

Size variation of Neogene *Reticulofenestra* coccoliths from Indian Ocean DSDP Cores

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ABSTRACT - Data is presented here on *Reticulofenestra* coccolith size distribution patterns from 122 Mid-Miocene to Pliocene samples from Deep Sea Drilling Project sites in the Western Indian Ocean and Red Sea. A clear pattern is revealed with a dramatic size reduction event occurring in the Late Miocene (nannofossil zone NN10). As a result of this event nannofloras from the interval above it are readily distinguishable by the absence of specimens longer than 5 microns; this interval is termed the "small *Reticulofenestra* interval". Assemblages from above and below this interval contain large specimens but they can be reliably distinguished by different size distribution patterns within them. Analogous data from other studies is reviewed, possible causes of the pattern are discussed, and its biostratigraphic application described. The Neogene taxonomy of the genus *Reticulofenestra* is revised and four new combinations are proposed.

INTRODUCTION

Although there are excellent high resolution nannofossil zonations for the Neogene (Martini 1971, Okada & Bukry 1980, Theodoridis 1984) in practice they are often extremely hard to apply since many of the marker species used are rare, ecologically restricted, or vulnerable to diagenesis. In well preserved pelagic sediments these problems are not important, but in the less favourable conditions routinely encountered during applied work they can greatly reduce the biostratigraphic resolution. So it is of considerable interest to attempt to extract the maximum amount of information from the more common nannofossils. *Reticulofenestra* coccoliths are particularly promising since they are the most abundant and widespread element of the nannofloras, and are diagenetically resistant.

Biostratigraphic problems of this kind were encountered during a study of the Neogene of the Makran of Pakistan (Platt et al 1985). In consequence a study was made of reference samples from Indian Ocean Deep Sea Drilling Project (DSDP) cores. In particular *Reticulofenestra* size variation was systematically observed. This work provided strong evidence for a surprisingly simple, consistent, and useful pattern of size variation, as described here.

METHODOLOGY

Measuring Technique. All work was carried out using conventional light microscopy, and coccolith size was measured using an eyepiece graticule. At the highest magnification (x200) the graticule divisions corresponded to 0.64 microns on the specimen, which provided the limit of resolution. This is adequate for recording variation in maximum dimension, i.e. length, since there is wide variation in length (<3 to >10 microns). This resolution is inadequate, however, for investigating variations in form, since other parameters, such as

coccolith width, central area length or rim width correlate strongly with length (Backman 1980, Young 1989). Electron microscopy, or image analysis equipment, is needed to quantitatively investigate the residual variation in these parameters independent of length. Hence, in order to make measuring fast enough for routine work, only the single parameter of coccolith length was measured.

For each sample the length of about one hundred randomly selected specimens was measured. The technique was to measure about twenty specimens in one area of a slide, moving from one specimen to the nearest unmeasured specimen, then moving to another area of the slide. In all cases low density smear slides were used.

Taxa included. The *reticulofenestra* coccoliths form an homogeneous group distinguished by their structure and readily recognisable by both light and electron microscopy (Fig. 1). They dominate coccolith assemblages from the Eocene to the Recent. Genera are primarily distinguishable by central area and rim structure. In the Middle Miocene to Early Pliocene interval *reticulofenestra* coccoliths lack distinctive structures and show little variation other than in size and degree of central area closure. Variation in both these parameters is continuous and so it is difficult to deal with the group other than as a single plexus, the genus *Reticulofenestra*. Coccoliths with wall cycles that have grown inwards to close the central area are placed in a separate genus, *Dictyococcites*, by many authors (e.g. Haq 1971, Backman 1980, Pujos 1985, Perch-Nielsen 1985), but not by others (e.g. Wise 1983, Driever 1988, Gallagher 1989). I support the latter view since this variation is probably ecophenotypic: intermediates occur; the closed central area forms are more common at high latitudes (Burns 1975, Haq 1980, Backman 1980, 1984); similar variation occurs within the coccoliths of the living

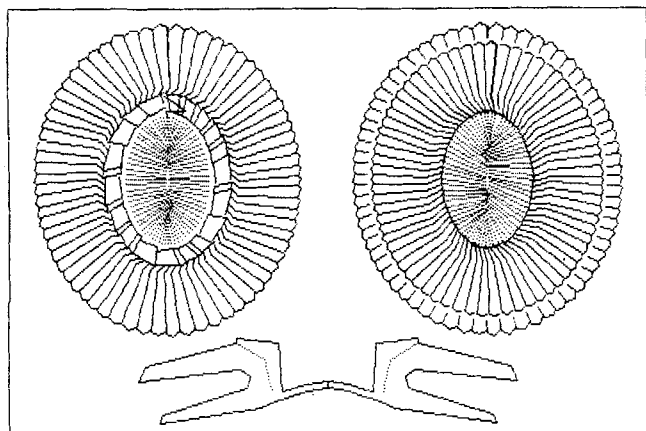


Fig. 1. *Reticulofenestra pseudumbilicus*. Computer generated illustration of a typical *R. pseudumbilicus* coccolith, seen in distal (left) and proximal (right) view, and in cross-section (below). In life the coccolithophore cell is surrounded by a coccosphere formed of several such coccoliths. The coccolith is constructed of a cycle of 30 to 60 intricate crystal units (Young 1989), but has a simple shape and shows little structural variability. Most other Neogene "species" of *Reticulofenestra* are essentially size defined variants of *R. pseudumbilicus*.

species *Emiliania huxleyi* (Burns 1977, Heimdal & Gaarder 1981, my obs). All encountered reticulofenestrids were included in the size counts of Middle Miocene to Early Pliocene assemblages. This had the advantage that selection of specimens for measuring was not dependent on subjective taxonomic assignments.

In the Late Pliocene there are distinctly different assemblages with the appearance of coccoliths with slits between the distal shield elements (*Reticulofenestra lacunosa*) and of coccoliths with a bridge across the central area (*Gephyrocapsa* spp.). *Gephyrocapsa* specimens were not included in the size counts but all members of the *Reticulofenestra minutula* - *Reticulofenestra lacunosa* group were included (see systematic taxonomy, and Fig. 9 for use of names).

Biostratigraphy. The samples were dated by combining data from the Initial Reports (Whitmarsh *et al.*, 1974, Fisher *et al.*, 1974, Simpson *et al.*, 1974, Davies *et al.*, 1974), subsequent studies (Theodoridis 1984), and my own observations (Young 1987). They were then assigned ages in Ma using the time scale of Haq *et al.*, (1987).

DATA PRESENTATION

The raw counting data is presented in Figures 3-5, without manipulation. Each diagram gives the data from a single DSDP site as a series of compressed size / frequency histograms for individual samples. On these histograms the horizontal scale is coccolith length and the vertical scale is relative frequency. Both scales are linear, and the size intervals are those recorded (i.e. increments of 0.64 microns). Only two adjustments have been made to the data, both primarily to cope with the occasional very abundant small specimens. First, abundances have been calculated relative to

the abundance of specimens over two microns, rather than of all specimens. Thus the presence of abundant small specimens in a sample does not depress the indicated abundances of the other specimens. Second, any relative abundances over 0.4 are rounded down to 0.4, this prevents histograms overlapping. Operator bias was reduced by performing all data reduction and plotting by computer.

The vertical positioning of the histograms within the diagrams is based on the age determined by conventional biostratigraphy. Nannofossil zones, chronometric ages and sample numbers (Core-Section) are given beside the vertical axes of the diagrams. Site locations are indicated on the map (Fig. 2).

