Palaeoenvironmental turnover across the Palaeocene/Eocene boundary at the Stratotype section in Dababiya (Egypt) based on benthic foraminifera

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ABSTRACT

The Global Stratotype Section and Point for the Palaeocene/Eocene (P/E) boundary was defined at Dababiya Quarry (Egypt) at the base of the carbon isotope excursion (CIE). We present the first detailed analysis of Palaeocene–Eocene benthic foraminifera from Dababiya, in order to infer the palaeoenvironmental turnover across the P/E boundary. At Dababiya, the CIE coincides with a major turnover in foraminiferal assemblages; the last occurrence of *Angulogavelinella avnimelechi*, at the base of the CIE, may be correlated to the main phase of extinction of deep-sea benthic foraminifera. Benthic foraminifera indicate that stressful conditions such as oxygen deficiency, carbonate dissolution, and changes in food supply, persisted at the sea floor over most of the CIE interval. The main phase of recovery of benthic foraminifera is recorded *c.* 250 cm above the P/E boundary, and it may be linked to increased productivity and oxygenation at the sea floor.

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Introduction

The Palaeocene/Eocene (P/E) boundary interval is marked by a negative shift in $\delta^{13}C$ values [commonly known as the carbon isotope excursion (CIE)] in carbonates in marine and continental sections. During this interval, one of the most abrupt global warming events in the Cenozoic occurred (Zachos *et al.*, 2001). A major faunal turnover, including a major extinction of deep-sea benthic foraminifera (e.g. Thomas, 1990, 2003), an acme of the tropical–subtropical planktic foraminiferal genus *Acarinina* (e.g. Arenillas and Molina, 1996; Kelly *et al.*, 1998), distinctive assemblages of calcareous nannoplankton (Aubry, 1995; Bralower, 2002), an acme of the dinoflagellate *Apectodinium* at middle and high latitudes (Crouch *et al.*, 2001), and the rapid radiation of mammals on land (Koch *et al.*, 1992), occurred during this warm period, which has been called the initial Eocene thermal maximum (IETM) or the Palaeocene–Eocene thermal maximum (PETM). Although the ultimate cause of the CIE is not well known, the dissociation of methane hydrates along the continental margins is a plausible

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hypothesis to account for the injection of ^{13}C-depleted carbon into the atmospheric and oceanic reservoirs (Dickens *et al.*, 1997). Deep-sea benthic foraminifera suffered major extinction at the time of the shift in $\delta^{13}C$ values in bulk carbonates, benthic and planktic foraminifera (Thomas, 2003), whereas benthic foraminifera from marginal and epicontinental basins show lesser extinction or temporary assemblage changes. Along the southern margin of Tethys (Egypt, Israel), the upwelling of low-oxygen intermediate water into the epicontinental basin led to increased biological productivity and anoxia at the sea floor before and during the IETM (Speijer and Schmitz, 1998; Speijer *et al.*, 2000; Speijer and Wagner, 2002). Low oxygen conditions during the IETM have also been documented in the northeastern Peri-Tethys (Gavrilov *et al.*, 2003).

The Global Stratotype Section and Point (GSSP) for the P/E boundary was defined at the Dababiya Quarry, in Egypt (Dupuis *et al.*, 2003). During the late Palaeocene and early Eocene this part of the Tethys was occupied by an epicontinental basin, deepening in a NNW direction from neritic to uppermost abyssal (Said, 1990; Speijer *et al.*, 2000). The lithology, mineralogy, carbon isotope stratigraphy, and planktic foraminiferal biostratigraphy of the Dababiya section were described by Dupuis *et al.* (2003) and

Berggren and Ouda (2003), but the benthic foraminifera have not been described in detail. We carried out the first detailed analysis of benthic foraminiferal assemblages across the Palaeocene–Eocene transition at Dababiya, in order to infer the palaeoenvironmental turnover, to document the extinction of benthic foraminifera in the type section, and to correlate the benthic foraminiferal turnover in that section to the extinction of benthic foraminifera in the deep sea.

