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BIOGEOGRAPHIC AND ECOLOGIC PATTERNS IN CALCAREOUS NANNOPLANKTON IN THE ATLANTIC AND PACIFIC OCEANS DURING THE TERMINAL CRETACEOUS

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ABSTRACT: Calcareous nannoplankton biogeography in the Cretaceous ocean has been analyzed from their floral composition at a time-slice spanning the upper parts of the *Micula prinsii* Zone (approximately the latest 10-60 kyr of the Cretaceous) at DSDP (Deep Sea Drilling Project) sites from low (16°) through middle (37°) paleolatitudes in both the Northern and the Southern Hemisphere. The study is based on relative abundance data of 44 species at Sites 356, 525A, and 527 from the South Atlantic, Sites 384 and 548A from the North Atlantic, and Site 465A from the Pacific Ocean.

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No significant changes occurred in the nannoplankton flora at any of the sites during the terminal 10-60 kyr of the Maastrichtian. This suggests that a stable environment persisted through the end of the Cretaceous and that a sudden catastrophic event that affected the calcareous nannoplankton was the cause of their nearly total extinction at the end of the Cretaceous.

Most species of late Cretaceous calcareous nannoplankton are believed to be cosmopolitan and therefore to exhibit only minor biogeographical differences. Ecologic preferences could, however, be distinguished for various species. On the basis of a correspondence analysis two major floral assemblages were distinguished: one Tethyan and one Transitional assemblage. The Tethyan assemblage, dominating at Sites 465A, 356, 384, and 548A, was composed of a large group of almost all taxa encountered. The Transitional assemblage, dominating at Sites 525A and 527 (Walvis Ridge), was composed of *Micula decussata, M. murus, Ceratolithoides aculeus, C. kamptneri, Lithraphidites quadratus*, and *Prediscosphaera majungae*.

In addition, three subassemblages could be distinguished within the Tethyan assemblage. A Tethyan low-latitude subassemblage was distinguished at the North Pacific Site 465A due to enhanced abundances of four species, *Watznaueria barnesae, Manivitella pemmatoidea, Loxolithus armilla*, and *Cylindralithus serratus.* A warm Tethyan subassemblage was found at Site 356 in the South Atlantic with enhanced abundances of *Discorhabdus ignotus, Corollithion exiguum, Zygodiscus erectus, Z. crux, Microrhabdulus undosus, Rhagodiscus asper, R. angustus, R. reniformes*, and *R. splendens.* A shallow and cool Tethyan subassemblage was encountered at the North Atlantic Site 548A which had greater relative abundances of *Nephrolithus frequens, Lucianorhabdus cayeuxii, Ahmuellerella octoradiata, Arkhangelskiella cymbiformis, Cretarhabdus surirellus,* and *Prediscosphaera majungae.*

Key words: Cretaceous, Maastrichtian, Calcareous nannoplankton, Coccoliths, Biogeography.

RESUMEN: Se analiza la biogeografía del nanoplankton calcáreo en el océano Cretácico a partir de su composición floral, en un lapso que comprende la parte superior de la zona de *Micula prinsii* (los últimos 10- 60 ka del Cretácico). Para esta reconstrucción se emplean testigos DSDP (Deep Sea Drilling Project) obtenidos en paleolatitudes bajas y medias (entre 16° y 37°) de ambos hemisferios. El trabajo se fundamenta en la cuantificación relativa de 44 especies en los DSDP*Sites* 356, 525A y 527 del Atlántico Sur, 384 y 548A del Atlántico Norte y 465A del Océano Pacífico. No se han observado cambios significativos en la nanoflora en ninguno de los testigos analizados durante los últimos 10- 60 ka del Cretácico final, lo sugiere la persistencia de un ambiente estable a lo largo del fin del Cretácico. La causa de la práctica total desaparición de dicha nanoflora al final del Cretácico se interpreta como consecuenciade un repentino evento catastrófico.

La mayoría de especies de nanoplancton calcáreo del Cretácico parecen ser cosmopolitas, mostrando escasas diferencias biogeográficas. Pueden distinguirse, sin embargo, algunas preferencias paleoecológicas. En base a un análisis de correspondencia se han distinguido dos asociaciones nanoflorísticas principales: una del Tethys y otra Transicional.

La asociación del Tethys domina los testigos 465A, 356, 384 y 548A, y está compuesta por un gran número de taxa. La asociación Transicional domina los testigos 525A y 527 (Walvis Ridge), y se compone de *Micula decussata, M. murus, Ceratolithoides aculeus, C. kamptneri, Lithraphidites quadratus* y *Prediscosphaera majungae.*

En la asociación del Tethys se han diferenciado asimismo tres subasociaciones: 1) Subasociación del Tethys de latitudes bajas en el testigo 465A del Pacífico Norte, fundamentalmente dominada por las especies *Watznaueria barnesae, Manivitella* *pemmatoidea, Loxolithus armilla* y *Cylindralithus serratus.* 2) Subasociación del Tethys cálida, localizada en el testigo 356C en el Atlántico S, con dominio de *Discorhabdus ignotus, Corollithion exiguum, Zygodiscus erectus, Z. crux, Microrhabdulus undosus, Rhagodiscus asper, R. angustus, R. reniformes* y *R. splendens.* 3) Subasociación del Tethys somera y fría, identificada en el testigo 548A del Atlántico Norte, con dominio de *Nephrolithus frequens, Lucianorhabdus cayeuxii, Ahmuellerella octoradiata, Arkhangelskiella cymbiformis, Cretarhabdus surirellus* y *Prediscosphaera majungae.*

Palabras clave: Cretácico, Maastrictiense, Nanoplancton calcáreo, Cocolitos, Biogeografía.

INTRODUCTION

The study of biogeographical and ecologic patterns is an important approach to a better understanding of the relationships between the organisms and their environment in the present and ancient oceans. Temperature may be the main factor controlling the distribution of marine pelagic organisms. The study of the paleobiogeographic history of fossil species assemblages at different times in the geological past can be used for inferences about time-related changes in the climatic oceanographic system. For example, earlier paleobiogeographical studies have demonstrated the existence of paleocurrent directions and paleoclimatic zones and their displacements with time. A number of studies has been carried out on the biogeographic patterns of various groups of planktonic microfossils in the Tertiary ocean. These studies were either based on continuous sections from different deep-sea sites (Haq *et al.*, 1977), or selected time-slices comprising sediments deposited during 0.5-1 m.y. from some geological transect (Haq, 1980; Hodell & Kennett, 1985). Few quantitative studies have dealt with the biogeography of Cretaceous planktonic microfossils. Roth & Bowdler (1981), Roth & Krumbach (1986), and Thierstein (1981) analyzed calcareous nannofossil distribution at time-slices of a duration from some million years up to about 10 m.y.

Malmgren (1991) carried out a quantitative study of the biogeography of planktonic foraminifera in the terminal Cretaceous, and Widmark & Malmgren (1992) carried out a study of the biogeographic patterns of benthic foraminifera during the same time-interval. Sliter (1977) distinguished three major bioprovinces of planktonic foraminifera in the Late Cretaceous: the Tethyan Realm, extending between about 30°S to 30°N, the Austral/Boreal Realm in the southern and northern high latitudes, respectively, and a Transitional Realm in between these realms. Malmgren (1991) distinguished three major faunal assemblages from a quantitative study of terminal Cretaceous planktonic foraminifera: a warm Transitional assemblage, a warm Tethyan assemblage, and a cool Tethyan assemblage.

Quantitative variations in calcareous nannofossil assemblages and their biogeographic and ecologic significance were analyzed in samples from the uppermost part of the Cretaceous. The samples were derived from six Deep Sea Drilling Project (DSDP) sites (Fig. 1, Table 1): Site 356 from the São Paulo Plateau (South Atlantic), Site 384 from the *J*-Anomaly Ridge (North Atlantic), Site 465A from the Hess Rise (North Pacific), Sites 525A and 527 from the Walvis Ridge (South Atlantic), and Site 548A from the Goban Spur (North Atlantic). The assemblages of calcareous nannofossils were analyzed at each site for a time-slice comprising the final 10-60 kyr of the Cretaceous. Several samples from this interval were investigated at each site, since a single sample may not be representative of the flora in the terminal Cretaceous at that site and since a sequence of samples provides a means of assessing the temporal stability of the assemblage structure through this crucial interval of the Cretaceous.

MATERIAL AND METHODS

In order to enable a comparison of calcareous nannoplankton floras from the same time interval at the various sites, a geochronology was established on the basis of magnetostratigraphy and calcareous nannofossil stratigraphy. Estimates of sedimentation rates are based on the assumption that the base of subchron C29R occurred 0.28 m.y. before the K-T boundary and that the base of the *Micula prinsii* Zone occurred 0.2 m.y. before the K-T boundary in the North Pacific (BERGGREN *et al.*, 1985; SHACKLETON *et al.*, 1984a; ZACHOS & ARTHUR, 1986; HENRIKSSON, 1993).

