica* in the zone (= Zone 4). Distinguishing the two species in this part of the range is difficult, suggesting that the two names refer to the same lineage". Although *R. gartneri* is rarely named in published papers, its disappearance always coincides with the appearance of *R. pseudoumbilica*, and their morphological characteristics are sufficiently alike for such a lineage.

7. Conclusion

The small and medium-sized Reticulofenestrids take a significant place in almost all the calcareous sediments, in all the oceans, since at least the very latest Eocene. The present study proved that they have to be observed much more than a "background". It is evident that naming them necessitates some care, but I demonstrated that the criteria employed could be very simple with an optical microscope; a simplified taxonomy is sufficient to obtain satisfactory stratigraphical and/or paleogeographical results with Reticulofenestrids.

Only very few species, which have synchronous highest or lowest occurrences, can be used as datums s. s. The other ones have their appearances spread out during several Ma between extreme latitudes. Such spatiotemporal distributions can be used almost as datums, because none of them has random appearances or extinctions. They are due to spatial migrations through time, related to the latitudinal environment gradient: cold water species appeared first at very high latitudes and then they colonized the middle and low ones; warm water species appeared at the Equator and then they migrated to higher latitudes. Most of the Reticulofenestrids disappeared almost synchroneously, at periods when major climatic events – such as the onset of the Antarctic and Northern glaciations – occurred. All these observations have to be further demonstrated in the future, but they emphasize the importance of the impact of the paleoclimate on the "birth" and "death" of the species.

Acknowledgements

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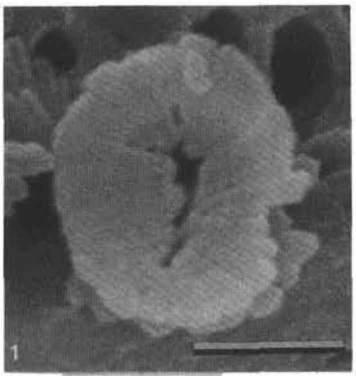
Plate 1

Figs. 1– 7: *Reticulofenestra minuta.*
Figs. 8–11,12a: *Reticulofenestra minutula minutula.*
Figs. 12b,18–21: *Reticulofenestra minutula haqii.*
Figs. 13–17: *Reticulofenestra doronicoides.*
Figs. 22–25: *Dictyococcites productus.*
Figs. 26–29: *Dictyococcites perplexus.*

Scale for SEM photos = 1 µm, for optical photos = 5 µm.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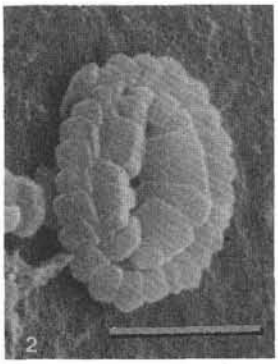
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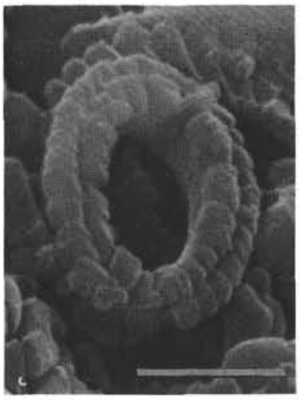
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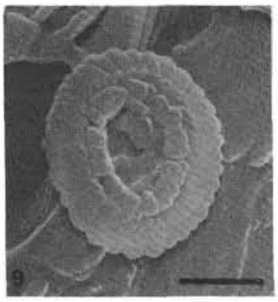
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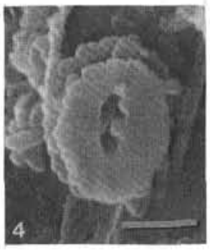
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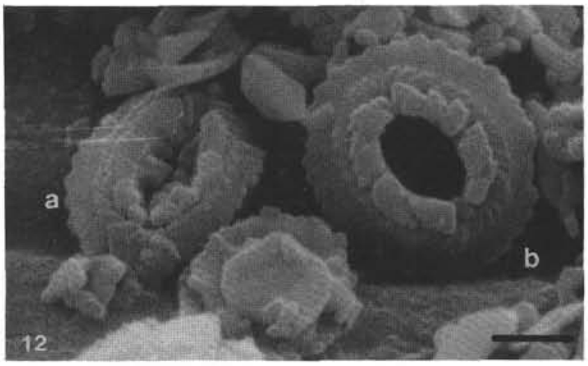

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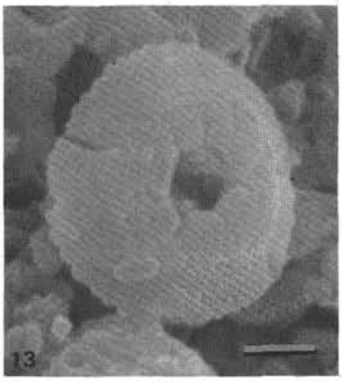
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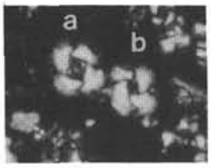