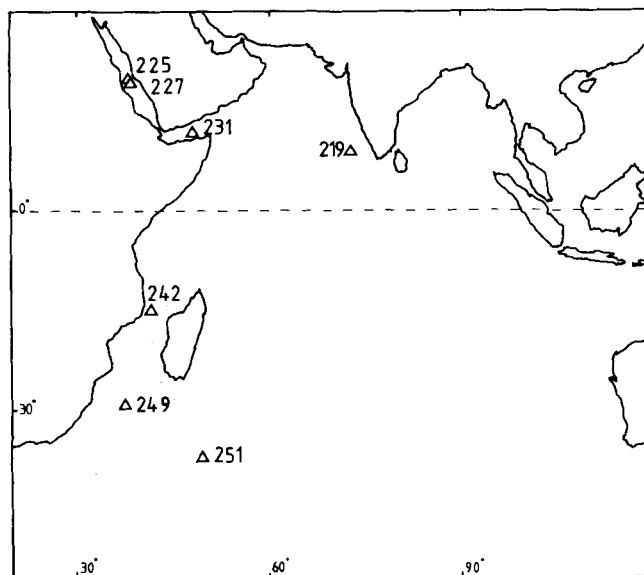


Fig. 2. The Indian Ocean. Map showing location of the Deep Sea Drilling Project Sites from which studied material came. Mercator projection.

RESULTS

Main Results, DSDP Sites 219, 223, 231, and 242

The results from the four sites with reasonably continuous successions are given in Figures 3 and 4. These are discussed together since the results are very similar in each case; even though the sites are separated by thousands of kilometres (Fig. 2). They can be subdivided into four intervals, as discussed below, with reference to the standard nannofossil zones of Martini (1971).

A. NN6 to early NN10. The size distribution patterns in all the samples from this interval show similar features. They are unimodal with a broad spread of sizes, typically 2-10 microns. Despite the general similarity of all the size distributions, a general trend can also be detected of size increase through this interval. This is shown particularly by variation in the modal length, maximum length is nearly constant. Thus although all samples contain significant numbers of specimens over 5 microns long these only constitute the majority of the assemblages in the later samples.

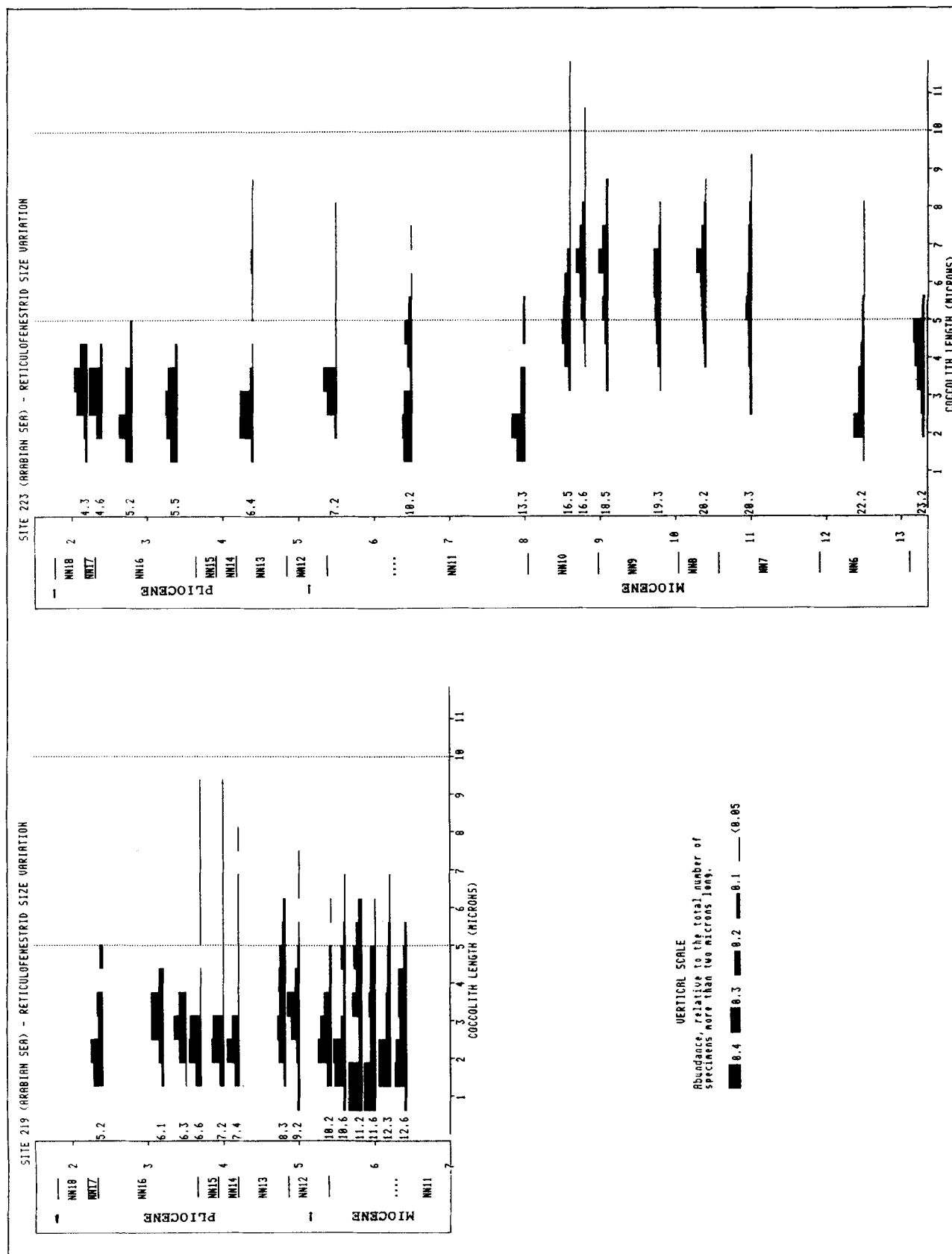


Fig. 3. Reticulofenestrid coccolith size variation with geological age, DSDP Sites 219 and 223. Data in left hand margins are geological periods, nannofossil zonation, age in Ma, sample reference (see text for details).