Location	Site 356	Site 384	Site 465A	Site 525A	Site 527	Site 548A
Latitude	28°S	40°N	34°N	29°S	28°S	49°N
Longitude	41°W	52°W	179°E	3°E	2°E	12°W
Waterdepth (m)	3175	3909	2161	2467	4428	1251
	(1)	(2)	(3)	(4)	(5)	(6)
K-T boundary	29-3,33	13-3,33	33-3,144	42-2,11	32-4,50	28-7,40
Depth (mbsf)	411.83	167.93	62.44	451.71	280.00	471.40
Base*	(7)	(8)		(9,10)	(9,10)	(11)
Subchron C29R (m)	7.5	1.1	---	5.0	6.6	4.6
Base*			(12)			
M. prinsii Zone (m)			2.3			
Estimated sedimentation rate (cm/kyr)	2.5	0.4	1.2	1.7	2.2	1.5

* Distance below K-T boundary.
References: (1) PERCH-NIELSEN *et al.* [1977], (2) TUCHOLKE *et al.* [1979],
(3) VALLIER *et al.* [1981], (4) MOORE *et al.* [1984a], (5) MOOE *et al.* [1984b],
(6) GRACIANSKY *et al.* [1985], (7) ZACHOS & ARTHUR [1986],
(8) LARSON & OPDYKE [1979], (9) SHACKLETON *et al.* [1984a],
(10) CHAVE *et al.* [1984], (11) TOWNSEND [1985], (12) HENRIKSSON [1993].

Table 1. Data for DSDP sites: present-day locations and water dfepths, location of the K-T boundary and thicknesses of the Crataceous portion of Subchron C29R and the *M.prinsii* Zone in Site 465A. Sedimentatión rates are stimated under the assumption that the base ob Subchron C29R occurred O.28 m.y. below the K-T boundary (BERGGREN *et al.*, 1985; SHACKLETON *et al.*, 1984a), and that the base of the *M.prinsii* Zone was 0.2 m.y. below the K-T boundary (HENRIKSSON, 1993).

Sedimentation rates are variable at the different sites during the latest Maastrichtian, ranging from 0.4 cm/kyr at Site 384 to 2.5 cm/kyr at Site 356 (Table 1). Samples were selected from a time-slice representing the final 10-60 kyr of the Cretaceous at the various sites (Fig. 1). Most sites were sampled at regular intervals of about 10-20 cm, except for Site 356 where the sampling interval was 20-50 cm. Data on depths in sites and ages below the K-T boundary are presented in Table 2. Smear slides for analyses of nannofossil content were made from raw samples. These slides were analyzed at random viewfields in random transects over the entire slide, using crossed nicols in a light microscope. The number of specimens counted in each sample was approximately 500.

Totally 68 species of calcareous nannoplankton species were identified. Those species that were present in more than half of the samples in at least one of the sites and with at least one relative abundance exceeding 1% were included in this study. Forty-four species met these requirements and were used as input variables in a correspondence analysis. Selected species are listed with references in the Appendix.

Correspondence analysis was applied in order to study the differences in the calcareous nannoplankton floral assemblages among the various sites and to assess biogeographic and ecologic patterns in the terminal Cretaceous ocean. An objective was to determine whether major differences in calcareous nannoplankton assemblages are tied to time-related changes through the interval studied at individual sites or related to variability along paleolatitudinal or other transects. Correspondence analysis permits simultaneous plots of sample points and species points on the same coordinate axis, facilitating interpretations of species associations responsible for clustering of the samples (Benzécri, 1973; Malmgren *et al.*, 1978).

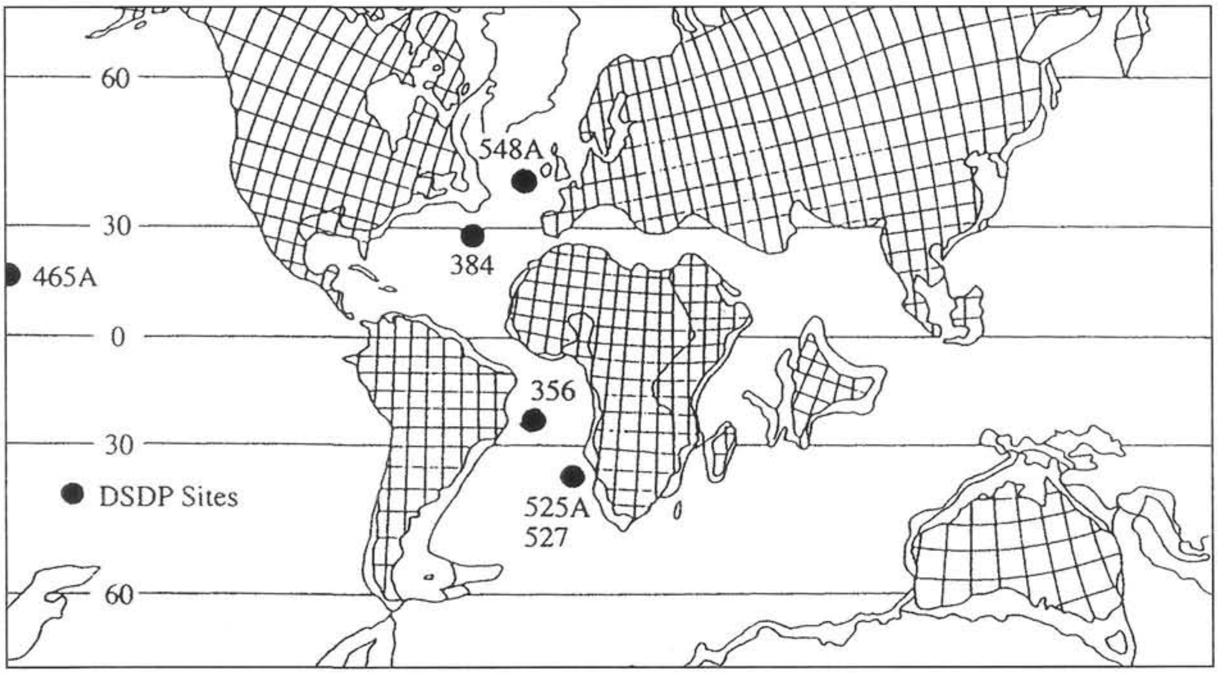

Fig. 1. Paleolocations of DSDP sites used in the present study at about the time of the K-T boundary (at about 65 Ma). These sites were used to study ecologic and biogeographic patterns in terminal Cretaceous calcareous nannoplankton.

RESULTS

The first three correspondence axes account for 76% of the variability in the 28-dimensional sample space and the 44-dimensional species space. The first axis accounts for 40%, the second axis for 24%, and the third axis for 12% of the variation.

The locations of the samples along the first and second, and second and third axis are shown in Figs. 2 and 3, respectively. The results show that samples from the same site cluster together. Differences in calcareous nannoplankton floras among sites clearly dominate over time-related changes at individual sites as the

Site	core	interval (cm)	Depth in site (mbsf)	Age below K-T (kyr)
356	29-3	54-55	412.04	10
		80-82	412.30	20
		100-102	412.50	30
	29-4	4-5	413.04	50
384	13-3	34-36	167.95	<10
		50-52	168.11	50
465A	3-3	148-149	62.48	<10
		4-5	62.54	10
		12-13	62.62	20
		20-22	62.70	<30
525A	40-2	47-48	452.08	20
		59-60	452.20	30
		69-70	452.30	<40
		78-79	452.39	40
		92-93	452.53	<50
		100-102	452.61	50
527	32-4	57-59	280.08	<10
		68-69	280.19	10
		87-89	280.38	20
		107-108	280.58	30
		133-134	280.83	40
	32-5	7-8	281.08	50
548A	29-1	4-5	471.54	10
		14-15	471.64	20
		34-35	471.84	30
		54-55	472.04	40
		64-65	472.14	50
		84-85	472.34	60

Table 2. Data for DSDP samples used in this study; depths in sites and ages below the K-T boundary.

major controlling force behind the configuration of sample points. Plots of the scores of the first through third correspondence axes against age below the K-T boundary show that calcareous nannoplankton floras remained stable through the 50-60 kyr before the K-T boundary extinction event (Fig. 4). As a consequence, there was only a minor change in the flora through the terminal Cretaceous and no significant decreases or turnovers that could predict the almost total extinction of calcareous nannoplankton at the K-T boundary. This clearly indicates that there should have been some sudden catastrophic event that caused the mass extinctions of calcareous nannoplankton species.

The first correspondence axis distinguishes the Walvis Ridge Sites 525A and 527 from the other sites (Fig. 2). The Tethyan Realm (Site 465A, 384, 356, and 548A) is clearly separated from the Transitional sites (525A and 527). The second axis distinguishes the low-latitude Tethyan (Pacific) Site 465A (Figs. 2, and 3), whereas the third axis distinguishes Sites 356 and 548A from the remaining sites (Fig. 3).

