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Gradual mass extinction, species survivorship, and long-term environmental changes across the Cretaceous-Tertiary boundary in high latitudes

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Gradual mass extinction, species survivorship, and long-term environmental changes across the Cretaceous-Tertiary boundary in high latitudes

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ABSTRACT

Stable-isotope and planktic foraminiferal analyses across the Cretaceous/Tertiary (K/T) boundary transition at Nye Klov indicate longterm oceanic instability associated with global sea-level fluctuations, a gradual mass extinction, and decreased magnitude of the δ^{13} C shift in high latitudes.

Oceanic instability, which began at least 100 kyr before the K/T boundary and continued for about 300 kyr into the Tertiary, was accompanied by a gradual faunal turnover. The maximum sea-level lowstand during latest Maastrichtian is recorded about 75 cm below the K/T boundary. A sea-level rise first in evidence at 20 cm to 40 cm below the boundary continued into Zone P0 (boundary clay). This sea-level rise was accompanied by 2 °C of cooling in surface and bottom waters prior to the K/T boundary. δ^{13} C values remained relatively stable up to 10 cm below the K/T boundary. A negative shift of 0.5 to 1.0 per mil occurred in the boundary clay in both planktic and benthic foraminifera. The surface to deep δ^{13} C gradient remained nearly unchanged, in contrast to low latitudes, where this gradient is virtually eliminated. No sudden mass extinction occurred in this cosmopolitan, high-latitude fauna, and nearly all Cretaceous taxa thrived well into the Tertiary, when they gradually disappeared. Shallow seas, dominated by Cretaceous survivor taxa and a well-developed oxygen minimum zone, prevailed during the earliest Tertiary. Short-term sea-level lowstands are marked by hiatuses at the top of Zones P0 and P1a about 50 kyr and 230 kyr after the K/T boundary, respectively. Rising sea level reestablished normal marine conditions about 300 kyr to 350 kyr after the K/T boundary, coincident with the first post-K/T boundary recovery of the Tertiary fauna and extinction of Cretaceous survivors. During this

time, high-latitude regions temporarily acted as centers of origin and dispersal for planktic foraminifera.

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Long-term oceanic instability, gradual faunal turnover, absence of a sudden mass extinction, and greatly diminished δ^{13} C shift in high latitudes suggest that a K/T boundary bolide impact was not the primary cause for the K/T boundary faunal transition. Moreover, these data strongly imply that the destructive effects of the bolide impact would have been greatest in low latitudes and negligible in high latitudes.

INTRODUCTION

Was the Cretaceous/Tertiary (K/T) boundary mass extinction a sudden geological event caused by an Earth-impacting giant asteroid or comet, or did this mass extinction occur more gradually over a few hundred thousand years? Many scientists now favor a large bolide impact to explain the Chicxulub feature in the Caribbean (Hildebrand and Boynton, 1990; Izett, 1991; Sigurdsson and others, 1991; Smit and others, 1992), accompanied by a smaller second impact (Manson crater) in North America. There is no consensus, however, as to the impact origin of these structures (Officer and others, 1992), the glassy spherules of Haiti (Jéhanno and others, 1992; Lyons and others, 1992), or the socalled impact-generated tsunami deposits of Haiti, Texas, or Mexico (Keller, 1989a; Donovan and others, 1988; Jéhanno and others, 1992). Moreover, an increasing number of scientists now interpret the K/T boundary deposits as the products of two rather closely spaced events. They disagree, however, as to whether these two events were both bolide impacts (Izett, 1991), or volcanism followed by a bolide impact (Jéhanno and others, 1992). Widespread, anomalously high iridium (Ir) concentrations, often associated with spinels found at the second event marking the K/T boundary, represent strong support for an extraterrestrial event (Robin and others, 1991, 1992). The first event is characterized by a thick and structurally complex deposit of sand, shale, and a "spherule bed" which some interpret as the tsunami-wave deposit generated by the K/T boundary impact (Smit and others, 1992), a gravity flow deposit (Stinnesbeck and others, 1993), another earlier bolide impact (Izett, 1991), or earlier volcanism unrelated to the K/T boundary impact (Jéhanno and others, 1992).

What effect did a bolide impact have on Earth's biota 65.4 m.y. ago? Impact proponents have long argued that a large bolide impact caused the extinction of nearly the entire Cretaceous biota. They argue that a sun-blocking dust cloud caused a nuclear winter and the cessation of photosynthesis, thus wiping out the base of the food chain and subsequently other organisms, including invertebrates and dinosaurs (Alvarez and others, 1980; Smit, 1982, 1990; Smit and others, 1992). Unfortunately, the existing data base for both dinosaurs and invertebrates is poor and totally inadequate to elucidate the shortterm nature and rate of extinction. Surlyk (1990) cited poor stratigraphic records and sampling as problems, which may modify diversity patterns and result in artificial range truncation (Signor and Lipps, 1982). Ward (1990) used the Signor-Lipps sample effect to argue that patterns of gradual extinction support an impact-generated mass extinction, if one assumes that rare specimens have not yet been found. Unfortunately, a test of this hypothesis is highly impractical, nor does the available evidence support it. Because of the poor record for macrofossils, evidence for the alleged mass extinction has been based primarily on planktic foraminifera. These singlecelled, microscopic organisms with calcare-

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ous shells have populated the oceans between equation and poles for more tilating says. Their skeletal remains, together with nannoplankton, compose most of the calcareous biogenic marine sediments above the carbonate compensation depth. Planktic foraminifera are therefore ideally suited to illuminate the detailed nature of extinction, whether sudden or gradual, and any diversity changes across the Cretaceous-Tertiary transition.

The record of planktic foraminiferal extinctions across the K/T boundary has not been without controversy. Some studies reported the sudden extinction of virtually the entire Cretaceous fauna at the K/T boundary (Smit, 1982; Smit and Romein, 1985; D'Hondt and Keller, 1991; Liu and Olsson, 1992). This pattern, however, appears to be an artifact of a widespread hiatus resulting from nondeposition or erosion (MacLeod and Keller, 1991a, 1991b). Other studies which reported less catastrophic and more gradual extinction patterns from shallower continental shelf and slope sections (Keller, 1988, 1989a, 1989b; Canudo and others, 1991) were generally considered anomalous, with pre-K/T boundary disappearances of species attributed to sampling effects, and Cretaceous species survivorship attributed to reworking. These attributions are now considered to be incorrect (MacLeod and Keller, in press).

Particularly troubling to catastrophists has been the El Kef, Tunisia record, which shows a systematic pattern of gradual extinctions that cannot be dismissed as random sampling error. This extinction pattern shows the early disappearance of large, complex, and ornamented tropical species followed by smaller less-ornamented species, and the survivorship of small cosmopolitan species into the Tertiary (Keller, 1988). Even more troubling is the Brazos, Texas, record, which shows that in the marginal Gulf of Mexico, a lowdiversity, cosmopolitan, Cretaceous assemblage not only survived the K/T boundary event, but thrived well into the Tertiary (Keller, 1989a). This record cannot be dismissed as the result of reworking, as suggested by Liu and Olsson (1992), because Cretaceous species in Tertiary sediments have a Tertiary isotopic signal (Barrera and Keller, 1990).

The Brazos record has generally been considered an anomaly and hence not representative of environmental conditions at K/T boundary time. Indeed, the shallow marginal Gulf of Mexico was probably a stressed environment, with salinity and density fluctuations that favored species tolerant of wideranging conditions. Such species, however,

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were also cosmopolitan and numerically dominated in northern (Stevns Klint, Schmitz and others, 1992) and southern high latitudes (Keller, 1993). In contrast, tropical and subtropical taxa were most vulnerable to environmental fluctuations, and those taxa seem to have disappeared gradually during the 100,000 to 300,000 yr preceding the K/Tboundary. By K/T boundary time, cosmopolitan taxa dominated the oceans from equator to poles (Schmitz and others, 1992; Keller, 1993). This type of extinction and survivorship pattern is not indicative of a catastrophic impact, but rather implies long-term oceanic and environmental instability. Moreover, this would imply that extinction patterns in high and low latitudes should be significantly different, if they are related to long-term environmental instabilities; but if they were caused by a large extraterrestrial bolide impact, they would be substantially the same.

In this report, we document the planktic foraminiferal and stable-isotope records during the latest Maastrichtian to early Tertiary at Nye Klov; compare them with the nearby Stevns Klint section (Schmitz and others, 1992) and the tropical record of Brazos, Texas; evaluate differences in species-richness values across latitudes; and discuss the implications of these results for the K/T boundary bolide-impact scenario.

METHODS

Samples were collected for the entire exposed sedimentary sequence at Nye Klov, beginning 6 m below and ending 13 m above the Cretaceous/Tertiary boundary. Samples from 50 cm below to 2 m above the K/T boundary were taken at 5-cm to 10-cm intervals, as compared to 20 cm to 50 cm for the remainder of the section. A total of 72 samples were analyzed for this study. Samples were processed for foraminiferal analysis by standard micropaleontological techniques, and quantitative counts were based on washed sample splits (using a microsplitter) of 300-400 individuals in the size fraction >63 μ m. The remaining sample residue was searched for rare species. All specimens were picked from each sample split, mounted on microslides for a permanent record and identified. Preservation of planktic foraminifera is good with little recrystallization of original shell calcite except for the fish clay which marks the K/T boundary. In the first cm(0-1 cm) at the base of the Tertiary (fish-clay layer), all planktic foraminifera are dissolved, and only the more solution-resistant benthic species are present. The effects of dissolution decrease upsection

over the next 7 cm (samples at 3 cm, 5 cm, 7 cm), as shown by increasing numbers of well-preserved planktic foraminifera. The relative abundance of species is shown in Table 1.

For stable-isotope analyses, monospecific samples of the benthic foraminifer Cibicidoides succeedens (size fraction 150-250 µm) and the planktic foraminifers Heterohelix globulosa (size fraction 105-180 µm) and Rugoglobigerina rugosa (size fraction 105-180 µm) were measured. All analyses are listed in Table 2. Only well-preserved foraminiferal tests were chosen for stable-isotope analysis. Preservation of foraminiferal calcite was evaluated based on Scanning Electron Microscope (SEM) observations. All specimens show some secondary calcite overgrowth, with diagenetic alteration most severe just above the K/T boundary (0-7 cm). It is possible that diagenesis altered δ^{18} O isotopic compositions in this interval. In contrast, δ^{13} C values are little affected by calcite replacement (Keigwin and Corliss, 1986).

LITHOSTRATIGRAPHY AND BIOSTRATIGRAPHY

The 19 m of exposed sediments at the Nye Klov section of northwestern Denmark span the Cretaceous-Tertiary boundary transition. The lower 6 m consists of light colored chalks with a varying abundance of bryozoans. The K/T boundary (at 0 m) is marked by a fewcentimeter-thick, clay-rich, dark gray marl with rust at its base and an Ir anomaly of 1.6 ppb (Nazarov and others, 1983; Hansen and others, 1986). Above the clay-rich layer, the lower 6.5 m of Tertiary sediments consists of gray marly chalks interbedded with 10- to 20cm-thick flint nodule layers. From 6.5 m to the top of the section at 13 m, tan chalk sedimentation resumes, with varying abundances of bryozoans and invertebrate fossils. About four beds of flint and flint nodules occur in this interval (Fig. 1).

