Benthic Foraminiferal Faunas and Trophic Regimes at the Terminal Cretaceous Tethyan Seafloor

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We quantified the horizontal distribution of Late Cretaceous (late Maastrichtian) benthic foraminifera for 10 upper bathyal to abyssal localities, that cover a wide range of environmental settings throughout the Tethyan realm. For the first time, a quantitative faunal study is performed in order to identify and explain the differences between Late Cretaceous benthic foraminiferal faunas from the deep open ocean and from the shallower marginal seas of the Tethys.

The results from correspondence analysis indicate that the main arrangement of the various sites coincides with a paleobathymetric ranking, which we consider to be primarily a reflection of gradients in trophic resources and oxygen levels. Five benthic foraminiferal assemblages were found to characterize bathymetrically and latitudinally different environmental settings within the Tethyan realm: (1) a Marginal Tethyan Assemblage (e.g., large Cibicidoides spp. and Sliteria varsoviensis) characteristic of the relatively highly fertile environment of the southern Central Tethyan margin, (2) an Abyssal Tethyan Assemblage (e.g., Aragonia spp. and Nuttallides truempyi) that signifies the more oligotrophic deep open-ocean conditions in the Western Tethys, (3) a Northwestern Tethyan Assemblage containing some high latitude ("boreal") faunal elements (e.g., Gavelinella pertusa and Stensioeina pommerana) characteristic of the northernmost part of the Western Tethys, (4) a Shallow Bathyal Assemblage (e.g., Bolivinoides draco and Eouvigerina subsculptura), which is composed of more or less ubiquitous taxa, and finally, (5) a Deep Bathyal Assemblage (e.g., Bulimina trinitatensis and Gavelinella beccariiformis), which also has a mostly ubiquitous distribution except for the shallow sites of the southern margin of the Central Tethys, where it is virtually absent. Morphotype analysis of the total fauna reveals distinct differences in proportions of endobenthic and epibenthic morphologies between the various sites, but a clear trend between the deep open ocean and the marginal seas cannot readily be discerned. However, a comparison of the proportions of morphotypes within the five assemblages resulting from correspondence analysis signifies clear trends between the various environmental settings. This enables us to distinguish various trophic regimes within the Tethyan realm; yet, we found no faunal indications of either true oligotrophic or eutrophic settings. We conclude that large areas of the latest Cretaceous bathyal environment of the Tethys were more or less mesotrophic in character, but nevertheless, abundance-patterns of morphogroups within each of the five assemblages were found to reflect depth-related gradients, which in turn are influenced by variations in food availability and oxygen concentration at the seafloor.

INTRODUCTION

The study of paleobiogeographic patterns is an important approach to a better understanding of the relationships between organisms and their environment in the geological past. Only a few quantitative studies on the paleoecology of Late Cretaceous benthic foraminifera have been carried out using multivariate statistics (Kuhnt and Moullade, 1991; Widmark and Malmgren, 1992a; Widmark, 1995). Kuhnt and Moullade (1991) investigated Campanian and Maastrichtian abyssal agglutinated foraminiferal faunas from six DSDP/ODP holes in the North Atlantic and found an environmentally determined response in these faunas, mainly controlled by the oxygenation of the bottom waters and the availability of calcium carbonate. Widmark and Malmgren (1992a) analyzed a time slice encompassing the terminal 20 to 50 ky of the Cretaceous from six DSDP holes in the Atlantic and Pacific Oceans. They found a clear biogeographic trend among the bathyal benthic foraminiferal faunas that appeared to be controlled by the proximity of the various sites to a low latitude high-productivity belt. Widmark (1995) extended the study of Widmark and Malmgren (1992a) by including late Maastrichtian (Abathomphalus mayaroensis Zone) material from 18 additional DSDP/ODP holes in the Atlantic, Indian, Pacific, and Southern Oceans representing a wide range of paleodepths and paleolatitudes. He suggested that the main global latitudinal contrast in deep-sea benthic foraminifera faunas reflects latitude-related differences in trophic levels and oxygenation. High latitudes were dominated by various epifaunal, oligotrophic/high-oxygen taxa suggesting the existence of a high-latitude deep-water source producing relatively cool, oxygen-rich deep waters, whereas the low-latitude faunas were inferred to be influenced by warm, saline, less oxygenated deep waters based on high abundance and diversities of various infaunal, eutrophic/low-oxygen (buliminid) taxa (Widmark, 1995). A similar paleoceanographic setting has also been suggested by several stable-isotope studies (e.g., Brass et al., 1982; Saltzman and Barron, 1982; Barrera et al., 1987; Barrera and Huber, 1990; Kennett and Barker, 1990; Barrera, 1994; MacLeod and Huber, 1996). Studies on upper bathyal faunas from the southern Central Tethyan margin (north Africa) also suggested the prevalence of rather high trophic conditions at the sea floor, probably induced by upwelling (Speijer and Van der Zwaan, 1996).

In the present study we focus on the geographic distribution of benthic foraminifera in the Late Cretaceous (late Maastrichtian) Tethyan realm, representing a wide range of paleoenvironments including deep ocean in the Western (Central Atlantic) Tethys to shallower marginal seas of the Central (Mediterranean) Tethys (Fig. 1). The aim of
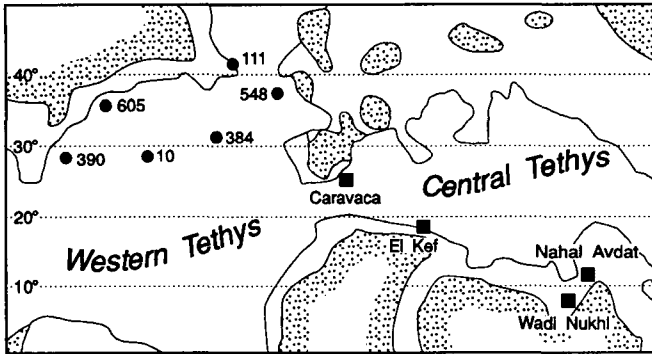
FIGURE 1—Paleo-locations of the various DSDP sites and landbased sections during the latest Maastrichtian (about 65 Ma). Base map from Keller (1992) and paleolatitudes as well as paleolatitudinal locations of sites and sections from Camoin et al. (1993). Dotted areas show continental areas from North Africa below to North America and Europe above.

the study is to identify and explain differences between benthic foraminiferal faunas in terms of depth and latitude related gradients of trophic and oxygen levels in order to provide a better understanding of the bathyal environment during the time just before the dramatic biogeosphere perturbations at the Cretaceous/Paleogene boundary (KPgB). Our timeslice study may serve as a baseline for future time-series studies on faunal change across the KPgB and thereby facilitate faunal evaluations in terms of extinctions, originations, and migrations.

MATERIALS AND METHODS

Latest Cretaceous benthic foraminifera from a wide range of paleodepths throughout the Western (Central Atlantic) and Central (Mediterranean) Tethys were analyzed. For convenience we refer to studied parts of the present-day Central and North Atlantic as Western Tethys during Cretaceous times. The material was obtained from six Western Tethyan DSDP sites including the North American Basin, Orphan Knoll, *J*-Anomaly Ridge, Blake Nose, Goban Spur, and off New Jersey (Holes 10, 111, 384, 390A, 548A, and 605, respectively), three landbased sections from the southern margin of the Central Tethys, including El Kef (Tunisia), Wadi Nukhl (Egypt), and Nahal Avdat (Israel), and one landbased section from the northern margin of the Central Tethys represented by the Caravaca section in southern Spain (Fig. 1).

Lithologies at the various DSDP sites range from nannofossil-foraminiferal oozes to chalks and limestones, all of which indicate more or less open-ocean environments with low terrigeneous influence; the landbased sections from the marginal Central Tethys, on the other hand, are dominated by marls, pointing to a stronger terrestrial influence at these sections. Inferred paleolatitudes of the various DSDP sites and landbased sections at 69.5–65 Ma were obtained or estimated from Camoin et al. (1993). Information on lithology, as well as inferred paleolatitude and paleodepth (see below) of the various sites and sections is given in Table 1.

The 32 samples analyzed herein were prepared according to conventional procedures, including disaggregation in water and washing through a 63 μm sieve. After drying,

the sand fraction was sieved over a 125 μm screen and the larger fraction was used for generation of compositional data. In most cases when analyzing DSDP material, the entire sample available was used for the foraminiferal analysis; for samples from landbased sections, representative samples were obtained by using an Otto Microsplitter. The sample size (i.e., number of specimens per sample) ranged between 114 and 826 (Table 2).

Substantial effort was put into the calibration of the taxonomies used by the two authors in order to conduct a reliable quantitative analysis. Nevertheless, more than 250 taxa were identified at generic or specific level. The faunas contain both calcareous and agglutinated benthic foraminifera, and they are dominated by the suborder Rotaliina. Those taxa with a mean relative abundance greater than or equal to 2% (based on the relative abundance of taxa in each sample) at any of the sites included in the survey were regarded as sufficiently abundant to be reliably used for the quantitative analysis. A faunal reference list for the 66 selected taxa is given in Appendix I. These 66 taxa constitute a major portion (70–88 %) of the benthic foraminiferal fauna throughout the study area and can therefore be considered to be representative for the benthic foraminiferal faunas in the Tethyan slope–basin environment during the terminal Cretaceous. Finally, correspondence analysis was employed in order to identify differences between benthic foraminiferal faunas in the Tethyan Realm.

BIOSTRATIGRAPHIC FRAMEWORK

All samples are from the uppermost Maastrichtian planktonic foraminiferal *Abathomphalus mayaroensis* Zone, representing the uppermost Cretaceous. The *A. mayaroensis* Zone was recognized at all DSDP sites, except for Site 390, according to various DSDP site reports. However, close examination of the planktonic foraminiferal fauna in sample 390A-11 cc yielded a few specimens of its biozonal index species *A. mayaroensis,* which made it possible to include this sample in the survey. Samples from the uppermost meter of the Maastrichtian at Caravaca are within the upper part of the *A. mayaroensis* Zone (Smit, 1982; Canudo et al., 1991). Speijer and Van der Zwaan (1996) allocated the El Kef samples used herein to the upper part of the *A. mayaroensis* Zone based on the biostratigraphy of Brinkhuis and Zachariasse (1988) and Nederbragt (1992), whereas the samples from Wadi Nukhl were assigned to the *Plummerita reicheli* Zone, which corresponds to the upper part of the *A. mayaroensis* Zone (Masters, 1993). Finally, the sample from Nahal Avdat was taken just below the KPgB from the calcareous nannofossil *Nephrolithus frequens* Zone (Romein, 1979a,b), which is also widely accepted to represent the uppermost Maastrichtian (e.g., Perch-Nielsen, 1985 and references therein). A listing of the samples analyzed, with depth below sea floor (mbsf; when appropriate) and position below the KPgB, is given in Table 2.

PALEOBATHYMETRIC FRAMEWORK

Paleodepths of the DSDP sites as given in the literature range from outer neritic-upper bathyal to abyssal and are

TABLE 1—Data on locations, lithologies of samples, inferred paleobathymetries, paleobathymetric information in the literature and the method used in cited references, and paleolatitude (at 69.5–65 Ma; Camoin et al., 1993) of the various sites and sections analyzed. Figures in parentheses refer to sources of information.