The configurations of species points along the first and second, and second and third correspondence axes are shown in Figs. 5 and 6, respectively.

Typical Tethyan species are not distinguished since no particular species seem to be restricted to the Tethyan Realm; according to Perch-Nielsen (1979) there are almost no specific Tethyan species. An assemblage of six species is associated with the Transitional Walvis Ridge sites: *Micula decussata, Micula murus, Lithraphidites quadratus, Prediscosphaera majungae, Ceratolithoides aculeus*, and *C. kamptneri* (Fig. 5). The relative abundances of these species at the different sites are shown in Figure 7 and Table 3.

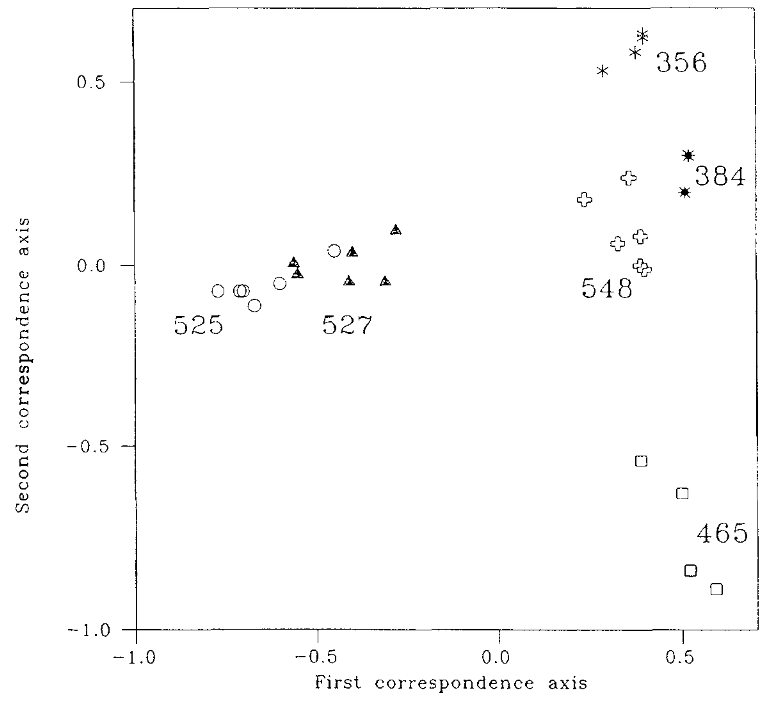

Fig. 2. Distribution of scores of samples for the various sites along the first two correspondence axes. This plane accounts for 64% of the variability in sample and species space. The first axis distinguishes the Walvis Ridge Sites 525A and 527 from the other sites.

The entire group of transitional species represents an average relative abundance of 58% at Site 525A and 48% at Site 527, whereas these species represent approximately 10-15% at the other sites. The most dominant species, *M. decussata,* shows relative abundances of 35-51% at Site 525A and 26-42% at Site 527, compared to less than 12% at any of the other sites. The other species, *M. murus, C. aculeus, C. kamptneri, L. quadratus*, and *P. majungae*, are also more abundant in the Walvis Ridge sites with average relative proportions of 13-14%, whereas the other sites have abundances of 6-7%.

Four species are associated with the low-latitude Tethyan (Pacific) Site 465A (Fig. 6): *Watznaueria barnesae, Cylindralithus serratus, Manivitella pemmatoidea,* and *Loxolithus armilla.* The relative proportions of these species compared to those at the other sites are shown in Figure 8 and Table 3. The dominant species in Site 465A is *W. barnesae* with an average relative abundance of 41%, compared to 8-18% at the other sites. *Loxolithus armilla* is only encountered (in the counts of 500 specimens) at this site. The other two species, *M. pemmatoidea* and *C. serratus*, are clearly more abundant at Site 465A with an average relative abundance of 4% compared to proportions of 0.2-1.1% at the other sites. These dominant species compose a group that represents 48% of the total assemblage at Site 465A. At the other sites these species make up only 8-18% of the floras.

The species that cluster with Site 356 along the second and third correspondence axes are assumed to be representative of a warm-water (Atlantic) subassemblage. These species are: *Rhagodiscus splendens, R. angustus, R. asper, R. reniformes, Discorhabdus ignotus, Corollithion exiguum, Microrhabdulus undosus, Zygodiscus crux,* and *Z. erectus* (Fig. 6). These species are all present in

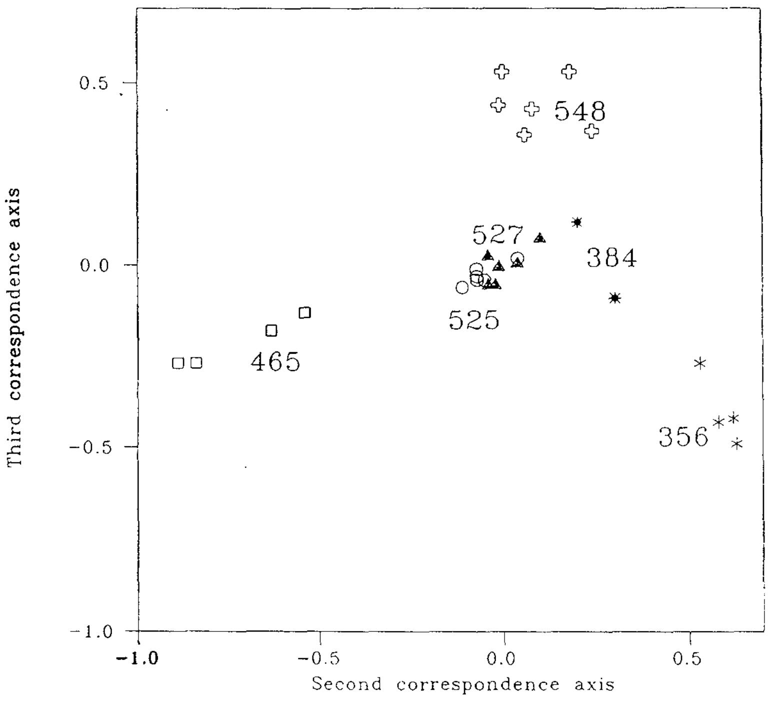

Fig. 3. Distribution of scores of samples on the second and third correspondence axes. This plane accounts for 36% of the variability of species abundances of the different samples. The second axis separates the low-latitude Tethyan (Pacific) Site 465A from the other sites. The third axis orders the sites according to paleotemperature (see Table 4).

low numbers at Site 356 (an average of 12%). Site 384 shows the second highest abundance of these species (an average of 6%), whereas at the other sites these species are almost absent (Fig. 9; Table 3).

The species which are shown by the third correspondence axis to be indicative of Site 548A are here interpreted as representative of a shallow and cool environment: *Nephrolithus frequens, Arkhangelskiella cymbiformis, Ahmullerella octoradiata, Lucianorhabdus cayeuxii, Cretarhabdus surirellus,* and *Prediscosphaera majungae* (Fig. 6). The relative proportions of these species compared to the other sites are shown in Figure 10 and Table 3. The comparatively shallow water depth at this site (200-500 m; GRACIANSKY *et al.*, 1985) might be a