The K/T transition in Denmark has been studied by numerous workers, and much of the early literature is published in two proceedings volumes of Birkelund and Bromley (1979). Studies of the 1980s largely concentrated on the geochemistry and origin of the K/T boundary fish clay, primarily at Stevns Klint (a short review is given in Schmitz and others, 1992). Few studies have reported on iridium in the Nye Klov section (Nazarov and others, 1983; Hansen and others, 1986), but no detailed geochemical analyses of the K/T boundary clay are known to us. This may be largely because the K/T boundary clay is not

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TABLE 1. RELATIVE PERCENT ABUNDANCE OF PLANKTIC FORAMINIFERA ACROSS THE K/T TRANSITION AT NYE KLOV, DENMARK

			KLO	V, DEN	MARK						
Meters below K/T boundary	6.00	5.00	4.50	4.00	3.50	3.00	2.50	2.00	1.75	1.50	
Giobotruncana arca Giobigerinelloides aspera Globigerinelloides subcarinatus Globigerina monmouthensis	0.65 19.54 0.33	8.18 0.51	0.28 9.55	10.70	11.01	20.09	4.33	4.88	0.86	4.55	
Globotruncanella caravacaensis Globotruncanella petaloidea			0.28								
Guembelitria cretacea	2.20	1.53	0.28	3.36	0.58	0.91	1.00	1.05	9.71	4.24	
Guembelitria danica Guembelitria trifolia	2.28	6.14	5.34	6.12	8.41	6.39	6.00	10.10	11.43	11.52	
Hedbergella holmdelensis Hedbergella monmouthensis	4.23 0.33		10.11	4.59 0.61	5.22	5.02	1.00 1.00	2.44	1.14	2.12	
Heterohelix complanata Heterohelix glabrans	9.45	11.00	8.71	11.93	3.77	10.05	5.67	9.76	10.29	3.03	
Heterohelix globulosa Heterohelix navarroensis	63.19	58.06 0.51			71.01	57.08	80.33 0.33	71.43	65.14	74.24 0.30	
Planoglobulina brazoensis		R	R		R	-		_	R	0.50	
Planoglobulina carseyae Rugoglobigerina macrocephala		R	R			R	R	R	R		
Rugoglobigerina rugosa											
Chiloguëmbelina crinita Chiloguembelina midwayensis											
Chiloguembelina waiparaensis	•									•	
Woodringina claytonensis Woodringina hornerstownensis Eoglobigerina danica Eoglobigerina eobulloides											
Eoglobigerina fringa Eoglobigerina simplicissima											
Eoglobigerina trivialis											
Globanomalina pentagona Globanomalina taurica											
Globanomalina tetragona Globoconusa conusa											
Globoconusa daubjergensis Igorina spiralis	<u> </u>										
Morozovella inconstans											
Murciglobigerina aquiensis Murciglobigerina chascanona											
Parvularugoglobigerina eugubina Parvularugoglobigerina longiapertura											
Planorotalites compressus											
Subbotina moskvíní Subbotina pseudobulloides											
Subbotina triloculinoides											
Subbotina varianta Juveniles no identification									0.57	0.30	
Total number counted	307	391	356	327	345	219	300	287	350	330	
Meters below K/T boundary	1.25	1.00	0.75	0.50	0,40	0.30	0.20	0.15	0.10	0.05	
Globotruncana arca		1 22	10.00	0.04	4.40	2.24	1.04	1.60	1 25	1 97	
Globigerinelloides aspera Globigerinelloides subcarinatus	3.71	1.32	18.89	2.84	4.40	2.24	1.94	3.58	1.32	2.83	
Globigerina monmouthensis Globotruncanella caravacaensis									2.19		
Globotruncanella petaloidea		0.33									
Guembelitria cretacea Guembelitria danica	2.65 15.38	5.96 13.25	4.33 17.34	1.89 19.24	1.17 17.89	1.28 15.06	13.87	1.10 12.95	2.19 7.02	0.47 8.96	
Guembelitria trifolia			0.93	0.63	0.88	0.96	2.26	0.83	1.75	3.77	
Hedbergella holmdelensis Hedbergella monmouthensis	1.59 0.80	2.98 1.32	2.79	0.63	0.29	0.64		0.55			
Heterohelix complanata	7.43	9.93	5.57	17.35	17.30	16.03	30.00	16.25	17.11	6.60	
Heterohelix glabrans Heterohelix globulosa	68,44	61.92	0.31 50.15	55.21	55.72	63.46	51.61	61.43	62.72	67.92	
Heterohelix navarroensis			R						1.32 R		
Planoglobulina brazoensis Planoglobulina carseyae		R	R						ĸ		
Rugoglobigerina macrocephala Rugoglobigerina rugosa							0.32	2.20	3.51	8.02	
Chiloguembelina crinita							0.02	0.28		0.02	
Chiloguembelina midwayensis Chiloguembelina waiparaensis											
Woodringina claytonensis											
Woodringina homerstownensis Eoglobigerina danica											
Eoglobigerina eobulloides											
Eoglobigerina fringa Eoglobigerina simplicissima											
Eoglobigerina simplicissima Eoglobigerina trivialis											
Eoglobigerina simplicissima											
Eoglobigerina simplicissima Eoglobigerina trivialis Globanomalina pentagona											

as distinct and well developed as at Stevns Klint. Stratigraphic studies of Nye Klov are generally limited to short reports on various Danian and Cretaceous species present. Interestingly, in addition to 'Globigerina' eugubina, Eoglobigerina danica, and Chiloguembelina spp., common small Cretaceous taxa are reported, including Heterohelix spp., Hedbergella sp., Rugoglobigerina sp., Globigerinella sp., and Guembelitria cretacea (Bang, 1979). As Cretaceous species in Danian deposits were generally considered reworked, there were no further investigations of these faunas. To us, these reports of small common Cretaceous taxa in Danian deposits were reminiscent of the faunal assemblages observed at Brazos, Texas (Keller, 1989a), which led us to collect and study the Nye Klov section. Our stratigraphic results are discussed below.

Figure 1 shows the sequence of Danian datum events at Nye Klov relative to the highresolution planktic foraminiferal zonation of Keller (1988, 1993; Canudo and others, 1991). Although this zonation was originally developed for low latitudes (Smit, 1982; Keller, 1988), the cosmopolitan nature of early Tertiary faunas allows global application into high latitudes (Keller, 1993). Figure 1 illustrates that the K/T transition at Nye Klov is biostratigraphically complete (that is, all biozones are present), but one and probably two intrazonal hiatuses occur in Zones P0 and P1a. The uppermost Maastrichtian is unzoned because the index taxa A. mayaroensis, P. deformis, or P. elegans are absent (see also Hultberg and Malmgren, 1987). A continuous uppermost Cretaceous sedimentation record appears to be present, however, when Nye Klov is compared with Stevns Klint (Schmitz and others, 1992).

The basal Tertiary Zone P0 ranges from the first appearance (FAD) of Tertiary species at the base of the boundary clay to the first appearance of Parvularugoglobigerina eugubina and/or P. longiapertura. At Nye Klov, the base of Zone P0 is inferred to be at the base of the boundary fish clay, although planktic foraminifera are dissolved in the boundary clay (0-1 cm) and partially dissolved in the next 5 cm (Table 1). Parvularugoglobigerina longiapertura (P. eugubina is rare) first appears 9 cm above the boundary clay and marks the P0/P1a boundary. Zone P0, therefore, spans less than 10 cm at Nye Klov, and it is likely that part of this zone is missing due to dissolution or nondeposition.

The last appearance (LAD) of Parvularugoglobigerina longiapertura occurs at

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Meters below K/T boundary	1.25	1.00	0.75	0.50	0.40	0.30	0.20	0.15	0.10	0.05	
Globoconusa daubjergensis Igorina spiralis Morozovella inconstans Murciglobigerina aquiensis					_						
Murciglobigerina chascanona Parvularugoglobigerina eugubina											
Parvulanugoglobigerina longiapertura Planorotalites compressus											
Subbotina moskvini											
Subbotina pseudobulloides Subbotina t ri loculinoides											
Subbotina varianta											
Juveniles no identification											
Total number counted	377	302	323	317	341	312	310	363	228	212	
Meters below K/T boundary	0.02	0.005	0.01	0.03	0.05	0.07	0.09	0.15	0.20	0.30	
Globotruncana arca Globigerinelloides aspera	2.66	4.11		2	1.69	0.85	1.74	4.20	1.83	1.75	
Globigerinelloides subcarinatus Globigerina monmouthensis	3.80	3.20		2	2.54	5.08	3.91	1.05	1.83	3.07	
Globotruncanella caravacaensis	5.00	5.20			0.85	5.00	5.91	1.05	0.46	5.07	
Globotruncanella petaloidea Guembelitria cretacea	0.38				10.17	8.47	6.09	4.90	6.88	0.44 6.58	
Guembelitria danica	0.76	5.02		1	4.24	13.56	9.13	11.19	13.76	17.54	
Guembelitria trifolia Hedbergella holmdelensis	2.28	0.46		3	2.54 2.54	1.69	8.26	15.38	11.93	10.96	
Hedbergella monmouthensis		0.40			<i>2.3</i> 4	1.09	1.74	4.20	2.75	0.44	
Heterohelix complanata Heterohelix glabrans	4.94	1.83		4 2	0.85	5.93	1.74	2.80	6.88	1.75	
Heterohelix globulosa Heterohelix navarroensis	73.38	69.86		12	66.10	72.88	65.65	51.75	47.25	53.95	
Planoglobulina brazoensis Planoglobulina carseyae	R	R									
Rugoglobigerina macrocephala Rugoglobigerina rugosa	11.03	15.07		9	7.63	3.39			1.38		
Chiloguembelina crinita Chiloguembelina midwayensis							1.30				
Chiloguembelina waiparaensis						2.54	0.87	1.75	1.38	1.32	
Woodringina claytonensis Woodringina homerstownensis Ecolobiantina danica							0.43	0.70	•		
Eoglobigerina danica Eoglobigerina eobulloides Eoglobigerina frinca								0.35	0.46		
Eoglobigerina fringa Eoglobigerina simplicissima								0.35	0.46		
Eoglobigerina trivialis Globanomalina pentagona											
Globanomalina taurica Globanomalina tetragona											
Globoconusa conusa		<u>.</u>						0.70	0.46	0.44	
Globoconusa daubjergensis Igorina spiralis											
Morozovella inconstans Murciglobigerina aquiensis											
Murciglobigerina chascanona								.			
Parvularugoglobigerina eugubina Parvularugoglobigerina longiapertura							1.30	0.35 1.05	0.92	0.44 2.19	
Planorotalites compressus											
Subbotina moskvini Subbotina pseudobulloides											
Subbotina triloculinoides											
Subbotina varianta Juveniles no identification							0.43				
Total number counted	263	219		35*	118	135	230	286	218	228	
Meters below K/T boundary	0.40	0.50	0.80	0.90	1.00	1.10	1.20	1.40	1.60	1.85	
Globotruncana arca											
Globigerinelloides aspera Globigerinelloides subcarinatus	2.78	5.29	2,88	4.21	0.77	1.77	3.86	3,20	1.14		
Globigerina monmouthensis	3.82		2.06	1.87	0.77	0.44	1.29	0.46	1.70		
Globotruncanella caravacaensis Globotruncanella petaloidea	0.35 0.69	0.44 0.44	1.65	0.93 0.47		3.10	1.72	1.37		0.53	
Guembelitria cretacea	7.99	4.85	3.29	3.27	7.69	4.87	7.30	5.02	5.68	1.59	
Guembelitria danica Guembelitria trifolia	14.58 7.99	11.45 3.52	14.81 7.41	16.36 0.47	16.92 5.38	7.52 0.88	10.73	6.85	4.55	7.41	
Hedbergella holmdelensis		200			5.30	5.00					
Hedbergella monmouthensis	2.78			0.93							
Heterohelix complanata Heterohelix glabrans	5.21	3.96	2.06		5.38	3.10	2.58	1.83		0.53	
Heterohelix globulosa	50.00	55.07	41.98	43.93	30.00	23.89	19.31	12.33	15.34	12.70	
Heterohelix navarroensis Planoglobulina brazoensis											
Planoglobulina carseyae											

LAD of P. longiapertura and/or P. eugubina to the FAD of Subbotina varianta, or from

ary (Table 1).

