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SIZE VARIATIONS IN LATE MIOCENE *RETICULOFENESTRA* AND IMPLICATION FOR PALEOCLIMATIC INTERPRETATION

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Key words: Reticulofenestra, late Miocene, orbital forcing, seasonality.

ABSTRACT

The major diameter of the placoliths of the genus *Reticulofenestra* varies in parallel at DSDP Sites 552A

and 609 (North Atlantic Ocean) in Miocene sediments. In the lower part of the sections the mean diameter is about 5.5 μm . During Chron 5 two diameter classes occurs: the smallest have a mean diameter of 3 to 4 μm , the largest of 8 μm . The ratio between these two classes shows frequencies similar to the orbital cycles. Frequencies related to the precession cycles are dominant. It is speculated that *Reticulofenestra* had two ecovariants, and that their respective abundance is a reflection of seasonality.

RIASSUNTO

Il diametro maggiore dei placoliti del genere *Reticulofenestra* varia in parallelo nei sedimenti miocenici dei Sites DSDP 552A e 609 (Nord Atlantico). Nella parte inferiore delle sezioni il diametro medio è circa 5.5 μm . Durante il Chron 5 si hanno due classi di diametro: la più piccola ha un diametro medio di 3-4 μm , la più grande di 8 μm . Il rapporto fra queste due classi mostra frequenze simili ai cicli orbitali. Dominano le frequenze collegate ai cicli di precessione. Si ipotizza che *Reticulofenestra* abbia due ecovarianti e che la loro rispettiva abbondanza sia un fenomeno stagionale.

INTRODUCTION

The concept of species is a controversial topic among paleontologists. To be meaningful, this concept in paleontology should be as close as possible to the biological one. Unfortunately it remains often restricted to a typological concept based only on morphology. IMBRIE (1957) ex-

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plained that the difficulty in using a biological concept in paleontology results essentially from three practical problems: (1) the inadequacy of morphological data, (2) the biased frequency distribution and (3) the incompleteness of the available fossil record. When dealing with the calcareous nanofossils, the last two problems can usually be eluded. It is possible to recognize differential dissolution which may bias the frequency distribution, and continuous sections through deep sea sediments are available. The inadequacy of the morphological data remains a severe obstacle, however, because the living Coccolithophoridae exhibit polymorphism, dithecatism, ecological morphotypes, and have a complex life cycle (AUBRY, 1989). There is little chance that the paleontologist may be able to reconstitute the elements of the life cycle of fossil species and it is rare when dithecatism or dimorphism is observed. On another hand, it might be possible to recognize morphologic variations related to paleoenvironmental changes and to characterize ecologic morphotypes. Primary production is influenced directly or indirectly by climatic controls (RAYMONT, 1980). It has been shown that the Coccolithophoridae are sensitive to variations in temperature and in concentration in nutrients (see review in TAPPAN, 1980). During the last decade our understanding of the past climates has improved significantly. It has been shown that Pleistocene climates fluctuated as a response to variations of the earth orbital parameters (MILANKOVITCH cycles) (HAYS *et al.* 1976).

The aim of this paper is to examine the size variations of the late Miocene reticulofenestrids as a possible result of climatic evolution. At times when large global climatic changes occurred, as during the late Miocene (*e.g.*, KENNETT, 1967; SHACKLETON and KENNETT, 1975; ADAMS *et al.* 1977), the relations between intra-interspecific variations and paleoclimatology are of prime importance to approach the reticulofenestrid specific concepts. In an attempt to characterize the temporal intraspecific variation in species of the genus *Reticulofenestra* during the late Miocene, a quantitative study of the size variation of their placoliths has been undertaken. In this study, changes in the placolith size through the upper Miocene sediments recovered at DSDP Sites 552A and 609 are determined.

CURRENT TAXONOMY

As many as eight species are distinguished among the late Miocene reticulofenestrids mainly

based on placolith length and size of the central opening (Table 1). They are *Reticulofenestra pseudoumbilicus* (GARTNER) GARTNER 1969, *R. minutula* (GARTNER) GARTNER 1969, *R. minuta* ROTH 1970, *R. gelida* GEITZENAUER 1972, *R. haqii* BACKMAN 1978, *Dictyococcites productellus* BUKRY 1975, *D. perplexus* BURNS 1975 and *D. antarcticus* HAQ 1976.

GENERIC LEVEL

BLACK (1967) indicated that coccoliths assigned to the genus *Dictyococcites* have a "large central opening which is occupied by a grid of calcite bars meeting along the major diameter of the ellipse" (*op. cit.* p. 141). Black's diagnosis refers only to the proximal side of the coccoliths. The genus *Reticulofenestra* HAY, MOHLER and WADE 1966 also includes "placoliths with a large central opening spanned by a reticulate or lacy net" (*op. cit.* p. 386). Arguing that the size of the central reticulate membrane which spans the central opening and may close it is not a valid character, STRADNER and EDWARDS (1968) emended the genus *Reticulofenestra* and established *Dictyococcites* as a synonym of *Reticulofenestra*. Although this synonymy is usually accepted (GALLAGHER, 1989) some workers continue to use the genus *Dictyococcites* as emended by BACKMAN (1980) who indicated that on the distal side the central area is "closed or virtually closed" (*op. cit.* p. 48). Since in our samples a continuum from virtually closed central area ("little pore") to entirely open is observed (see below) the genus *Dictyococcites* is not recognized as useful for this study.

SPECIES LEVEL

Reticulofenestra with an open central area

From the original descriptions that GARTNER (1967) gave of *Reticulofenestra minutula* and *R. pseudoumbilicus* it appears that the only difference between the two taxa resides in their size. The former one is a "small" placolith; its holotype is 4.4 μm long. The difference in the number of elements in the shields of the taxa (45 in *R. minutula*, 70 in *R. pseudoumbilicus*) is not a valid distinction since BACKMAN (1980) has shown that the number of elements in the shields increases with the overall size of the placolith.