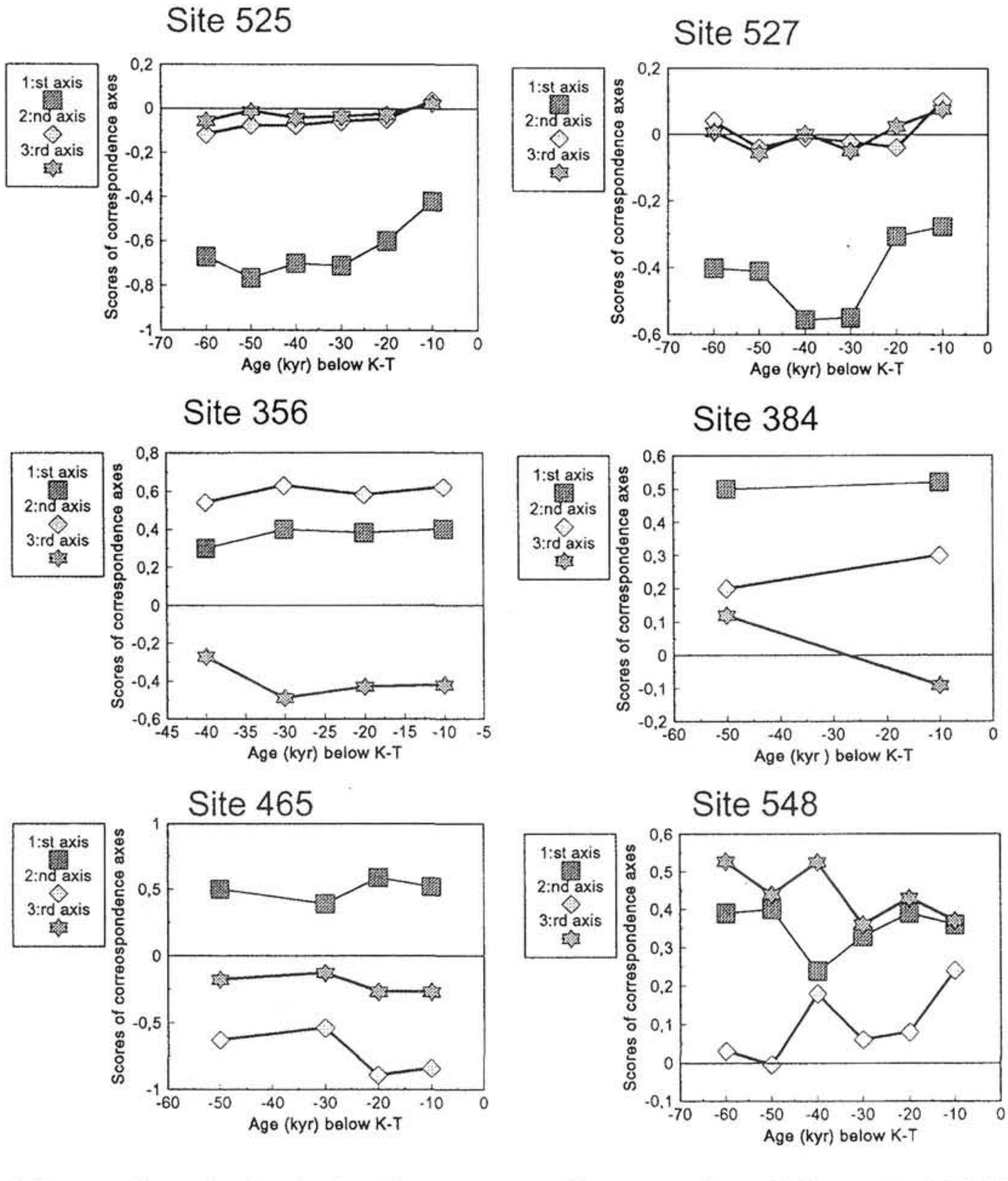

Fig. 4. Scores of samples for the first three correspondence axes through the terminal 10-60 kyr of the Cretaceous at the various DSDP sites. Sample points are approximatively relative to geologic time. The plots suggest that no significant change occurred in the calcareous nannoplankton flora prior to the K-T boundary extinctions. This also suggests that the Atlantic and Pacific Oceans were stable with regard to the paleoceanographic conditions during this time.

major cause behind the floral assemblage characterizing Site 548A. *Arkhangelskiella cymbiformis* and *L. cayeuxii* have been reported to be more common in shelf areas (Perch-Nielsen, 1979; Thierstein, 1981). This shallow and cool-water flora represents a relative abundance of 13% at Site 548A, whereas it

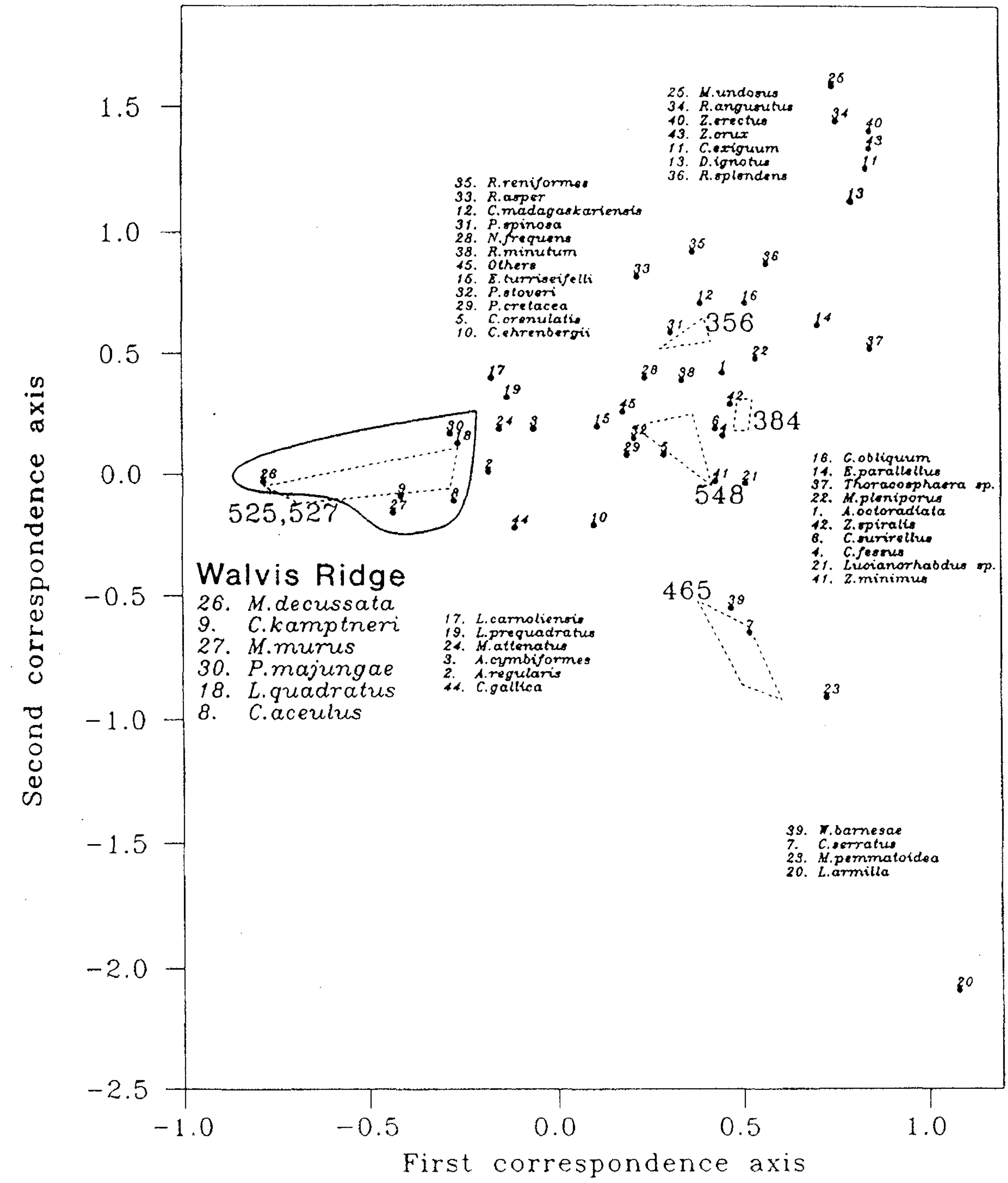

Fig. 5. Configuration of species loadings along the first and second correspondence axes. Species clustering with particular groups of sample points are characteristic of these samples. Scatter polygons indicate the locations of the samples from the different sites (derived from Fig. 3). The Walvis Ridge Sites (525A and 527) are separated from the other sites due to higher abundances of six species (M. decussata, M. murus, C. aculeus, C. kamptneri, L. quadratus, and P. majungae).