1.2 m to 3.9 m above the K/T boundary at Nye Klov. This interval is marked by maximum abundances of Eoglobigerina danica and Chiloguembelina waiparaensis and the extinction of Cretaceous survivor taxa except for Guembelitria cretacea (Table 1). The upper 7 m of the section is in Zone P1c, which extends from the FAD of S. varianta to the FAD of Morozovella trinidadensis. At Nye Klov, the section terminates below the FAD of M. trinidadensis. Zone P1c can be subdivided based on the FAD of Morozovella inconstans, which first appears 7.4 m above the K/T boundary at Nye Klov. Subzone P1c(1) is characterized by the extinction of E. danica, maximum abundances of Globoconusa daubiergensis, and abundant Murciglobigerina aquiensis, M. chascanona, Subbotina pseudobulloides, S. varianta, Globanomalina pentagona, and Planorotalites compressus (Table 1). This interval, which marks the first post-K/T boundary recovery of marine plankton, is coincident with the resumption of tan chalk sedimentation.

1.2 m above the K/T boundary and marks the Pla/Plb boundary. Zone Pla can be subdivided based on the FAD of Subbotina pseudobulloides, which first appears in the upper half of the zone. As that species is not present with P. longiapertura at Nye Klov, only the lower part, Subzone P1a(1), seems to be present. The upper part, Subzone P1a(2), is removed by a hiatus marked by the abrupt and common (22%) occurrence of Eoglobigerina danica at 1.1 m above the K/T bound-

The succeeding Zone P1b extends from the

Chronostratigraphy

The age of the K/T transition exposed at Nye Klov can be estimated based on stratigraphic correlation with coeval sequences for which there are paleomagnetic records. The age of the Maastrichtian sediments, however, is difficult to estimate. Sedimentation rates of the bryozoan-rich chalks of the uppermost Maastrichtian have been previously estimated at about 10 cm/1,000 yr (Kaminski and Malmgren, 1989; Schmitz and others, 1992). This depositional rate is a maximum average over the entire Maastrichtian (7.5-8.0 Ma), that assumes continuous sedimentation in the thickest section of the basin (700 m near Stevns Klint). These rates are probably substantially too high for the terminal Maastrichtian and cannot be applied to the uppermost Maastrichtian at Nye Klov.

Planoglobulina carseyae Rugoglobigerina macrocephal

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			TAB	LE 1. (C	ontinued	!)				
Meters below K/T boundary	0,40	0.50	0.80	0.90	1.00	1.10	1.20	1.40	1.60	1.85
Rugoglobigerina rugosa Chiloguembelina crinita Chiloguembelina midwayensis Chiloguembelina waiparaensis	1.04	0.88 3.08	18.52	0.47 20.09	0.77 26.92	22.57	27.04	39.73	40.34	0.53 29.10
Woodringina claytonensis Woodringina homerstownensis Eoglobigerina danica Eoglobigerina eobulloides Eoglobigerina fringa	0.69	1.76		0.93	0.77	22.57	18.45	26.94	25.57	45.50
Eoglobigerina simplicissima Eoglobigerina trivialis Globanomalina pentagona Globanomalina tetragona Globaconusa conusa		0.44	0.41		0.77			0.46	0,57	
Globocomusa daubjergensis Igorina spiralis Morozovella inconstans	1.39	3.08	3.70	5.61	2.31	4.42	2.58	1.37	4.55	
Murciglobigerina aquiensis Murciglobigerina chascanona Parvulangoglobigerina eugubina Parvulangoglobigerina longiapertura Planorotalites compressus Subbotina moskvini Subbotina moskvini Subbotina priedobulloides Subbotina triloculinoides Subbotina varianta Juveniles no identification	3.47		0.41	0.47	1.54	5.31 0.44	2.58 0.43	0.46 0.46	0.57	0.53
Total number counted	288	227	243	214	130	226	233	219	176	189
Meters below K/T boundary	2.00	2.10	2.40	2.70	3.30	3.90	4.35	4.90	5.20	5.70
Globotruncana arca Globigerinelloides aspera Globigerinelloides subcarinatus Globigerina montmouthensis Globotruncanella caravacaensis	0.34			0.84						
Globotruncanella petaloidea Guembelitria cretacea Guembelitria danica Guembelitria trifolia Hedbergella holmdelensis Hedbergella monmouthensis	2.73 3.75	2.42 3.23	0.95 3.79	2.11 3.80	4.20 2.10 1.40	3.22 0.96	6.02 5.73 2.01	1.94 2.90	1.64 0.23 1.41	
Heterohelix complanata Heterohelix glabrans Heterohelix glabulosa Heterohelix navarroensis Planoglobulina brazoensis Planoglobulina carseyae Rugoglobigerina mucrosephala Rugoglobigerina nugosa	8.87	1.61 9.68	0.47 6.16	1.27 4.22	1.40	0.32 0.32				
Chiloguembelina crinita Chiloguembelina midwayensis Chiloguembelina waiparaensis	25.60	0.40 16.53	27.01	1.27 17.72	18.18	0.32 16.08	0.29 9.17	2.26	1.41	
Woodringita claytonensis Woodringina homerstownensis Eoglobigerina danica Eoglobigerina eobulloides Eoglobigerina fringa	55.29	65.73	59.72	66.24	69.23	27.33 0.32	14.90	13.23	14.05	8
Eoglobigerina implicissima Eoglobigerina trivialis Globanomalina pentagona Globanomalina taurica Globanomalina tetragona Globoconusa conusa							0.29 0.29	0.32 0.32 3.87 0.65	1.87 1.64	1
Globoconusa daubjergensis Igorina spiralis Morozovella inconstans	2.39				2.10	10.61	53.01	64.52	68.62	35
Murciglobigerina aquiensis Murciglobigerina chascanona Parvularugoglobigerina eugubina Parvularugoglobigerina longiapertura									2.34 0.70	
Planorotalites compressus Subbotina moskvini Subbotina pseudobulloides Subbotina triloculinoides Subbotina varianta Juveniles no identification	0.34	0.40		0.84 2.11	0.70	3.22 1.29 0.64	5.73 2.01 0.29	1,61 5.81 2.90	1.87 2.81 0.23 1.41	
Total number counted	293	248	211	237	143	311	349	310	427	44*
Meters below K/T boundary	6.40	6.70	6.90	7.15	7.40	7.70	8.00	8.30	8.50	8.80
Globotruncana arca										

Globotruncana arca Globigerínelloides aspera

A better estimate of depositional rates can be obtained for the earliest Tertiary. Paleomagnetic stratigraphy places the top of Zone P1a at the base of Chron 29N (Channell and Dobson, 1989; MacLeod and Keller, 1991a, 1991b). The interval between the K/T boundary and the top of Chron 29R (Zones P0 and P1a) is estimated between 230,000 and 280,000 yr (Channell and Dobson, 1989; Herbert and D'Hondt, 1990; MacLeod and Keller, 1991b). Zone P0 is estimated at about 40,000 to 50,000 yr. If no hiatuses were present, sedimentation rates for Zone P0 would average 0.18 cm to 0.22 cm/1,000 yr; and those for Zone P1a, 0.61 cm/1,000 yr, similar to Caravaca, Spain (0.2 cm and 0.5 cm/1,000 yr, respectively). As hiatuses seem to be present in both zones at Nye Klov and Caravaca, these average depositional rates are probably significantly too low. In contrast, sedimentation rates at the more complete El Kef section are 1.4 cm and 3.7 cm/1,000 yr for Zones P0 and P1a, respectively (MacLeod and Keller, 1991).

The first post-K/T boundary recovery in planktic foraminifera was previously interpreted to be in Zone P1c from about 300,000 to 350,000 vr after the K/T boundary (Keller, 1988, 1989b; Keller and Benjamini, 1991). At Nve Klov, this recovery occurs in the lower part of Zone P1c or Subzone P1c(1) between 5 m and 6.5 m above the K/T boundary and immediately preceding the resumption of tan chalk deposition in the Tertiary. Assuming a 120,000-vr duration for P1b and P1c(1), depositional rates averaged 4.4 cm/1,000 yr for this interval. Depositional rates in the succeeding chalks are probably higher, but no estimate can be given here because the section terminates below the top of Subzone P1c(2).

Placement of the K/T Boundary

In most K/T sequences, the boundary is easily identified based on one or more of the following: (1) a lithologic break from chalk or marl deposition of the Cretaceous to a thin layer of dark, organic-rich, and CaCO₃-poor clay (boundary clay) followed by increasingly carbonate-rich clays and marls; (2) a 2- to 3-mm oxidized "red layer" at the base of the boundary clay; (3) anomalously high iridium values generally concentrated in the red layer and often associated with spinels (Robin and others, 1991, 1992); (4) a negative δ^{13} C shift in marine plankton (fine fraction carbonate or planktic foraminifera); (5) the first appearance of Tertiary planktic foraminifera, usually within 1 cm to a few centimeters above the red