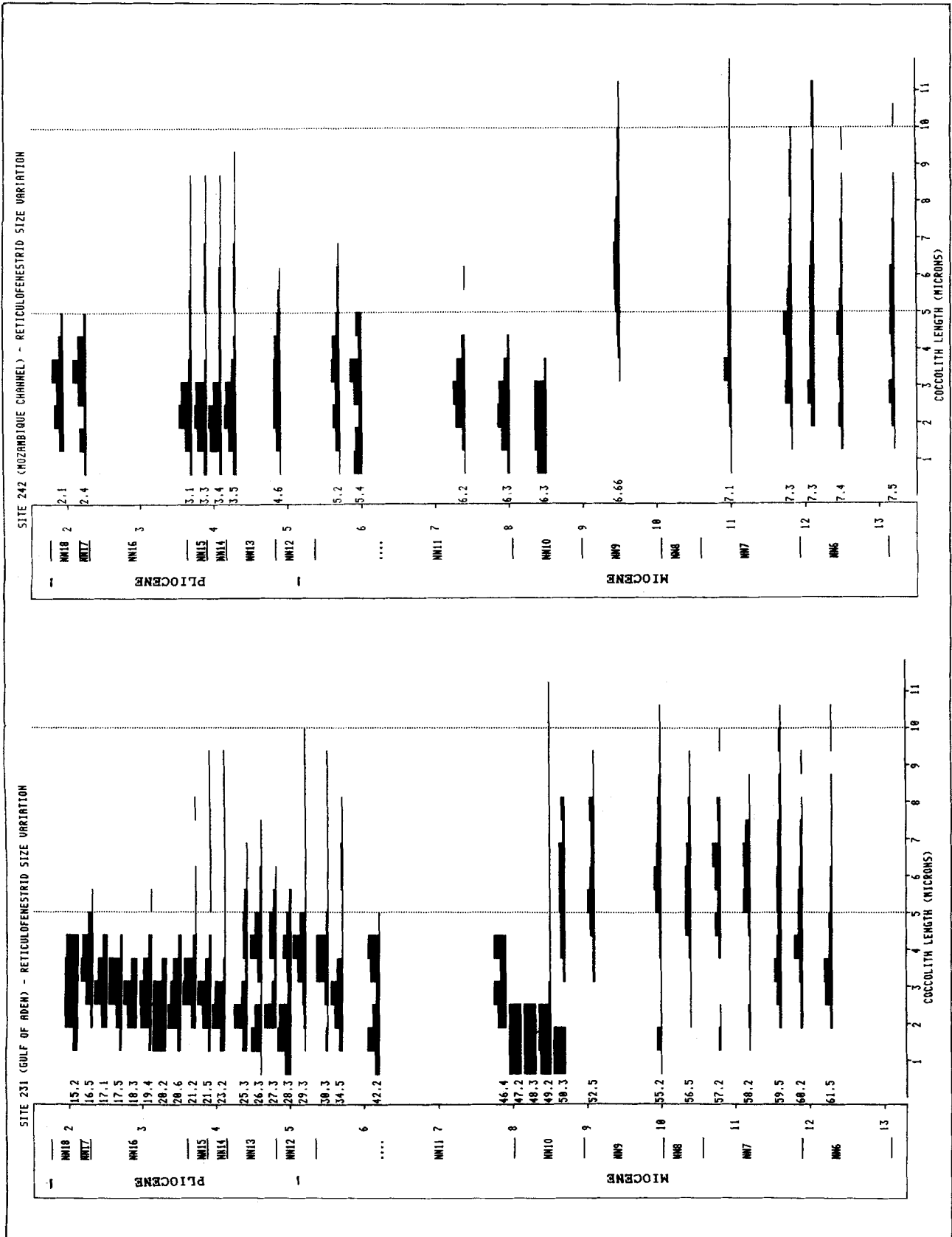


Fig. 4. Reticulofenestrid coccolith size variation with geological age, DSDP Sites 231 and 242. Date in left hand margins are geological periods, nannofossil zonation, age in Ma, sample reference (see text for details).

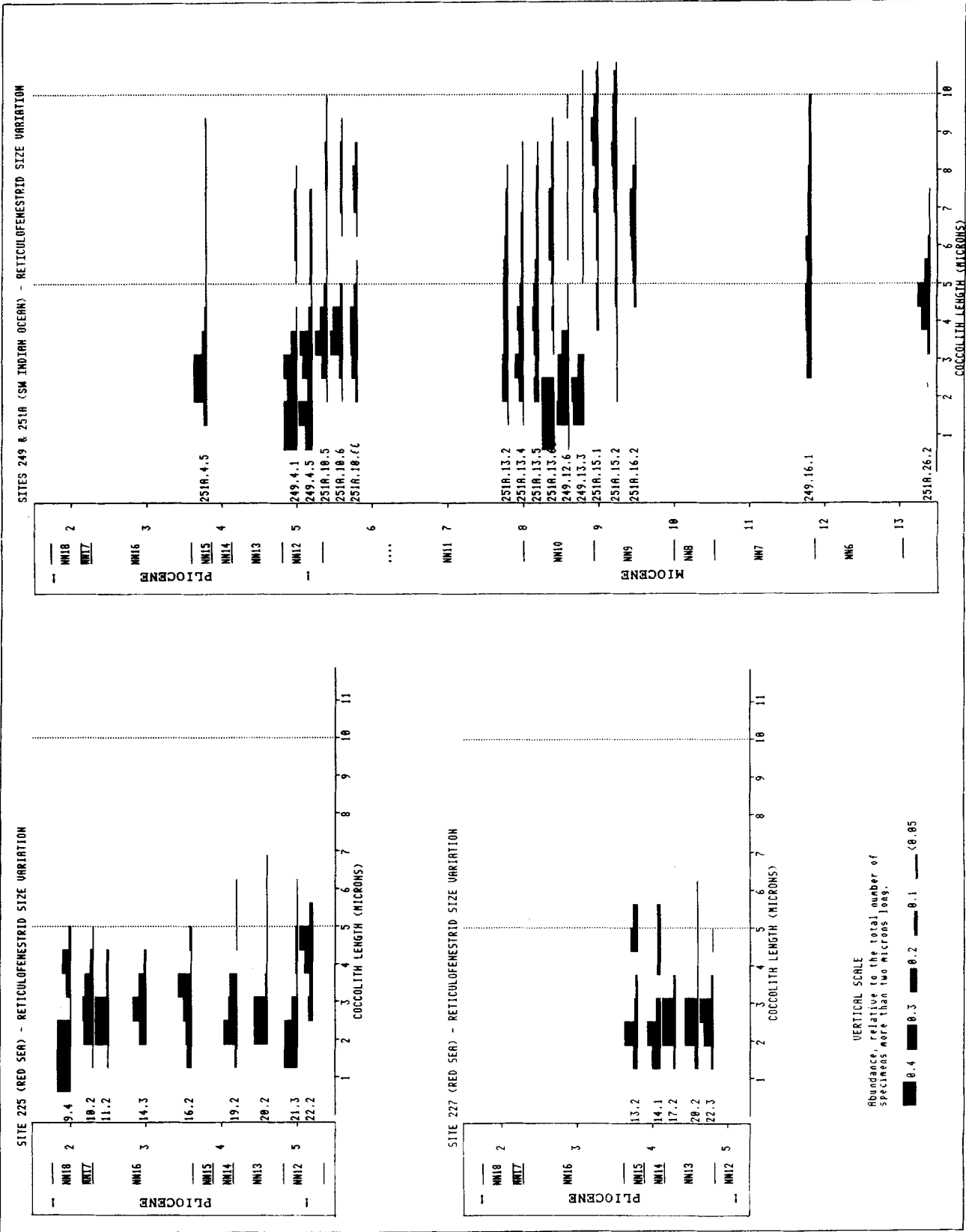


Fig. 5. Reticulofenestrid coccolith size variation with geological age, DSDP Sites 2225, 227, 249 and 251A. Data in left hand margins are geological periods, nanofossil zonation, age in Ma. sample reference (see text for details).

B. Late NN10 to early NN11 - "Small *Reticulofenestra* Interval". Within zone NN10 there is a dramatic decrease in maximum, minimum, and modal size, with coccoliths over five microns long virtually disappearing, and smaller specimens increasing in abundance (in both relative and absolute terms). The samples from this interval contain the most distinctive *Reticulofenestra* assemblages. For convenience I have termed it the "small *Reticulofenestra* interval", by analogy with the Pleistocene small *Gephyrocapsa* interval (Gartner 1977, Rio 1982).

C. Late NN11 to NN15. During this interval the reticulofenestrids again show a wide range of size variation, as in the first interval. The size distribution patterns, however, are strongly skewed toward the smaller specimens, so the bulk of specimens are always less than 5 microns long, and large specimens (>c.7microns) are always rare. Within the smaller size range several samples show evidence of bimodality with a frequency minimum around 3-3.5microns. It is thus possible to describe the *Reticulofenestra* coccolith assemblage in this interval as being formed of three components: very small coccoliths (<3microns); small coccoliths (3-5microns); and larger coccoliths (>5microns). There appears, however, to be a complete intergradation of morphology between the three groups.

There is some evidence of size increase through this interval, particularly in maximum length. However, this cannot be a simple uniform size increase trend since 7-10 micron long coccoliths are present in both top NN11 and NN14-15 age samples, but are generally absent from Earliest Pliocene, NN12-13 age samples. This is most clearly seen in Site 231 (Fig. 4), and was also noted in material from the Makran (unpublished data). The simplest interpretation is perhaps that there are two size increase trends separated by a minor size reduction event near the top of the Miocene. However, owing to the restricted number of samples and the low relative abundance of the larger specimens this suggestion can only be tentative.