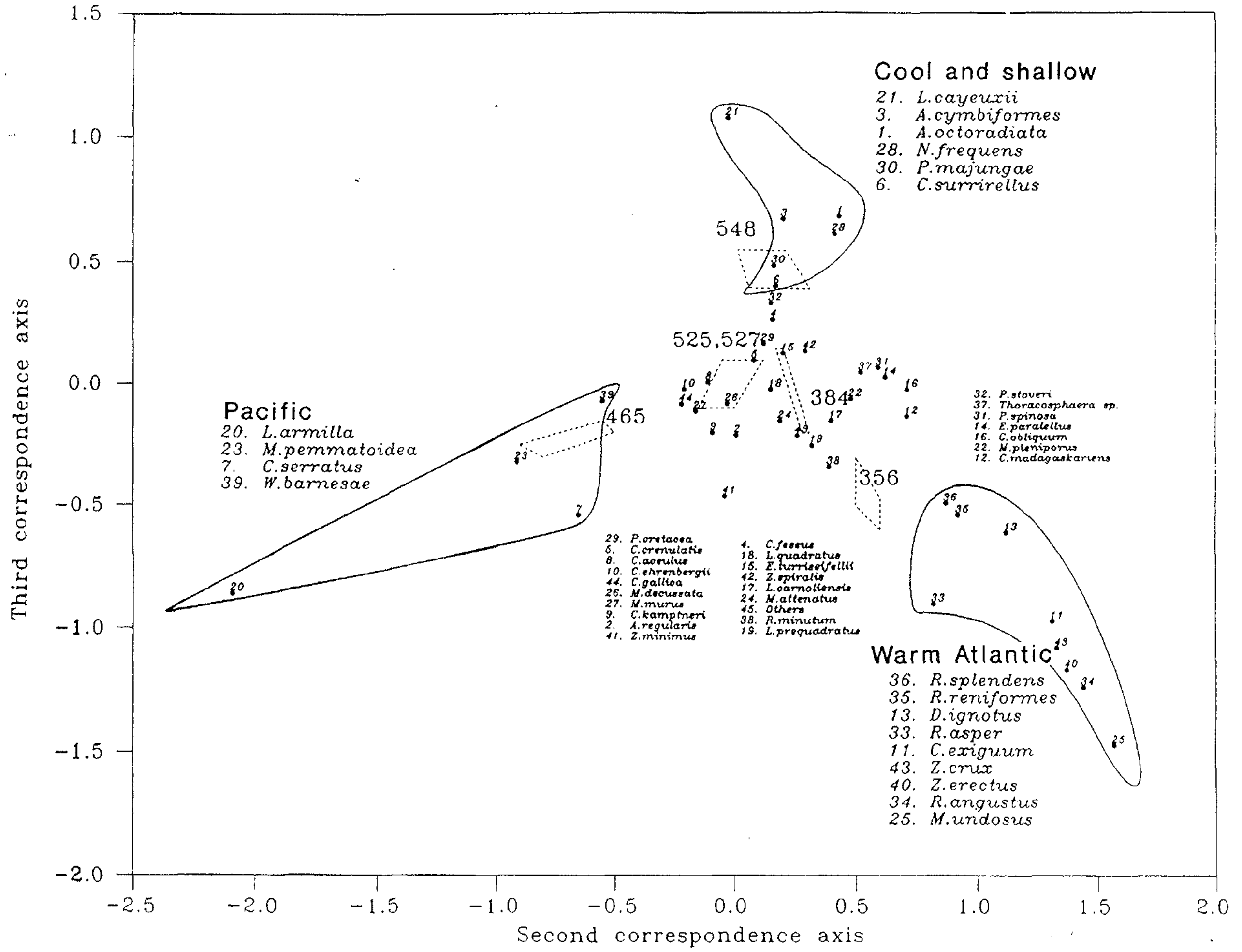

Fig. 6. Distribution of species loadings along the second and third correspondence axes. Species that cluster with sample points are characteristic of these samples. Scatter polygons indicate the placements of the samples of the different sites (derived from Fig. 4). Site 465A stands out from the other sites along the second correspondence axis due to higher abundances of four species. (W. barnesae, L.armilla, C.serratus, and M.pemmatoidea). The third axis seems to order the sites along a temperature gradient, and therefore species preferring warm waters cluster with Site 356 and species preferring cooler waters cluster with Site 548.

represents approximately 4% at the other Atlantic sites and only 2% at Site 465A. *Prediscosphaera majungae* is about equally abundant at Site 527 and Site 548A and is therefore assumed to be representative of similar latitudes in both hemispheres.

Species that show intermediate scores on the first three correspondence axes are assumed to lack biogeographic or ecologic preferences. This group consists of 20 species that were either equally abundant at all sites or showed only minor differences among sites (Table 3).

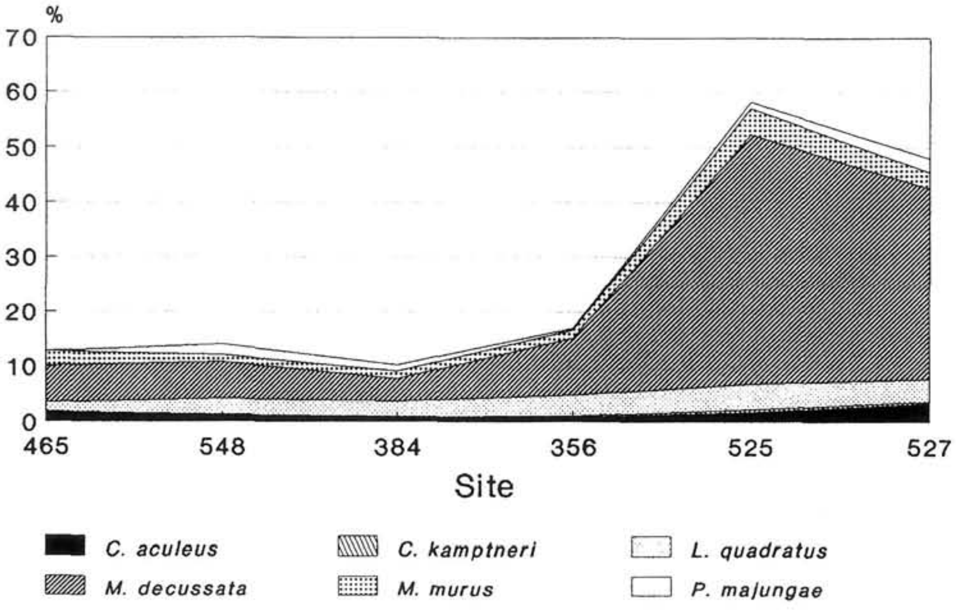

Fig. 7. Relative abundances at the various DSDP sites of species more abundant at the transitional Sites 525A and 527. Means and ranges of the different species are presented in Table 3.

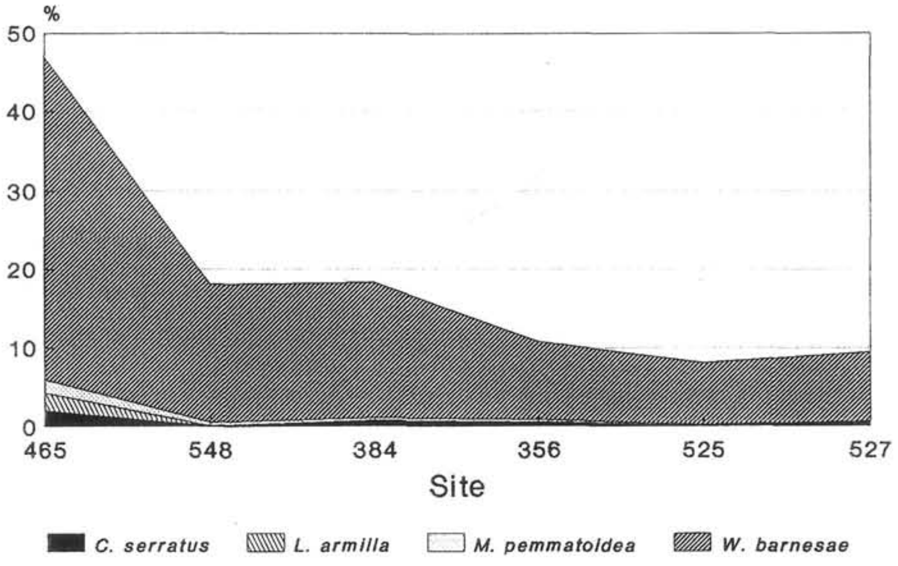

Fig. 8. Relative abundances at the various DSDP sites of species that are characteristic of the low-latitude Tethyan (Pacific) Site 465A. Means and ranges of the different species are presented in Table 3.

DISCUSSION

The results of this investigation do not appear to be controlled by differences in preservation among the various sites. After death and settling onto the sea floor, calcareous nannoplankton specimens are subject to partial or complete chemical dissolution. Dissolution operates differently on separate species, and differences in the strength of dissolution among the different sites should be known to be able to infer real biogeographic and ecologic signals. The degree of fragmentation of

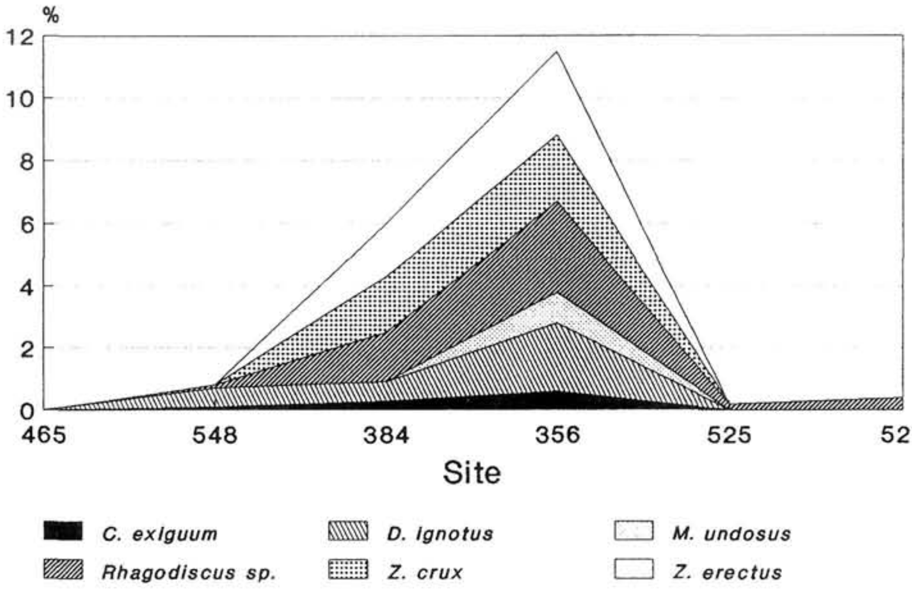

Fig. 9. Relative abundances at the various DSDP sites of species that show enhanced abundances at the warmest Site 356 (Atlantic). Means and ranges of the different species are presented in Table 3.