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Meters below K/T boundary	6.40	6.70	6.90	7.15	7.40	7.70	8.00	8.30	8.50	8.80		
Globigerinelloides subcarinatus Globigerina monmouthensis Globotruncanella caravacaensis Globotruncanella petaloidea Guembeliaria cretacea Guembeliaria cretacea Guembeliaria cretacea Guembeliaria che ante Hedbergela holmdelensis Hedbergella monmouthensis	0.58	2.40	0.70	3.54	0.96	0.96	1.27	2.52	0.74	1.69		
Heterohelix complanata Heterohelix glabrans Heterohelix glabulosa Heterohelix navarroensis Planoglobulina brazoensis Planoglobulina brazoensis Planoglobulina carseyae Rugoglobigerina macrocephala Rugoglobigerina rugosa Chiloguembelina crinita Chiloguembelina midwayensis Chiloguembelina waiparaensis	2.31	0.96	0.35 0.35	0.88 9.29	0.96 1.91 8.92	0.96 0.64 5.45	1.59 0.32	1.26				
Woodringina claytonensis Woodringina homerstownensis Eoglobigerina danica Eoglobigerina ebulloides Eoglobigerina fringa Eoglobigerina simplicissima Eoglobigerina trivialis	10. 9 8	10.58	1.05	10.62	5.10	3.21 0.96	0.64	0.63		0.85		
Globanomalina pentagona	3.47	9.13	2.80	0.88	4.14	4.17	2.87	2.52	2.60	2.54		
Globanomalina taurica Globanomalina tetragona Globoconusa conusa		3.85				1.28	0.32					
Globoconusa daubjergensis	42.77	40.87	42.66	19.47	19.43	24.36	36.94	27.04	29.00	33.90		
Igorina spiralis Morozovella inconstans	2.31				2.23	2.88	0.64 4.14	2.52	1.49 2.60	0.85 2.54		
Murciglobigerina aquiensis	9.83	25.00	33.22	25.66	21.66	36.22	29.94	27.67	27.88	36.44		
Murciglobigerina chascanona Parvularugoglobigerina eugubina Parvularugoglobigerina longiapertura	2,31		4.55	2.65	1.27	4.17	6.37	7.86	7.81	4.24		
Planorotalites compressus Subbotina moskvini	7.51	0.48	3.15	7.96	11.78	6.41	10.51	12.58	14.50	11.02		
Subbotina pseudobulloides	9.83	3.85	1.75	8.41	11.15	4.17	3.50	12.89	11.90	5.93		
Subbotina triloculinoides Subbotina varianta	8.09	2.88	8.74	10.62	2.87 6.05	4.17	1.27	0.63 1.57	1.49			
Juveniles no identification					0.32							
Total number counted	173	208	286	226	314	312	314	318	269	118		
Meters below K/T boundary	9.20	9.40	9.80	10.20	10.60	10.80	11.30	11.60	12.00	12.30	12.50	13.00
Globotruncana arca Globigerinelloides aspera Globigerinelloides subcarinatus Globigerina momouthensis Globotruncanella caravacaensis Globotruncanella petaloidea Guembeliara cretacea Guembeliara cretacea Guembeliara cretacea Guembeliara trifolia Hedbergella holmdelensis Hedbergella monmouthensis	2.00	0.67										
Heterohelix complanata Heterohelix glabrans Heterohelix glabruosa Heterohelix navarroensis Planoglobulina carseyae Rugoglobigerina macrosephala Rugoglobigerina macrosephala Chiloguembelina crimita Chiloguembelina midwayensis Chiloguembelina waiparaensis	1.50	0.33		0.30			0.84	2.97	0.61	0.30	0.72	9.42
Woodringina claytonensis Woodringina homerstownensis Eoglobigerina danica Eoglobigerina eobulloides Eoglobigerina fringa Eoglobigerina simplicissima Eoglobigerina thivialis Globanomalina tentagona Globanomalina tentagona Globacomusina tanica Globacomusia conusa	0.50 3.50	2.34	1.69 0.56	0.30 0.91 5.45	2.77	2.60 7.14 0.32	0.84 3.77	1.49	2.45	1.82	0.72	1.39
Globoconusa daubjergensis Igorina spiralis Morozovella inconstans Murciglobigerina aquiensis	37.00 1.50 3.50 20.50	18.39 2.01 5.35 33.11	23.66 0.56 2.25 16.90	20.30 0.61 3.03 25.76	17.85 2.77 12.62 20.92	18.83 1.62 12.99 14.29	21.34 11.72 19.25	28.47 5.69 30.45	14.42 9.82 42.64	10.61 11.52 51.82	13.26 9.32 54.48	11.36 8.59 44.60

layer and Ir anomaly; and (6) the disappearance of the remaining surviving tropical and subtropical Cretaceous species, but survivorship of unspecialized cosmopolitan taxa. At Nye Klov, all of these criteria, except for the red layer and spinels, are present and mark the K/T boundary.

The coincidence of these lithological, geochemical, and paleontological criteria is unique in the geological record and virtually insures that the stratigraphic placement of the K/T boundary is uniform and coeval in marine environments across latitudes. Any of these criteria used in isolation, however, diminish the stratigraphic resolution of the K/T boundary and may introduce artificial diachroneity into this boundary event. The first appearance of Tertiary species seems to be a very reliable indicator for the K/T boundary because they are usually found within 1 cm to a few centimeters above the red layer, Ir anomaly, and δ^{13} C shift (Smit, 1982; Smit and Romein, 1985; Keller, 1988, 1989a, 1989b, 1993; Canudo and others, 1991). The fewcentimeters discrepancy between these geochemical anomalies and the first appearance of Tertiary species is generally due to carbonate dissolution in the boundary clay. The suggestion that the mass extinction of all but one Cretaceous species should define the K/T boundary (Smit, 1982, 1990; Olsson and Liu, 1992) is not practical because only specialized tropical and subtropical forms disappeared, whereas most high-latitude and cosmopolitan taxa survived. Equally impractical is the suggestion that the first abundance increase in the Cretaceous survivor Guembelitria defines the K/T boundary (Olsson and Liu, 1992) because species abundance peaks are not unique events, but rather reflect favorable environmental conditions. Guembelitria are isotopically light species which thrive in shallow neritic environments. Their abundance peaks range over at least 200,000 to 300,000 yr of the earliest Tertiary and reflect shallow-water environments associated with sea-level lowstands. Olsson and Liu's (1992) criteria applied to the Gulf Coast may introduce diachroneity of as much as 300,000 yr in placement of the K/T boundary, as well.

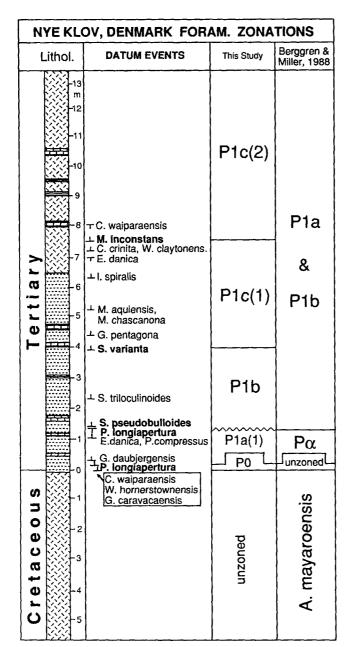
The lithological, geochemical, and paleontological criteria outlined above have been successfully applied at Stevns Klint and Nye Klov (Schmitz and others, 1992; this study), as well as in sections at Agost and Caravaca in Spain (Smit, 1990; Canudo and others, 1991), El Kef, Tunisia (Smit, 1982; Keller, 1988; Keller and Lindinger, 1989), the eastern Tethys (Keller and others, 1990; Keller and Benjamini, 1991), Deep Sea Drilling Project

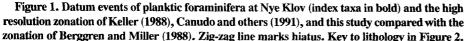
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	TABLE 1. (Continued)												
Meters below K/T boundary	9.20	9.40	9.80	10.20	10.60	10.80	11.30	11.60	12.00	12.30	12.50	13.00	
Murciglobigerina chascanona Parvularugoglobigerina eugubina Parvularugoglobigerina longiapertura	6.50	21.07	24.23	22.12	24.62	14.94	16.32	18.32	3.37		1.08	5.54	
Planorotalites compressus Subbotina moskvini	6.00	8.70	6.76	9,70	6.46	15.58	18,83	9.16	13.80	16.06	15.77	10.80	
Subbotina pseudobulloides Subbotina triloculinoides	7.00 1.00	6.02	5.63 3.66	7,58 0,91	10.77	7.47 0.97	10.46	2.72	10.74	6.06 0.30	1.79 0.36	4.43 0.55	
Subbotina varianta Juveniles no identification	2.00	2.68	2.54 0.56	2.42 0.61	1.23	3.25	0.42	0.74	1.84 0.31	1.52	1.43	1.11 1.11	
Total number counted	200	299	355	330	325	308	239	404	326	330	279	361	

Note: R << 1%; very rare species are listed as "R". Samples with strong carbonate dissolution and fewer than 100 individuals are marked by asterisks and actual numerical abundance, rather than percent values, are given.





(DSDP) Sites 577 and 528 (D'Hondt and Keller, 1991) and Antarctic Ocean Drilling Program (ODP) Site 738 (Thierstein and others, 1991; Schmitz and others, 1991; Keller, 1993). In all of these sections, the placement of the K/T boundary is unquestioned. It is only in the Brazos River sections where placement of the K/T boundary is controversial. In those sections, some paleontologists have placed the K/T boundary at the hiatus either at the base of a shell-hash bed (tsunami deposit of Bourgeois and others, 1988), where most of the tropical taxa disappear (Montgomery and others, 1992); at the top of the "tsunami" bed (Hansen and others, 1987); or about 15 cm to 17 cm above the "tsunami" deposit at a 2-mm-thin, red-brown layer which coincides with the first appearance of Tertiary planktic foraminifera and nannofossils (Jiang and Gartner, 1986; Keller, 1989a) and the δ^{13} C shift (Barrera and Keller, 1990). The paleontological controversy, which was largely due to the fact that no unequivocal bolide impact signature (including Ir anomaly and spinels) was found, may now be resolved. R. Rocchia and E. Robin (1992, written commun.) have now found maximum Ir concentrations in the 2-mm, red-brown layer 15 cm above the "tsunami" bed where Jiang and Gartner (1986) and Keller (1989a, 1989b) placed the K/T boundary based on the first appearance of Tertiary species and a $\delta^{13}C$ shift.

PLANKTIC FORAMINIFERAL TURNOVER

Nye Klov and Brazos Compared

The faunal turnover in planktic foraminifera across the latest Maastrichtian to early Tertiary at Nye Klov is illustrated in Figure 2. For comparison, the tropical section from Brazos, Texas, is shown in Figure 3. Note the striking similarities in the Cretaceous species survivorship patterns of these two geographically and latitudinally disparate sections. In both localities, Heterohelix globulosa is the dominant species, averaging 50% to 60% of the faunal assemblage. This species declines at, or immediately after, the K/T boundary and disappears at the top of Zone P1a or in Zone P1b along with all other Cretaceous survivors, except for Guembelitria. Guembelitria species are the second most abundant group, averaging about 20% in the meter below the K/T boundary and dominating in the early Danian. Globigerinelloides aspera and Heterohelix complanata are also common in both sections. Species endemic to either lo-

- TABLE 2	STABLE ISOTOPE ANALYSES	S OF NYE KLOV FORAMINIFERA
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Meters below K/T	C. succeedens		H. globulosa		R. rugosa		Meters	C. succ	eedens	H. glo	bulosa	R. rugosa	
DEIOW IN/I	S ¹⁸ O	S ¹³ C	S ¹⁸ O	S ¹³ C	S ¹⁸ O	S ¹³ C	above K/T	S ¹⁸ O	S ¹³ C	S ¹⁸ O	S ¹³ C	S ¹⁸ O	S ¹³ C
-6.00 m*	-1.25	1.81	-1.52	1.57			+0.01 m	-0.75	2.12				
-5.00 m*	-1.11	1.73					+0.01 m*	-0.74	2.17				
~4.50 m*	-1.15	1.68	-1.51	1.09			+0.03 m	-0.78	1.99				
-4.00 m*	-1.01	1.84					+0.05 m*	0.90	1.78				
-3.50 m*	-1.14	1.79	-1.30	1.27			+0.05 m	-1.34	1.70	-1.37	1.09	-1.42	2.57
-3.00 m*	-1.25	1.79					+0.07 m			-0.98	1.29	-1.28	2.27
-2.50 m*	-1.04	1.91	-1,48	1.47			+0.09 m			-1.37	1.14		
-2.00 m*	-1.06	1.80					+0.15 m	-1.29	1.35	-1.26	1.11		
-1.75 m*	-1.09	1.79	-1.34	1.14			+0.20 m	-1.25	1.48	-1.39	1.15		
-1.50 m*	-1.18	1.81					+0.30 m			-1,47	1.14		
-1.25 m*	-1.12	1.90					+0.40 m	-1.28	1.53	-1.46	1.12		
-1.00 m*	-1.12	1.89					+0.50 m	-1.11	1.48	-1.52	1.10		
-0.75 m*	-1.04	1.94	-1.49	1.57			+0.80 m	-0.86	1.51	-1.30	1.10		
-0.50 m*	-0.95	2.05	-1.40	1.42			+0.90 m	-1.03	1.64	-1.43	1.00		
-0.40 m*	~0.99	2.04					+1.00 m	-1.29	1.55				
-0.40 m	-1.07	1.96	~1.48	1.35			+1.10 m	-0.99	1.67	-1.38	1.11		
-0.30 m*	-1.19	1.99					+1.20 m	-0.89	1.73	-1.42	1.10		
-0.30 m	-1.13	1.85	-1.45	1.46			+1.40 m	-0.99	1.75				
-0.20 m*	-1.14	2.02					+1.60 m	-0.78	1.92				
-0.20 m	-1.23	1.67	-1.40	1.32	-1.70	2.44	+2.00 m	-0.73	1.86				
-0.15 m*	-1.16	2.03											
-0.15 m	-1.25	1.94			-1.92	2.45							
-0.11 m			-1.39	1.33									
~0.10 m*	-1.10	2.03											
-0.10 m	-0.86	1.75	~1.51	1.68	-1.83	2.47							
-0.08 m			-1.53	1.47	-1.63	2.43							
-0.07 m			-1.53	1.44									
-0.05 m*	-0.94	2.14											
-0.05 m	-0.91	1.98	-1.51	1.65	-1.85	2.48							
-0.02 m					-1.51	2.59							
~0.015 m			-1.24	1.31									
-0.01 m	-0.86	1.86											
~0.005 m					-1.58	2.57							

*Stable-isotope analyses of C. succeedens done at the University of Gothenburg, Sweden; all other analyses done at the University of Michigan, Ann Arbor, Michigan.

cality are rare during the latest Maastrichtian. Differences include the more common presence of *Hedbergella* spp. at Nye Klov and the common presence of *Heterohelix navar*roensis, *Pseudoguembelina costulata*, and *P. excolata* at Brazos, as compared to their near absence at Nye Klov.