BACKMAN (1978, p. 111) described *R. haqii* as "a small, elliptical reticulofenestrid with a small central opening". He indicated to be smaller than *R. pseudoumbilicus*, but no comparison with *R. minutula* was made. When describing *R. pseudoumbilicus*, GARTNER (1967) emphasized the

TABLE 1 - Main characteristics of upper Miocene *Reticulofenestra* from their original descriptions (P=Placolith length, A = Central area length, O = Central opening length)

SPECIES	<i>R. minutula</i>	<i>R. pseudo-umbilicus</i>	<i>R. minuta</i>	<i>R. gelida</i>	<i>R. productella</i>	<i>R. perplexa</i>	<i>R. antarctica</i>	<i>R. baqii</i>
	GARTNER 1967 GARTNER 1969	GARTNER 1967 GARTNER 1969	ROTH 1970	GETZENAUER 1972	BUKRY 1973 GALLAGHER 1989	BURNS 1975 WISE 1983	HAQ 1976	BACKMAN 1978
OCCURRENCE	Pliocene	Pliocene	Oligocene	upper Pliocene	Pleistocene	middle upper Miocene	Miocene	upper Miocene lower Pliocene
	Trinidad	Gulf of Mexico	Alabama	Pacific (sub-antarctic)	Pacific	Antarctic	Antarctic	Vera bassin
SIZE GIVEN BY AUTHOR	small		very small	6 to 12 μm	small: 3 to 8 μm	?	small: 4 to 7 μm	small: 3 to 5 μm
SIZE HOLOTYPE	P = 4.4 A = 3.2 O = 2	8.4 5.2 2.8	1.5 .86 .05	10.2 6.8 2.2	3.2 2.1 1.9	? ? ?	5.7 3.1 0	4.6 2.3 1
NUMBER OF ELEMENTS	45	70	26	68-74	28-38		60-80	40-50
MARGIN	protrude distally	may be decorated by large coarse crystallites						may distally consist of coarse crystallites
CENTRAL AREA	Open	Differs in size within the species. May be covered by a lacy network of bars that join along a longitudinal fissure at the center of the placolith.	1/3 of the coccolith covered by a coarse grille with twisted bars	Opening small circular to slit-like	Virtually close along a median slit	Closed. Well developed. Tortuous central line which is aligned with the long axes of the placolith central line suture.	Solid central area showing a long central furrow.	Small central opening (1-1.5 μm)

fact that the "elliptical central area differs in size within the species". No indication of the intra-specific variation of central opening in *R. minutula* was given. The holotype of *R. haqii* shows a smaller central opening than the holotype of *R. minutula* although both holotypes are of comparable sizes. Based on a quantitative study of the total placolith area versus the central opening area of Miocene-Pliocene *Reticulofenestra*, BACKMAN (1980, p. 44) concluded that his results were "not conclusive with regard to the taxonomic status of *R. haqii* and *R. minutula*". However, he considered it premature to unite the two taxa in a single species, mainly because of the small sample size he studied.

Reticulofenestra minuta was described from Oligocene sediments as "a very small species of *Reticulofenestra*" (ROTH, 1970, p. 850). A quantitative comparison between this form, *R. minutula* and *R. haqii* was performed by BACKMAN (1980) who concluded that distinction of *R. minuta* from the other two taxa through numerical parameters was not conclusive. Despite the non conclusive results of his study, BACKMAN (1980) proposed to separate the three species as follows:

- Specimens smaller than 3 μm were assigned to *R. minuta*.
- Specimens ranging from 3 to 5 μm which have a central opening larger than 1.5 μm were referred to *R. minutula*.
- Specimens of the same size but with a smaller central opening were assigned to *R. haqii*.

In addition, specimens larger than 5 μm are placed in *R. pseudoumbilicus* (BACKMAN, 1980). The criteria used by BACKMAN (1980) to subdivide the Neogene *Reticulofenestra* into 4 species are arbitrary: First, the original descriptions refer to size in a qualitative way ("small" or "very small"). Second, quantitative studies do not provide conclusive scatter allowing these specific subdivisions. BACKMAN's measurements (1980) indicate rather gradational changes from one taxon to another; therefore, size should not be used as a specific criteria.

The size of *Reticulofenestra gelida* (GEITZNAUER, 1972), ranges from 6 to 12 μm . This form has a small central opening. Following BACKMAN (1980) it is regarded as a junior synonym of *R. pseudoumbilicus*.

Reticulofenestra with closed central area

The late Miocene *Reticulofenestra* species with a closed central area are *R. productella*, *R. antarctica* and *R. perplexa*. *Reticulofenestra productella* is a placolith with a central area virtually closed

along a median slit. Its size ranges from 3 to 8 μm (BUKRY, 1975). *R. perplexa* was described as a "medium-sized elliptical placolith, with closed central area" and with "a central suture line running part way across the central part of the central area" (BURNS, 1975, p. 594). Because of a probable scaling error in BURNS's figure captions (BURNS, 1975, p. 589; WISE, 1983) the size of the holotype and that of the three paratypes are unknown. WISE (1983) estimated the length of the holotype to be 5 to 6 μm , based on the estimated length (5 μm) of a specimen of *Isthmolithus recurvus* illustrated in the same plate as the holotype of *R. perplexa* (BURNS, 1975, p. 589, fig. 17). In addition to the fact that 5 μm is unusually short for *I. recurvus* (AUBRY, *pers. com.*, 1989), we find inappropriate to guess the size of a holotype based upon comparison with a specimen which size has been a priori estimated. *Reticulofenestra antarctica* (HAQ, 1976) is a "small elliptical to subcircular placolith from 4 to 7 μm in length (rarely up to 8 μm), with a solid central area showing a long central furrow on both proximal and distal sides" (*op. cit.*, p. 561). BACKMAN (1980) considered it as a junior synonym of *R. perplexa*. The size is the character used to differentiate *R. productella* from *R. perplexa*. GALLAGHER (1989) gave a size of 5.0-6.0 μm for the latter and 3.5-4.5 μm for the former. BACKMAN (1980) proposed to restrict the concept of *R. productella* to include only forms with a size under 3.5-4.5 μm . However, BACKMAN (1980) did not emend this species. BUKRY (1975) stated that *R. productella* ranges in size between 3 and 8 μm , thus allowing large intraspecific variations in this form. Since the size range of *R. productella* overlaps entirely with that of *R. perplexa*, and because no morphologic differences are apparent between both taxa, the two species are regarded as synonymous.

We may conclude, from the literature, that only 3 late Miocene species of *Reticulofenestra* should be retained: *R. minutula*, *R. pseudoumbilicus* and *R. productella*.