Location			Lithology	Inferred paleo-bathymetry	Paleo-bathymetry (in literature)	Method (used in reference)	Paleo-latitude (2)
DSDP sites							
10	Central Atlantic	N. American basin	Foram nanno chalk ooze*	abyssal (3100 m)	3100 m (13)	backtracking (13)	29°N
111	North Atlantic	Orphan Knoll	Chalk ooze*	upper bathyal (~500 m)	~300 m (8)	forams and ostracods (8)	41°N
384	Central Atlantic	J-Anomaly Ridge	Nanno chalk*	abyssal (3400 m)	3400 m (13)	backtracking (13)	31°N
390	Central Atlantic	Blake Nose	Marly nanno ooze*	lower bathyal (1200 m)	600–1600 m (1)	subsidence and sed. accumulation rates (1)	29°N
548	Central Atlantic	Goban Spur	Foram nanno chalk*	middle bathyal (~800 m)	outer shelf–upper slope (11)	nannos and forams (11)	38°N
605	Central Atlantic	Off New Jersey	Clay-rich foram nanno limestone*	middle bathyal (~800 m)	~2400 m (5) 600–1800 m (10)	see text (5) forams (10)	36°N
Land-based sections							
El Kef	Tunisia		Marl (12)	upper bathyal (~400 m)	u. bathyal–outer shelf (6) u. bathyal (4) 150–350 m (7) 150–300 m (9) 300–500 m (12)	forams (6, 7, 12) ostracods (4, 9)	18°N
Wadi Nukhl	Egypt		Marl (12)	upper bathyal (~400 m)	300–500 m (12)	forams (12)	9°N
Nahal Avdat	Israel		Marl (12)	upper bathyal (~400 m)	300–500 m (12)	forams (12)	11°N
Caravaca	Spain		Marl (3)	middle bathyal (~800 m)	600–1000 m (3) 200–600 m (7)	forams (3, 7)	25°N

* Data on lithologies are taken from the various DSDP Site Reports. References: (1) Benson et al. (1978); (2) Camoin et al. (1993); (3) Coccioni and Galeotti (1994); (4) Donze et al. (1982); (5) Jansen and Kroon (1987); (6) Keller (1988); (7) Keller (1992); (8) Laughton et al. (1972); (9) Peypouquet et al. (1986); (10) Saint-Marc (1987); (11) Snyder et al. (1985); (12) Spiejer and Van der Zwaan (1996); (13) Tucholke and Vogt (1979).

based on backtracking, subsidence curves, ostracoda, foraminifera, or nannofossil data. On the basis of our own benthic foraminiferal data we agree with most of the inferred paleodepths except for those of Sites 111 and 548. Outer neritic-to-upper bathyal deposition at Sites 111 and 548 was determined from foraminifera and ostracoda (Laughton et al., 1972) and nannofossils and foraminifera (Snyder et al., 1985), respectively, which is too shallow considering the benthic foraminiferal faunas that we quantified at these sites. We found significant mean relative abundance of several bathyal species at both Sites 111 and 548: *Gavelinella beccariiformis* (7.6 and 6.0%, respectively), *Nuttallides truempyi* (0.2 and 3.8%), *Cibicidoides hyphalus* (16.8 and 9.6%), and *C. velascoensis* (3.5 and 0.5%). The upper bathymetric limit for *N. truempyi* has been suggested by Berggren and Aubert (1983) to be within the depth range of 500–600 m (upper bathyal), which suggests that the paleodepth of Site 111 was close to the upper ecological limit (~500 m) of this species, whereas Site 548 was probably somewhat deeper (~800 m) based on the consistent occurrence of *N. truempyi.*

Inferred paleodepths in the literature for Site 605 represent a wide depth range from 600–1800 m (Saint-Marc,

1987) to about 2400 m (Jansen and Kroon, 1987); the former depth estimate was based on the episodic occurrence of *N. truempyi* during the Paleocene. The latter depth estimate, on the other hand, was based on the paleodepth model of Hardenbol et al. (1981) (assuming that the subsidence caused by lithospheric cooling was negligible since the Maastrichtian; see Jansen and Kroon, 1987) and the constant relative abundance of benthic foraminiferal superfamilies throughout the section studied. Since *N. truempyi* is absent, but other bathyal species such as *G. beccariiformis* and *C. hyphalus* are present in significant numbers (1.2% and 5.7%, respectively) we rather agree on the shallower part (500–800 m) of the depth range suggested by Saint-Marc (1987) for Site 605. Depths of deposition of the various landbased sections are more homogeneous ranging from upper-to-middle bathyal depths, based on ostracod and foraminiferal data (Donze et al., 1982; Peypouquet et al., 1986; Keller, 1988, 1992; Coccioni and Galeotti, 1994; Speijer and Van der Zwaan, 1996). These estimates are roughly compatible with our interpretations; only the paleodepth estimates for Caravaca (Spain) vary considerably between 200–600 m (Keller, 1992) and 600–1000 m (Coccioni and Galeotti, 1994). We

TABLE 2—Depth in hole (when appropriate) and depth below top of Cretaceous section for the samples analyzed herein, position of samples within the biozones, and number of specimens (N) encountered in each sample. Figures within parentheses refer to sources of information.

Samples/Biozone	Depth in Hole (mbsf)	Depth below top Cret. (m)	N
K/Pg boundary	292.00*	0.00	
10-10-1, 120–126 cm	293.23	−1.23	184
10-10-2, 120–126 cm	294.73	−2.73	217
10-10-3, 64-70 cm	295.67	−3.67	170
10-10-4, 104–110 cm	297.57	−5.57	114
10-10-5, 106–112 cm	299.09	−7.09	343
Base *A. mayaroensis*			
Zone	299.50*	−7.50	
K/Pg boundary	182.13*	0.00	
111A-11-2, 5–19 cm	183.62	−1.50	834
Base *A. mayaroensis*			
Zone	183.90*	−1.78	
K/Pg boundary	167.93*	0.00	
384-13-3, 34–36 cm	167.95	−0.02	244
384-13-3, 50–52 cm	168.11	−0.18	285
384-13-4, 3–18 cm	169.17	−1.24	369
Base *A. mayaroensis*			
Zone	177.70*	−9.77	
K/Pg boundary	112.00*	0.00	
390A-11 cc	113.57	−1.57	261

Sample within *A. mayaroensis* Zone (see text for explanation)

Samples/Biozone	Depth in Hole (mbsf)	Depth below top Cret. (m)	N
K/Pg boundary	471.40*	0.00	
548A-29-1, 14–15 cm	471.65	−0.25	338
548A-29-1, 34–35 cm	471.85	−0.45	412
548A-29-1, 54–55 cm	472.05	−0.65	285
548A-29-1, 64–65 cm	472.15	−0.75	397
548A-29-1, 84–85 cm	472.35	⁻0.95	424
Base *A. mayaroensis*			
Zone	485.50*	−14.10	
K/Pg boundary	759.81(7)	0.00	
605-66-3, 53–68 cm	762.80	−2.99	476
605-66-4, 43–58 cm	764.05	−4.24	346
Base *A. mayaroensis*			
Zone	793.17*	−33.36	

El Kef, Tunisia

Samples/Biozone	Depth below top Cret. (m)	N
K/Pg boundary	0.00	
AFN 540	−0.05	215
AFN 539	−0.25	203
AFN 538	−0.45	267
AFN 537	−0.65	231
AFN 536	−0.85	227
AFN 534	−1.50	198
AFN 532	−2.50	226
AFN 530	−3.50	231
AFN 528	−4.50	256

Samples within *A. mayaroensis* Zone (1,4,8) (see text for explanation)

Wadi Nukhl, Egypt

Samples/Biozone	Depth below top Cret. (m)	N
K/Pg boundary	0.00	
S 704	−1.20	234
S 702	−2.30	209
S 701	−3.10	173

Samples within *P. reicheli* Zone (3,8) (see text for explanation)

Nahal Avdat, Israel

Samples/Biozone	Depth below top Cret. (m)	N
K/Pg boundary	0.00	
IR 53	<0.50	268

Sample within *N. frequens* Zone (5, 8) (see text for explanation)

TABLE 2—Continued.

Samples/Biozone	Depth in Hole (mbsf)	Depth below top Cret. (m)	N
Caravaca, Spain			
K/Pg boundary		0.00	
CAR 1		−0.30	317
CAR 2		−0.60	299

Samples within *A. mayaroensis* Zone (2,6) (see text for explanation)

* Information is obtained from appropriate DSDP Site report. References: (1) Brinkhuis and Zachariasse (1988); (2) Canudo et al. (1991); (3) cf. Masters (1993); (4) Nederbragt (1992); (5) Romein (1979a,b); (6) Smit (1982); (7) Smit and Van Kempen (1987); (8) Speijer and Van der Zwaan (1996).

agree on the deeper range (of ~800 m) for this section on the basis of (1) the overall resemblance with other middle bathyal faunas analyzed world wide (Widmark, 1995); and (2) the absence of many Midway-fauna species (Berggren and Aubert, 1975) that are very frequent in our material from the upper bathyal (~400 m) sites of the southern Central Tethyan margin (see further text). In the following, we adopt the bathymetric scheme employed by Van Morkhoven et al. (1986), i.e., neritic = 0–200 m, upper bathyal = 200–600 m, middle bathyal = 600–1000 m, lower bathyal = 1000–2000 m, and abyssal > 2000 m.

RESULTS

Correspondence Analysis

Correspondence analysis permits simultaneous plots of observation (sample) and variable (taxon) points on the same coordinate axes, which facilitates interpretation of the assemblages that are responsible for clustering the samples (David et al., 1974; Malmgren et al., 1978; Saint-Marc and Berggren, 1988; Kuhnt and Moullade, 1991; Widmark and Malmgren, 1992a,b; Widmark, 1995). This method is applied here in order to emphasize the differences between the various benthic foraminiferal faunas, based on both the species occurrences as well as the relative proportions of the 66 selected taxa in the Western and Central Tethys during the latest Cretaceous.

Figure 2 shows the clustering of samples (marked by hatched areas) and taxa along the first two correspondence axes. The groupings of samples into clusters of the same site in combination with the grouping of sites from similar domains (bathymetrically and/or geographically) implies (1) that the faunal composition is quite stable within a single site (or domain) and (2) that the outcome of the correspondence analysis reflects true environmental gradients between the deep open ocean and shallower marginal settings within the Tethyan realm. The first two axes account for 38% of the variability (23 and 15%, respectively). The relatively "low" eigenvalues for the first two axes is due to the lack of a constantly dominant taxon, which can be expected when data from such a range of different environments are processed. The first axis shows a compositional contrast between deep ocean faunas and upper bathyal faunas of the southern Central Tethyan margin by plotting the deepest faunas (Sites 10 and 384) to the left and faunas of the southern margin of the Cen-
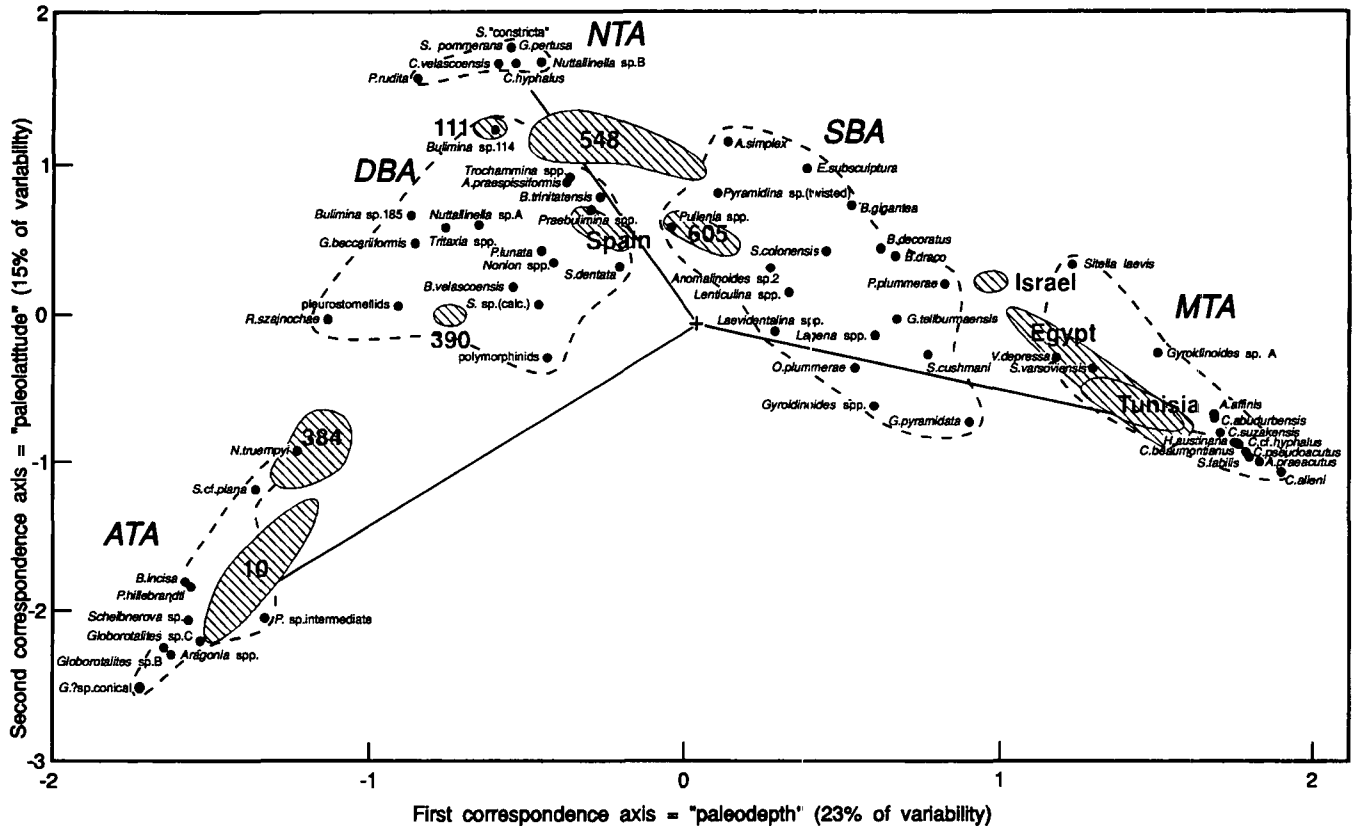
FIGURE 2—Taxa and samples (indicated by hatched areas) plotted along the first two correspondence axes. Analysis based on 66 taxa and 32 samples, the first and second axes account for 38% of the variability (23 and 15%, respectively). The five benthic foraminiferal assemblages identified are indicated by dashed lines: ATA = *Abyssal Tethyan Assemblage*; DBA = *Deep Bathyal Assemblage*; NTA = *Northwestern Tethyan Assemblage*; SBA = *Shallow Bathyal Assemblage*; MTA = *Marginal Tethyan Assemblage*. The plus sign (+) at center of plot indicates the mean loading of the taxa, while the three solid lines radiating from the mean taxa loading (+) mark the three main directions of variability within this plane in multivariate space.
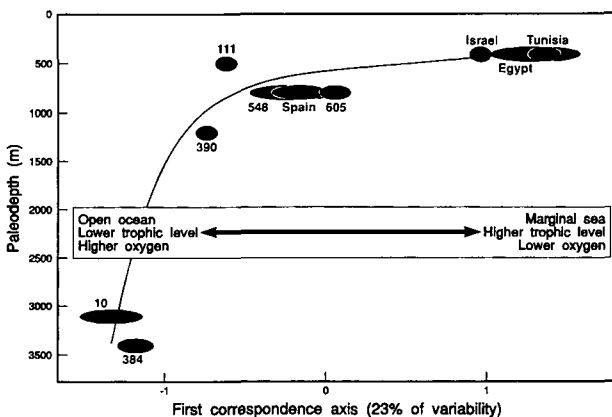
FIGURE 3—Diagram showing the first axis scores of samples plotted against the paleodepths inferred for the various sites/sections (see Table 1); note the strong correlation between paleodepth and the main faunal trend in the data set. Paleodepth is considered to be highly interrelated with environmental gradients (trophic level, oxygenation) from the deep open ocean to the shallow marginal sea.