Strong faunal similarities between the boreal sea Nye Klov and Brazos, Texas, sections continue into the earliest Tertiary Zones P0 and P1a as seen in the Cretaceous species survivorship patterns. Faunal differences are significantly more prominent in the evolving taxa beginning in Zones P1a and P1b and mark the onset of an inverse trend in species richness in high latitudes, as discussed below.

The Case for Cretaceous Species Survivorship

Similarities in Cretaceous species patterns in the earliest Tertiary of sections as widely separated as Texas and Denmark indicate that these taxa are survivors. No reworking process could produce such a systematic species-abundance pattern, let alone reproduce it halfway around the earth. Only the belief that all Cretaceous species were killed in a catastrophicmass extinction at the K/Tboundary (Smit, 1982, 1990; Olsson and Liu, 1992) would lead one to question the reality of the species patterns observed at Brazos and Nye Klov. Fortunately, there is an objective and definitive test of species survivorship based on the δ^{13} C isotopes of the species in question. If the Cretaceous species in the earliest Tertiary sediments are reworked, they should have Cretaceous isotopic signals; if they lived in the earliest Tertiary, they should have Tertiary signals. As the δ^{13} C signals between the Cretaceous and Tertiary are significantly different due to a negative δ^{13} C shift at the K/T boundary, this test should unequivocally mark the species as either reworked or *in situ*.

In an earlier study, such a test was done for *Heterohelix globulosa* at Brazos, Texas (Barrera and Keller, 1990). Figure 4 illustrates δ^{18} O and δ^{13} C measurements of *H. globulosa* and the benthic foraminifer *Lenticulina*. These results show that *H. globulosa* in Tertiary sediments has Tertiary signals, with δ^{13} C values gradually getting 3.0 permil lighter in Zone P0. Clearly, *H. globulosa* is a Cretaceous survivor in the Gulf of Mexico region.

We have made the same stable isotopic measurements for *H. globulosa* and the benthic species *Cibicidoides succeedens* at Nye Klov (Fig. 5). Just as at Brazos, Texas, δ^{13} C values of *H. globulosa* and the benthic foraminifer *Cibicidoides succeedens* in Tertiary sediments are significantly lighter than those in Cretaceous sediments. Therefore, *H. globulosa* populations in Tertiary sediments at Nye Klov also represent Cretaceous survivors, and we assume that the other Cretaceous species consistently present in Tertiary sediments at both Nye Klov and Brazos are, as well. This assumption is supported by stable isotopic values of another Cretaceous survivor, *Guembelitria danica* at Nye Klov (E. Barrera and G. Keller, unpub. data).

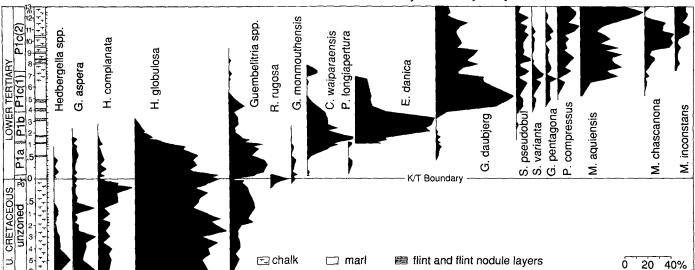
Gradual Mass Extinction in High Latitudes

Perhaps the most striking feature of the K/T transition at Brazos and Nye Klov is the absence of species extinctions directly associated with the K/T boundary (Figs. 2, 3), as also observed in the Indian Antarctic Ocean Site 738 (Keller, 1993). All dominant species survived, terminally declining in relative abundances either before or soon after the K/T boundary, except for the shallow-water Guembelitria group, which thrived into the earliest Tertiary. At Nye Klov, 7 species, or 41%, survived well into Tertiary Zone P1b, or for about 300,000 yr. Three species (R. rugosa, H. holmdelensis, and H. monmouthensis), or 18%, may have survived for a shorter time (Zones P0 to lower P1a, or about 50,000 to 100,000 yr). The remaining 7 species (41%) of the Cretaceous assemblage (G. arca, G. subcarinatus, G. petaloidea, H. glabrans, H. navarroensis, P. brazoensis, and P. carseyae) are rare and sporadically present in the 6 m below the K/T boundary (Table 1; see also Stevns Klint in Schmitz and others, 1992). Two of these species (G. subcarinatus and H. navarroensis) seem to be survivors in low latitudes (Keller, 1988, 1989a). Only one of the seven species disappears at the K/T boundary at Nye Klov (P. carseyae, Table 1). A similar gradual extinction pattern in planktic foraminifera has been observed in the Indian Antarctic Ocean Site 738 (Keller, 1993). Moreover, palynomorphs and invertebrate fossils in sections on Seymour Island also show gradual extinction patterns across the K/T boundary (Zinsmeister and others, 1989; Askins, 1992). In comparison with high latitudes, at Brazos, Texas, 46% of the Cretaceous species disappeared 10 cm to 15 cm below the K/T boundary at a short hiatus coinciding with a sea-level lowstand at the base of a shell-hash bed ("tsunami"), whereas 54% survived into the earliest Tertiary (Keller, 1989a). At El Kef, Tunisia, 22%, or 10 species, survived well into the Tertiary (Zones P1a to P1b), but the remainder of the species disappeared between 25 cm below and 7 cm above the K/T boundary (Keller, 1988).

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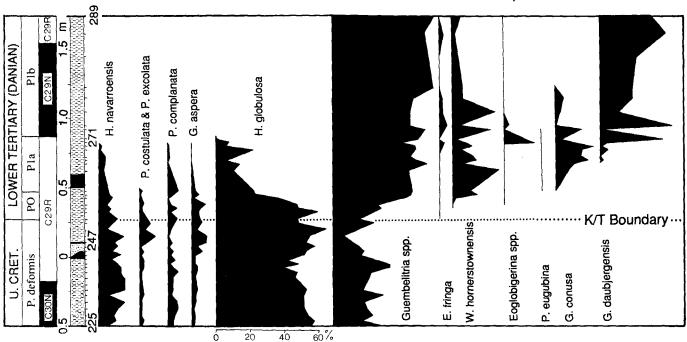
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Planktic Foraminiferal Turnover across the Cretaceous - Tertiary Boundary at Nye Klov, Denmark

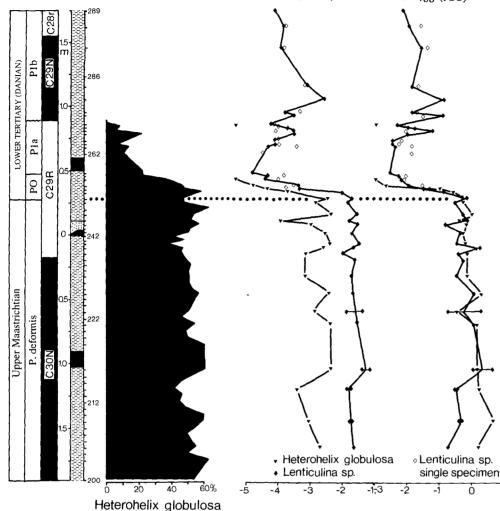
Figure 2. Planktic foraminiferal turnover across the Cretaceous-Tertiary transition at Nye Klov, Denmark. Note the absence of species extinctions at the K/T boundary and the survivorship of all dominant Cretaceous taxa into the Tertiary.



K/T Transition in Planktic Foraminifera at Brazos, Texas

Figure 3. Planktic foraminiferal turnover across the Cretaceous-Tertiary transition at Brazos, Texas (from Keller, 1989a). Note the similarity with the faunal turnover at Nye Klov, the absence of species extinctions at the K/T boundary, and the survivorship of all dominant Cretaceous taxa into the Tertiary.

Significantly, survivorship patterns exhibited at all four geographically separated localities indicate that (1) only small, unornamented, cosmopolitan taxa survived; (2) many of these taxa were abundant throughout the Maastrichtian, whereas others were present in small numbers, and they numerically expanded only when larger, more specialized taxa began to disappear during the latest Cretaceous. Unspecialized survivor taxa were able to tolerate wide-ranging temperature, oxygen, and water-density conditions. Their dominance at Nye Klov during the latest Maastrichtian and earliest Tertiary reflects both the high-latitude location and the shallow-water (100–200 m) environment in the Danish basin, which was probably characterized by salinity, temperature, and oxy-



BRAZOOVALOGO from gsabulletin.gsapubsor & Augusto 9, 2014 813 C % (PDB)

Figure 4. Carbon- and oxygenisotope values of the planktic foraminifer *Heterohelix globulosa* and benthic foraminifer *Lenticulina* spp. and the relative abundance of *H. globulosa* across the K/T boundary at Brazos, Texas (data from Barrera and Keller, 1990). Note the gradual $3.0\% \delta^{13}$ C shift in Zone P0 parallel with the decline in *H. globulosa* abundance and the reduction in the surface to deep gradient.

gen fluctuations. Their dominance in the tropical region of Brazos, Texas, during the same time interval reflects the stressed conditions of this shallow-water, marginal sea. There, most large, tropical taxa, which lived at depths greater than 200 m, were excluded by shallow-water depth, and salinity and oxygen fluctuations, that also excluded many other taxa (Keller, 1989a). In contrast, in the deeper Tethyan continental-shelf environment of El Kef, Tunisia, most large, complex tropical forms are present. Those taxa, however, gradually disappeared below the K/T boundary as the cosmopolitan survivor group increased significantly in relative abundance (Keller, 1988), indicating deteriorating environmental conditions beginning well before the K/T boundary event.

The present quantitative planktic foraminiferal data set implies that environmental conditions in the tropics gradually became detrimental to specialized, large, complex forms some time before the K/T boundary, permitting dominance of small unspecialized cosmopolitan taxa (see MacLeod and Keller, in press). At or near the K/T boundary, the surviving specialized tropical and subtropical taxa disappeared, apparently due to a major drop in surface productivity as inferred from the δ^{13} C shift of about 3 permil and the elimination of a surface-to-deep carbon-13 gradient (Zachos and Arthur, 1986; Zachos and others, 1989; Keller and Lindinger, 1989). Only small unspecialized cosmopolitan taxa survived this event. In the high latitudes (including the Antarctic; Keller, 1993), where cosmopolitan taxa dominated during the latest Maastrichtian, the K/T boundary event does not appear to have had any immediate detrimental consequences (see also Zinsmeister and others, 1989; Askins, 1992). Consequently, environmental effects of the K/T boundary event were most severe in the low latitudes and diminished into high latitudes. [Note that of the Antarctic Ocean ODP Sites, only Site 738 has a continuous K/T boundary record, whereas Site 690 (Stott and Kennett, 1990a, 1990b) and Site 750 (Zachos and others, 1992) have hiatuses with Zones P0 and P1a missing (see Keller, 1993; E. Barrera and G. Keller, unpub. data).] Already stressed tropical environments such as Brazos, however, were not affected because specialized taxa had been eliminated at an earlier time. This interpretation is supported by stable-isotope data (discussed below) which indicate that the negative $\delta^{13}C$ shift and decrease in the surface-to-deep gradient of the low latitudes is negligible or even absent in the high latitudes.