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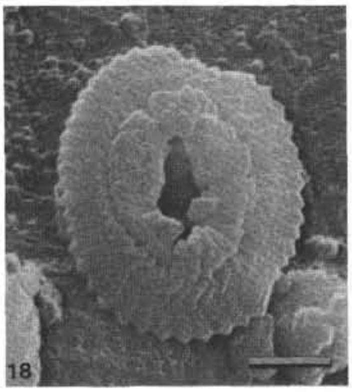
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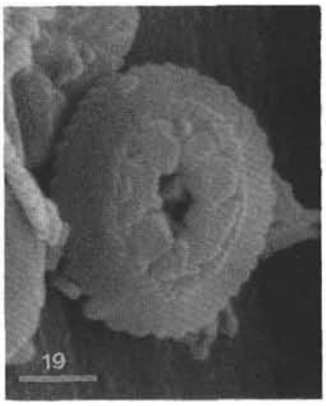
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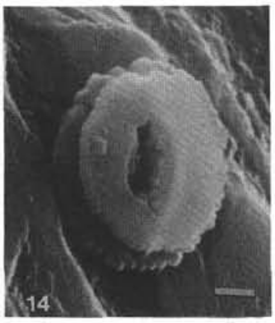
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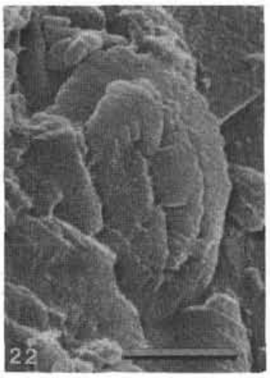
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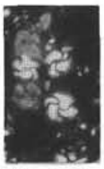
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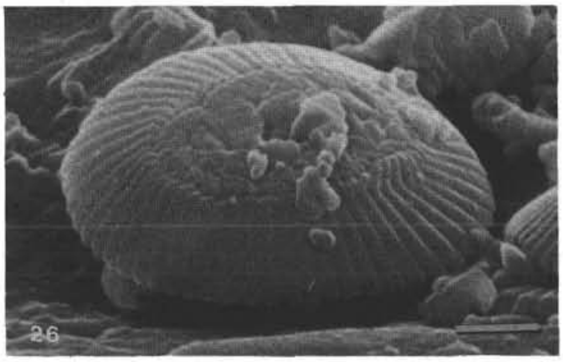
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Plate 2

Figs. 1– 3: *Reticulofenestra gartneri.*
Figs. 4– 8: *Reticulofenestra scrippsae* and *Reticulofenestra hesslandii.*
Figs. 9–12: *Reticulofenestra daviesi.*
Figs. 13–17,18a: *Reticulofenestra pseudoumbilica pseudoumbilica.*
Figs. 18b–c,19–22: *Reticulofenestra pseudoumbilica gelida.*
Fig. 23: *Reticulofenestra insignita.*

Scale for SEM photos = 1 µm, for optical photos = 5 µm.