tral Tethys to the right in Figure 2. Faunas from intermediate (bathyal) environments cluster in the middle of the plot. Figure 3 depicts this environmental trend (described by the first correspondence axis) as a function of paleodepth (Table 1), which, of course, is highly interrelated with environmental parameters such as organic fluxes and oxygen levels (i.e., "Open ocean—Lower trophic level—Higher oxygen" versus "Marginal Sea—Higher trophic level—Lower oxygen"). The main faunal contrast along the first correspondence axis is marked by a number of Midway-fauna species (Berggren and Aubert, 1975), such as various *Anomalinoides* and *Cibicidoides* species that occur throughout the samples from the southern margin of the Central Tethys (i.e., the sections in Tunisia, Egypt, and Israel). This Midway-fauna was originally recorded in, and named after, the lower Paleocene Midway Formation in Texas (Plummer, 1927; Kellough, 1965) and is also commonly associated with marls and shales deposited in neritic environments in Europe and North Africa (e.g., Brotzen, 1948; LeRoy, 1953; Berggren and Aubert, 1975; Salaj et al., 1976; Luger, 1985; Speijer, 1995). In the following we refer to Midway-fauna species *sensu lato*, i.e., species that are characteristic of Paleocene neritic environments rather than just described or reported from the type area by Plummer (1927) and/or Kellough (1965). On the other end of the spectrum, the deep Western Tethys

TABLE 3—Mean relative abundances of taxa selected for the quantitative analysis and their contribution to the "Marginal Tethyan", "Abyssal Tethyan", and "Northwestern Tethyan" Assemblages, respectively. Accounts of the taxa loadings along the first correspondence axis as well as the allocations of hyaline taxa into the two basic morphogroups (epi- and endobenthics; see Corliss, 1985; Corliss and Chen, 1988) are also given (pleurostomellinids, lagenids, agglutinated, and planispiral taxa are omitted from morphotypic analysis due to the uncertainty of microhabitat preferences among such test morphologies).

	First axis score	Morpho-type	10	384	111	548	390	Spain	605	Tunisia	Egypt	Israel
Marginal Tethyan Assemblage (MTA)												
Cibicidoides alleni	1.897	epi.	—	—	—	—	—	—	—	0.4	2.4	—
Anomalinoides praeacutus	1,833	epi.	—	—	—	—	—	—	—	0.4	4.4	—
Sitella fabilis	1.808	endo.	—	—	—	—	—	—	—	6.8	—	—
Cibicidoides pseudoacutus	1.798	epi.	—	—	—	—	—	—	—	3.1	10.9	1.1
Cibicides beaumontianus	1.779	epi.	—	—	—	—	—	—	—	2.3	—	—
Cibicidoides cf. hyphalus	1.766	epi.	—	—	—	—	—	—	—	4.1	1.0	1.1
Heterostomella austinana	1.753	—	—	—	—	—	—	—	—	5.7	1.1	0.4
Cibicidoides suzakensis	1.713	epi.	—	—	—	0.1	—	—	—	3.6	5.5	1.5
Cibicidoides abudurbensis	1.706	epi.	—	—	—	—	—	—	—	1.5	10.1	6.0
Anomalinoides affinis	1.673	epi.	—	—	—	—	—	—	—	2.4	0.6	3.7
Gyroidinoides sp. A	1.510	epi.	—	—	—	—	—	—	—	—	3.2	2.6
Sliteria varsoviensis	1.296	epi.	—	—	0.5	0.2	—	0.2	5.9	7.7	1.6	3.0
Sitella laevis	1.237	endo.	—	—	—	—	—	—	—	—	—	2.2
Valvalabamina depressa	1.184	epi.	—	—	0.7	0.4	1.1	—	1.9	2.7	3.6	1.5
Proportion of total fauna (%)			—	—	1.2	0.7	1.1	0.2	7.7	40.7	44.5	23.1
Abyssal Tethyan Assemblage (ATA)												
Gavelinella? sp. conical form	−1.690	epi.	4.6	1.3	—	—	—	—	—	—	—	—
Globorotalites sp. B	−1.646	epi.	4.0	2.6	—	0.1	—	—	—	—	—	—
Aragonia spp.	−1.620	endo.	7.2	3.5	—	0.1	0.7	—	0.1	—	—	—
Bulimina incisa	−1.581	endo.	1.3	3.6	—	—	—	—	—	—	—	—
Paralabamina hillebrandti	−1.563	epi.	0.8	2.2	—	—	0.4	—	—	—	—	—
Scheibnerova? sp.	−1.551	epi.	5.1	0.4	—	—	4.1	0.5	—	—	—	—
Globorotalites sp. C	−1.531	epi.	6.4	1.9	0.4	0.1	—	0.2	—	0.1	0.2	—
Sitella cf. plana	−1.352	endo.	9.8	17.6	3.9	0.5	3.4	1.5	2.1	—	—	—
Paralabamina sp. interm. form	−1.316	epi.	3.2	1.3	0.2	—	1.5	—	—	0.2	—	—
Nuttallides truempyi	−1.228	epi.	11.8	2.6	0.2	3.8	9.4	0.3	—	—	—	—
Proportion of total fauna (%)			54.2	37.1	4.7	4.6	19.5	2.4	2.2	0.3	0.2	—
Northwestern Tethyan Assemblage (NTA)												
Cibicidoides velascoensis	−0.587	epi.	—	—	3.5	0.5	—	0.6	0.9	—	—	—
Gavelinella pertusa	−0.552	epi.	—	—	2.1	1.5	—	—	—	—	—	—
Nuttallinella sp. B	−0.483	epi.	—	—	0.6	2.5	1.5	—	—	—	—	—
Spiroplectammina "constricta"	−0.533	—	—	—	3.6	3.9	—	—	—	—	—	—
Stensioeina pommerana	−0.548	epi.	—	—	2.7	2.4	—	0.8	—	—	—	—
Cibicidoides hyphalus	−0.532	epi.	—	0.6	16.8	9.6	—	1.6	5.7	—	—	—
Pyramidina rudita	−0.850	endo.	0.1	0.3	8.8	—	3.0	—	—	—	—	—
Proportion of total fauna (%)			0.1	0.9	38.1	20.4	4.5	3.1	6.6	—	—	—

(Sites 10 and 384) is characterized by well-known bathyal Velasco-fauna species, such as *Nuttallides truempyi, Paralabamina hillebrandti,* and *Aragonia* spp. The Velasco fauna was established by Berggren and Aubert (1975) and named after the lower Paleocene Velasco Formation (Mexico), which foraminifera first were described by Cushman (1925, 1926) and White (1928a,b, 1929). The Velasco fauna has, from general geological considerations, been regarded as representing bathyal, deep-sea environments (e.g., Van Morkhoven et al., 1986; Saint-Marc, 1987). Other Velasco-fauna taxa (such as *Gavelinella beccariiformis, Cibicidoides hyphalus, C. velascoensis, Bulimina trinitatensis, B. velascoensis,* etc.) are therefore not surprisingly found at upper to middle bathyal sites (i.e., Sites 111, 390, 548, 605, and in Spain) where they distributionally have their center of gravity, and from which they gradually decrease in abundance towards both "environmental end-members" of the first correspondence axis (see Tables 3–4).

The second correspondence axis shows the contrast in faunal composition between the relatively shallow mid-latitude Sites 111 and 548 and the deeper low-latitude Sites 10 and 384 in the Western Tethys. Figure 4 illustrates the sample scores on the second axis plotted against paleolatitude of the various sites in order to demonstrate this latitude-related gradient. The deep, low-latitude, assemblage characteristic of Sites 10 and 384 (mentioned above) is contrasted along the second axis by a northern assemblage, which in part may represent a more boreal component in Late Cretaceous deep-sea benthic foraminiferal biogeography.

Benthic Foraminiferal Assemblages

Three well-defined clusters of taxa can be recognized along the three main directions in multivariate space on the plane of the first two correspondence axes (Fig. 2). The three clusters of taxa (assemblages; Table 3) are associated with sample clusters that are similar in faunal compo-

TABLE 4—Mean relative abundances of taxa selected for the quantitative analysis and their contribution to the "Shallow" and "Deep" bathyal Assemblages, respectively. Accounts of the taxa loadings along the first correspondence axis as well as the allocations of hyaline taxa into the two basic morphogroups (epi- and endobenthics; see Corliss, 1985; Corliss and Chen, 1988) are also given (pleurostomellinids, lagenids, agglutinated, and planispiral taxa are omitted from morphotypic analysis due to the uncertainty of microhabitat preferences among such test morphologies).