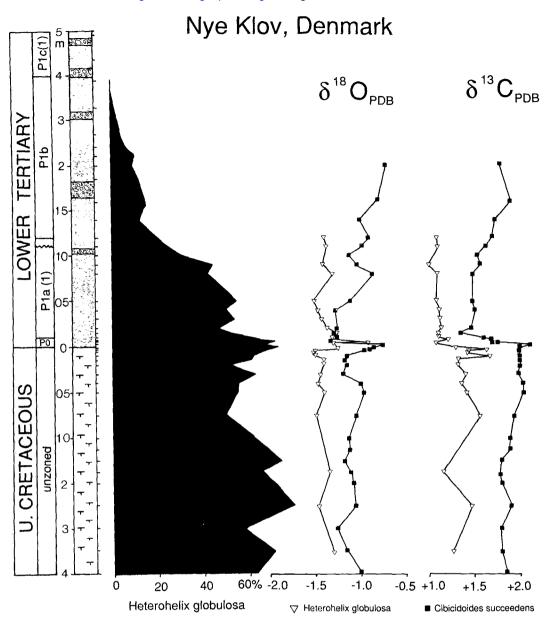


Figure 5. Carbon- and oxygen-isotope values of the planktic foraminifer H. globulosa and benthic foraminifer Cibicidoides succeedens and the relative abundance of H. globulosa. Note the reduced magnitude of the $\delta^{13}C$ shift (0.5%) at Nye Klov as compared with Brazos (3.0‰), the absence of a reduced surface to deep gradient, and the similarity in the relative abundance distribution of the Cretaceous survivor species H. globulosa.

PRE-K/T BOUNDARY FAUNAL AND ENVIRONMENTAL CHANGES

Recent sequence stratigraphic studies (Haq and others, 1987; Hallam, 1989; Donovan and others, 1988) have shown that the uppermost Cretaceous drop in sea level culminated just before the K/T boundary and was followed by a sea-level rise that may have amounted to as much as 130 m. The early Tertiary sea-level rise has been documented by sequence stratigraphic studies as well as paleoecological analyses (Vail and others, 1977; Haq and others, 1987; Hancock and Kauffman, 1979; Matsumoto, 1980; Weimer, 1984; Schmitz and others, 1992; MacLeod and Keller, 1991a, 1991b). These studies indicate that the long-term transgressive cycle, which extended throughout early Paleocene time, was interrupted during the early Danian by at least two short-term sea-level lowstands. The first of these short-term lowstands culminated near the P0/P1a boundary. and the second probably reached its maximum in the upper part of Zone P1a. The intervals of time that appear to be missing in most early Tertiary sequences correspond to this lower Paleocene interval of protracted sea-level instability (Keller, 1989a, 1993; Canudo and others, 1991; Keller and Benjamini, 1991; MacLeod and Keller, 1991a, 1991b). In the Stevns Klint section, we have documented this long-term sea-level instability based on stable isotopes as well as planktic and benthic foraminiferal analyses (Schmitz and others, 1992). Here we document these environmental changes at the more complete Nye Klov section based on stable isotopes and planktic foraminiferal analyses.

Evidence for Latest Maastrichtian Sea-Level Lowstand

There is evidence of two major environmental changes at Nye Klov. First, a faunal change, at 2.5 m to 3.0 m below the K/T boundary at Nye Klov as well as at Stevns Klint (Schmitz and others, 1992), marks a sealevel lowstand. Second, a faunal event marks a sea-level rise beginning just below and continuing across the K/T boundary. The faunal

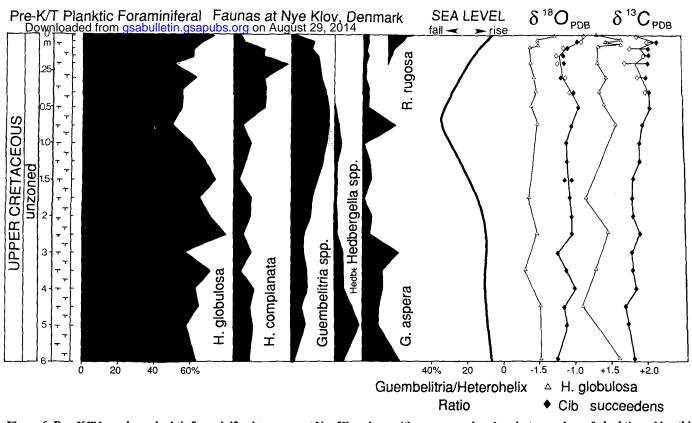


Figure 6. Pre-K/T boundary planktic foraminiferal turnover at Nye Klov along with oxygen- and carbon-isotope values of planktic and benthic foraminifera and relative changes in sea level.

and isotopic variations associated with this environmental change are part of the K/T transition event.

Latest Maastrichtian planktic foraminiferal faunas at Nye Klov are illustrated, along with stable-isotope measurements of benthic and planktic foraminifera, in Figure 6. A low-diversity fauna consisting of a few cosmopolitan taxa of the genera *Heterohelix*, *Hedbergella*, *Globigerinelloides*, and *Guembelitria* dominates. Relative abundances change between 2.5 m and 3.0 m below the K/T boundary with the decline of *G. aspera* and *Hedbergella* spp. and concurrent rise in *Guembelitria* spp. This faunal change indicates a sea-level lowstand for the following reasons.

Planktic foraminifera live primarily in the upper 200–300 m of the water column. Within this interval, they are depth stratified as shown by stable-isotope ranking of individual species (Douglas and Savin, 1978; Boersma and Shackleton, 1981; Stott and Kennett, 1990a; Keller, 1985). In the Cretaceous ocean, large taxa (globotruncanids, planoglobulinids, pseudotextularids) generally lived in deeper waters, whereas small taxa (heterohelicids, guembelitrids, hedbergellids, globigerinelloids) generally lived in the upper 100–200 m of the water column. Depth stratification excluded deeper-water taxa from shallow-water, continental-shelf regions. At Nye Klov, as well as at Stevns Klint, the deeper-dwelling Maastrichtian index taxa *Abathomphalus mayaroensis* is absent, and *Pseudotextularia deformis* and *P. elegans* are extremely rare in the shallow-water environment (<200 m) of the Danish basin at this time.

Among the shallow-water taxa, Guembelitria (trifolia, cretacea) species are consistently the isotopically lightest group and are inferred to live closest to the ocean surface. Moreover, those species are known to dominate nearshore or shallow continental shelves or basins, and they are nearly absent in the open ocean (Sliter, 1972; McGowran and Beecroft, 1985; Keller, 1988, 1989a, 1989b; Kroon and Nederbragt, 1990; D'Hondt and Keller, 1991). Hedbergellids and globigerinelloids, isotopically heavier than guembelitrids and heterohelicids, seem to occupy deeper waters. The increased abundance of Guembelitria spp. beginning 2.5 m to 3.0 m below the K/T boundary at Nye Klov and Stevns Klint (Schmitz and others, 1992), and the decreased abundance of deeper-dwelling species (*G. aspera, Hedbergella* spp.) therefore suggest shallowing of the Danish basin at this time. The shallowing indicated by these planktic foraminifera is also supported by benthic foraminifers at Stevns Klint, where a shallowing from outer to mid-shelf depth is indicated (Schmitz and others, 1992).

Heterohelix globulosa is generally most abundant in continental-shelf regions and decreases in open-marine environments (Sliter, 1972; Keller, 1988, 1989a; D'Hondt and Keller, 1991). Being isotopically heavier than Guembelitria, but lighter than globigerinelloids or hedbergellids, it is inferred to occupy water depths between those groups (Stott and Kennett, 1990a; E. Barrera and G. Keller, 1990 and unpub. data). The temporary decrease in abundance of H. globulosa coincident with maximum Guembelitria abundances at Nye Klov and Stevns Klint also suggests a shallowing environment. These paleobathymetric changes can be summarized by values of the Guembelitria/Heterohelix (surface/subsurface) ratio (Fig. 6). High values of this ratio indicate shallower conditions, whereas low values indicate deeper water. This paleobathymetric index indicates

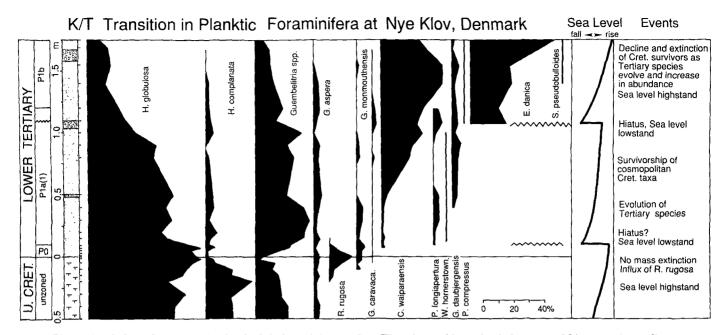


Figure 7. K/T boundary transition in planktic foraminifera at Nye Klov along with sea-level changes and hiatuses (zig-zag lines).

that a maximum sea-level lowstand occurred about 1 m below the K/T boundary at Nye Klov. At Stevns Klint, where benthic foraminifera support the planktic foraminiferal depth index, the sea-level lowstand reached its maximum between 1 m and 2.5 m below the K/T boundary (Schmitz and others, 1992). Stable-isotope values in both planktic and benthic foraminifers remained virtually unchanged (Fig. 6), implying that this sealevel lowstand was not accompanied by any significant temperature or productivity changes.

K/T BOUNDARY TRANSITION

Evidence for Sea-Level Highstand

The Guembelitria/Heterohelix paleobathymetric index ratio indicates that sea level rapidly rose following the latest Maastrichtian lowstand (Fig. 6). This is evident in the decreasing abundance of Guembelitria spp. and increased abundance of H. globulosa. A sealevel rise at this time is also supported by the sudden influx of Rugoglobigerina rugosa. Rugoglobigerinids are open-ocean, surface dwellers (Boersma and Shackleton, 1981; Barrera and Huber, 1990; Schmitz and others, 1992). Their sudden influx into the Danish basin at 20 cm below the K/T boundary indicates a sea-level transgression. Planktic foraminiferal assemblages illustrated in Figure 7 indicate that sea level continued to rise across the K/T boundary and into the earliest Tertiary Zone P0. Rising sea level is suggested by the continued presence of R. rugosa, decreased abundance of the shallow-water Guembelitria spp., and increased abundance of H. globulosa. Deposition of the boundary clay (fish clay) occurred during a sea-level highstand as earlier reported by Ekdale and Bromley (1984). A rapid rise in the sea level across the K/T boundary was also observed in Spain (Canudo and others, 1991) and El Kef, Tunisia (Peypouquet and others, 1987; Brinkhuis and Zachariasse, 1988). It is difficult to determine, however, when the sealevel rise ended because a hiatus which marks the top of the fish clay at Stevns Klint (Schmitz and others, 1992) may also be present at Nye Klov. It is reasonable to assume that this hiatus marks erosion associated with the sea-level lowstand that followed the K/T boundary transgression. Evidence for a hiatus and sea-level lowstand at the P0/ P1a boundary is widespread: the eastern Tethys (Keller and others, 1991; Keller and Benjamini, 1991), Spain (Canudo and others, 1991), U.S. Gulf Coast (Donovan and others, 1988; Olsson and Liu, 1992), Antarctic Indian Ocean Site 738C (Keller, 1993), and numerous deep-sea sections (MacLeod and Keller, 1991a, 1991b).