D. NN16 to NN18, Late Pliocene. The last occurrence of *R. pseudumbilicus* (i.e. large *Reticulofenestra*) is the marker event for the NN15/16 boundary. In the data this is reflected by the absence of specimens over 5 microns above NN15 although as they are rare in any case this does not have a very marked effect on the appearance of the assemblages. In addition the subsequent assemblages are almost entirely unimodal, with the dominant size, 2.5-4 microns approximately corresponding to the frequency minimum in the previous bimodal distributions. Also larger specimens show distinctive "lacunosa" morphology (slitting between the rays of the distal shield, more open central area, and lower ellipticity).

Red Sea Sites, 225 and 227

The results from these sites (Fig. 5) are of some interest since the largest *Reticulofenestra* specimens are missing, possibly an ecological effect related to the restricted nature of the Red Sea at this time. Nonetheless the results are plainly

comparable to those from the other sites and the last occurrences of specimens over five microns are still apparent.

South West Indian Ocean Sites, 249 and 251A

The data from these sites (Fig. 5) is limited and of rather poor quality, in particular the biostratigraphy is not as good as for the other sites, and preservation is rather worse. I did not want, however, to exclude data which was contradictory to the general model presented.

The results from the NN6-NN9 interval (samples 251A-26-2 to 251A-15-1) are similar to those from the other sites. The small *Reticulofenestra* interval is arguably represented by samples 251A-13-6 to 249-13-3 but since there are some large specimens still present in these samples it is much less distinct than at the other sites. The three samples above these (251A-13-2 to 251A-13-5) have lower modal size than in the early samples, but again the presence of large specimens reduces this contrast. The youngest assemblages (Samples 251A-4-5 to 251A-10-CC) are similar to those of this age from the other sites.

The poor development of the small *Reticulofenestra* interval in this area may be an artifact related to the problems noted above. Alternatively it may be related to the higher latitude of these sites (35-40° as opposed to <25°).

COMPARABLE STUDIES

The last occurrence of large *Reticulofenestra* and the end of the Early Pliocene is well established as a global event, it forms an important datum in all Pliocene nannofossil zonations. Beyond this the literature contains few explicit indications that Neogene reticulofenestrids show systematic size variation patterns. There are, however, several studies which can be used to investigate whether the patterns described above also hold outside the Western Indian Ocean.

Other biometric studies. The most extensive biometric study published on Miocene reticulofenestrids is that of Backman (1980). He did detailed work mainly on the, high latitude, N. Atlantic DSDP Site 116. His work was, however, primarily taxonomic through time (Backman 1980, figs. 5 & 24) could be interpreted as giving evidence for a Late Miocene small *Reticulofenestra* interval, but is not directly comparable with mine [N.B. size data is given in terms of "placolith area", this parameter is undefined but appears to equal $2 \cdot 2.5 \times \text{length}^2$].

For the Pliocene Driever (1988) has recently completed a very detailed study using Mediterranean land sections. The Early Pliocene *Reticulofenestra* assemblages described are predominantly bimodal or negatively skewed - with abundant small specimens (<4microns) and rare large one (his figs. 18-25). Interestingly he found that the large specimens increased in size through the Early Pliocene (NN12-15); from about 5 to 9microns (his figs. 27-28,33). These results are in excellent agreement with my, limited, data for this period (Site 231, Fig. 4 and Section 3.1C).

Quantitative studies using detailed taxonomy. From his biometric work Backman (1980) proposed a rationalized subdi-

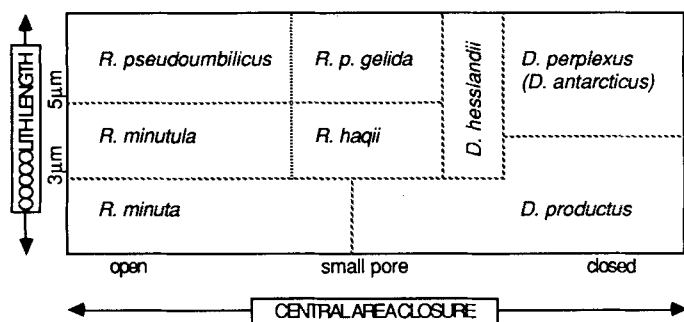


Fig. 6. Conventional taxonomic subdivision of Miocene *Reticulofenestra* coccoliths, after Backman (1980), Pujos (1987) etc. This classification subdivides the group according to coccolith length and degree of central area closure. Central area closure is probably an unstable ecophenotypic character and is not used in this paper. N.B. (1) The genus *Dictyococcites* is used for specimens with closed central areas. (2) *D. perplexus* and *D. hesslandii* are rarely reported above the Miocene. (3) *R. doronicoides* is usually used in place of *R. minutula* in the Late Pliocene. (4) The boundary sizes vary slightly between authors. (5) An emended version of this taxonomy is recommended in the systematics section (see also Fig. 9).

vision of the reticulofenestrids based on size and central area opening (summarised in Fig. 6). The scheme has been adopted by several authors, with only minor changes to the species definitions. Some of these have presented quantitative information on the species abundances which can be compared with my data.

Haq (1980) studied variations in nannofossil assemblages in 44 Miocene samples from 23 South Atlantic DSDP sites. The information is given in terms of principal components analysis so details are obscure, but major trends can be seen. The *R. pseudumbilicus* - *R. haqii* component shows a marked drop around 10Ma (probably within NN10; he uses an undefined time scale), with a correlative increase in the *D. minutus* component (his figs. 6 & 7). This could correspond to the start of the small *Reticulofenestra* interval. Lohmann & Carlson (1981) conducted a similar study of Pacific material, with arguably similar results, which they interpreted in terms of climatic control. Again, however, use of multivariate analysis and an uncorrelated numerical time-scale makes data re-interpretation tenuous.

Pujos (1985, 1987) recorded quantitatively variations in the abundance of reticulofenestrid species in samples from Central Pacific DSDP Sites 571-575, Leg 85. This is the most readily comparable study to mine and the results are very similar. There is a distinct small *Reticulofenestra* interval (*R. minuta* dominant, and *R. pseudumbilicus* absent) at all sites. Also the assemblages below are dominated by large to medium forms (*R. pseudumbilicus*, *R. minutula*, *D. perplexus* and *D. hesslandii*) whilst those above are characterised by small to medium forms (*R. minuta*, and *R. minutula* with rare *R. pseudumbilicus*). Unfortunately the relevant interval (NN9-early NN11) is represented by sediments which are stratigraphically

condensed and in which the marker discoaster species are rather rare. As a result of these factors the timing of events is rather uncertain but the *Reticulofenestra* assemblage development is at least broadly correlative with that seen in the Indian Ocean.

Routine Studies. Events as marked as the small *Reticulofenestra* interval might be expected to be detected during routine studies, however, in most cases only one or two divisions of the *Reticulofenestra* group are made and even semi-quantitative abundance information is not always given. Thus in the Indian Ocean DSDP reports the small *Reticulofenestra* interval can be discerned in the data given by Boudreaux (1974) for Site 223, but not in the data of Roth (1974) or Theodoridis (1984) for Site 231, or of Muller (1974) for Site 242. Of Indian Ocean Sites I did not study there is evidence for it at Site 214 (Gartner 1974), and possibly Site 220 (Boudreaux 1974). Outside the Indian Ocean the interval is discernible in the data of Jiang & Gartner (1984, DSDP Leg 74, S. Atlantic), and more ambiguously of Martini (1981, DSDP Leg 59, Central Pacific); but few of the reports checked contain suitable information from the relevant interval.

Analogous studies. Several workers have recently investigated size variation patterns in coccoliths of other ages and have found biostratigraphically dependable patterns, notably: Backman & Hermelin (1986), Palaeogene *Reticulofenestra*; Matsuoka & Okada (1989), Rio (1982), *Gephyrocapsa*; Girgis (1983), Maastrichtian *Arkhangelskiella*; Romein (1979), Palaeocene *Cruciaplacolithus*.

DISCUSSION OF THE SIZE VARIATION TRENDS

Validity and extent

If the size variation trends had only been documented from one site then they could have been interpreted as a preservational artifact, or even a random effect. However, since three well separated sites independently show virtually the same pattern the most reasonable explanation is that these patterns represent primary variation in the nannofossil population within the study area, i.e. low latitude Western Indian Ocean.