Materials and methods

The GSSP of the P/E boundary is in eastern Egypt, and occurs in the Esna Shale Formation in Dababiya Quarry, 35 km south of Luxor (Dupuis *et al.*, 2003). The 130-m-thick Esna Formation consists of monotonous grey to brown-green marls and shales with abundant and generally well-preserved microfossils. The GSSP is in the lower part of the Esna Formation, at the contact between the marly Esna 1 and Esna 2 Units. The latter unit contains a succession of five beds that were formally described and named 'Dababiya Quarry Beds 1–5' (Dupuis *et al.*, 2003). The CIE (as recognized in bulk organic matter) occurs within the Dababiya Quarry Beds (DQBeds), which contain phosphatic dissolution levels in which calcareous foraminifera are almost absent (Figs 1 and 2). The P/E boundary has been placed at
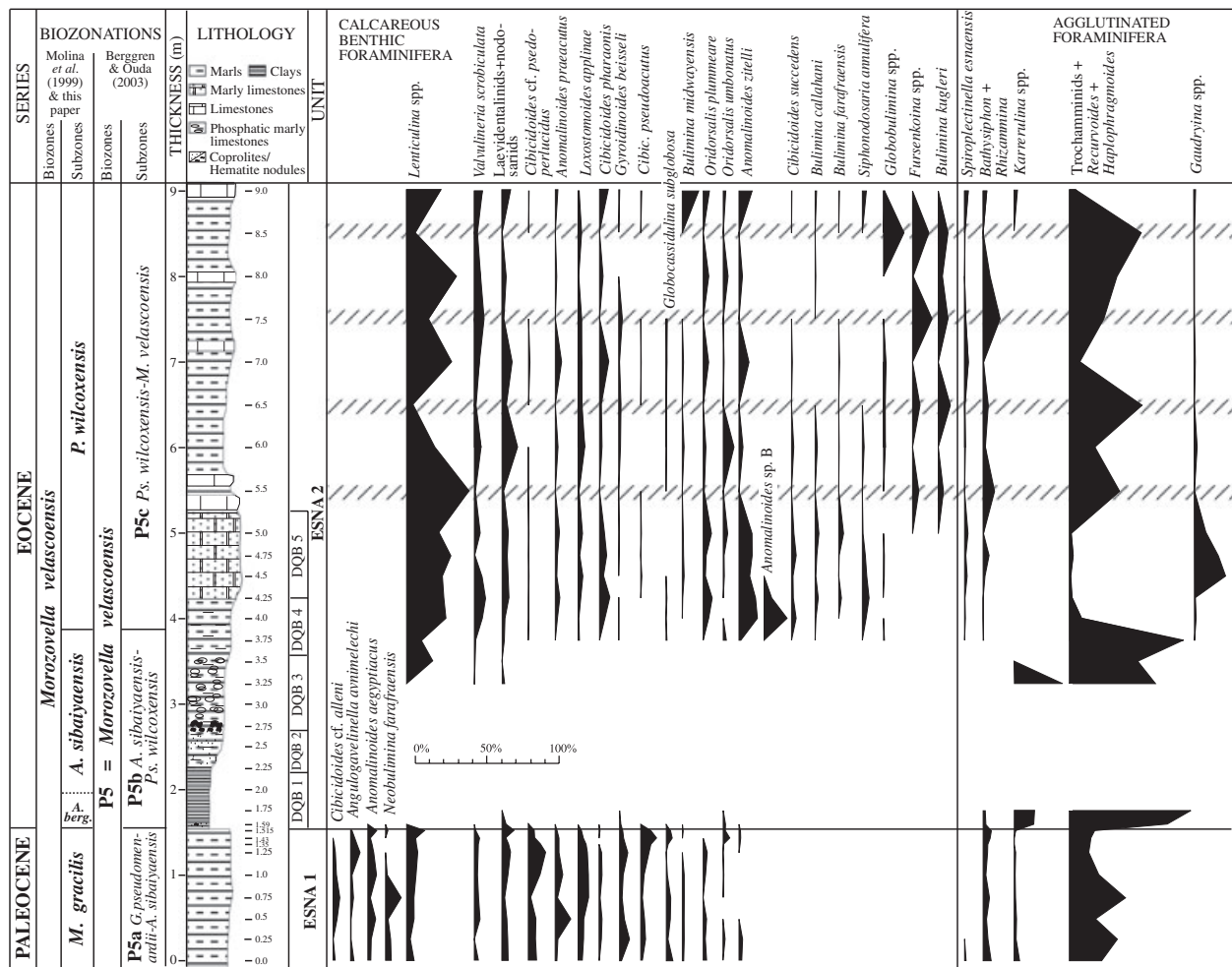
Fig. 1 Benthic foraminiferal turnover across the Palaeocene/Eocene boundary at Dababiya section. The dashed areas in the lower Eocene correspond to the levels with abundant pyritized foraminifera. Species that make up 4–9% of the assemblages in at least one sample have been considered as 'common taxa'. A. berg. = A. berggreni Subzone.

the base of the CIE, at the contact between the marly Esna 1 Unit and the dark, laminated non-calcareous clayey DQB 1 (Dupuis *et al.*, 2003).