δ¹³C Record of Foraminifera

In an effort to determine the environmental conditions accompanying the sea-level transgression across the K/T boundary, we have measured the isotopic values of R. rugosa, H. globulosa, and one benthic foraminifer (C. succeedens) at Nye Klov and Stevns Klint (Figs. 8, 9). At Stevns Klint, δ^{13} C values of benthic foraminifera become 0.3 permil heavier coincident with the sea-level rise. In the K/T boundary fish clay, there is a negative shift of about 1.0 permil. δ^{13} C values of surface-water dwellers R. rugosa and H. globulosa remain nearly the same during the pre-K/T boundary sea-level rise. No data are available for planktic foraminifera in the fish clay because of carbonate dissolution and a hiatus which removed Zones P0 and P1a at Stevns Klint. A more complete K/T boundary transition is present at Nye Kloy (Fig. 9). where benthic foraminifera indicate a paleodepth of 100-200 m during the earliest Tertiary. There, a negative δ^{13} C shift of 0.5 to 0.6 permil occurs in both benthic (C. succeedens) and planktic (H. globulosa) foraminifera, and the surface to bottom gradient remains nearly constant. The $\delta^{13}C$ shift, however, which generally begins at the K/T boundary, as also shown here in benthic foraminifera, seems to have started 5 cm below the K/T boundary with H. globulosa. In contrast, δ^{13} C values of the surface dweller R. rugosa remain stable and increase slightly across the K/T boundary. A negative δ^{13} C shift may be suggested by the last occurrence of this species in Zone P0. Generally, δ^{13} C shifts have been observed only in planktic foraminifera. The presence of this shift in both planktic and benthic foraminifera at Nye Klov, as well as

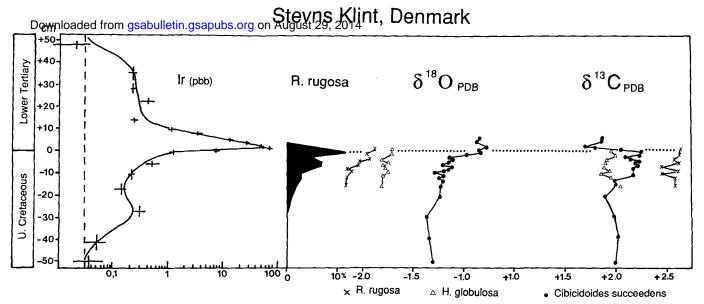


Figure 8. Iridium-, oxygen-, and carbon-isotope values of planktic and benthic foraminifera and relative abundance of *Rugoglobigerina rugosa* across the K/T boundary at Stevns Klint (data from Rocchia and others, 1984; Schmitz and others, 1992). Note the cooling observed in planktic and benthic foraminifera beginning below the K/T boundary.

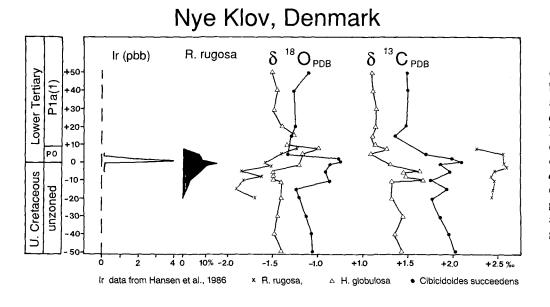


Figure 9. Iridium-, oxygen-, and carbon-isotope values of planktic and benthic foraminifera and relative abundance of *Rugoglobigerina rug-osa* across the K/T boundary at Nye Klov. (Ir data from Hansen and others, 1986). Note the delayed cooling observed in surface waters (*R. rug-osa, H. globulosa*) as compared to deeper waters (*C. succeedens*), the gradual δ^{13} C shift into Zone P0, and absence of reduced surface-to-deep gradient.

Brazos (Fig. 4), seems to be related to the shallow depositional environment (within the photic zone) of these sections.

We interpret the heavier δ^{13} C values prior to the K/T boundary fish clay in the Stevns Klint benthic foraminifera and Nye Klov planktic foraminifera as indicative of increased organic matter at thermoclinal depth and on the sea floor. This may have been due to low-oxygen conditions associated with the sea-level rise. The 0.5 to 1.0 permil negative shift beginning near the K/T boundary and in the fish clay is correlative with the K/T boundary δ^{13} C shift observed in low-latitude sections (Zachos and Arthur, 1986; Zachos and others, 1989; Keller and Lindinger, 1989), including Brazos, Texas (Fig. 4). In low latitudes, however, this negative δ^{13} C shift in surface waters is about 3.0 permil, or several times larger than in the high-latitude Danish sections (Keller and Lindinger, 1989; Barrera and Keller, 1990; Schmitz and others, 1992). The δ^{13} C shift, associated with the elimination of the surface to deep gradient in low latitudes, is generally interpreted as the near shut-off of surface-water productivity in the marine realm (Zachos and Arthur, 1986; Zachos and others, 1989). Our data from Nye Klov and Stevns Klint indicate that this near shut-off in surface productivity did not occur in northern high latitudes. There, the decrease in surface productivity was minimal, and the surface-to-deep gradient remained nearly the same. Moreover, there is no evidence of a δ^{13} C shift in the Antarctic Indian Ocean ODP Site 738C, but rather a slight increase in δ^{13} C values of fine fraction and bulk carbonates (Thierstein and others, 1991; E. Barrera and G. Keller, unpub. data). [The δ^{13} C shift identified as K/T boundary at Site 690 (Stott and Kennett, 1989, 1990a) and Site 750 (Zachos and others, 1992) actually oc-

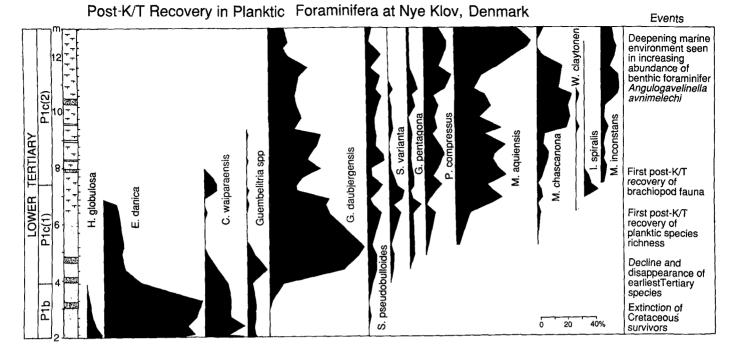


Figure 10. Post-K/T recovery in planktic foraminifera at Nye Klov, Denmark. Note that the extinction of Cretaceous cosmopolitan taxa coincides with the resumption of carbonate sedimentation and the first post-K/T radiation in planktic foraminifera about 300,000 to 350,000 yr after the K/T boundary.

curred in Zone P1b (with Zones P0 and P1a missing, E. Barrera and G. Keller, unpub. data).] These isotopic data imply that the tropics were most severely affected by the K/T boundary δ^{13} C event and that the effect was greatly diminished or even absent in high latitudes.

Another very surprising difference in $\delta^{13}C$ values between high and low latitudes is the inverted δ^{13} C gradient in high latitudes (Figs. 8, 9). Planktic foraminifera, living in surfacewater habitats, are expected to have higher δ^{13} C values relative to benthic foraminifera. This is not the case at Nye Kloy, Stevns Klint (Figs. 8, 9), or Antarctic Ocean Site 738 (E. Barrera and G. Keller, unpub. data), where biserial and triserial planktic foraminifera (H. globulosa, C. waiparaensis, Guembelitria danica), which live at thermoclinal depths, show consistently lighter δ^{13} C values relative to the benthic foraminifer C. succeedens. Only the near-surface dweller R. rugosa shows the expected heavier values (Figs. 8, 9). The consistency of this inverted δ^{13} C gradient for biserial taxa in three high-latitude sections, but absence at Brazos, Texas (Fig. 4), suggest that it is not due to a vital effect. Our data suggest that biserial taxa (and the triserial Guembelitria danica) seem to have lived in the oxygen minimum zone where δ^{13} C values may be more negative than

on the sea floor. Although Boersma and Premoli-Silva (1988) earlier suggested that biserial taxa may be oxygen minimum zone dwellers, this is the first stable isotopic evidence to that effect. These data imply that a strong oxygen minimum zone was present at K/Tboundary time in high latitudes, where, in contrast to low latitudes, surface productivity remained high.

δ¹⁸O Record of Foraminifera

 δ^{18} O measurements of planktic and benthic foraminifera indicate temperature changes associated with the sea-level rise and the K/T boundary event. At Stevns Klint and Nye Klov, benthic δ^{18} O values increased about 0.5 permil beginning about 10 cm below the K/T boundary and remained high during deposition of the fish clay (Zone P0); whereas planktic values increased beginning about 3 to 5 cm below the K/T boundary. After the K/T boundary, from the top of Zone P0 to the base of Subzone P1a(1) at Nye Klov, planktic and benthic measurements temporarily reach the same level. Thereafter, benthic and planktic δ^{18} O values diverge, with planktic values increasing to pre-K/T boundary levels (Fig. 9). These stable isotopic values are not an artifact of bioturbation, as indicated by 1-cm interval sample analyses for the 15 cm preceding the K/T boundary at Stevns Klint which show a consistent trend (Schmitz and others, 1992).

We interpret the 0.5 permil heavier benthic δ^{18} O values, beginning prior to the K/T boundary and continuing across the fish clay, as cooling of about 2 °C in the bottom water of the Danish basin. Cooling of surface water was somewhat delayed. This relation may imply an influx of cooler, deeper waters with the sea-level rise beginning prior to the K/T boundary. During deposition of the fish clay, both surface and deep-water temperatures remained cool. The convergence of benthic and planktic values in Zone P0 may indicate the absence of thermal stratification in the Danish basin. This interval also coincides with nondeposition or a short hiatus at Nye Klov, a major hiatus at Stevns Klint, and a sea-level lowstand. Divergence of benthic and planktic foraminifers in P1a(1) indicates that thermal stratification had resumed (Fig. 9).

POST-K/T ENVIRONMENTAL CHANGES

The faunal record of Nye Klov (Fig. 7) suggests that sea levels remained relatively low during early Tertiary Zone P1a, as indicated by high abundances of *Guembelitria* spp. The faunal assemblages are still dominated by

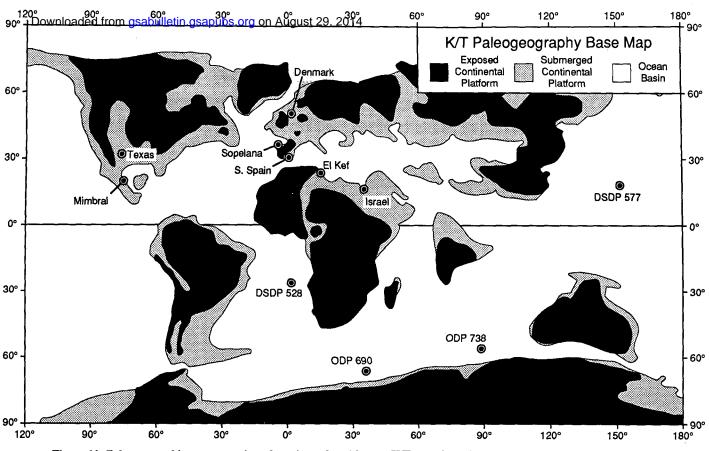


Figure 11. Paleogeographic reconstruction of continental positions at K/T boundary time and localities of sections studied.