SCHMIDT (1979) and DRIEVER (1988) from respectively upper Miocene and lower Pliocene Mediterranean sections found that the size of the placolith of *R. pseudoumbilicus* changed through time. During the late Miocene and the early Pliocene, an increase in mean size is observed from around 6 μm to 8 μm . This illustrates well the intraspecific variation of the size of the placolith of *R. pseudoumbilicus*. The time factor is also important. It is expected that a detailed study of relationship between time and placolith size of all the reticulofenestrids present during a given time

interval would reveal the bounds which exist between intraspecific and interspecific variations.

MATERIAL AND METHODS

SITE

Placoliths of the genus *Reticulofenestra* come from the upper Miocene calcareous nannofossil oozes and chinks recovered at DSDP sites 552A and 609 in the North Atlantic (Fig. 1). The placoliths of *Reticulofenestra* dominate the assemblages with *Coccolithus pelagicus*.

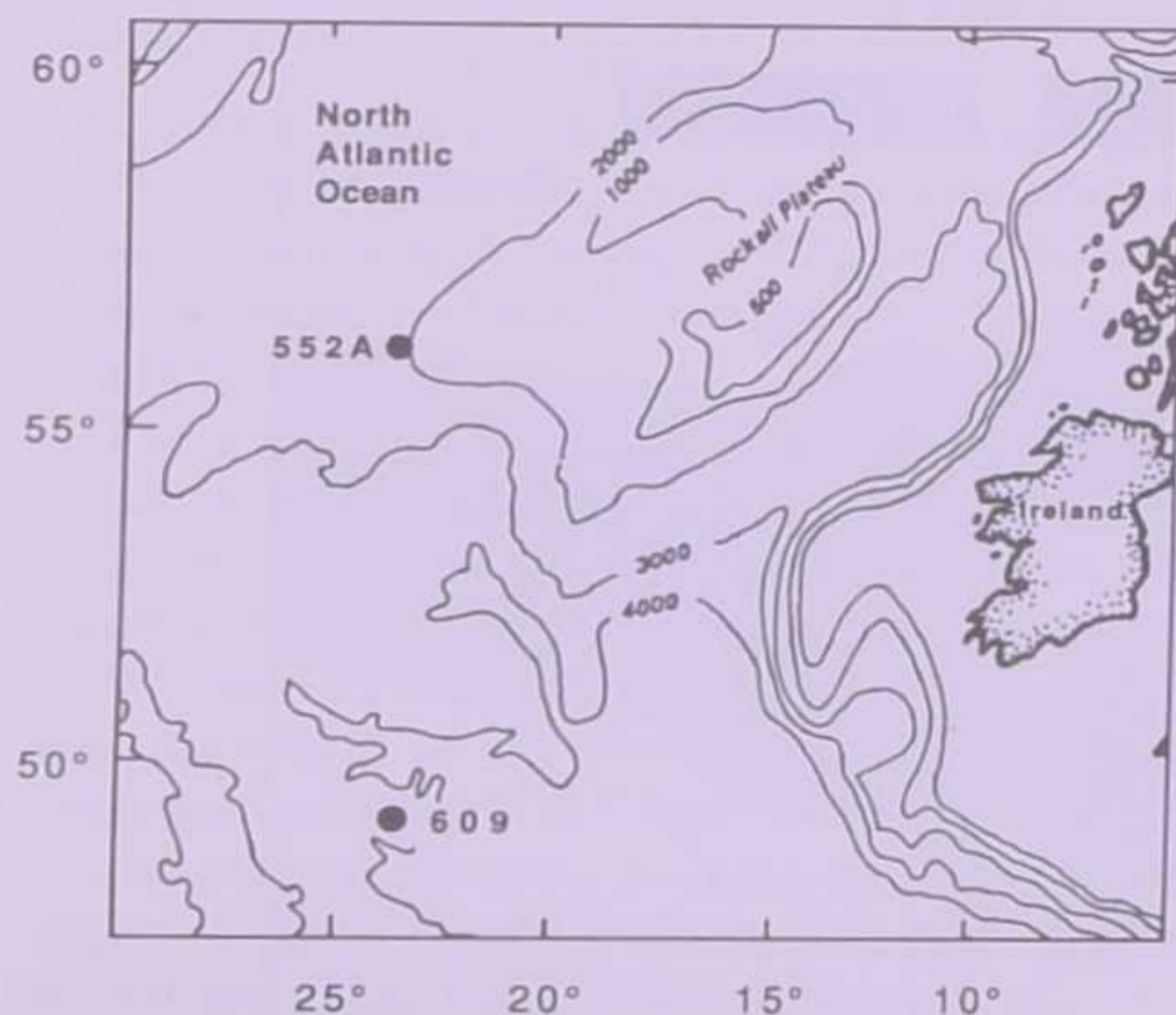


FIG. 1 - Location of DSDP sites 552A and 609.

The stratigraphy at Site 552A was established through magnetostratigraphy, biostratigraphy and stable isotope stratigraphy (KEIGWIN *et al.*, 1986; BEAUFORT and AUBRY, 1990). The stratigraphy at Site 609 is primarily based on magnetostratigraphy (CLEMENT and ROBINSON, 1987).

Smear slides were made from samples taken every 10 cm between 104 and 152 m at Site 552 A and every 20 cm between 313 and 360 m at Site 609. Considering the high sedimentation rates at these sites, ~30m/my and ~60 m/my respectively, the sampling interval allows a resolution of about 3000 years.

Placolith of *Reticulofenestra*: Biometry

In order to check if the size of the central opening was a discriminating parameter the reticulofenestrids, the total length of the placolith and that of the central opening were measured on the first 60 placoliths encountered while scanning a smear slide. A test was performed on three samples randomly chosen at 107.40, 127.92 and 143.60 m from Site 552A. The results are presented in figure 2. The size of the central opening