We studied 32 samples from the upper 1.57 m of Unit Esna 1 (Palaeocene) and the lower 7.5 m of Unit Esna 2 (Eocene) in subsection (DBH) where the GSSP was formally defined. The DBH subsection spans the middle part of the planktic foraminiferal *Morozovella velascoensis* Zone (Zone P5).

In order to avoid the loss of small taxa, quantitative studies were based on representative splits of about 300 specimens of benthic foraminifera larger than 63 μm (Table 1). Benthic foraminiferal morphotype analysis (Table 2), and changes in the abun-dance of selected taxa and in genus richness allowed us to infer probable microhabitat preferences and environmental parameters (e.g. Bernhard, 1986; Jorissen *et al.*, 1995). The Fisher-α diversity index and the H(S) Shannon–Weaver information function were calculated in order to document possible changes in diversity (Murray, 1991).

Palaeobathymetry

Benthic foraminiferal assemblages contain abundant representatives of the Midway-type fauna (Berggren and Aubert, 1975), such as *Angulogaveli-nella avnimelechi*, *Bulimina midwayen-sis*, *Cibicidoides* cf. *alleni*, *Cibicidoides succedens*, *Loxostomoides applinae*, *Osangularia plummerae* and *Siphogen-erinoides eleganta* (Fig. 1), as well as other taxa that were common at *c.* 150–200 m depth (e.g. *Bulimina cal-lahani*, *Bulimina farafraensis*, *Cibici-doides pharaonis*, *Cibicidoides pseudoperlucidus*, *Lenticulina* spp., *Oridorsalis plummerae*, *Spiroplectinel-la esnaensis*, *Valvulineria scrobiculata*; Speijer and Schmitz, 1998). The upper-depth limit of species such as *Bulimina midwayensis*, *Cibicidoides* cf. *alleni* and *Osangularia plummerae*, is located at middle sublitoral depths (50–100 m; Van Morkhoven *et al.*, 1986). These data suggest that upper Palaeocene and lower Eocene sediments from Dababiya were deposited in an outer shelf environment (*c.* 150–200 m depth), in agreement with Spei-
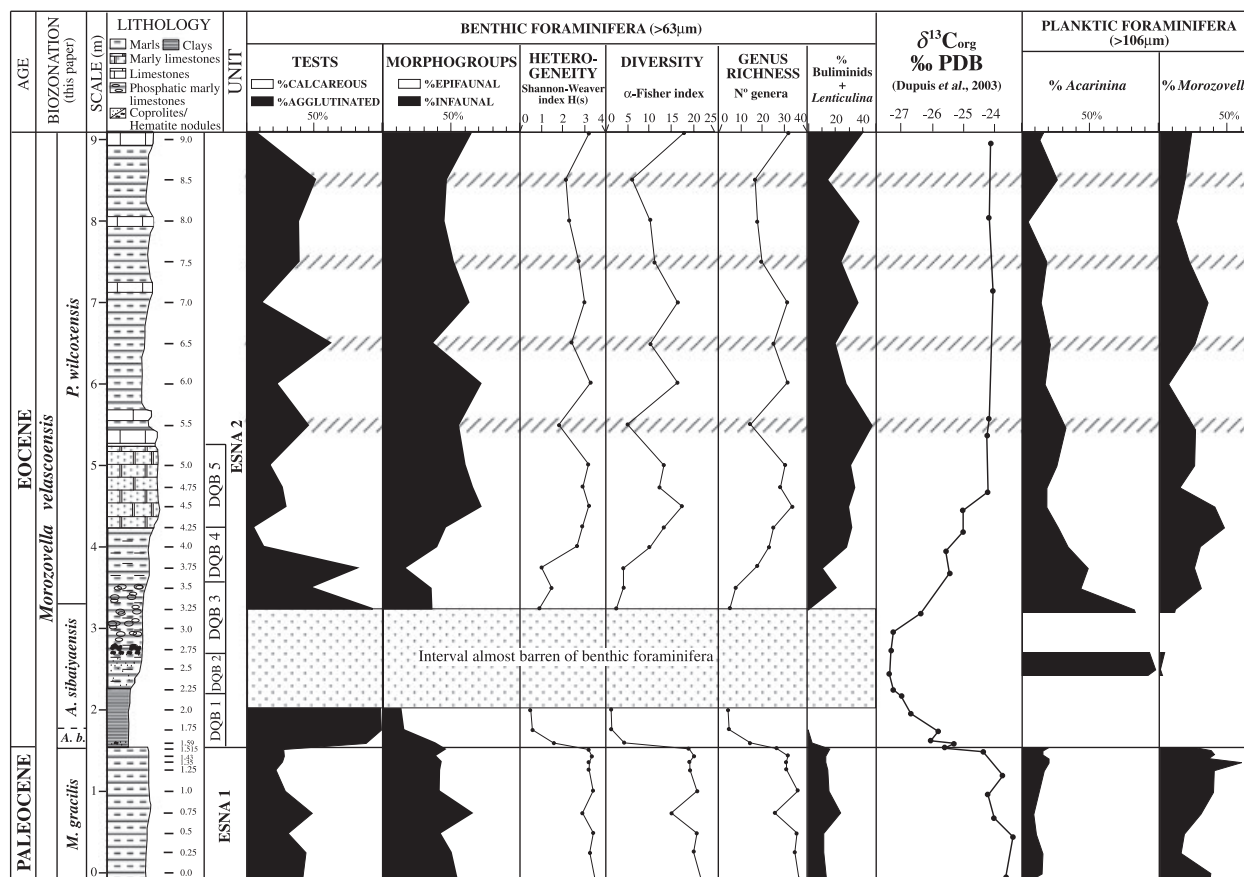
Fig. 2 Benthic foraminiferal indices, $\delta^{13}C$ values (Dupuis *et al.*, 2003) and percentages of the planktic foraminifera *Acarinina* and *Morozovella* across the Palaeocene/Eocene boundary at Dababiya section. *A. b.* = *A. berggreni* Subzone; CIE = carbon isotope excursion; IETM = initial Eocene thermal maximum.