	First axis score	Morpho-type	10	384	111	548	390	Spain	605	El Kef	Egypt	Israel
Shallow Bathyal Assemblage (SBA)												
Gaudryina pyramidata	0.909	—	1.2	0.4	0.5	0.2	1.1	—	—	1.3	6.2	5.6
Pseudouvigerina plummerae	0.829	endo.	—	—	0.7	0.8	—	1.1	0.1	1.2	1.8	2.2
Sitella cushmani	0.779	endo.	1.2	—	0.8	0.5	2.6	0.2	2.7	3.2	1.5	6.7
Gyroidinoides tellburmaensis	0.668	epi.	0.2	0.4	1.8	0.1	1.5	—	2.1	2.2	0.5	1.9
Bolivinoides draco	0.653	endo.	—	—	0.5	0.7	—	2.3	1.1	1.3	0.3	5.2
Bolivinoides decoratus	0.629	endo.	—	—	2.2	0.2	—	0.2	—	1.0	0.8	1.1
Lagena spp.	0.610	—	0.6	0.9	0.5	1.0	0.4	2.9	1.5	3.1	0.6	0.7
Gyroidinoides spp.	0.599	epi.	1.9	1.3	0.2	1.0	0.4	1.5	1.4	3.2	3.7	1.1
Oridorsalis plummerae	0.534	epi.	1.3	0.8	0.8	0.9	2.6	2.9	—	2.0	4.7	3.0
Brizalina gigantea	0.528	endo.	—	—	0.4	3.6	—	0.2	—	1.1	5.7	3.0
Sitella colonensis	0.458	endo.	1.1	0.3	0.7	6.2	1.9	0.2	7.5	4.9	0.2	0.7
Eouvigerina subsculptura	0.393	endo.	—	—	0.8	4.3	0.7	0.5	—	0.3	2.8	22.8
Lenticulina spp.	0.333	—	1.1	1.5	3.6	2.1	2.6	3.4	3.6	2.9	5.5	1.1
Anomalinoides sp. 2	0.275	epi.	—	—	—	—	2.2	1.1	2.7	0.5	—	—
Laevidentalina spp.	0.292	—	0.7	1.7	0.1	0.9	0.4	4.9	1.1	2.4	0.2	1.1
Anomalinoides simplex	0.139	epi.	—	—	0.1	2.7	—	—	—	0.3	1.6	0.4
Pyramidina sp. 150 (twisted)	0.093	endo.	—	—	—	—	—	—	2.5	—	—	—
Pullenia spp.	−0.046	—	—	2.5	2.1	2.7	1.9	1.5	4.4	1.3	0.6	3.0
Proportion of total fauna (%)			9.1	9.9	16.9	27.9	18.4	22.7	30.8	32.4	36.7	59.7
Deep Bathyal Assemblage (DBA)												
Reussella szajnochae	−1.127	endo.	4.1	4.5	8.0	0.9	7.5	0.5	—	—	—	—
pleurostomellids	−0.903	—	1.2	1.6	0.8	0.8	1.5	2.3	0.4	—	—	—
Bulimina sp. 185	−0.875	endo.	0.1	0.8	0.8	0.7	3.0	0.3	—	—	—	—
Gavelinella beccariiformis	−0.846	epi.	2.0	10.1	7.6	6.0	6.7	6.7	1.2	—	—	0.4
Tritaxia spp.	−0.767	—	1.9	0.9	2.4	2.1	1.1	0.6	0.9	—	—	0.7
Nuttallinella sp. A	−0.657	epi.	0.3	—	0.4	0.5	6.0	2.4	—	—	—	—
Bulimina sp. 114	−0.610	endo.	0.1	—	—	1.1	3.4	0.3	—	—	—	—
Bulimina velascoensis	−0.546	endo.	0.3	0.3	0.1	—	1.9	—	2.2	—	—	—
Spiroplectammina spp. (calc.)	−0.461	—	0.8	0.1	0.1	0.1	1.5	0.2	3.4	—	—	—
Paralabamina lunata	−0.456	epi.	0.8	2.2	1.9	2.2	3.4	—	1.0	0.4	1.0	1.9
polymorphinids	−0.432	—	2.6	2.6	1.3	1.1	0.7	2.4	1.7	1.1	0.5	0.4
Nonion spp.	−0.417	—	0.1	0.7	—	—	—	2.4	1.6	—	—	—
Anomalinoides praespissiformis	0.373	epi.	—	1.1	0.6	1.2	—	1.8	4.1	—	—	—
Trochammina spp.	−0.359	—	—	—	—	—	—	3.2	—	—	—	—
Praebulimina reussi	−0.297	endo.	3.2	3.6	0.6	11.2	2.6	14.4	8.2	1.0	4.7	0.4
Bulimina trinitatensis	−0.279	endo.	—	—	0.1	—	2.2	3.6	2.1	—	—	—
Spiropectammina dentata	−0.201	—	0.6	0.2	—	—	—	—	5.2	—	—	—
Proportion of total fauna (%)			18.0	28.7	24.9	28.0	41.6	41.2	32.2	2.5	6.2	3.7

sition and thus represent certain environmental conditions. A *Marginal Tethyan Assemblage* (MTA) is characteristic of the upper bathyal environment of the southern margin of the Central Tethys and loads higher than +1 along the first correspondence axis. The MTA is opposed by an *Abyssal Tethyan Assemblage* (ATA) in the deep Western Tethys, which roughly plots between -2 and - 1 and -1 and -3 along the first and second axes, respectively. The third cluster of taxa is represented by a *Northwestern Tethyan Assemblage* (NTA), that is characteristic for the higher latitudes of the Western Tethys and loads most positively (>1) on the second correspondence axis.

A majority of the taxa included in the analysis is more or less present throughout the study area. These ubiquitous taxa, which plot in the middle (between about -1 and +1 along the first axis and below +1 on the second axis) of Figure 2, can be divided into two intergrading assemblages. Between about -1 and 0 on the first axis are the

taxa situated that may be allocated to a *Deep Bathyal Assemblage* (DBA; see Table 4) since they are more abundant in the bathyal to abyssal environments than in the environments of the southern margin of the Central Tethys. The other assemblage can be defined as a *Shallow Bathyal Assemblage* (SBA; Table 4) that consists of the taxa plotting between 0 and +1 along the first axis due to their high abundance in the upper bathyal environments of the southern margin of the Central Tethys compared to the deep Western Tethys. Figure 5 and 6 depict a graphic representation of the distribution of the five assemblages in terms of their mean relative abundance at various paleo-depths and paleolatitudes. A closer account of each of these assemblages is given in the following.

Marginal Tethyan Assemblage (MTA)

Characteristic for the MTA assemblage (Fig. 5A) are a number of Midway-fauna (*s.l.*) species, including *Anomal-*
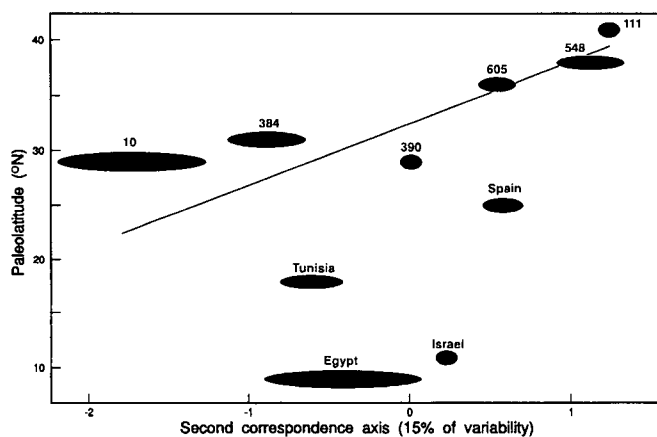
FIGURE 4—Illustration of the (weak) correlation between second axis sample scores and paleolatitudes of the sites/sections (see Table 1) within the Western and Central Tethys. This subordinate, paleolatitudinal trend that separates the northern sites and faunas from the ones of lower latitudes may reflect a more pulsed food supply resulting from the seasonal productivity cycle and/or cooler, well-oxygenated conditions that influences higher latitude ecosystems.

inoides affinis, A. praeacutus, Cibicidoides alleni, C. pseudoacutus, C. suzakensis, C. abudurbensis, C. cf. *hyphalus,* and *Valvalabamina depressa,* together with *Cibicides beaumontianus, Gyroidinoides* sp. A, *Heterostomella* spp., *Sitella fabilis, Sitella laevis,* and *Sliteria varsoviensis.* This assemblage is almost completely restricted to the southern margin of the Central Tethys where it constitutes between 23 and 45% of the fauna. Outside this area the MTA is absent or occurs in much lower frequencies (between 0.2 and 7.7%); the latter high value is represented by Site 605 due to common *S. varsoviensis* that occurs in as much as 5.9% at that site (Table 3).

Abyssal Tethyan Assemblage (ATA)

This assemblage (Fig. 5B) consists of *Aragonia* spp., *Bulimina incisa, Gavelinella*? sp. conical form, *Globorotalites* sp. B, *Globorotalites* sp. C, *Paralabamina hillebrandti, Paralabamina* sp. intermediate form, *Scheibnerova*? sp., *Sitella* cf. *plana,* and *Nuttallides truempyi.* The ATA makes up 37–54% of the faunas at the abyssal Western Tethyan sites and about 20% at the lower bathyal Site 390, but only between 2.2 and 4.7% in the other, middle-bathyal Tethyan environments. On the southern margin of the Central Tethys (i.e., Tunisia, Israel, and Egypt) the frequencies of the ATA is as low as 0–0.3% (Table 3).

Northwestern Tethyan Assemblage (NTA)

Cibicidoides hyphalus, C. velascoensis, Gavelinella pertusa, Nuttallinella sp. B, *Pyramidina rudita, Spiroplectammina* "constricta", and *Stensioeina pommerana,* characterize the NTA (Fig. 5C), which occurs in much higher abundances (20–38%) at the higher latitude Sites 111 and 548 compared to the abyssal, low-latitude Sites 10 and 384 where it occurs in only 0.1–0.9%. In the rest of the Western Tethyan sites (i.e., 390 and 605) and Spain it makes up between 4.5 and 6.6% of the faunas, whereas it is completely absent at the southern margin of the Central Tethys (Ta-

ble 3). Three species belonging to this assemblage (i.e., *S.* "constricta", *G. pertusa,* and *Nuttallinella* sp. B) probably represent a true boreal component in Late Cretaceous benthic foraminiferal biogeography; they have not been encountered elsewhere during the course of a global biogeographic survey conducted on the same time slice by the senior author (Widmark, unpublished data).

Shallow Bathyal Assemblage (SBA)

The SBA (Fig. 6A) is an ubiquitous assemblage that includes a number of Maastrichtian bi-, tri-, and multiserial taxa, such as *Bolivinoides decoratus, B. draco, Brizalina gigantea, Eouvigerina subsculptura, Pseudouvigerina plummerae, Pyramidina* sp. (twisted), *Sitella colonensis,* and *S. cushmani,* together with *Anomalinoides* sp. 2, *Anomalinoides simplex, Gaudryina pyramidata, Gyroidinoides* spp., *G. tellburmaensis, Laevidentalina* spp., *Lagena* spp., *Lenticulina* spp., *Oridorsalis plummerae,* and *Pullenia* spp. The SBA shows a clear preference toward upper bathyal environments on the southern margin of the Central Tethys (32–60%) compared to the deep Western Tethys where it is much less abundant (9-10%); at upper to lower bathyal depths in the Western Tethys and Spain this assemblage occurs in intermediate abundances ranging between 18 and 31% (Table 4).

Deep Bathyal Assemblage (DBA)

Several characteristic Velasco-fauna species such as *Gavelinella beccariiformis, Bulimina velascoensis,* and *B. trinitatensis,* make up this ubiquitous assemblage (Fig. 6B). Other taxa of the DBA are represented by *Anomalinoides praespissiformis, Bulimina* sp. 114, *Bulimina* sp. 185, *Nonion* spp., *Nuttallinella* sp. A, *Paralabamina lunata,* pleurostomellids, polymorphinids, *Praebulimina reussi, Reussella szajnochae, Spiroplectammina dentata, Spiroplectammina* spp. (calcareous), *Tritaxia* spp., and *Trochammina* spp. The DBA is much more frequent in Spain and Western Tethyan bathyal (25–42%) and abyssal (18-29%) environments than in the upper bathyal environment of the southern margin of the Central Tethys, where it only constitutes between 2.5 and 6.2% of the entire benthic foraminiferal fauna (Table 4).

DISCUSSION AND INTERPRETATION

The biogeographic and bathymetric distribution of fossil as well as Recent deep-sea benthic foraminifera are controlled by the ambient environment, which is determined by physical, chemical, and biological parameters. Some parameters, such as salinity and temperature, mainly depend on water mass characteristics, whereas others, such as food and oxygen levels, may vary considerably within a given water mass or oceanic basin due to differential food supply from surface waters.