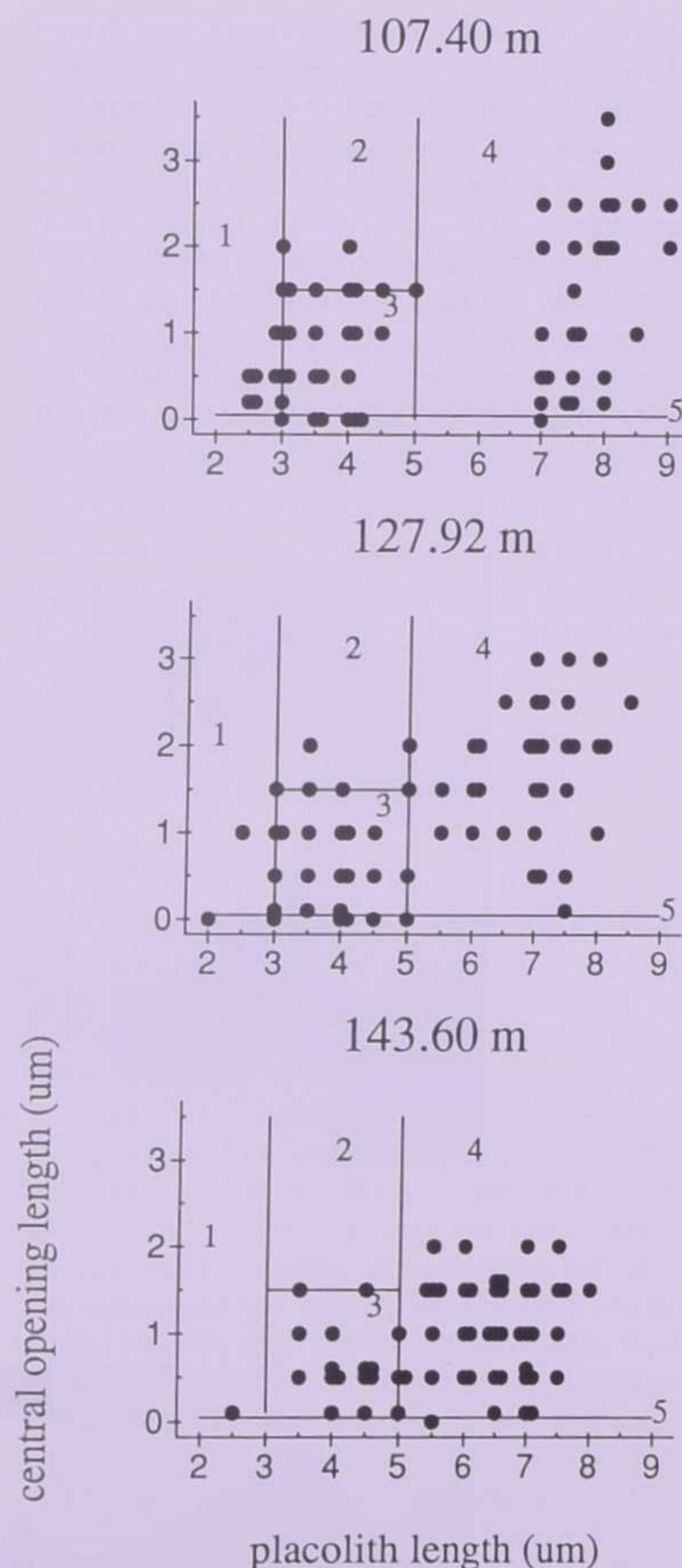


FIG. 2 - Size of the placolith and the central opening in three 552A samples (60 individuals in each). The 5 lines correspond to the taxonomic boundaries used by BACKMAN (1980) to differentiate: 1: *Reticulofenestra minutula*; 2: *R. minuta*; 3: *R. baqii*; 4: *R. pseudoumbilicus* and 5: *R. gelida*; *Reticulofenestra* with closed central area.

does not appear to be a good discriminating factor since no clusters are seen in these three samples. A continuum from forms with a closed central area to forms with an open one was observed, although it was not possible to quantify this continuum under the light microscope. The placo-

liths larger than 5 μm with a closed central area which were observed did not present a slit in the central area but a "small pore". In fact very few specimens with a slit were observed during this study.

The size of the placoliths allows separation of two clusters in the first sample (at 107.40 m). However in the second sample (at 127.92 m) the clusters are not well individualized, and in the third sample no cluster is seen. A detailed quantitative study was therefore undertaken in an attempt to understand size variations in the late Miocene *Reticulofenestra* of the North Atlantic.

LONG TERM VARIATIONS

MEASUREMENTS

Twenty one samples per site were selected and the long diameter of the first 30 placoliths of *Reticulofenestra* encountered was measured. The number of samples and specimens/sample was estimated large enough to describe in a qualitative way the variations of the diameter of the placoliths (no statistics are made from these data). The results are plotted as a contour map (Fig. 3).