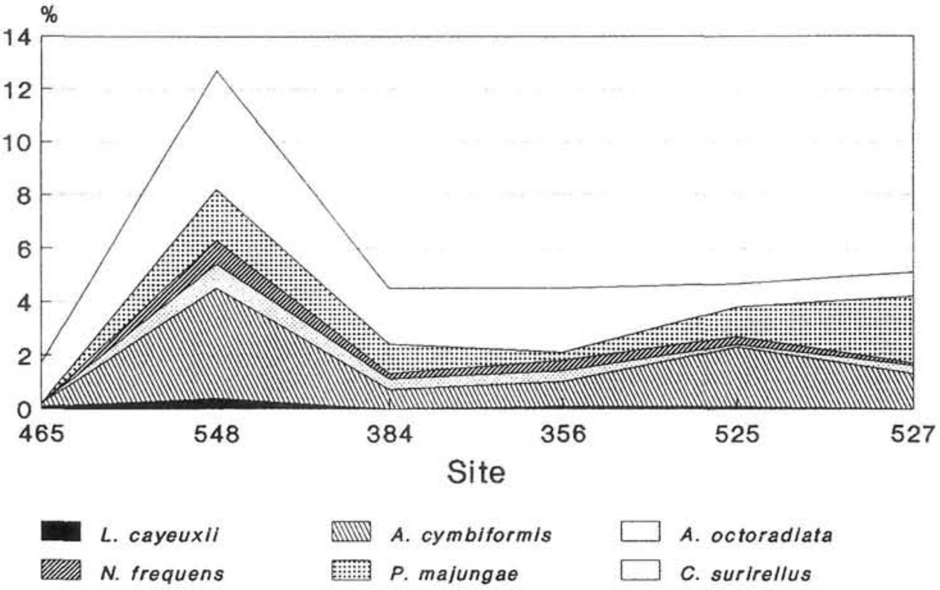

Fig. 10. Relative abundances at the various DSDP sites of species that show greater abundances at the shallow and cool-water Site 548A (Atlantic). Means and ranges of the different species are presented in Table 3.

	Site 465A	Site 548A	Site 384	Site 356	Site 525A	Site 527
Species indicative of the Walvis Ridge sites						
Transitional assemblage						
M. decussata	6.7	6.7	4.1	10.3	45.5	34.7
	(4.6-8.7)	(5.5-7.4)	(3.9-4.3)	(8.7-11.8)	(35.0-51.4)	(26.0-41.8)
M. murus	2.6	1.3	1.3	1.5	4.8	3.0
	(2.2-3.4)	(0.9-1.8)	(1.2-1.4)	(1.0-1.9)	(3.9-6.0)	(2.5-3.8)
C. aceulus	1.7	1.3	0.9	0.9	1.8	3.4
	(1.1-2.0)	(1.0-2.2)	(0.6-1.2)	(0.8-1.0)	(1.0-2.9)	(2.2-5.6)
C. kamptneri	0.3	0.1	0.1	0.3	0.5	0.4
	(0.0-0.6)	(0.0-0.2)	(0.0-0.2)	(0.0-0.6)	(0.0-1.0)	(0.2-0.6)
L. quadratus	1.5	2.8	2.8	3.7	4.6	4.1
	(1.0-2.0)	(2.5-3.3)	(2.6-2.9)	(2.3-5.2)	(3.1-5.5)	(3.3-4.8)
P. majungae	0.0	1.9	1.1	0.3	1.1	2.5
	(0.0-0.0)	(0.8-2.9)	(0.8-1.4)	(0.0-0.4)	(0.6-1.6)	(0.4-4.7)
Low-latitude Tethyan subassemblage (Pacific)						
C. serratus	2.1	0.1	0.8	0.6	0.1	0.6
	(1.3-2.8)	(0.0-0.4)	(0.4-1.2)	(0.2-1.2)	(0.0-0.4)	(0.2-1.0)
M. pemmatoidea	1.7	0.4	0.3	0.3	0.1	0.1
	(0.8-2.3)	(0.0-0.9)	(0.2-0.4)	(0.0-0.6)	(0.0-0.4)	(0.0-0.4)
L. armilla	2.2	0.0	0.0	0.0	0.0	0.0
	(1.4-3.4)	(0.0-0.0)	(0.0-0.0)	(0.0-0.0)	(0.0-0.0)	(0.0-0.0)
W. barnesae	41.0	17.6	17.2	9.9	7.9	8.8
	(33.3-46.2)	(11.8-22.9)	(16.6-17.7)	(8.0-11.4)	(6.8-10.0)	(6.7-10.9)
Warm-water Tethyan subassemblage (Atlantic)						
D. ignotus	0.0	0.6	0.6	2.2	0.0	0.0
	(0.0-0.2)	(0.0-1.2)	(0.4-0.8)	(1.0-3.7)	(0.0-0.0)	(0.0-0.0)
C. exiguum	0.0	0.1	0.3	0.6	0.0	0.0
	(0.0-0.0)	(0.0-0.2)	(0.2-0.4)	(0.2-1.0)	(0.0-0.0)	(0.0-0.0)
Z. erectus	0.0	0.0	1.7	2.7	0.0	0.0
	(0.0-0.0)	(0.0-0.0)	(1.6-1.9)	(1.7-4.2)	(0.0-0.0)	(0.0-0.0)
M. undosus	0.0	0.0	0.0	1.0	0.0	0.0
	(0.0-0.0)	(0.0-0.0)	(0.0-0.0)	(0.6-1.3)	(0.0-0.0)	(0.0-0.0)
Z. crux	0.0	0.0	1.8	2.1	0.0	0.0
	(0.0-0.0)	(0.0-0.0)	(0.8-2.9)	(1.7-2.3)	(0.0-0.0)	(0.0-0.0)
R. asper	0.0	0.0	0.0	0.5	0.1	0.1
	(0.0-0.2)	(0.0-0.0)	(0.0-0.0)	(0.0-1.1)	(0.0-0.2)	(0.0-0.4)
R. angustus	0.0	0.1	0.4	1.7	0.0	0.0
	(0.0-0.0)	(0.0-0.4)	(0.2-0.6)	(1.0-2.5)	(0.0-0.0)	(0.0-0.2)
R. reniformes	0.0	0.0	0.4	0.4	0.0	0.2
	(0.0-0.0)	(0.0-0.0)	(0.4-0.4)	(0.0-0.1)	(0.0.-0.0)	(0.0-0.6)
R. splendens	0.0	0.0	0.8	0.3	0.1	0.1
	(0.0-0.0)	(0.0-0.2)	(0.6-1.0)	(0.0-0.8)	(0.0-0.4)	(0.0-0.2)
Shallow and cool Tethyan subassemblage (Atlantic)						
L. cayeuxii	0.1	0.4	0.0	0.1	0.1	0.0
	(0.0-0.4)	(0.0-1.1)	(0.0-0.0)	(0.0-0.2)	(0.0-0.2)	(0.0-0.0)
A. cymbiformis	0.1	4.1	0.7	0.9	2.2	1.3
	(0.0-0.4)	(3.3-7.6)	(0.6-0.8)	(0.4-1.5)	(1.6-3.5)	(0.6-2.5)
A. octoradiata	0.0	0.9	0.4	0.4	0.1	0.3
	(0.0-0.0)	(0.2-1.9)	(0.4-0.4)	(0.2-0.6)	(0.0-0.2)	(0.0-0.6)
C. surrirellus	1.5	4.5	2.1	2.4	0.9	0.9
	(1.1-2.0)	(3.8-5.7)	(2.1-2.2)	(0.8-3.8)	(0.4-1.2)	(0.4-2.1)
N. frequens	0.0	0.9	0.2	0.4	0.3	0.1
	(0.0-0.0)	(0.4-1.1)	(0.2-0.2)	(0.2-0.6)	(0.0-0.9)	(0.0-0.2)
P. majungae	0.0	1.9	1.1	0.3	1.1	2.5
	(0.0-0.0)	(0.8-2.9)	(0.8-1.4)	(0.0-0.4)	(0.6-1.6)	(0.4-4.7)

Table 3. Means and ranges (within parentheses) of relative abundances of different species. Four different species assemblages could be distinguished (see for explanation).