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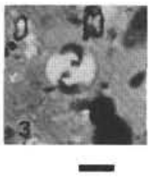
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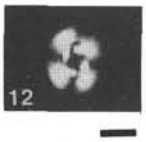
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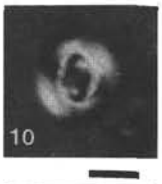
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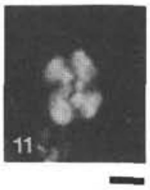
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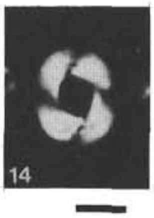
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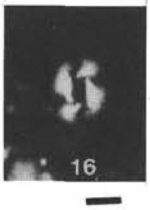
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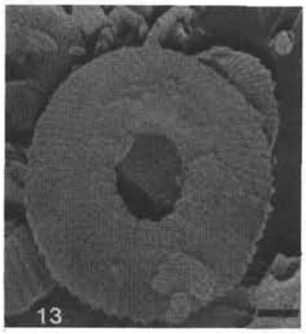
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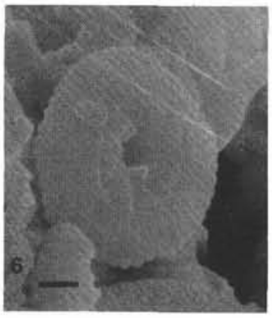
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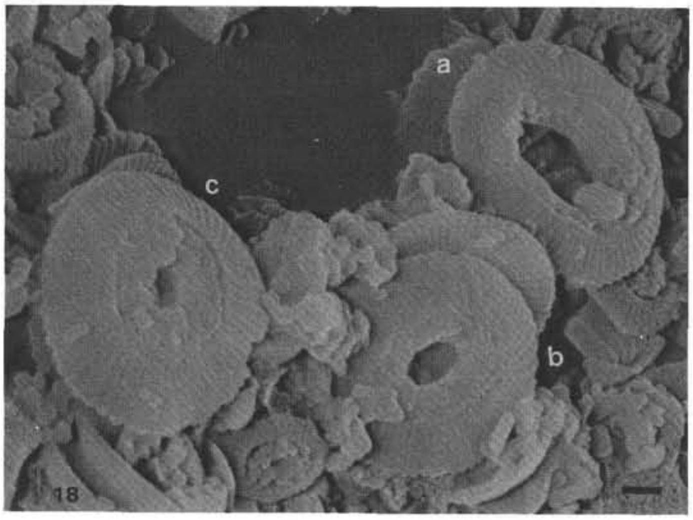
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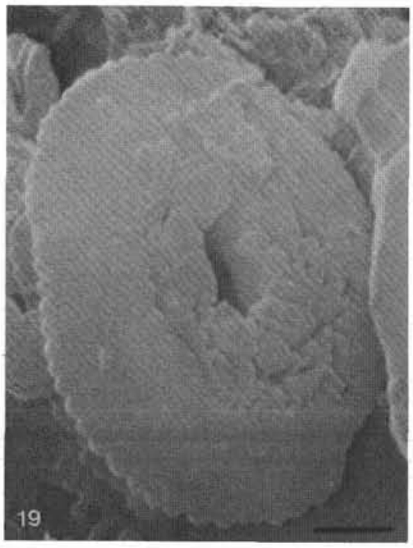
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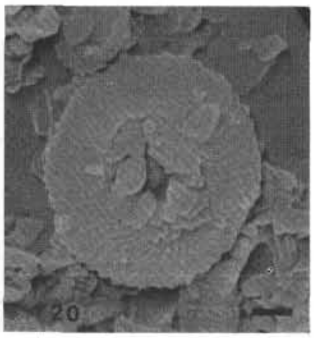
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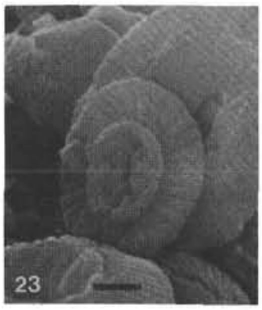
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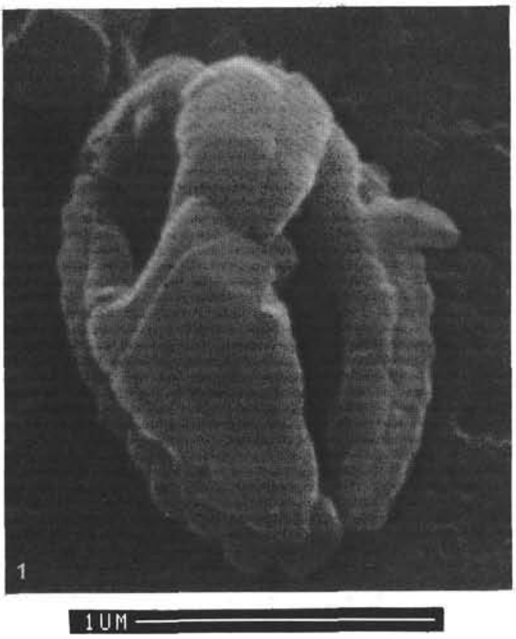
Plate 3

Gephyrocapsa theyeri n. sp.

Fig. 1 : Holotype.
85, Site 572, Hole A, 15–3, 0.1 cm.
Figs. 2–3 : Optical photo.
Figs. 4–4': Stereoscan photos of the holotype.

Scale for SEM photos = 1 µm, for optical photos = 5 µm.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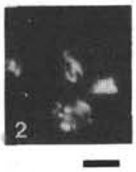
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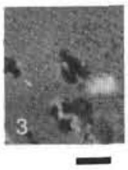
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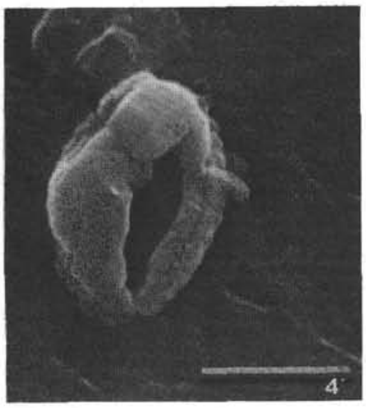
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