The evidence from published work, discussed above, is not conclusive but does suggest that the small *Reticulofenestra* interval is also discernible in the Eastern Indian Ocean (Site 214), the Central Pacific and the South Atlantic. The contrast between the NN6-9 interval (large *Reticulofenestra* dominated) and the NN11-15 interval (small *Reticulofenestra* dominated) is harder to detect in published records, but is shown in the data of Pujos (1985). The work of Driever (1988) suggests that Mediterranean *Reticulofenestra* size distribution patterns were similar during the Pliocene to those of the Indian Ocean.

At high latitudes the record is complicated by poorer dating, and by the presence of forms with closed central areas, nonetheless several authors have looked closely at reticulofenestrid coccoliths from high latitude material. So it is unlikely that an event as obvious as the small *Reticulofenestra* interval would have gone unnoticed.

In conclusion it seems probable, that the size variation

patters documented here may hold more or less universally at low latitudes (c.0-30°), but it is likely that they are at least modified at higher latitudes.

Possible Causes

The size variation patterns can be interpreted in a range of ways. The two extreme possibilities are, first, that they represent the effect of change in ecological factors such as climate on a genetically unchanging population. Second, that they reflect evolutionary change without environmental change. It is not possible to decide conclusively between these, and the spectrum of intermediate possibilities, without information on a range of other topics including: how widespread these changes are, particularly at high latitudes; the biological significance of coccolith size variation; and how climate changed during the Neogene. At present there is too much uncertainty in all these topics for conclusions based on them to be meaningful. Indeed arguments could be constructed from present knowledge to support either of the two extreme possibilities.

Nonetheless, since size range and modal size vary independently it seems reasonable to suggest that the patterns should not be interpreted in terms of a simple response to a single external factor, such as temperature. Also a simple ecological control might be expected to produce much less stable patterns. My suspicion is that the direct control is evolutionary, i.e. that the size variation patterns are a product of genotypic variation. An ecological influence (as opposed to control) is, however, extremely likely.

Taxonomic Interpretation

In the preceding discussion I have avoided taxonomic subdivision of the group, however, for many purposes taxonomy is essential. Unfortunately there are many different possible ways of dividing the group depending on both taxonomic philosophy and the causal interpretations discussed above. In Figure 7 three hypothetically possible schemes are illustrated based on rigorous application of different premises. In Figure 7/D a suggested compromise is given.

Purely morphological. In Figure 7/A a strictly morphological classification is shown based on convenient size divisions. This has the advantage of being objective and can be used to convey observations on size variation concisely and consistently. It is, however, an explicitly arbitrary classification which does not reflect any possible evolutionary trends.

Evolutionary, monospecific. Figure 7/B shows the very different result of using an age related classification based on the assumption that the events at the end of NN15 and within NN10 constitute natural breaks within an evolving lineage. This approach has the considerable advantage that all members of a single taxon of a single age are given the same name. It has the practical disadvantage that identical specimens of different ages may be assigned to different taxa and so can only be named when the age of the sample has been determined.

Evolutionary polyspecific. Figure 7/C shows a third possibility, based on the assumption that the variation is due to a number of separate taxa being present at most intervals. On this basis it is most important to describe the typical form of each taxon, and to trace how this varies through time. The definitions of boundaries between taxa are less important, since it is to be expected that some overlap in the size of taxa may occur. This model is only valid if the taxa are genuine species, which is by no means certain since despite occasional bimodality there is a continuous range of variation in size and other criteria do not provide independent support for division into these taxa.

Discussion, compromise scheme. Each of these schemes has some validity, and is attractive in some respects, and for some purposes; but a single scheme needs to be adopted in order that nomenclature has any meaning - note the very different extents of *R. pseudumbilicus* in the three diagrams (Figs. 7/A-C).

Separation of the larger specimens (>3microns) in the Late Pliocene group is almost certainly justifiable, since associated with the change in size variation is a parallel change in the structural variability of the group. In addition to simple reticulofenestrids *R. lacunosa* morphotypes appear, with slitted shields, lower ellipticity and wider central areas. Apparently an evolutionary change in the variation potential of the group occurred at this interval and so it seems wholly reasonable to divide the lineage at this level, as on Figure 7/B. Identical coccoliths nonetheless do occur above and below the boundary.

In the NN11-NN15 interval the three-fold *minuta* - *haqii* - *pseudumbilicus* division as proposed by Backman seems to be justified by the data, although due to the presence of intermediates between these groups and the lack of independent evidence for them being separate I am inclined to regard them as varieties rather than species.

In the NN6-NN9 interval these divisions have less justification. The five micron division between *R. haqii* and *R. pseudumbilicus* often corresponds to the peak of the unimodal size frequency distributions of this interval. Thus it is tempting to use different taxonomy for this interval, as per Figure 7/C. However, there is no independent evidence that the small *Reticulofenestra* interval is an evolutionary event, so this approach which requires the creation of new taxa, or radical revision of the definitions of old ones, would be premature. If further research proves that the small *Reticulofenestra* interval is an evolutionary break, as suggested in Figures 7/B,C it would then be appropriate to revise the taxonomy. For the present I suggest the compromise indicated on Fig. 7/D, applying perhaps artificially, the Late Miocene-Pliocene taxa to this interval since they do permit objective description of the assemblages, and can be used to investigate the changes in them.