	Site 465A	Site 548A	Site 384	Site 356	Site 525A	Site 527
Species without biogeographic preference						
C. crenulatis	1.7	1.5	4.3	1.2	0.7	1.4
	(0.6-4.0)	(0.7-2.0)	(4.0-4.5)	(0.4-2.5)	(0.4-1.1)	(0.4-2.3)
A. regularis	2.4	1.1	1.9	2.7	2.2	4.3
	(2.2-2.8)	(0.6-2.0)	(1.4-2.5)	(1.9-3.3)	(1.4-3.4)	(1.0-6.9)
Thoracosph. sp.	0.0	0.0	1.8	0.1	0.0	0.0
	(0.0-0.2)	(0.0-0.0)	(1.4-2.2)	(0.0-0.2)	(0.0-0.0)	(0.0-0.2)
R. minutum	0.5	0.4	1.5	1.4	0.2	0.8
	(0.2-1.0)	(0.0-0.9)	(0.8-2.3)	(0.4-2.5)	(0.0-0.5)	(0.2-1.5)
P. cretacea	9.4	15.8	13.2	11.7	7.2	9.6
	(7.6-12.0)	(12.5-18.6)	(13.0-13.4)	(8.9-13.1)	(5.9-8.8)	(7.9-13.3)
P. spinosa	0.3	2.8	1.8	4.1	0.9	1.1
	(0.0-0.6)	(2.2-4.1)	(1.4-2.2)	(2.9-5.3)	(0.4-1.6)	(0.6-1.7)
P. stoveri	3.6	11.9	12.3	4.7	4.2	6.0
	(2.1-5.5)	(7.6-15.2)	(10.9-13.8)	(4.2-5.2)	(2.1-6.4)	(5.3-8.1)
G. obliquum	0.0	0.3	1.2	0.5	0.0	0.2
	(0.0-0.0)	(0.0-0.9)	(1.0-1.4)	(0.2-0.8)	(0.0-0.2)	(0.0-0.4)
L. carnoliensis	0.0	0.2	0.2	0.5	0.2	0.5
	(0.0-0.2)	(0.0-0.4)	(0.0-0.4)	(0.2-0.6)	(0.0-0.4)	(0.0-1.0)
L. prequadratus	0.2	0.2	0.4	0.7	0.5	0.5
	(0.0-0.4)	(0.0-0.4)	(0.4-0.4)	(0.4-1.1)	(0.0-1.0)	(0.2-0.9)
C. madagask.	0.1	1.4	0.4	2.6	0.2	0.7
	(0.0-0.4)	(0.6-2.5)	(0.2-0.6)	(1.9-3.2)	(0.0-0.5)	(0.2-1.5)
M. pleniporus	0.0	0.9	0.7	1.4	0.1	0.3
	(0.0-1.2)	(0.2-1.5)	(0.6-0.8)	(0.6-1.7)	(0.0-0.4)	(0.0-0.8)
E. paralellus	0.1	0.8	1.0	1.0	0.1	0.1
	(0.0-0.4)	(0.2-1.4)	(0.6-1.4)	(0.4-2.1)	(0.0-0.2)	(0.0-0.2)
E. turriseifellii	1.3	2.4	2.7	2.1	1.5	1.7
	(1.0-2.2)	(1.1-3.9)	(2.2-3.1)	(1.7-2.5)	(0.2-2.9)	(1.0-2.5)
M. attenatus	0.4	0.5	0.3	1.0	0.6	1.1
	(0.2-0.6)	(0.0-0.9)	(0.2-0.4)	(0.6-1.2)	(0.0-1.4)	(0.8-1.7)
Z. minimus	2.0	0.4	1.8	1.9	0.4	0.7
	(1.6-2.2)	(0.0-1.0)	(1.2-2.4)	(1.4-2.7)	(0.0-1.0)	(0.2-1.7)
C. ehrenbergii	6.5	3.8	3.4	3.5	4.0	3.0
	(5.5-7.3)	(2.3-5.9)	(3.3-3.4)	(2.5-4.4)	(2.9-5.0)	(1.8-4.4)
C. fessus	1.5	2.8	3.8	1.8	0.5	1.3
	(1.1-2.0)	(1.0-3.7)	(3.3-4.3)	(1.5-2.3)	(0.0-1.0)	(0.6-2.6)
Z. spiralis	1.9	3.9	2.7	3.8	0.9	1.0
	(1.6-2.2)	(2.4-4.9)	(2.1-3.4)	(1.9-5.4)	(0.4-1.6)	(0.4-1.6)
C. gallica	1.7	1.1	1.2	0.8	1.9	1.0
	(0.8-2.7)	(0.4-2.3)	(1.0-1.4)	(0.4-1.5)	(1.0-2.9)	(0.4-2.4)
Rest of flora	4.1	4.1	4.9	8.9	3.3	4.3
	(2.8-5.8)	(2.7-4.4)	(4.7-5.1)	(6.5-11.2)	(1.2-5.3)	(2.2-6.9)

Table 3. (cont.)

planktonic foraminiferal tests has been employed as an index of calcite dissolution (for example, Arrhenius, 1952; Berger, 1970; Malmgren, 1983, 1987). For interpretations of dissolution effects a combination of the degree of fragmentation and benthonic foraminiferal abundance was used by Malmgren (1991). Dissolution was moderate (percentage of fragments 10-40% and percentage of benthonic foraminifera <10%) at all sites (Fig. 11).

The result of this study suggests that the dominant controlling force of the biogeographic patterns at the investigated sites is the extension of the Tethyan Realm and the circulation patterns in this realm (Fig. 2).

The second correspondence axis documents a floral difference between Site 465A and the other Tethyan sites (Figs. 2 and 3). This may be due to the location of Site 465A in a more open-ocean environment, or a distinct difference in paleoceanographic conditions in the Pacific and the Atlantic at this time, resulting from a difference in circulation patterns within oceans.

The third axis orders the sites along a temperature gradient (Fig. 3). Stable isotope temperature estimates show that Site 356 was the warmest and Site 548A the coolest of the investigated sites during the end of the Cretaceous (Table 4). This axis distinguishes Site 548A which cluster to the extreme from Site 356; this is due to the cool and shallow environment at Site 548A (200-500 m; Graciansky *et al.*, 1985) in the terminal Cretaceous.

Comparisons with other investigations of ecologic or biogeographic patterns in Late Cretaceous calcareous nannofossils are difficult because earlier studies were either not quantitative or based on broad time-slices comprising several million years. Thierstein≠s (1976; 1981) studies of biogeographic patterns in calcareous nannofossils during the last 15 m.y. of the Cretaceous and the study by Perch-Nielsen (1979) may, however, be used for comparisons with the distributional patterns found here. Table 5 compares the results of previous biogeographic studies with those obtained here.

According to Thierstein (1981) the abundance of *Micula decussata* (syn. *M. staurophora*) is highest at middle latitudes, but its distribution is to some degree controlled by differences in preservation. However, the great abundances of this species in only highly dissolved samples have later been questioned, since many well preserved sections contain great abundances of this species (Eshet *et al.*, 1992).

Micula murus, C. aculeus, C. kamptneri, and *L. quadratus* are more abundant at the Transitional sites (525A and 527). Previous studies state that *M. murus, C. aculeus*, and *L. quadratus* are somewhat more abundant at middle latitudes than low latitudes (Thierstein, 1976), and this inference is in agreement with the

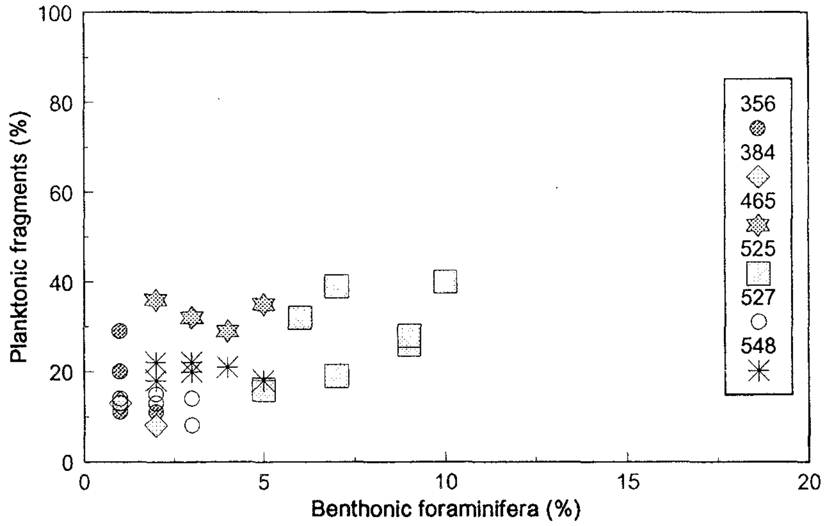

Fig. 11. Relationship between relative abundance of fragments of planktonic foraminifera (in relation to whole and fragmented test) and relative abundance of benthonic foraminifera (in relation to total foraminiferal content) at the various sites (after Malmgren, 1991).

present study. *Prediscosphaera majungae* is almost equally abundant at Site 527 and Site 548A and appears to be a cool-water species.