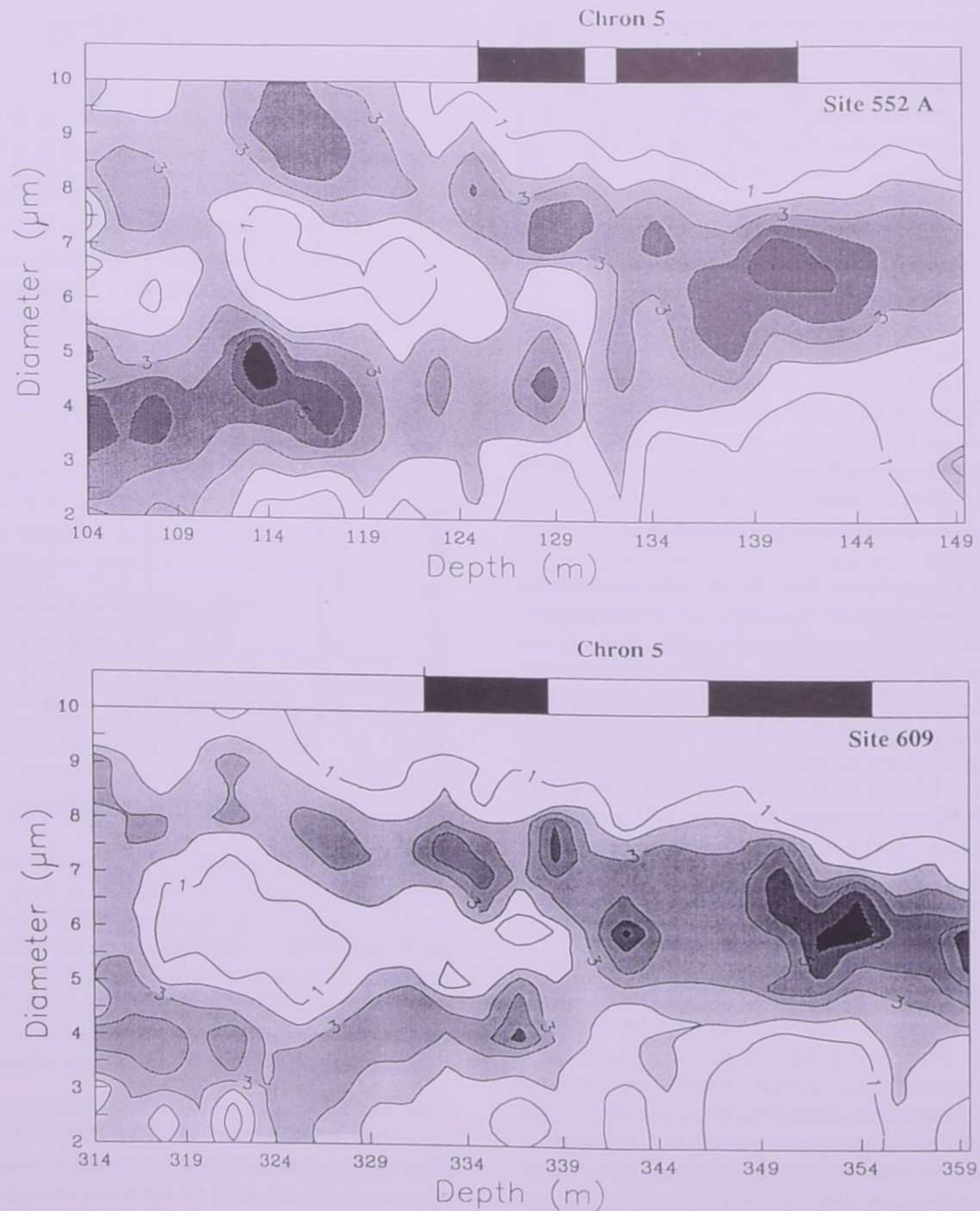


FIG. 3 - Contour plot of the size distribution of the placoliths of *Reticulofenestra* in the upper Miocene sediments of 552A and 609.

The length of the major diameter of the placoliths varies in parallel during the late Miocene at DSDP sites 552A and 609. In the lower part of the sections the mean diameter is about 5.5 μm . Above, in the upper part of Chron 5 (130 m at Site 552A, 338 m at 609) two diameter classes occur: In the smallest the mean diameter is 3 to 4 μm , in the largest it is about 8 μm . In most of the samples analyzed from this upper part of the sections the two classes are so well differentiated that they appear easily at a first glance in the light microscope.

IMPLICATIONS

The fact that the size distribution changes synchronously at Sites 552A and 609 exclude physical causes such as winnowing or differential dissolution. A biased frequency distribution is not at the origin of this pattern.

The size break at 5 or 5.5 μm that most authors use is suitable only in the upper part of the sections. Below it is clearly inadequate since the mean size exactly equals the size break. SCHMIDT (1979) already noticed this problem while studying placoliths of *Reticulofenestra* from lower Messinian sediments of Crete.

The size distribution pattern observed in the upper Miocene of DSDP Sites 552A and 609 can be interpreted in three different ways:

One possible explanation is that three unrelated species are present in the assemblages. One has a mean diameter of 5 to 6 μm and is dominant in the lower part (lower part of Chron 5 and below) of the sections. Above (upper part of Chron 5 and above) a small size and a large size species dominate the assemblages.

Another possibility is that the pattern observed results from an evolutionary process, an ancestral medium sized species evolving into two daughter species (a small one and a large one).

A last explanation is that the variation in size corresponds to intraspecific variations of a single taxon.

In the first hypothesis the overlap in size existing between the 3 hypothetical "species" exclude any practical way to separate between them. Mainly for practical reason this hypothesis is rejected. The second hypothesis is not tenable for two reasons. First, small and large forms existed before the hypothesized evolution from middle sized forms into smaller and larger ones occurred: *R. minuta* was described from Oligocene sediments and the stratigraphic ranges given for most of the late Miocene *Reticulofenestra* extend far below the upper Miocene (GALLAGHER, 1989).

Small specimens are also present in the lower part of our records (Fig. 3).

Second, DRIEVER (1988) observed that in lower Pliocene sediments from Crete *R. pseudoumbilicus* has a mean diameter of 5.5 to 6 μm , which corresponds to the size of our supposed ancestral medium sized *Reticulofenestra*. If the second hypothesis was correct, it would imply that the hypothetical mother species gave rise to two daughter species during the late Miocene, which had converged during the younger part of the Pliocene and diverged again since DRIEVER (1988) shows an increase in diameter of the placolith of *R. pseudoumbilicus* in the early Pliocene. It is difficult to explain the observations by this type of iterative and fast evolution. We prefer to explore the third hypothesis.

SHORT TERM FLUCTUATIONS

INTRODUCTION

It is now well established that during the Pleistocene and the Holocene climates were strongly influenced by the periodical variations of the earth orbital parameters (MILANKOVITCH theory of climates) (HAYS *et al.*, 1976). Calcareous nanofossil assemblages variations (ratio between *C. pelagicus* and *Reticulofenestra*) and stable isotopic records in upper Miocene sediments from DSDP Site 552A display large fluctuations which are interpreted to reflect MILANKOVITCH periodicities (BEAUFORT and AUBRY, 1990). In order to decipher possible short term variations (in the band of MILANKOVITCH cycles) in the size of the placolith of *Reticulofenestra* during the late Miocene, a short interval between 125 and 126 m at Site 552A was studied in detail. The placolith of fifty randomly taken specimens were measured in 10 slides (sampling interval: 10 cm) (Fig. 4). These measurements indicate that the mode of the two classes does not vary significantly in such a small interval but that the importance of one class relative to the other changes considerably.