Cretaceous survivors, and numerical abundances of evolving new Tertiary species are correspondingly low. A hiatus marked by the sudden and abundant (22%) first appearance of Eoglobigerina danica occurs near the top of Subzone P1a(1) (1.1 m; Fig. 7). The upper Subzone P1a(2) is missing at this hiatus. A short hiatus is also present at this interval at Brazos, Texas (Keller, 1989a), the eastern Tethys (Keller and others, 1990; Keller and Benjamini, 1991), and Antarctic Indian Ocean Site 738C (Keller, 1993). Benthic foraminiferal data suggest that this hiatus marks another global sea-level lowstand associated with widespread erosion (Keller, 1992; Mac-Leod and Keller, 1991a, 1991b).

After the Zone P1a/P1b hiatus, a deepening marine environment is indicated at Nye Klov by the decreasing abundance of shallowwater *Guembelitria* spp. At the same time, the biserial species *Chiloguembelina waiparaensis*, which may be tolerant of lowoxygen conditions, began to dominate the faunal assemblages in the subsurface environment. *Eoglobigerina danica* dominated as *C. waiparaensis* declined in the upper part of Zone P1b. Stable-isotope values of planktic and benthic foraminifera continued to diverge (Fig. 9), suggesting increased thermal stratification. All Cretaceous survivor taxa decreased in abundance and disappeared by the end of Zone P1b, or about 300,000 yr after the K/T boundary.

Post-K/T Boundary Recovery

The first post-K/T boundary recovery in planktic foraminifera at Nye Klov occurred in Subzone P1c(1) or about 300,000 to 350,000 yr after the K/T boundary (Keller, 1988, 1989a, 1989b). Figure 10 shows that this recovery is associated with the decline and disappearance of the earliest Tertiary species, including chiloguembelinids, guembelitrids and eoglobigerinids, and the extinction of the remaining Cretaceous survivors. Characteristic of this recovery is the expansion of species populations, which first evolved in Zone P1a, and the rapid evolution of new species. Rather surprisingly, this evolving fauna appears to be more diverse in high northern and southern latitudes (Keller, 1993) than in the tropical and subtropical ocean. For instance, species evolving at this time in high latitudes include Murciglobigerina aquiensis, M. chascanona, and Igorina spiralis (Fig. 10). Those species are not present in low latitudes until much later in Paleocene time. In contrast, virtually all low-latitude taxa are present in high latitudes. This suggests a more favorable environment for speciation at high latitudes at this time, followed later by species migration into low latitudes, as discussed below.

There are some tantalizing similarities in the environmental indicators associated with this first post-K/T boundary recovery of planktic foraminifera. In both low and high latitudes, high carbonate sedimentation resumed for the first time in Zones P1c after the K/T boundary (Keller, 1988, 1993; Keller and others, 1990). At Nye Klov, bryozoan chalk deposition resumed between 6 m and 7 m and coincided with the first post-K/T boundary recovery of brachiopod faunas (Surlyk and Johanson, 1984; Surlyk, 1990). At Site 738 in the Antarctic Ocean, chalk sedimentation also resumed in Zone P1c after an interval of laminated clay sedimentation in Zones P0 and P1a (Keller, 1993). At El Kef and the eastern Tethys, δ^{13} C values returned to nearly pre-

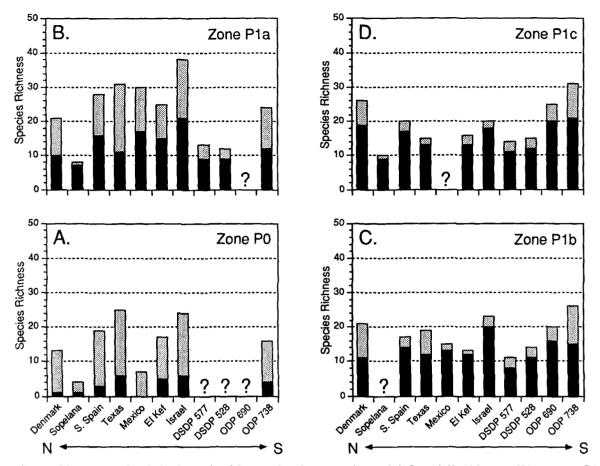


Figure 12. Geographic patterns of variation in species richness values for composite planktic foraminiferal faunas of biozones P0, P1a, P1b, and P1c. Localities are arrayed along a north-south transect. Black pattern marks Tertiary species; stipple pattern marks Cretaceous survivor species. Question marks indicate that biozone is missing in that particular region (from MacLeod and Keller, in press).

K/T values in Zone P1c (Keller and Lindinger, 1989; Magaritz and others, 1992), indicating recovery of the marine environment. A generally deepening ocean in the Tethys region is associated with this recovery (Keller and Benjamini, 1991; Keller, 1992). In the Danish Basin, at Nye Klov, a deepening marine environment is also indicated by increasing abundance of the upper-slope to outershelf benthic foraminifer *Angulogavelinella avnimelechi*, suggesting a paleodepth of >200 m. We still do not understand either the long delay of this post-K/T recovery or the reason for the recovery.

HIGH LATITUDES MORE FAVORABLE FOR SPECIATION?

A survey of species richness (number of species present) in the early Tertiary Zones P0 to P1c in 11 localities and 19 sections, spanning from the northern boreal sea to the Antarctic Ocean (Fig. 11), provides strong evidence for an inverse trend in species richness in high latitudes (MacLeod and Keller, in press). Instead of lower species richness, as generally expected for high latitudes, species richness increases, indicating a more favorable environment beginning in Zone P1b. These unexpected results are tabulated in Figure 12. Note that both evolving new species (black) and Cretaceous survivors (shaded) are tabulated. This inverse species richness trend is present in Zone P1c even if Cretaceous survivor taxa are excluded. Multiple investigator bias does not account for this inverse trend, because all localities were studied by the same investigators using the same species concepts.

The basal Tertiary Zone P0 (Fig. 12A) shows relatively high species richness in low latitudes (question marks indicate localities where this zone is missing). The majority of taxa present are Cretaceous survivors. In Zone P1a, species richness remains strong in low latitudes with the evolution of many new species (Fig. 12B). There is little change in the Cretaceous survivor group. Although not evident in the species richness pattern, faunal differences between high and low latitudes begin in Zone P1a with the evolution of highlatitude species Eoglobigerina danica and Chiloguembelina waiparaensis (Fig. 2). In Zone P1b, species richness declines in low latitudes (except for Israel) due to the extinction of some Tertiary species as well as the extinction of nearly all Cretaceous survivors (Fig. 12C). Most Cretaceous survivor taxa continue in high latitudes. The anomalously high species richness in Israel at this time is due to diachronous extinction of several taxa (E. fringa, E. edita, G. conusa, G. taurica; Keller and Benjamini, 1991). In Zone P1c, the inverse species richness trend is established with significantly higher numbers of species in the northern boreal seas (Denmark) and the Antarctic Ocean (Sites 690, 738; Fig. 12D). Increased species diversity in high latitudes at this time is due to both the continued survival of Cretaceous taxa and the evolution of new species (Igorina spiralis, Murciglobigerina aquiensis, M. chascanona, Globoconusa ex-

tensa) which do pot appear in low latitudes until the late Paleocene (Keller, 1988, 1989a, and 1993; Canudo and others, 1991; Keller and Benjamini, 1991).

These data strongly suggest that during early Tertiary time, high-latitude regions acted as centers of origin and dispersal for planktic foraminifera. How long this inverse trend continued is unclear due to a lack of comparable data for the late Paleocene. Environmental conditions that fostered this trend remain enigmatic. Stable isotopic data indicate that the major difference between high and low latitudes is in surface productivity. It is well known that surface productivity dropped significantly in low latitudes beginning at the K/T boundary and did not recover until 350 to 500 kyr later (Zones P1c to P1d; Zachos and Arthur, 1986; Zachos and others, 1989; Keller and Lindinger, 1989). Less well known is the fact that surface productivity remained nearly constant in high latitudes as discussed above for the Danish sections and by E. Barrera and G. Keller (unpub. data) for the Antarctic sections. It is likely that these favorable surface-water productivity conditions temporarily shifted the center of speciation and dispersal to high latitudes.

CONCLUSIONS

Our planktic foraminiferal and stable isotopic analyses of the K/T transition at Nye Klov and comparison with K/T boundary sections worldwide lead us to the following conclusions.

1. Long-term oceanic instability evident in sea-level fluctuations characterizes the K/T transition beginning at least during the past 100,000 yr of the Cretaceous and continuing for about 300,000 yr into the Tertiary. A maximum sea-level lowstand is recorded in the Danish sections about 1 m to 2 m below the K/T boundary, as is a sea-level rise beginning 20 cm to 40 cm (or 5,000 to 10,000 yr) below the boundary. The fish clay was deposited during a sea-level highstand. Two hiatuses or periods of nondeposition mark sea-level lowstands at the top of Zones P0 and P1a about 50,000 yr and 230,000 yr after the K/T boundary, respectively. Thereafter, sea level rose, and normal marine conditions were re-established.

2. No sudden mass extinction occurred in planktic foraminifera at the K/T boundary at Nye Klov. Instead nearly all species survived and thrived well into the Tertiary, when they gradually disappeared. At high latitudes, only unspecialized small cosmopolitan Cretaceous species tolerant of environmental fluctuations were able to this of the disappeared in low latitudes were large specialized forms. This evidence suggests that the effects of the K/T boundary event may have been more severe in low latitudes. At Nye Klov, and Antarctic Ocean Site 738, extinction of Cretaceous species coincides with the re-establishment of normal marine conditions in low latitudes and the first post-K/T boundary recovery of the Tertiary fauna about 300,000 to 350,000 yr after events marking the boundary.

3. The δ^{13} C shift is largest in the tropics (3.0‰), greatly reduced (0.5‰-1.0‰) in the high-latitude Nye Klov and Stevns Klint sections, and absent in the Antarctic Ocean (E. Barrera and G. Keller, unpub. data). The surface-to-deep $\delta^{13}C$ gradient was temporarily eliminated in the tropics but remained virtually unchanged in high latitudes, indicating that surface productivity remained stable in high latitudes. These data indicate that the environmental effects of the K/T boundary event were strongest in the tropical and subtropical oceans and diminished into high latitudes.

4. Biserial planktic foraminifers Heterohelix globulosa and Chiloguembelina waiparaensis and triserial Guembelitria danica show an inverted $\delta^{13}C$ gradient in high latitudes with lower δ^{13} C values relative to benthic foraminifers. $\delta^{13}C$ values are generally more positive in the upper water column than on the sea floor, except in the oxygenminimum zone. We therefore interpret these data to imply that those biserial and triserial taxa are low-oxygen-tolerant forms and that their high abundance in high latitudes indicates the presence of a well-developed oxygen-minimum zone during the K/T boundary transition.

5. During the early Tertiary (Zone P1c), high-latitude regions temporarily acted as centers of origin and dispersal for planktic foraminifera. This conclusion is indicated by the higher species richness in both northern and southern high latitudes as compared to low latitudes, and it is apparently due to the longer survivorship of Cretaceous taxa as well as the early evolution of new taxa in high latitudes before migration to lower latitudes.

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