During the last decade several papers have demonstrated that individual species of Recent deep-sea benthic foraminifera occupy different microhabitats, i.e., they live at different depths relative to the water/sediment interface (e.g., Corliss, 1985, 1991; Gooday, 1986; Mackensen and Douglas, 1989) and that there is a general relationship between the microhabitat and the morphology of the fora-
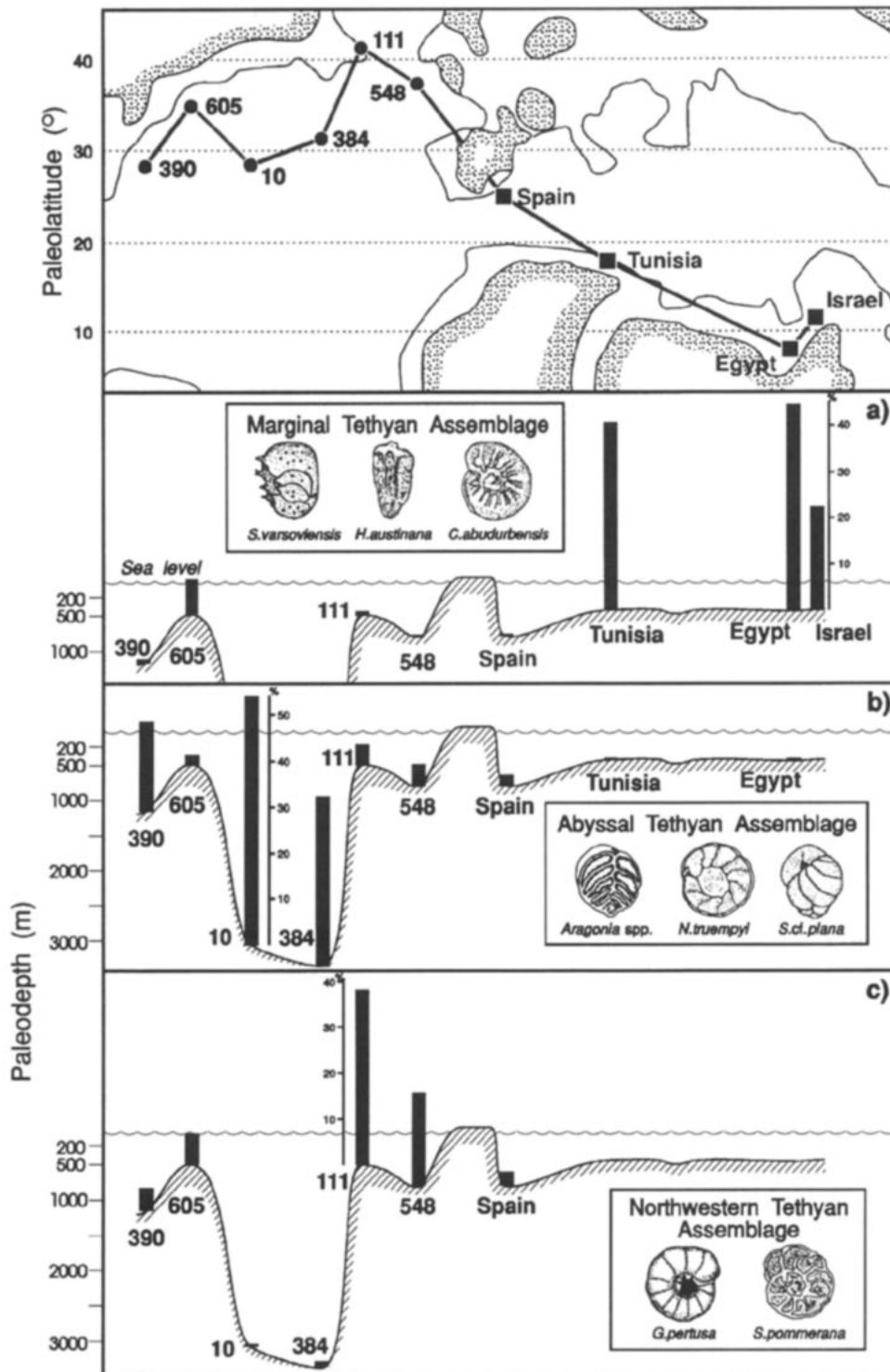
FIGURE 5—Lateral distribution (mean relative abundance) of the three main faunal assemblages (identified in Fig. 2) arranged along a transect across the study area. (A) *Marginal Tethyan Assemblage* (MTA) including some Midway-fauna species, such as *Anomalinoides affinis, A. praeacutus,* and large *Cibicidoides* spp. as well as *Cibicides beaumontianus, Heterostomella austinana, Sitella fabilis, Sliteria varsoviensis,* and *Valvalabamina depressa;* (B) *Abyssal Tethyan Assemblage* (ATA) consisting of e.g., *Aragonia* spp., *Bulimina incisa,* C, *Paralabamina hillebrandti, Sitella* cf. *plana,* and *Nuttallides truempyi;* (C) *Northwestern Tethyan Assemblage* (NTA) including such as *Cibicidoides hyphalus, C. velascoensis, Gavelinella pertusa, Pyramidina rudita, Spiroplectammina* "constricta", and *Stensioeina pommerana* (see also Table 3).
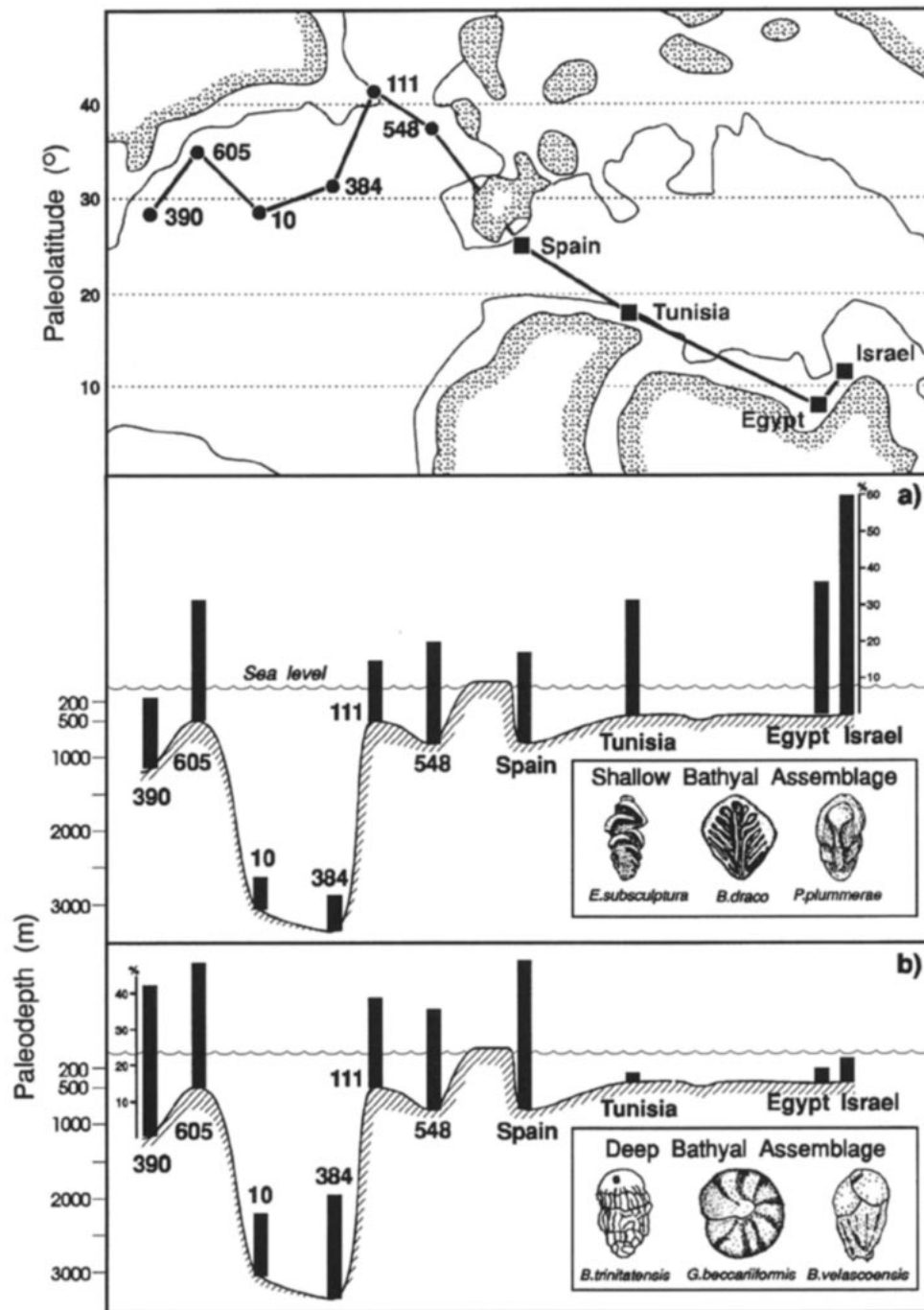
FIGURE 6—Lateral distribution (mean relative abundance) of the two bathyal assemblages (identified in Fig. 2) arranged along a transect across the study area. (a) *Shallow Bathyal Assemblage* (SBA) including a number of "buliminid" taxa, such as *Bolivinoides decoratus, B. draco, Brizalina gigantea, Eouvigerina subsculptura, Pseudouvigerina plummerae, Sitella colonensis, S. cushmani,* together with *Anomalinoides simplex, Gaudryina pyramidata, Gyroidinoides* spp., *G. tellburmaensis, Oridorsalis plummerae,* and most lagenids. (b) *Deeper Bathyal Assemblage* (DBA) encompassing several characteristic Velasco-fauna species such as *Gavelinella beccariiformis, Bulimina velascoensis,* and *B. trinitatensis,* along with *Anomalinoides praespissiformis, Paralabamina lunata,* pleurostomellids, polymorphinids, *Praebulimina reussi, Reussella szajnochae,* and *Spiroplectammina dentata* (see also Table 4).

miniferal test (Corliss, 1985; Corliss and Chen, 1988). Species found mainly on top of the sediment or within the top 0.5 cm are widely referred to as "epifaunal" and dominated by trochospiral test morphologies, whereas other species, which are found deeper in the sediment, are referred to as "infaunal" and exhibit a variety of bi-, tri-, and multiserial and planispiral test morphologies (Corliss, 1985; 1991); although the terms "infaunal" and "epifaunal" are widely used throughout the literature, they are rather inappropriate in this context since they suggest that the foraminifera live within or on top of other fauna, and therefore, we instead prefer to use the terms "endobenthic" and "epi-

benthic" (see also Walker and Miller, 1992). It has also been shown that generally benthic foraminiferal densities, as well as the densities and microhabitat depth of endobentic species are linked to the trophic structure (i.e., food availability) and/or oxygen levels of the ambient environment, but which of the two (food or oxygen) is the limiting factor on benthic foraminiferal densities and microhabitat depths is still under dispute (e.g., Gooday, 1986; Corliss and Chen, 1988; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Corliss, 1991; Barmawidjaja et al., 1992; Rosoff and Corliss, 1992; Sjoerdsma and Van der Zwaan, 1992; Jorissen et al., 1993; Rathburn and Corliss, 1994). Jorissen et al. (1995) proposed a conceptual model that explains the microhabitat (and morphotypic distribution) in terms of trophic conditions and oxygen concentrations. They suggested that toward the eutrophic end on the eutrophic-to-oligotrophic continuum, oxygen concentration is the limiting factor, whereas under oligotrophic conditions food is the main factor controlling benthic foraminiferal distribution and microhabitat depth; both eutrophic and oligotrophic conditions were found to invoke rather shallow microhabitat depths, in contrast to mesotrophic conditions, under which the deepest endobenthic fauna was developed.

In spite of all controversy on these matters throughout the literature, it is generally accepted that epibenthic species are less tolerant to low-oxygen levels than endobenthic species which flourish in environments where the food supply is high and the oxygen level is lower (often due to the oxidation of organic matter). Many endobenthic species are thus more opportunistic (r-selected) and are able to reproduce at higher turnover rates in order to profit from large food resources, whereas epibenthic species in general are equilibrium species (K-selected), which implies that they are able to sustain themselves under conditions with quite low food supply as long as the oxygen levels are kept at reasonably high levels. It is therefore agreed upon that generally high frequencies of endobenthic elongate (bi-, tri-, and multiserial) morphotypes indicate more eutrophic conditions with higher organic-carbon fluxes, whereas low oxygen level by itself does not necessarily favor any certain test morphology (see overview in Sen Gupta and Machain-Castillo, 1993). The absence of endobenthic morphotypes generally indicates opposite, oligotrophic (food-poor) and, therefore, rather well-oxygenated conditions, under which the remaining fauna (i.e., largely epibenthic morphotypes) may show a relation with surrounding water-mass characteristics. As soon as there is a significant change (or variation) in the trophic regime, then this relationship is overruled by the availability of food, which is a much stronger ecological factor than the physicochemical characteristics of the surrounding water mass. This generalized model could be questioned, however, due to the fact that high frequencies of some Recent epibenthic species (i.e., *Epistominella exigua* and *Alabaminella weddellensis*), of which *E. exigua* have formerly been used as a water-mass marker (e.g., Weston and Murray, 1984), have also been linked to sudden high inputs of phytodetritus (Gooday, 1988, 1994; Gooday and Lambshead, 1989) and these species thus are regarded as opportunistic (r-selected) species. This implies that they actually are distributionally controlled by large organic-carbon inputs that are quite restricted temporally and spatially;

this of course questions the general usage of epibenthic species as deep-water tracers as already pointed out by, for example, Corliss (1985), Thomas and Vincent (1987), Linke and Lutze (1993).