RATIO BETWEEN THE TWO SIZE FRACTIONS

Between 104 and 125 m at Site 552A and between 314 and 338 m at Site 609 the large placoliths were counted versus the small ones (<5.0 μm) in every samples. The sample size is about 300 specimens per sample at Site 552A and 200 at Site 609. The relative abundance of the two forms are presented on figure 5 on a time axis. The curves vary in a comparable way at both sites

Detail (1 peak) Site 552 A

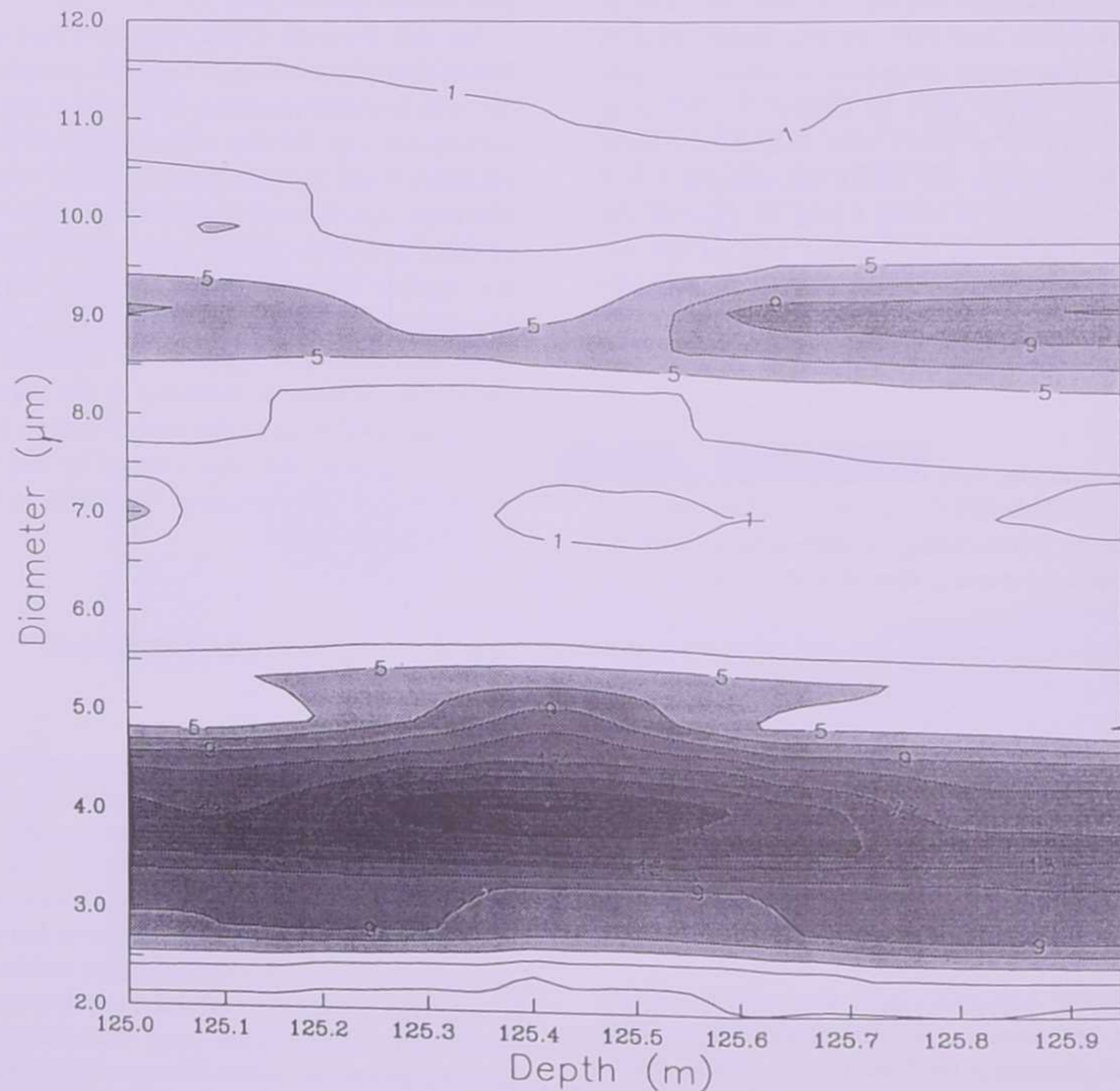


FIG. 4 - Contour plot of the size distribution of the *Reticulofenestra* on a short interval at 552A.

with high frequencies and amplitudes. A time series analysis was computed in order to extract the periods (if existing). A cubic spline was used to create series of equally spaced points in time (3000 years) from the original series. Once completed with zero padding (512 points) a discrete Fourier transform was computed on the series. The periodograms (Fig. 6) were smoothed (7 point-smoothing). At Site 552A the frequencies obtained are very similar to those predicted by the Milankovitch theory: 37 kyr is very close to 41 kyr (the period of the tilt) and 21.6 and 18.7 may correspond to the periods of the precession of the equinoxes (23 and 19 kyr). The large first peak is due to the non stationary pattern existing in the series (see Fig. 5). At Site 609 the peaks at 24.7 and 19.9 kyr probably correspond to the pre-

cession periods. The 30 kyr period is interpreted as the result of small variations in the sedimentation rate between the calibration points leading to small disturbances in the time model used.

At Site 552A the stable isotope records and the ratio *C. pelagicus* and *R. pseudoumbilicus* (BEAUFORT and AUBRY, 1990) show a greater importance of longer cycles than the size fluctuation do. Thus it is almost impossible to compare directly the size ratio curve with for example the $\delta^{18}\text{O}$ record. The suspected importance of the precession cycles in the records introduce the possibility of the effect of seasonal variation in the size of the placoliths of *Reticulofenestra*. If a species possesses two (winter and summer) variants characterized by a different size, the precession of the equinox will lead to periodic variations in the relative abundance of the two variants (Fig. 7).