Biostratigraphic use

Biostratigraphic application is more straightforward than

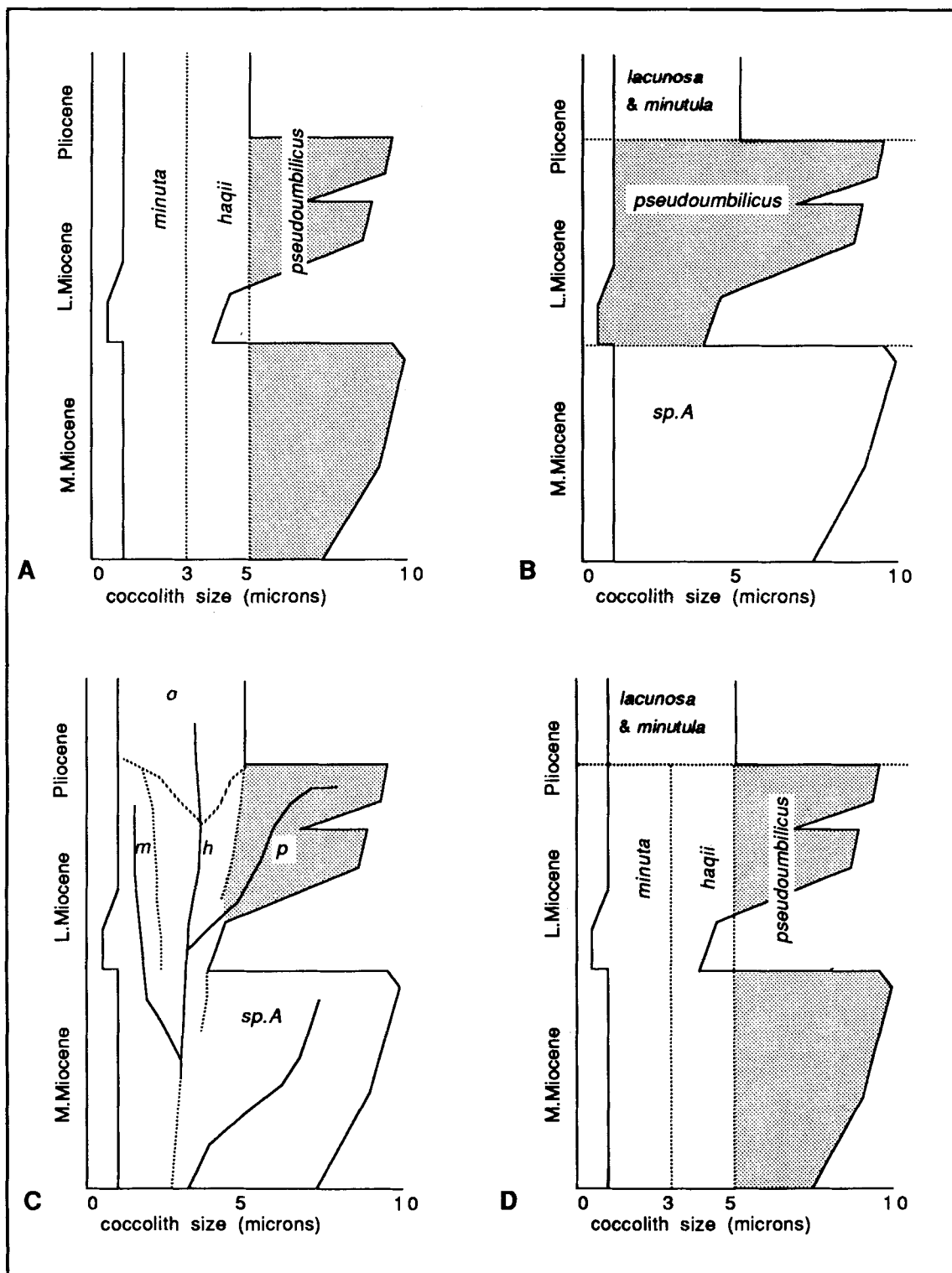


Fig. 7. Taxonomic interpretations of reticulofenestrid size variation. Four possible subdivisions of the Middle Miocene to Pliocene *Reticulofenestra* plexus, see text for discussion. In each diagram the size variation pattern observed in this study is indicated by the solid outline, dotted lines represent possible taxonomic subdivisions of this morphology-time space.

- A. Purely morphological subdivision.
- B. Evolutionary subdivision, assuming a single species, and that pattern is universally valid.
- C. Evolutionary subdivision, assuming a several species are present, and that pattern is universally valid.
- D. Proposed compromise scheme.

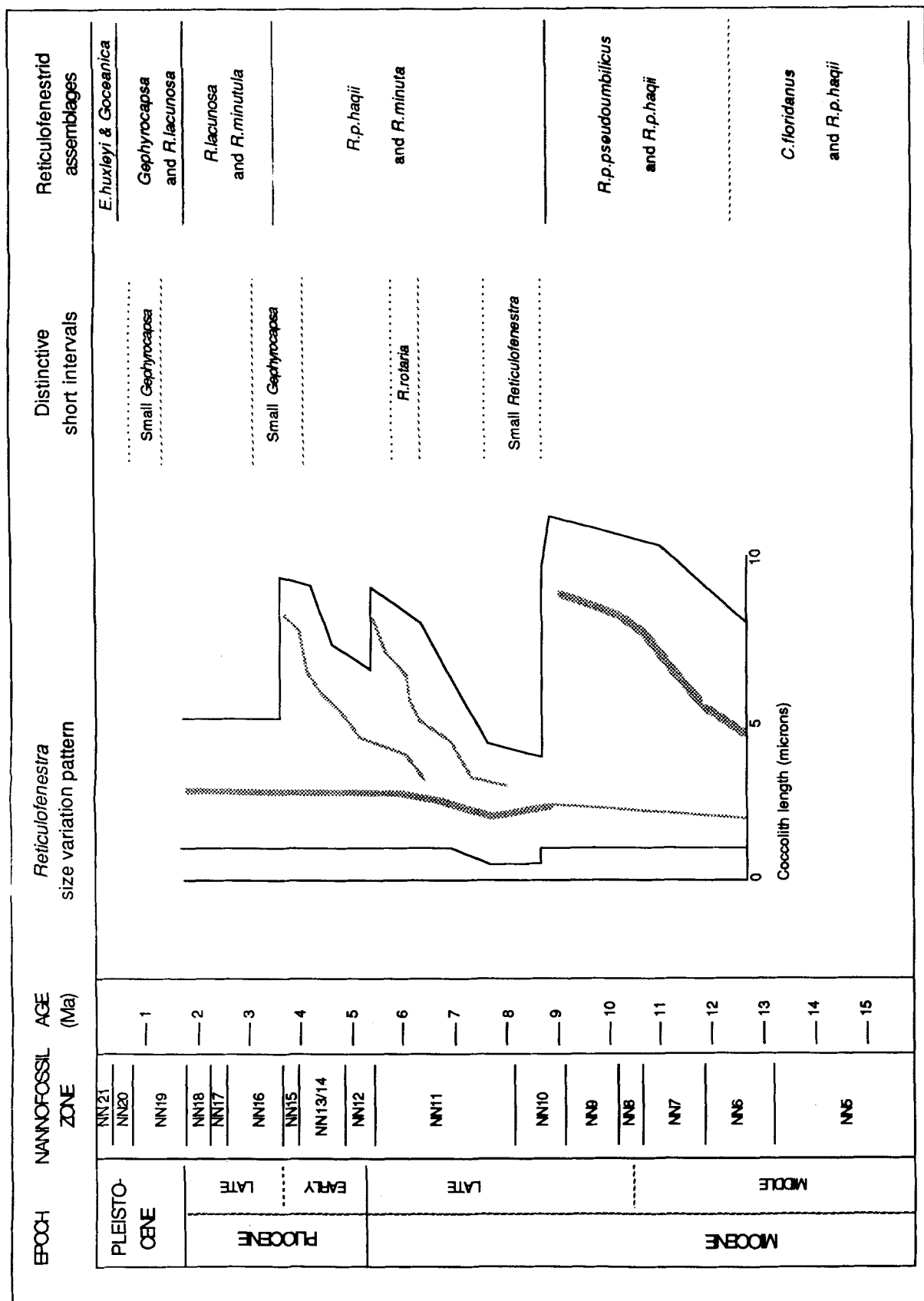


Fig. 8. Summary of biostratigraphic information available from reticulofenestrinids in Middle Miocene to Recent. Size variation pattern from data presented and reviewed here, stippled lines indicate shift in modal sizes. Short intervals indicate shifts in assemblages (see text). Reticulofenestrinid assemblages; dominant reticulofenestrinid taxa, synthesis from this paper. Within the Quaternary additional information can be retrieved from variation in *Gephyrocapsa* populations (Rio 1982, Matsuoka & Okada 1989).

taxonomic or casual analysis, since the patterns can be applied independently of any interpretations, although it would be nice to have a theoretical basis. Figure 8 summarises the biostratigraphic data available in the mid-Miocene to Recent interval, from reticulofenestrids. Some published information not discussed above is included in this synthesis. Five main assemblages can be recognised:

A. *Cyclicargolithus floridanus* and medium *Reticulofenestra pseudumbilicus*, NN5-6. Assemblages characterised by *C. floridanus* and medium (c.5micron) *R. pseudumbilicus*. *C. floridanus* dominates Oligocene and Early Miocene nanofloras then is rather gradationally replaced by *R. pseudumbilicus*. The last *C. floridanus* specimens occur in NN6 (Theodoridis 1984, my obs.).

B. Medium and large *Reticulofenestra pseudumbilicus*, NN6-9.

Assemblages dominated by specimens >4microns long. There appears to be a gradual increase in modal size during this interval, although maximum size does not change greatly.

C. Small and medium *Reticulofenestra*, NN10-15. Assemblages dominated by specimens <5microns long with a tail of larger specimens. Within this episode the small *Reticulofenestra* interval is characterised by absence of large specimens, and by very low modal size. Near the top of NN11 there is a short interval in which nearly circular *R. pseudumbilicus* specimens, *R. p. rotaria*, are present (Theodoridis 1984, my obs.).