Widmark (1995) suggested that the global distribution of Late Cretaceous benthic deep-sea foraminiferal faunas was mainly controlled by trophic level and oxygenation of the sea-floor and that their distribution also provided evidence for the existence of a relatively cold, and well oxygenated deep-water mass produced at high (southern) latitudes, simultaneously with the local production of warm saline deep waters in the (sub)tropics. Hence, the superior trend reflected by benthic foraminiferal faunas followed a latitudinal gradient due to generally more oligotrophic conditions in high latitude deep-water environments compared to those of the low-latitudes (Widmark, 1995). This conclusion was mainly based on the much higher relative abundances of endobenthic ("infaunal" in Widmark, 1995) eutrophic/low-oxygen taxa at lower latitudes than at higher latitudes and by the reversed abundance pattern of the epibenthic ("epifaunal" in Widmark, 1995) oligotrophic/high-oxygen taxa (Fig. 7).

The present overall faunal pattern in the Tethys deviates from the global pattern outlined by Widmark (1995) in that the main trend here goes in an apparent east-west (longitudinal) direction. As suggested before, this superior trend here coincides with a paleobathymetric gradient from the rather shallow upper-bathyal environment on the southern margin of the Central Tethys in the east to the abyssal Western Tethys (Fig. 3). In general, such a gradient is highly interrelated with a combination of the most crucial environmental parameters influencing benthic foraminiferal distribution, namely the trophic level and the oxygenation of the environment (e.g., Gooday, 1986; Corliss and Chen, 1988; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Corliss, 1991; Barmawidjaja et al., 1992; Rosoff and Corliss, 1992; Sjoerdsma and Van der Zwaan, 1992; Jorissen et al., 1993; Rathburn and Corliss, 1994). It is therefore reasonable to propose a working hypothesis, in which we assume that the Late Cretaceous deep, open-ocean environment, far below the locus of primary production in the euphotic zone, was relatively oligotrophic, being marked by low food fluxes arriving at the sea floor due to long exposure to grazing and bacterial degradation during sinking. Consequently, we can assume that oxygen levels were relatively high in these deep open-ocean settings, although this parameter is also influenced by aging of the water mass. This situation would be opposed by environmental conditions characterizing the upper bathyal environment of the southern margin of the Central Tethys, where the organic fluxes were supposedly much higher and the benthic faunas inhabit an environment that is situated within a weakly developed oxygen minimum zone (OMZ) (see also Peypouquet et al., 1986; Speijer and Van der Zwaan, 1996). Trophic regimes at the other sites would be intermediate between the extremes of the abyssal realm and the southern margin of the Central Tethys.

In order to test our working hypothesis we allocated the 52 hyaline taxa among our 66 selected taxa (lagenids, pleurostomellids, agglutinated, and planispiral taxa were omitted) into the two basic morphogroups (epibenthic and endobenthic; see Tables 3–4) and compared their relative
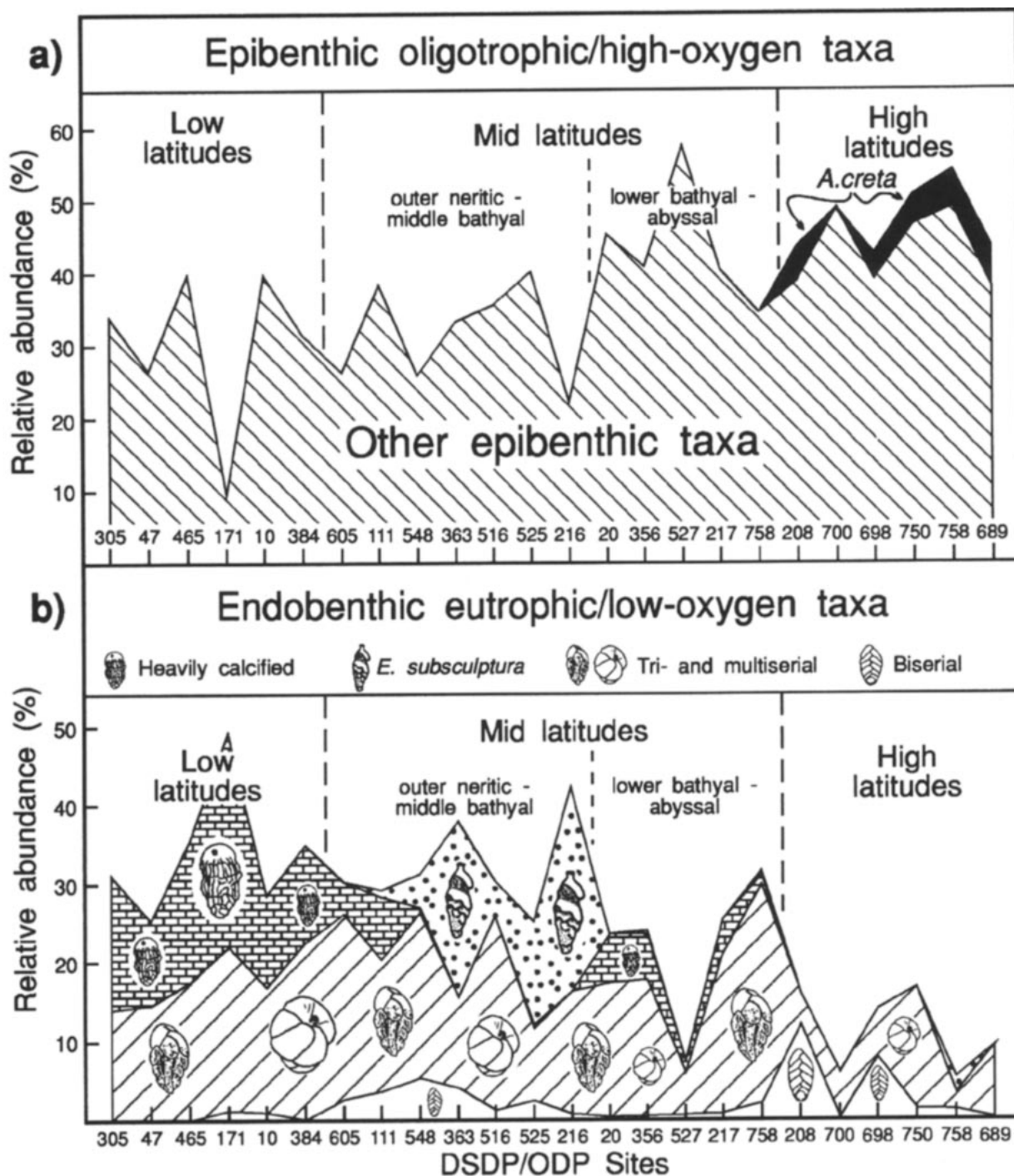
FIGURE 7—Global distribution of epibenthic (a) and endobenthic (b) morphotypes in terms of their relative abundance (% of entire benthic foraminiferal fauna) at the various sites analyzed in Widmark (1995) (figure modified from Widmark, 1995). Epibenthic taxa includes various trochospiral taxa (see Widmark, 1995); the epibenthic *Alabamina creta* has been given a special account since it may represent an opportunistic species comparable to the morphologically similar modern *Alabaminella weddellensis* (see Widmark, 1995). The global distribution of Late Cretaceous benthic foraminifera was suggested by Widmark (1995) to reflect latitudinal and bathymetrical gradients in trophic level and oxygenation.

abundances with the results of the global survey of Widmark (1995) here presented in Figure 7. The overall pattern in the proportions of the two basic morphotype categories (Fig. 8) displays no clearcut trend between the various Tethyan depositional settings. Epibenthics (strongly) dominate over endobenthics in the upper bathyal locali-

ties of Tunisia, Egypt, and Site 111 as well as in the abyssal Site 10, whereas the opposite holds true for the upper bathyal Israeli locality (mainly due to high abundance of *E. subsculptura*, 22.8%; Table 4) and to a lesser degree for the middle bathyal Spanish section and the abyssal Site 384. The remaining middle and lower bathyal sites show a
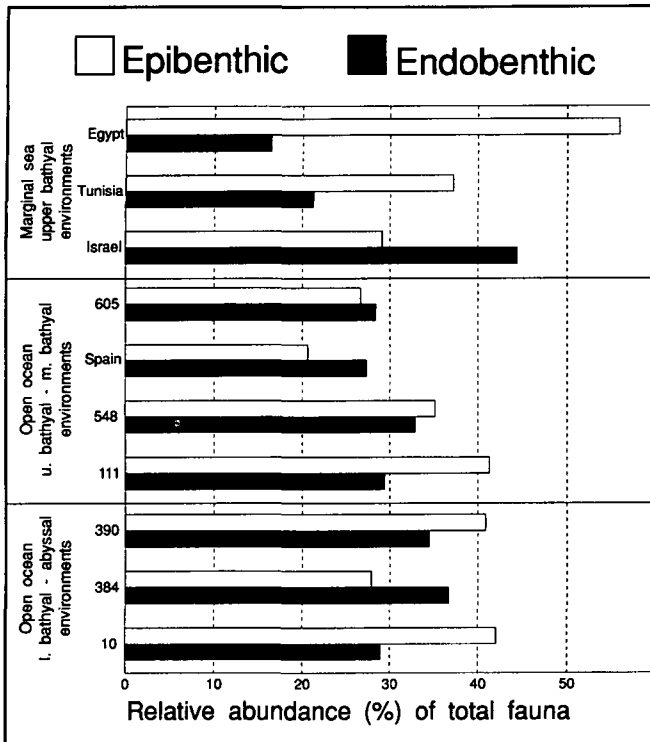
FIGURE 8—Relative abundance (%) of epibenthic and endobenthic morphotypes of the 52 hyaline taxa allocated in Tables 3–4. Sites and sections are vertically arranged according to the paleobathymetrical trend revealed by the first correspondence axis. A clear trend from shallow-to-deep settings cannot be discerned; i.e., epibenthics show surprisingly high abundances in the shallowest settings in contrast to what might be expected (see text).

FIGURE 9—Epibenthic-endobenthic morphotype proportions (%) within two of the five assemblages identified to signify various oceanographic settings in the study area. (a) The *Marginal Tethyan Assemblage* (MTA) is dominated by several trochospiral (epibenthic) Midway-fauna species that constitute a neritic faunal component; (b) The *Northwestern Tethyan Assemblage* (NTA) is clearly dominated by epibenthics that may reflect the more oligotrophic character of northern high-latitude bathyal environment (see text). The proportions of the two basic morphogroups were calculated according to the allocations of the hyaline taxa of the MTA and NTA, respectively, in Table 3.

more even balance in the proportions of the morphogroups.

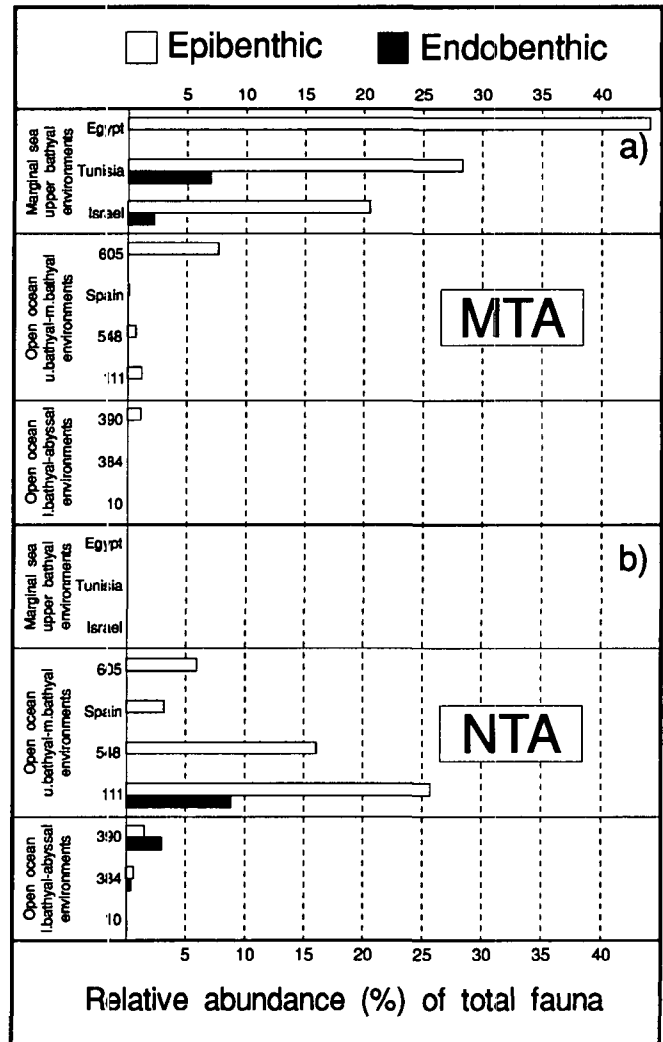In a more refined approach we tested how the two basic morphogroups within each of the five assemblages relate to the working hypothesis. Figures 9 and 10 combine the results from the correspondence analysis with the morphotype approach and show how the proportions of the two basic morphogroups are distributed among the five assemblages resulting from the correspondence analysis.