Watznaueria barnesae was most abundant at the low-latitude (Pacific) Site 465A. The preference for a low-latitude open-ocean environment is shared by *C. serratus, L. armilla,* and *M. pemmatoidea.* This preference was also noted for *W. barnesae* and *C. serratus* by THIERSTEIN (1981).

The warm Atlantic Site 356 showed enhanced abundances of several species although their abundances were low: *D. ignotus, C. exiguum, Z. erectus, Z. crux, M. undosus, R. asper, R. angustus, R. reniformes,* and *R. splendens. Microrhabdulus undosus* was only encountered at Site 356 and may require very warm waters.

Nephrolithus frequens showed the highest relative abundance at the coolest site (548A); this preference for cool water masses is well known, since this species is a biostratigraphic marker at high latitudes. This species may also prefer a shallow environment. *Ahmullerella octoradiata* is more common at Site 548A than at the other sites, and is generally more abundant at high latitudes (THIERSTEIN, 1981). Some of the other species encountered at Site 548A have been considered to be more abundant at high-latitude, marginal seas, namely, *A. cymbiformis* and *L. cayeuxii* (THIERSTEIN, 1976, 1981; PERCH-NIELSEN, 1979). *Cretarhabdus surirellus* was most abundant at the coolest Site 548A; the second greatest abundance of this species is encountered at the warmest Site 356. This observation is somewhat peculiar, and there might be an unknown factor controlling the distribution of this

Site	Paleodepths (m)	Paleolatitudes	Paleotemperatures (°C)
356	1000 (2)	23°S (1)	19-21 (9)
384	3000 (3)	29°N (1)	15-16 (9)
465A	1500 (4)	16°N (1,5)	16-18 (8)
525A	1100 (6)	36°S (1)	13-14 (10)
527	2700 (6)	36°S (1)	12-13 (10)
548A	200-500 (7)	37°N (1)	10-12 (11)

References: (1) ZACHOS & ARTHUR [1986], (2) PERCH-NIELSEN *et al.* [1977], (3) THIERSTEIN & OKADA [1979], (4) BOERSMA [1981], (5) VALLIER *et al.* [1981], (6) MOORE *et al.* [1984c], (7) GRACIANSKY *et al.* [1985], (8) BOERSMA & SCHACKLETON [1981], (9) BOERSMA *et al.* [1979], (10) SCHAKLETON *et al.* [1984b], (11) POAG *et al.* [1985].

Table 4. Estimates of paleodepths, paleolatitudes, and paleotemperatures for the different sites at about the time of the K-T boundary.

species. THIERSTEIN (1981) found a slight preference among low-and middle-latitude sites for *C. surirellus*, but it also showed abundance peaks at higher latitudes.

Several species showed no clear biogeographic patterns and were about equally abundant at the different sites. No clear biogeographic variation was found for *P. cretacea, M. pleniporus, C. ehrenbergii,* and *Z. spiralis* by THIERSTEIN (1981). *Prediscosphaera spinosa* showed some preferences for high latitudes in THIERSTEIN'S study (1981). *GARTNERago obliquum* and *E. turriseiffelii* also showed preferences for high latitudes, although they showed some peculiarities in distribution, which according to THIERSTEIN (1981), were either referable to high salinity or high productivity.

This study	Previous studies
Species indicative of the Walvis Ridge sites	
Transitional assemblage	
M. decussata	Middle latitudes (peculiar pattern)
M. murus	Middle (and low) latitudes
C. aculeus	Middle latitudes
C. kamptneri	---
L. quadratus	Middle latitudes
P. majungae	---
Low-latitudeTethyan subassemblage (Pacific)	
C. serratus	Low latitudes, open ocean
M. pemmatoidea	---
L. armilla	---
W. barnesae	Low latitudes, open ocean
Warm-water Tethyan subassemblage (Atlantic)	
D. ignotus	---
C. exiguum	---
Z. erectus	---
M. undosus	---
Z. crux	---
R. asper	---
R. angustus	---
R. reniformes	---
R. splendens	---
Shallow and cool Tethyan subassemblage (Atlantic)	
L. cayeuxii	High latitudes, marginal seas
A. cymbiformis	High latitudes, marginal seas
A. octoradiata	High latitudes
C. surirellus	Low-middle latitudes (peculiar pattern)
N. frequens	High latitudes
P. majungae	---

Table 5. Comparison of ecologic and biogeographic patterns of different calcareous nannoplankton species covered in this study to previous studies (THIERSTEIN, 1976, 1981; PERCH-NIELSEN, 1979).

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APPENDIX

Calcareous nannofossil species discussed in this paper in alphabetical order of their genus epithets. References to original descriptions are listed in the reference list. Further discussions and illustrations of the different taxa can be found in VERBEEK (1977) and PERCH-NIELSEN (1985).

Ahmuellerella octoradiata (GORKA 1957) REINHARDT 1964.
Ahmuellerella regularis (GORKA 1957) VERBEEK 1977.
Arkhangelskiella cymbiformis VEKSHINA 1959.
Ceratolithoides aculeus (STRADNER 1961) SISSINGH 1977.
Ceratolithoides kamptneri BRAMLETTE & MARTINI 1964.
Chiastozygus fessus (STOVER 1966) SHAFIK 1979.

This study	Previous studies
Species without biogeographic preference	
C. crenulatis	---
A. regularis	---
Thoracosph. sp.	---
R. munitus	---
P. cretacea	No pattern
P. spinosa	High latitude
P. stoveri	---
G. obliquum	High latitude (peculiar pattern)
L. carniolensis	---
L. prequadratus	---
C. madagaskariensis	---
M. pleniporus	No pattern
E. paralellus	---
E. turriseiffelii	High latitude (peculiar pattern)
M. attenuatus	---
Z. minimus	---
C. ehrenbergii	No pattern
C. fessus	---
Z. spiralis	No pattern
C. gallica	---

Table 5. (cont.)

Corollithion exiguum STRADNER 1961.
Corollithion madagaskariensis PERCH-NIELSEN 1973.
Cretarhabdus crenulatis BRAMLETTE & MARTINI 1964.
Cretarhabdus surirellus (DEFLANDRE & FERT 1954) REINHARDT 1970.
Cribrocorona gallica (STRADNER 1963) PERCH-NIELSEN 1973.
Cribrosphaerella ehrenbergii (ARKAHANGELSKY 1912) DEFLANDRE 1952.
Cylindralithus serratus BRAMLETTE & MARTINI 1964.
Discorhabdus ignotus (GORKA 1957) PERCH-NIELSEN 1973.
Eiffelithus parallelus PERCH-NIELSEN 1973.
Eiffelithus turriseiffelii (DEFLANDRE & FERT 1954) REINHARDT 1965.
GARTNERago obliquum (STRADNER 1963) REINHARDT 1970.
Lithraphidites carniolensis DEFLANDRE 1963.
Lithraphidites prequadratus ROTH 1978.
Lithraphidites quadratus BRAMLETTE & MARTINI 1964.
Loxolithus armilla (BLACK & BARNES 1959) NOEL 1965.
Lucianorhabdus cayeuxii DEFLANDRE 1959.
Manivitella pemmatoidea (MANIVIT 1965) THIERSTEIN 1971.
Microrhabdulus attenuatus BRAMLETTE & MARTINI 1964.
Microrhabdulus undosus PERCH-NIELSEN 1973.
Micula decussata VEKSHINA 1959.
Micula murus (MARTINI 1961) BUKRY 1973.
Misceomarginatus pleniporus WISE & WIND 1977.
Nephrolithus frequens GORKA 1957.
Prediscosphaera cretacea (ARKAHANGELSKY 1912) GARTNER 1968.
Prediscosphaera majungae PERCH-NIELSEN 1973.
Prediscosphaera spinosa (BRAMLETTE & MARTINI 1964) GARTNER 1968.
Prediscosphaera stoveri (PERCH-NIELSEN 1968) SHAFIK & STRADNER 1971.
Rhagodiscus angustus (STRADNER 1963) REINHARDT 1971.
Rhagodiscus asper (STRADNER 1963) REINHARDT 1967.
Rhagodiscus splendens (DEFLANDRE 1953) VERBEEK 1977.
Rhagodiscus reniformes PERCH-NIELSEN 1973.
Rotelappilus munitus (PERCH-NIELSEN 1973) PERCH-NIELSEN 1984.
Thoracosphaera sp. KAMPTNER 1927.
Watznaueria barnesae (BLACK & BARNES 1959) PERCH-NIELSEN 1968.
Zygodiscus crux (DEFLANDRE & FERT 1954) BRAMLETTE & SULLIVAN 1961.
Zygodiscus erectus (DEFLANDRE & FERT 1954) REINHARDT 1965.
Zygodiscus minimus BUKRY 1969.
Zygodiscus spiralis BRAMLETTE & MARTINI 1964.

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