D. *Reticulofenestra minutula* and *R. lacunosa*, NN16-18. Assemblages dominated by the *R. minutula* - *lacunosa* species plexus (*R. minutula*, *R.l. ovata*, *R.l. lacunosa*). These are less than 5 microns long in the Pliocene, and the most extreme form, *R.l. lacunosa*, has very characteristic morphology. In addition small (<3micron) *Gephyrocapsa* specimens are often present. This is particularly so in NN15 and the lowest part of NN16 (Samtleben 1978, Driever 1988, my obs.). The transition from *R. pseudumbilicus* to *R. minutula* - *lacunosa* (+*Gephyrocapsa*) flora is complex and gradational in detail (Driever 1988).

E. *Gephyrocapsa*, NN19-21. Assemblages dominated by *Gephyrocapsa* spp. with *E. huxleyi* in the youngest and *R. lacunosa* in older assemblages. This interval has been well studied and a very high resolution largely reticulofenestrid based zonation developed (Gartner 1977, Raffi & Rio 1979, Samtleben 1980, Matsuoka & Okada 1989).

For high resolution biostratigraphy the most interesting new feature in the floral sequence is the sharp drop in size at the beginning of the small *Reticulofenestra* interval. This seem to occur consistently within zone NN10. If it proves to be widely recognisable it should form a valuable addition to the standard nannofossil zonations. The minor *R. p. rotaria* and mid-Pliocene small *Gephyrocapsa* intervals may also prove useful (cf. Theodoridis 1984, Driever 1988). The general succession of assemblages is probably too gradational for high resolution work. Nonetheless it can be used for low resolutional work, to crudely date problematic samples or, more realistically, to test tentative age assignments based on

other criteria. It proved of real utility in this way in later studies of Makran material. For such dating it is not usually necessary to measure systematically a large number of specimens, since the distribution patterns are very different between the assemblages. A graticule is of course essential.

PRINCIPAL CONCLUSIONS

1. There are consistent variations in the size-frequency distribution patterns of *Reticulofenestra* coccoliths in the Neogene of the Western Indian Ocean.

2. The most prominent feature of this variation, the "small *Reticulofenestra* interval" can be detected in the data of other workers and is probably a widespread low-latitude event.

3. The *Reticulofenestra* coccoliths from above and below this interval show different size distribution patterns, but otherwise seem to be morphologically similar.

4. The start of the small *Reticulofenestra* interval, and the contrast in assemblages above and below it, have real biostratigraphic use, as a supplement to existing schemes.

5. Further work on this topic is needed to determine the extent, causes and taxonomic significance of the changes.

6. The success of this study suggest that equivalent studies on other nannofossil groups may be worthwhile.

SYSTEMATIC DESCRIPTIONS

The nomenclatural taxonomy of *Reticulofenestra* is extremely, confused, so discussion is needed here (see also Backman 1980, Pujos 1987, Driever 1988, Gallagher 1989). The system presented is based on the premise that if it is useful to arbitrarily sub-divide a continuous plexus then it is better to distinguish the taxa as varieties than species, this aspect is further discussed elsewhere (Young 1987, and in prep.). The scheme is summarised in Figures 7/D and 9. Only the genus *Reticulofenestra* is discussed here, and only Neogene species.

Interval	species	varieties	diagnoses
LATE PLIOCENE	<i>R. lacunosa</i>	<i>R.l. lacunosa</i>	>12 slits
		<i>R.l. ovata</i>	1-12slits
	<i>R. minutula</i>		no slits
EARLY PLIOCENE - MIOCENE	<i>R. pseudumbilicus</i>	<i>R.p. rotaria</i>	circular
		<i>R.p. haqii</i>	3-5µm
		<i>R.p. pseudumbilicus</i>	>5µm
	<i>R. minuta</i>		<3µm

Fig. 9. Summary of taxonomic subdivision of Neogene *Reticulofenestra* coccoliths as proposed in this paper.

CLASS Prymnesiophyceae Hibberd 1976
FAMILY Noelaerhabdaceae Jerkovic 1970

Family including *Noelaerhabdus*, *Reticulofenestra*, *Gephyrocapsa*, *Cyclicargolithus* etc., Synonyms Prinsiaceae, Gephycapsaceae. Since the family includes the Palaeogene genera *Toweius* and *Prinsius* which have rather more complex structures the term reticulofenestrids is used informally in this paper to designate the Neogene members of the family.

Genus *Reticulofenestra* Hay, Mohler & Wade 1966

As discussed above there is a major evolutionary change in reticulofenestrid assemblages around the NN15/16 boundary and so it is convenient to divide the *Reticulofenestra* lineage at this point, using different species names above and below the boundary, even though some morphotypes may be indistinguishable. The two segments of the lineage are discussed separately.

1. MID-MIOCENE AND EARLY PLIOCENE SPECIES

This segment of the lineage is divided by the small *Reticulofenestra* interval, but it is impossible to distinguish individual coccoliths from above and below the small *Reticulofenestra* interval and it is quite possible that the larger forms became geographically restricted during the small *Reticulofenestra* interval, rather than extinct. So the same taxonomy is applied throughout this time period.

Reticulofenestra minuta Roth 1970

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.

Description. Very small elliptical *Reticulofenestra* species, less than 3 microns long.

Dimensions. 1.5-3 microns.

Remarks. The holotype of this species is Oligocene, but the epithet has been extensively used in this sense. In some samples *R. minuta* appears quite distinct from *R. p. haqii*, in others there is a complete morphological gradation.

Coccoliths taganus Fonseca 1976 is similar, but with a closed central area. In the Late Pliocene and Pleistocene *R. minuta* is largely replaced by the small *Gephyrocapsa* plexus.

Reticulofenestra pseudumbilicus (Gartner 1967) Gartner 1969

Remarks. This species varies considerably in size, so it is convenient to subdivide it into two varieties. Forms with closed central areas are of importance at high latitudes, and a parallel set of varieties might usefully be used for them.

Reticulofenestra pseudumbilicus Gartner 1967 var. *pseudumbilicus*

1967 *Coccolithus pseudumbilicus* Gartner: 4, pl. 6, Figs. 1-4.

1969 *Reticulofenestra pseudumbilicus* Gartner: 598, pl. 2, Fig. 4.

Description. Medium to large elliptical variety of *R. pseudumbilicus*, over 5 microns long.

Remarks. The holotype of *R. pseudumbilicus* was described from Pliocene sediments of probable NN15 age.

Dimensions. 5-10 microns (occasionally up to 12 microns).

Reticulofenestra pseudumbilicus var. *haqii* Backman 1978 n. stat.

1978 *Reticulofenestra haqii* Backman: 29, pl. 1, Figs. 1-4, pl. 2, Fig. 10.

1978 *Reticulofenestra* sp. Haq & Berggren: 1190, pl. 1, Figs. 23-26.

Description. Small elliptical variety of *R. pseudumbilicus*. **Dimensions.** 3-5 microns

Remarks. The name *R. minutula* is often used in this sense but the holotype of *R. minutula* has a wide central area and reduced ellipticity, the paratypes have slitted shields, and *R. lacunosa* occurred in the type material. I believe it is a member of the *R. lacunosa* group. So use of the epithet *minutula* is not appropriate for *R. pseudumbilicus* varieties.

Reticulofenestra pseudumbilicus var. *rotaria* (Theodoridis 1984). n. stat.

1984 *R. rotaria* Theodoridis: 85, pl. 5, Figs. 1-4.

Description. Medium sized, circular, or very weakly elliptical, variety of *R. pseudumbilicus* with a wide central opening.

Dimensions. 5-7 microns

Remarks. The shape of this species sharply distinguishes it from normal *R. pseudumbilicus*. Nonetheless it is identical in other respects and intermediates between the two varieties occurred in all the samples in which I found it. Hence I consider it a variety of *R. pseudumbilicus* rather than a separate species.

Range. Short interval near the top of the NN11 Zone (= *R. rotaria* subzone of Theodoridis 1984), my observations agreed well with those of Theodoridis.