The MTA, characterizing the upper bathyal realm of the southern margin of the Central Tethys, is strongly dominated by epibenthics (Fig. 9A), many of which belong to the neritic Midway-fauna. This affinity to the Midway-fauna suggests that their dominance in the Tunisian and Egyptian sections is related to an influence that determines neritic benthic faunas. It might be that the low numbers of endobenthics reflect a poorly developed endobenthic habitat, due to a shallow critical oxygen level within the sediment, resulting from a high organic carbon input as in the conceptual microhabitat model of Jorissen et al. (1995). Alternatively, the neritic Midway taxa at the sites from the southern margin of the Central Tethys might be favored by a secondary food source in the form of degraded land derived organic matter. The fact that these taxa survived the oceanic fertility crisis at the K/PgB in contrast to many endobenthic taxa (of the SBA), could indeed suggest that the encountered epibenthic Midway taxa may have depended on non-marine food sources,

which could favor the latter alternative. Outside the southern margin of the Central Tethys, the only significant MTA-epibenthic component is found at Site 605 and accounts for about 8% of the entire fauna. This component largely results from the high numbers of *Sliteria varsoviensis* (Table 3), a species that is restricted to the Maastrichtian (Speijer and Van der Zwaan, 1996) and thus is not a Midway-fauna species.

Among the ubiquitous taxa of the SBA that exhibit a preference toward middle and upper bathyal environments, there is a much greater proportion of endobenthics in upper-to-middle bathyal environments than at lower bathyal-to-abyssal depths (Fig. 10A). Furthermore, the SBA endobenthics dominate over the SBA-epibenthic component at all sites/sections except at the lower bathyal
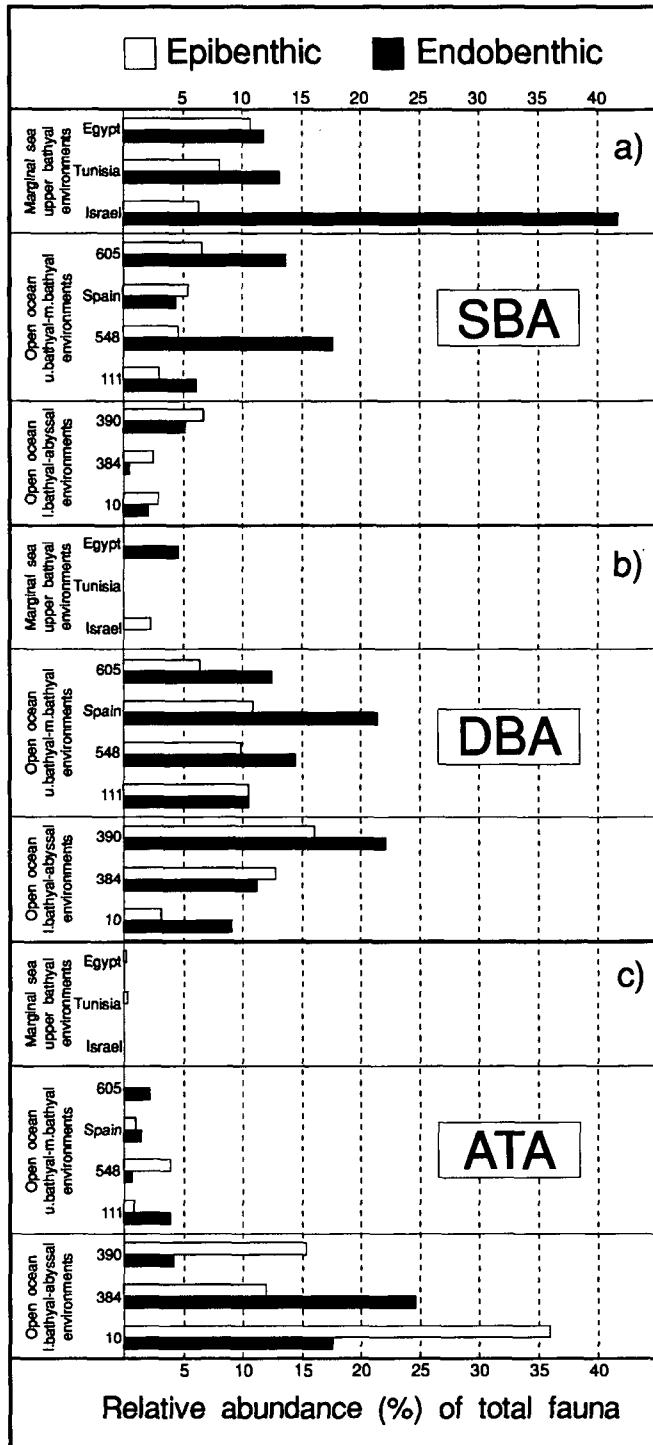
FIGURE 10—Epibenthic-endobenthic morphotype proportions (%) within three of the five assemblages identified to signify various oceanographic settings in the study area. (a) *Shallow Bathyal Assemblage* (SBA); (b) *Deep Bathyal Assemblage* (DBA); and (c) *Abyssal Tethyan Assemblage* (ATA). Endobenthics predominate the SBA in shallower bathyal settings (a), epibenthics are more abundant within the ATA in the deep ocean (c), whereas the two basic morphogroups of the DBA are rather evenly distributed throughout the bathyal realm (b) (see text). The proportions of the two basic morphogroups were calculated according to the allocations of the hyaline taxa of the SBA, DBA, and ATA, respectively, in Tables 3-4.

and abyssal ones (Sites 10, 384, 390) and the Spanish section at Caravaca. This trend suggests that the higher relative abundances of SBA endobenthics represent a response to the larger food-fluxes that are provided to the upper part of the bathyal environment compared to abyssal depths, and thus reflecting a higher trophic level of the upper part of the bathyal environment.

Within the DBA the proportions of two morphogroups are more evenly distributed, although there is a slight dominance of the endobenthic component at most sites (Fig. 10B), whereas the epibenthic component of the deepest ATA (Fig. 10C) exhibits an opposite abundance and distribution pattern to that of the SBA. Indeed, there is a clear response by the ATA epibenthics, which increase in relative abundance with increasing depth with the only exception of Site 384. This depth-related pattern of the ATA epibenthics is probably reflecting the increasing oxygen concentrations due to a smaller food supply that generally occur in deep ocean environments.

Surprisingly, however, and in spite of what one may expect from the oligotrophic character of the environment of the abyssal open ocean at the deepest Site 384, endobenthics predominate over the epibenthics both in terms of total endobenthic-epibenthic proportions (Fig. 8) and within the ATA (Fig. 10C). The endobenthic dominance at Site 384 is due to a conspicuously high abundance of a single, rather small, morphologically endobenthic species, *Sitella cf. plana*, which also occurs quite abundantly at the other abyssal Site 10. Assuming that these high numbers reflect an opportunistic strategy to profit from some sort of high (pulsed?) food supply, how then could sufficient food amounts reach to these depths in order to sustain such opportunistic populations? A possible scenario involves enhanced productivity that occurs when warm and cold waters from different surface currents are mixed as, for example, south of the present-day Labrador Sea. The situation during the Maastrichtian might have been similar as today in that a warm surface current along the eastern coast mixed with a (presumably) cold surface current from the north (see Camoin et al., 1993), resulting in enhanced productivity and relatively high food-fluxes at Sites 10 and 384. Therefore, it is not unlikely that the environment at these deep sites actually was more mesotrophic in character than expected for such deep settings.

In contrast to the other assemblages identified in the present data set, the NTA is entirely dominated by epibenthics (Fig. 9B). This may indicate a better oxygenation of the upper-to-middle bathyal environment at Sites 111 and 548 due to a possible presence of cooler, more oxygen-enriched intermediate waters at higher latitudes in the northwestern-Tethys and/or more seasonal food-fluxes typical of higher-latitude ecosystems, i.e., an northern-hemisphere analog to the environmental conditions reflected by the high southern latitude assemblage in Widmark (1995).

In summary, we can conclude from our initial test of the working hypothesis, which simply is based on the total proportions of the two basic morphogroups throughout the study area, that clearcut differences between marginal seas and deep, open-ocean settings within the Tethyan realm can not be inferred. This indicates that neither eutrophic, low diversity OMZ faunas nor truly oligotrophic faunas are present in our data set; the latter was indeed

already concluded by Widmark (1995). In the absence of the end members of the oligotrophic-eutrophic continuum, only more or less mesotrophic conditions can be inferred for the various latest Cretaceous upper bathyal-to-abyssal environments analyzed here. However, after evaluation of how the two basic morphogroups are distributed among the various assemblages (i.e., the SBA, DBA, and ATA) and how they correspond to the depth-related gradients, a clear pattern emerges: endobenthics dominate the SBA at the shallower sites, whereas the epibenthics of the ATA clearly outnumber the endobenthics (except for Site 384); the DBA occupies an intermediate position with a more even balance between the two basic morphogroups. We interpret this pattern as a benthic foraminiferal response to the higher food-fluxes (and lower oxygen levels) that may be anticipated in shallower environments and the lower food supply and better oxygenation that might be expected in deeper settings of the terminal Cretaceous seafloor.

SUMMARY AND CONCLUSIONS

Correspondence analysis, based on the 66 most common benthic foraminiferal taxa throughout the late Maastrichtian Western-and-Central Tethys, reveals ordered biogeographic and bathymetric patterns in this taxonomically highly heterogeneous fossil group:

(1) The clustering of faunas (sites) follows a paleobathymetric gradient, which we consider to be primarily a reflection of gradients in trophic and oxygen levels.
(2) The analysis reveals five assemblages: a *Marginal Tethyan Assemblage* (MTA) including a number of Midway-fauna species, such as *Anomalinoides affinis, A. praeacutus,* large *Cibicidoides* spp., and *Valvalabamina depressa,* and *Sliteria varsoviensis*; a *Shallow Bathyal Assemblage* (SBA) that includes a number of typical Late Cretaceous bi-, tri-, and multiserial taxa, such as *Bolivinoides draco, Brizalina gigantea, Eouvigerina subsculptura,* and *Sitella colonensis*; a *Deeper Bathyal Assemblage* (DBA) comprising an array of ubiquitous species of which some belong to the Velasco fauna, such as *Gavelinella beccariiformis, Bulimina velascoensis,* and *B. trinitatensis*; an *Abyssal Tethyan Assemblage* (ATA) consisting of, amongst others, *Aragonia* spp., *Bulimina incisa, Paralabamina hillebrandti, Sitella* cf. *plana,* and *Nuttallides truempyi*; and a *Northwestern Tethyan Assemblage* (NTA) partly made up by a boreal faunal component in latest Cretaceous benthic foraminiferal biogeography, including *Gavelinella pertusa, Nuttallinella* sp. B, and *Spiroplectammina* "constricta".
(3) Proportions of epibenthic vs. endobenthic morphogroup data indicate that the trophic levels of the various environments throughout our study area were more or less within the mesotrophic regime of the oligotrophic-to-eutrophic continuum.
(4) Evaluation of the epibenthic/endobenthic distribution within each of the five assemblages reveals, however, morphotypic responses to depth-related gradients, i.e., gradients in food supply (trophic level) and oxygen concentrations. Epibenthics of the Midway fauna dominates the MTA, which may indicate a poorly developed endobenthic habitat (due to high organic-carbon fluxes/oxygen deficiency) and/or the influence of a secondary

food source. Dominant endobenthics within the SBA reflect higher food fluxes/lower oxygen concentrations are reflected by at shallower depths, whereas dominant epibenthics of the deepest ATA at the deeper sites indicate lower food fluxes/higher oxygen concentrations; the DBA occupies an intermediate position in that the two basic morphogroups are more evenly distributed throughout the middle bathyal-to-abyssal sites.