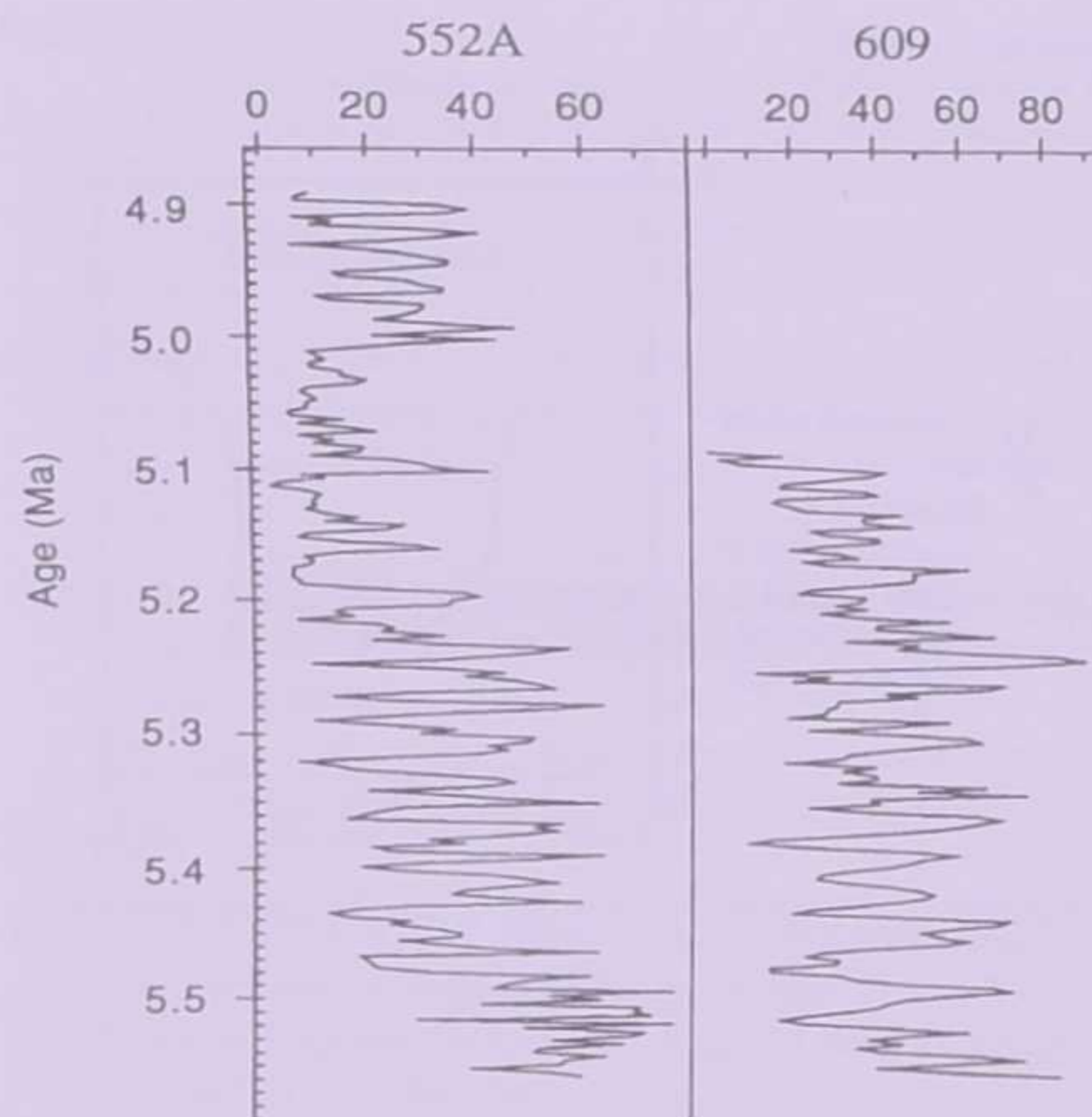


FIG. 5 - Ratio of the two size fraction of *Reticulofenestra* at sites 609 and 552A plotted on a time axes. (The uppermost Miocene is missing at Site 609).

DISCUSSION

Examples of size variation in the phytoplankton due to climatic factor are known. For example, the diatom *Coscinodiscus nodulifer* presents a bimodal size distribution, and fluctuations in the abundance of each mode during the Pleistocene follows climatic variations (BURCKLE and MC LAUGHLIN, 1977; ARRHENIUS, 1988). Also as a rule, the size of cells in the phytoplankton community as a reflexion of interspecific competition is influenced by factors such as temperature, nutrient concentration or depth of the mixed layer, and it varies seasonally (see HARRIS, 1986). If we assume that it is possible to extend this rule to intraspecific variation, we can postulate that the season cycle also affects the size distribution of a species with two morphotypes differentiated by cell size. The size of the placoliths of *Reticulofenestra* in our sample is positively correlated with the size of the coccosphere (cell size): the coccospheres with small placoliths which were encountered during this study were always smaller than the rare coccospheres with large placoliths (and even often of smaller than the placoliths itself). This implies that the two *Reticulofenestra* variants had different cell sizes.

From culture, BLACKWELDER (1976) shown that the size of the placoliths of *Emiliania huxleyi* var-