2. LATE PLIOCENE SPECIES

Within the Late Pliocene there are three basic reticulofenestrid morphotypes; forms with a bridge over the central area, *Gephyrocapsa*; forms with slits in the distal shield, variously termed *Pseudoemiliania lacunosa*, *Emiliania ovata* and *E. annula*; and simple forms with neither bridge nor slits, usually termed *Reticulofenestra minutula* or *R. doronicoides*. *Gephyrocapsa* is not discussed here, the other two forms are.

The presence of slits in the distal shield has been taken as a genotypic character, however, there is a continuous variation from large sub-circular coccoliths with many slits through medium sized moderate ellipticity coccoliths with a few slits to small elliptical coccoliths with no slits (McIntyre *et al.*, 1967, Samtleben 1979, Young 1989). This appears to be a good example of an allometric relationship between coccolith size and morphology within one species. It is quite different to the size - morphology relationship in *R. pseudumbilicus*, where increasing size results in minimal morphological change. Uniting all the forms as varieties of one species is tempting but would result in confusing nomenclature, and there is evidence that in the Pleistocene the forms become distinct. However, the continuity of the variation certainly makes it inappropriate to place the forms in separate genera. For this reason they are all placed in *Reticulofenestra*.

Reticulofenestra minutula (Gartner 1967) Haq & Berggren 1978.

non Coccolithus daronicoides Black & Barnes 1961: 142, pl. 25, Fig. 3.

- 1967 *Coccolithus minutulus* Gartner: *partim*: 3, pl. 5, Figs. 3-4.
 1971 *Gephyrocapsa reticulata* Nishida: 150, pl. 17, Figs. 1-7.
 1973 *Crenolithus daronicoides* (Black & Barnes); Roth: 731, pl. 3, Fig. 3.
 1978 *Reticulofenestra minutula* (Gartner); Haq & Berggren: 1190.
 1979 *Crenolithus daronicoides* (Black & Barnes); Samtleben: 919, pl. 3, Figs. 4,9,10.
 1979 *Reticulofenestra japonica* Nishida (*non. substit. pro G.reticulata*); 105, pl. 1, Figs. 1-3.
 1980 *Reticulofenestra japonica* Nishida; Nishida: 105, pl. 1, Figs. 1,5,17.
 1980 *Reticulofenestra minutula* (Gartner); Backman: 59, pl. 7, Figs. 3-5, 11,13.
 1985 *Reticulofenestra daronicoides* (Black & Barnes); Pujos (*invalid*): 594, pl. 1, Fig. 7.
 1987 *Reticulofenestra daronicoides* (Black & Barnes); Pujos: 247, pl. 1, Figs. 13-17.
 1988 *Reticulofenestra minutula* (Gartner); Driever: 117, pl. 1, Fig. 1, pl. 5, Figs. 3-6.
 1988 *Reticulofenestra daronicoides* (Black & Barnes); Young 1988:4.

Emended Diagnosis. Small elliptical *Reticulofenestra* species, without slits in the distal shield.

Dimensions. 3-5microns

Remarks. *R. minutula* specimens usually have wider central areas than typical *R.p.haqii* specimens, but this distinction is not of much practical use, distinction of the two is primarily by means of associated larger coccoliths.

The epithet *daronicoides* has often been used for this species, but the true identity of the holotype of *Coccolithus daronicoides* has been in doubt (Backman 1980). To resolve this point the topotypic material, Challenger dredging 338, was re-examined. The material is calcareous ooze with a well preserved Holocene nannoflora, and virtually no reworked Neogene material. The "discoasters" referred to in Black & Barnes (1961) are in fact coccoliths of the extant species *Hayaster perplexus*.

The only coccoliths matching the illustration and description of *C.daronicoides* appear to be specimens of *Gephyrocapsa oceanica* which have lost their bridge. So *C.daronicoides* should be considered a junior synonym of *G. oceanica*. This leaves *R minutula* as the name with priority.

Reticulofenestra lacunosa (Gartner 1969, ex Kamptner 1963) n.comb.

- 1963 *Ellipsoplacolithus lacunosus* Kamptner: 172, pl. 9, Fig. 50.
 1969 *Pseudoemiliana lacunosa* (Kamptner); Gartner: 595, pl. 2, Figs. 9-10.

Description. Species of *Reticulofenestra* with a variable number of irregular slits in the distal shield.

Remarks. Kamptner (1963) described *Ellipsoplacolithus lacunosus* as a paraspecies (provisional taxon), and so it was invalid (Loeblich & Tappan 1967). Gartner (1969) used the

epithet in a non-provisional sense, and as the type species of his genus *Pseudoemiliana*. The validity of this has been disputed (Loeblich & Tappan 1970, Gartner 1977), leading to rather variable taxonomic usage. Careful re-examination of the original descriptions in the light of the latest version of the ICBN (Greuter *et al.*, 1988) suggests that Gartner (1969) did validate *lacunosa*, and so this epithet does have priority over *ovata*, (S.E. van Heck pers comm 1989, and in press).

The species is strongly variable and there is a tendency for the larger more circular forms with more slits to become more common through time. So it is sometimes useful to divide the species; the degree of slitting is visible by light microscopy in reasonably well preserved material, and forms the most convenient arbitrary criterion for division.

Reticulofenestra lacunosa (Gartner 1969 ex Kamptner 1963). n.comb. var. *lacunosa*

- 1963 *Ellipsoplacolithus lacunosus* Kamptner: 172, pl. 9, Fig. 50.
 1969 *Pseudoemiliana lacunosa* (Kamptner); Gartner: 598, pl. 2, Figs. 9-10.
 1971 *Emiliana annula* (Cohen); Bukry: 1971, 1514.
 1977 *Pseudoemiliana lacunosa* (Kamptner); Gartner: 15, pl. 4, fig. 3.
 1979 *Pseudoemiliana lacunosa* (Kamptner); Samtleben: 919, pl. 3, figs. 2, 5, 12.
 1980 *Pseudoemiliana lacunosa* (Kamptner); Nishida: pl. 1, Fig. 13.
 1988 *Emiliana ovata* Bukry 1973; Driever (*partim*): pl. 6, Figs. 6-11, pl. 7, Figs. 1, 2, 5, 6, 8.

Emended Diagnosis. Circular to sub-circular variety of *R. lacunosa* with more than twelve slits in the distal shield.

Remarks. Use of the epithet *annula* for this form was based on misidentification of the holotype of *Cyclococcolithus annulus* Cohen 1964, which was probably a specimen of *Neosphaera coccolithomorphia* Lecal-Schaudler (1950). Similarly the holotype of *Coccolithus cricotus* Gartner 1967 was probably a coccolith of *Geminilithella rotula*.

Size. c. 4-8microns.

Reticulofenestra lacunosa var. *ovata* (Bukry 1973) n.comb. & stat.

- 1967 *Coccolithus minutulus* Gartner *partim*: pl. 5, figs. 3, 4, *non*. p. 3, pl. 5, Figs. 3-5.
 1973 *Emiliana ovata* Bukry: 678, pl. 2, Figs. 10-12.
 1973 *Pseudoemiliana lacunosa* (Kamptner) Gartner; Roth: pl. 3, fig. 6.
 1979 *Pseudomiliana lacunosa* (Kamptner) Gartner; Samtleben: 919, pl. 3, Figs. 2, 3, 5, 6.
 1979 *Reticulofenestra pacifica* Nishida: 106, pl. 1, Figs. 4-6.
 1980 *Reticulofenestra pacifica* Nishida; Nishida: pl. 1, Fig. 9.
 1980 *Pseudomiliana lacunosa* (Kamptner) Gartner; Backman: pl. 16, Figs. 12,13.
 1988 *Emiliana ovata* Bukry; Driever *partim*: pl. 1, Fig. 2, pl. 7, Figs. 3,4,7.

Emended diagnosis: Elliptical variety of *R. lacunosa* with less than twelve slits in the distal shield.

Size: c.3.5-5.5microns.

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