Clearly, our interpretation is based on a restricted data set from the Tethyan realm; our time-slice study is intended as a step up to the understanding of large scale patterns and processes of a specific, relatively stable, period. The validity of our hypothesis should be tested elsewhere in the Tethys and also by alternative faunal and/or geochemical productivity proxies. Our results could direct such studies to places of interest in our study area, such as Site 605, where there appears to be a strong discrepancy in paleodepth estimates, which might be related to the trophic regime. In addition, late Maastrichtian low diversity OMZ faunas are necessary to obtain an idea of truly eutrophic benthic environments of bathyal depths. Finally, geochemical studies are required to fully exploit the understanding on microhabitats and to determine whether there really is a general relationship between morphology of Maastrichtian taxa and their microhabitats.

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APPENDIX I

Faunal Reference List

The 66 taxa included in quantitative analysis; references (when applicable) clarify the species concepts used herein. The generic concepts of Loeblich and Tappan (1988) are used for taxa only assigned to genus level.

Anomalinoides praespissiformis = *Anomalina praespissiformis* Cushman and Bermudez, 1948, p. 86, pl. 15, figs. 1–3 = *Anomalina praeacuta* Vasilenko (Widmark and Malmgren, 1988, p. 75, Pl. 3, Fig. 2).

Anomalinoides affinis = *Anomalinoides affinis* (Hantken) (Speijer, 1994, p. 58, Pl. 6, Fig. 1).

Anomalinoides praeacutus = *Anomalinoides praeacutus* (Vasilenko) (Speijer, 1994, p. 60, Pl. 7, Fig 1).

Anomalinoides simplex = *Anomalinoides simplex* (Brotzen) (Speijer, 1994, p. 60, Pl. 9, Fig. 1).

Anomalinoides sp. 2 = *Anomalinoides* sp. 2 (Speijer, 1994, p. 62, Pl. 6, Fig. 1).

Aragonia spp. = *Aragonia* spp. (Widmark and Malmgren, 1992a, p. 393, Pl. 1, Fig. 9; 1992b, p. 110, Pl. 4, Fig. 5).

Bolivinoides decoratus = *Bolivinoides decoratus* (Jones) (Speijer, 1994, p. 46, Pl. 9, Fig. 2).

Bolivinoides draco = *Bolivinoides draco draco* (Marsson) (Speijer, 1994, p. 48, Pl. 1, Fig. 3).

Brizalina gigantea = *Coryphostoma incrassata gigantea* (Wicher) (Speijer, 1994, p. 52, Pl. 1, Figs. 4–5).

Bulimina incisa = *Bulimina incisa* Cushman (Widmark and Malmgren, 1992a, p. 393, Pl. 1, Fig. 1).

Bulimina sp. 114.

Bulimina sp. 185.

Bulimina trinitatensis = *Bulimina trinitatensis* Cushman and Jarvis (Widmark and Malmgren, 1992a, p. 393, Pl. 1, Fig. 4; 1992b, p. 111, Pl. 1, Fig. 7).

Bulimina velascoensis = *Bulimina velascoensis* (Cushman) (Widmark and Malmgren, 1992a, p. 393, Pl. 1, Fig. 5; 1992b, p. 111, Pl. 1, Fig. 6).

Cibicides beaumontianus = *Cibicides beaumontianus* (d'Orbigny) (Speijer, 1994, p. 56, Pl. 3, Fig. 2).

Cibicidoides abudurbensis = *Cibicidoides abudurbensis* (Nakkady) (Speijer, 1994, p 54, Pl. 4, Fig. 6).

Cibicidoides alleni = *Truncatulina alleni* Plummer, 1927, p. 144, Pl. 10, Fig. 4.

Cibicidoides hyphalus = *Gavelinella hyphalus* (Fisher) (Widmark and

Malmgren, 1988, p. 76, Pl. 4, Fig. 1) = *Cibicidoides hyphalus* (Fisher) (Widmark and Malmgren, 1992a, p. 393, Pl. 2, Figs. 10–11; 1992b, p. 111, Pl. 5, Figs. 1–2).

Cibicidoides cf. *hyphalus* = *Cibicidoides* cf. *hyphalus* (Fisher) (Speijer, 1994, p. 54; Pl. 5, Figs. 2–3).

Cibicidoides pseudoacutus = *Cibicidoides pseudoacutus* (Nakkady) (Speijer, 1994, p. 54, Pl. 7, Fig. 6).

Cibicidoides suzakensis = *Cibicidoides suzakensis* (Bykova) (Speijer, 1994, p. 54, Pl. 5, Fig. 1).

Cibicidoides velascoensis = *Cibicidoides velascoensis* (Cushman) (Widmark and Malmgren, 1992b, p. 111, Pl. 5, Fig. 5).

Eouvigerina subsculptura = *Eouvigerina subsculptura* McNeil and Caldwell (Widmark and Malmgren, 1992a, p. 393, Pl. 1, Fig. 8; 1992b, p. 111, Pl. 1, Fig. 8) = *Eouvigerina subsculptura* McNeil and Caldwell (Speijer, 1994, p. 48, Pl. 1, Fig. 7).

Gaudryina pyramidata = *Gaudryina pyramidata* Cushman (Widmark and Malmgren, 1988, p. 65, Pl. 5, Fig. 5; 1992a, p. 393, Pl. 6, Fig. 8; 1992b, p. 111, Pl. 10, Fig. 3) = *Gaudryina pyramidata* Cushman (Speijer, 1994, p. 44, Pl. 4, Fig. 1).

Gavelinella beccariiformis = *Gavelinella beccariiformis* (White) (Widmark and Malmgren, 1988, p. 75, Pl. 3, Fig. 5; 1992a, p. 393, Pl. 2, Figs. 7–9; 1992b, p. 111, Pl. 5, Fig. 3).

Gavelinella pertusa = *Gavelinella pertusa* (Marsson) (Brotzen, 1942, p. 41, Pl. 1, Figs. 1–2).

Gavelinella? sp. conical form = *Gavelinella?* sp. conical form (Widmark and Malmgren, 1992b, p. 111, Pl. 5, Fig. 4).

Globorotalites sp. B = *Globorotalites* sp. B (Widmark and Malmgren, 1992a, p. 394, Pl. 3, Figs. 1–3; 1992b, p. 111, Pl. 6, Fig. 1).

Globorotalites sp. C.

Gyroidinoides sp. A.

Gyroidinoides spp.

Gyroidinoides tellburmaensis = *Gyroidinoides girardanus* (Reuss) (Widmark and Malmgren, 1992b, p. 111, Pl. 6, Fig. 3) = *Gyroidinoides tellburmaensis* Futyan (Speijer, 1994, p. 62, Pl. 3, Fig. 1).

Heterostomella austinana = *Heterostomella austinana* Cushman (Speijer, 1994, p. 46, Pl. 1, Fig. 2).

Laevidentalina spp.

Lagena spp.

Lenticulina spp.

Nonion spp.

Nuttallides truempyi = *Nuttallides truempyi* (Nuttall) (Widmark and Malmgren, 1988, p. 69, Pl.1, Fig. 7; 1992a, p. 398, Pl. 5, Figs. 4–6; 1992b, p. 112, Pl. 2, Fig. 3).

Nuttallinella sp. A = *Nuttallinella* sp. A (Widmark and Malmgren, 1988, p. 71, Pl. 2, Fig. 2; 1992a, p. 398, Pl. 5, Figs. 7–9; 1992b, p. 112, Pl. 2, Fig. 5).

Nuttallinella sp. B.

Oridorsalis plummerae = *Oridorsalis plummerae* (Cushman) (Speijer, 1994, 58, Pl. 6, Fig. 8).

Paralabamina hillebrandti = *Neoeponides hillebrandti* Fisher (Widmark and Malmgren, 1988, p. 71, Pl. 2, Fig. 3) = *Paralabamina hillebrandti* (Fisher) (Widmark and Malmgren, 1992a, p. 398, Pl. 4, Figs. 7–9; 1992b, p. 112, Pl. 3, Fig. 1).

Paralabamina lunata = *Neoeponides lunata* (Brotzen) (Widmark and Malmgren, 1988, p. 71, Pl. 2, Fig. 5) = *Paralabamina lunata*

(Brotzen) (Widmark and Malmgren, 1992a, p. 402, Pl. 4, Figs. 10–12; 1992b, p. 112, Pl. 3, Fig. 3).

Paralabamina sp. intermediate form = *Neoeponides* sp. intermediate form (Widmark and Malmgren, 1988, p. 71, Pl. 2, Fig. 4) = *Paralabamina* sp. intermediate form (Widmark and Malmgren, 1992b, p. 112, Pl. 3, Fig. 2).

pleurostomellinids.

polymorphinids.

Praebulimina reussi = *Praebulimina* spp. (Widmark and Malmgren, 1992a, p. 402, Pl. 1, Fig. 6; 1992b, p. 112, Pl. 1, Fig. 11) = *Praebulimina reussi* (Morrow) (Speijer, 1994, p. 48, Pl. 1, Fig. 11).

Pseudouvigerina plummerae = *Pseudouvigerina plummerae* Cushman (Speijer, 1994, p. 48, Pl. 4, Fig. 2).

Pullenia spp.

Pyramidina rudita = *Pyramidina rudita* (Cushman and Parker) (Widmark and Malmgren, 1992a, p. 402, Pl. 1, Fig. 3; 1992b, p. 113, Pl. 1, Fig. 12).

Pyramidina sp. 150 (twisted).

Reussella szajnochae = *Reussella szajnochae* (Grzybowski) (Widmark and Malmgren, 1988, p. 69, Pl. 1, Fig. 6; 1992a, p. 402, Pl. I, Fig. 7; 1992b, p. 113, Pl. 1, Fig. 15).

Scheibnerova? sp. = *Scheibnerova?* sp. (Widmark and Malmgren, 1992a, p. 402, Pl. 3, Figs. 4–6; 1992b, p. 113, Pl. 6, Fig. 2).

Sitella colonensis = *Sitella colonensis* (Cushman and Hedberg) (Speijer, 1994, p. 50, Pl. 1, Fig. 8).

Sitella cushmani = *Buliminella* cf. *beaumonti* Cushman and Renz (Widmark and Malmgren, 1992b, p. 111, Pl. 1, Fig. 10) = *Sitella cushmani* (Sandidge) (Speijer, 1994, p. 50, Pl. 1, Fig. 9).

Sitella fabilis = *Sitella fabilis* (Cushman and Parker) (Speijer, 1994, p. 50, pl. 1, Fig. 10).

Sitella cf. *plana* = *Buliminella* cf. *plana* (Cushman and Parker) (Widmark and Malmgren, 1992a, p. 393, Pl. 1, Fig. 2).

Sitella laevis = *Sitella laevis* (Biessel) (Loeblich and Tappan, 1988, p. 512, pl. 563, Figs. 15–19).

Sliteria varsoviensis = *Sliteria varsoviensis* sp. n. (Gawor-Biedowa, 1992, p. 156, Pl. 33, Figs. 9–13) = *Gavelinella martini* (Sitter) (Speijer, 1994, p. 64, Pl. 2, Fig. 1).

Spiroplectammina "constricta".

Spiroplectammina dentata = *Spiroplectammina dentata* (Alth) (Widmark and Malmgren, 1988, p. 65, Pl. 5, Fig. 13; 1992b, p. 113, Pl. 10, Fig. 4).

Spiroplectammina spp. (calcareous) = *Spiroplectammina* spp. calcareous forms (Widmark and Malmgren, 1992a, p. 402, Pl. 6, Fig. 9; 1992b, p. 113, Pl. 10, Fig. 8).

Stensioeina pommerana = *Stensioeina pommerana* Brotzen (Speijer, 1994, p. 62, Pl. 2, Fig. 2).

Tritaxia spp.

Trochammina spp.

Valvalabamina depressa = *Valvalabamina depressa* (Alth) (Speijer, 1994, p. 56, Pl. 4, Fig. 5) = *Valvalabamina* sp. evolute form (Widmark and Malmgren, 1992a, p. 402, Pl. 3, Figs. 10–12; 1992b, p. 113, Pl. 4, Fig. 3) and *Valvalabamina* sp. involute form = *Anomalina* sp. a (Widmark and Malmgren, 1988, p. 75, Pl. 3, Fig. 3) = *Valvalabamina* sp. involute form (Widmark and Malmgren, 1992a, p. 402, Pl. 2, Figs. 4–6; 1992b, p. 113, Pl. 4, Fig. 2).