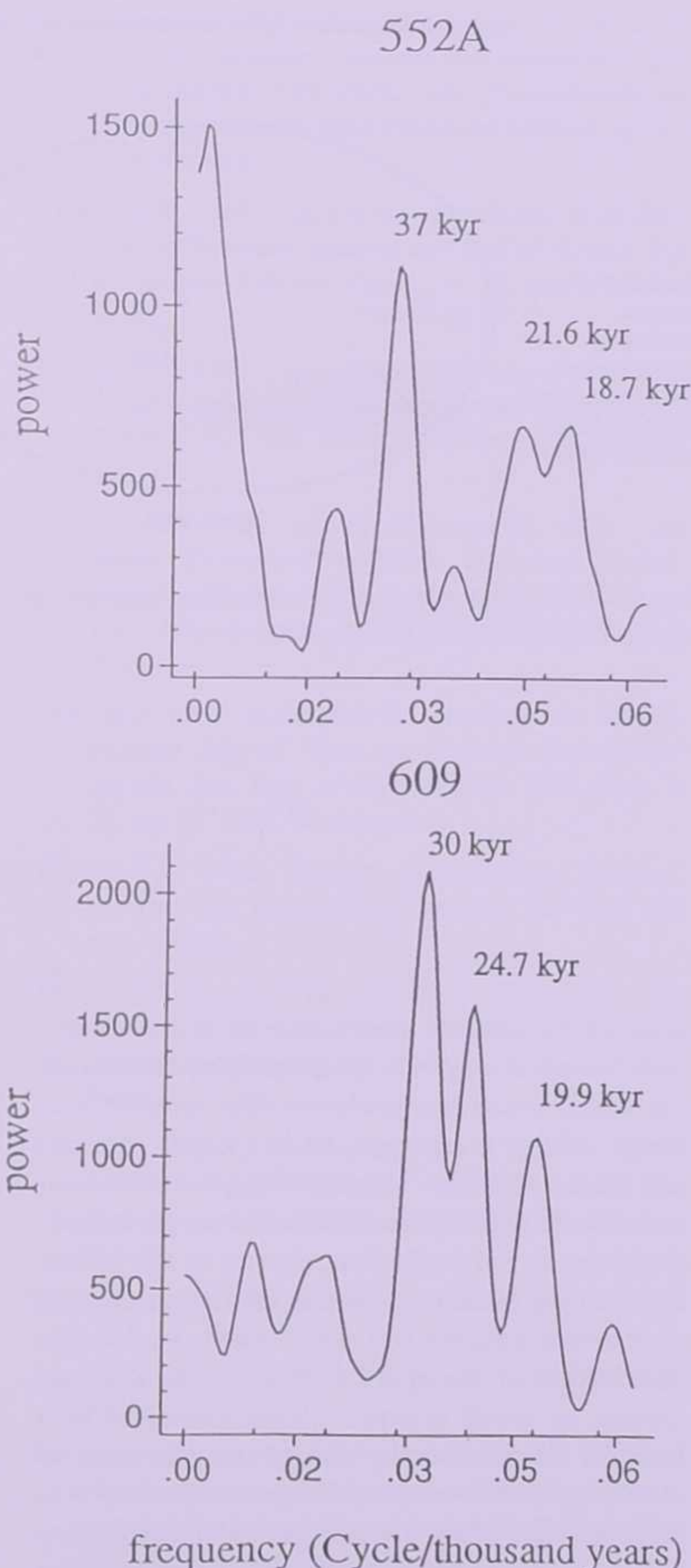


FIG. 6 - Periodograms of the two size ratio series.

ies with temperature (at low temperature the placoliths are larger). If temperature also affect the size of the placolith of *Reticulofenestra*, therefore placoliths secreted during winter would have been larger than those during summer.

If we assume a seasonal effect on the size of the placoliths of *Reticulofenestra*, this size should fluctuate with climatic variations. If so the precession of the equinoxes will lead to periodic varia-

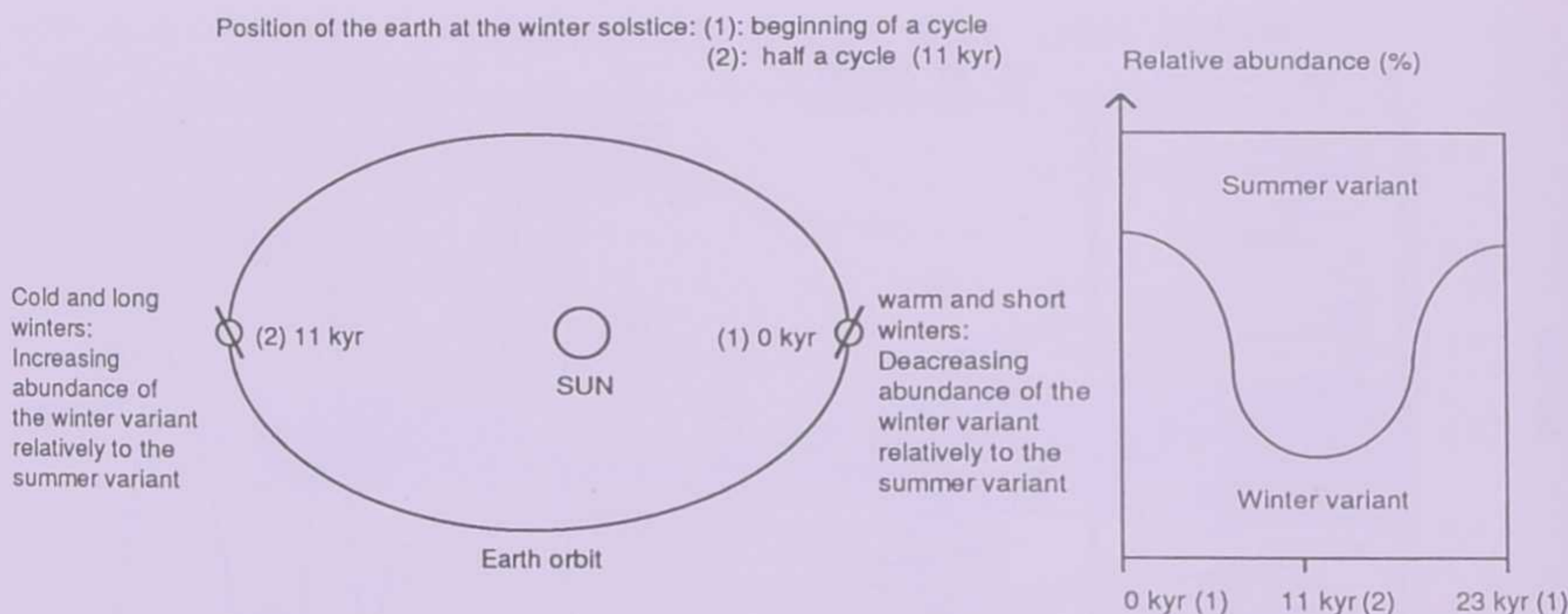


FIG. 7 - Theoretical effect of the precession cycle on the abundance of a winter variant of a single phytoplankton species in the Northern Hemisphere.

tions of the relative abundance of the two variants since a strong ~23 kyr periodicity dominates the winter insolation gradients (the summer gradients exhibit a stronger 40 kyr cycle) (YOUNG and BRADLEY, 1984). Thus the length of the winter taken in a biological sense will vary periodically (longer at the perihelion, shorter at the aphelion) leading to changes in the relative abundance of the two variants and, as a result, in the size distribution of the species (Fig. 7). As a consequence, we would interpret times dominated by a bimodal distribution the size of the placoliths of *Reticulofenestra*, as times when seasonality was stronger than times when a unimodal distribution existed. It is therefore tentatively suggested that seasonality increased during the late part of Chron 5.

CONCLUSIONS

From this analysis of the size of the placoliths of *Reticulofenestra* which occur in the upper Miocene sediments recovered from DSDP sites 552A and 609 it has been shown that:

(1) The length of the placolith is not a valid specific character, first because overlap occurs widely between species, second because size varia-

tions occur through time. The size of the central opening is not either a good parameter. Thus applying a typological taxonomical concept, it appears to be preferable to regroup the late Miocene *Reticulofenestra* in a single species.

(2) During Chron 5 two diameter classes occurred synchronously in the North Atlantic Ocean. This may prove to be a useful stratigraphic datum.

(3) The size distribution pattern observed during this study does not seem to result from an evolutionary process (mainly because the size fractionation in two classes is not found exclusively in the upper Miocene). An environmental interpretation is instead suggested. The presence of periodicities related to the precession cycle of the Earth orbit in the ratio of the two classes of placoliths implies a strong effect of seasonality on the *Reticulofenestra* assemblages. It follows that the latest Miocene (~5.5 to ~4.9 Ma) was a time of stronger seasonal contrasts than adjacent times intervals.

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