jer *et al.* (2000) and Speijer and Wagner (2002).

Foraminiferal assemblages

Upper Palaeocene benthic foraminiferal assemblages from Dababiya (uppermost 1.57 m of Unit Esna 1) are diverse and heterogeneous (Fig. 2). Agglutinated foraminifera are minor components of the assemblages (20–47%). Among calcareous taxa, *Anomalinoides praeacutus*, *Cibicidoides pseudoacutus*, *Cibicidoides pseudoperlucidus*, laevidentalinids, *Lenticulina* and *Neobulimina farafraensis* are most abundant (Fig. 1). Assemblages consist of a mixture of infaunal (39–62%) and epifaunal morphogroups. Planktic foraminiferal assemblages from the *Morozovella gracilis* Subzones are diverse and rich in tropical–subtropical species.

The last occurrences of *Angulogavelinella avnimelechi*, *Anomalinoides aegyptiacus* and *Neobulimina farafraensis* occurred at the P/E boundary. The agglutinated trochamminids, *Karrerulina*, *Haplophragmoides* and *Recurvoides* increased in abundance, while the percentage of infaunal morphogroups, the genus richness, diversity and heterogeneity of the assemblages decreased at the base of the CIE-interval (base of DQB 1; Fig. 2). The relative abundance of trochamminids increased within this bed up to 85%. Planktic foraminifera are rare, and their assemblages have a low diversity.

Samples from the upper part of DQB 1, DQB 2 and lower half of DQB 3 are almost barren of benthic foraminifera, whereas planktic foraminifera are common in the upper part of DQB 2 and in the lowermost

part of DQB 3 (sample 2.5), where a peak in the abundance of the genus *Acarinina* has been identified (Fig. 2). Very few, probably reworked benthic foraminifera were found in DQB 2 and in most part of DQB 3, so that we could not make palaeoenvironmental inferences based on this group.

Samples from the upper half of DQB 3 and the lower half of DQB 4 contain more common benthic foraminifera. Assemblages are dominated by agglutinated taxa, mainly trochamminids and *Karrerulina* spp., but the calcareous taxa *Lenticulina* spp., *Anomalinoides* spp. and *Hemirobulina* spp. are also common. Diversity indices remain very low (Fig. 2). Acarininids dominate the planktic foraminiferal assemblages.

The abundance of benthic foraminifera, the percentage of infaunal morphogroups, the genus richness,

Table 1a Benthic foraminiferal species counts in upper Palaeocene samples from Dababiya. For considerations on relative abundance of branching foraminifera (e.g. *Bathysiphon*, *Rhizammina*), we divided the number of pieces by 4, considering that on average about four pieces are representative of one specimen.

	DBH 0	DBH 0.25	DBH 0.5	DBH 0.75	DBH 1	DBH 1.25	DBH 1.35	DBH 1.40	DBH 1.43	DBH 1.45	DBH 1.5	DBH 1.515
Ammobaculites sp.			1		1	1	1					
Ammodiscus spp.	3	4	6	2	2	4	3		1			3
Ammomarginulina sp.		2										
Bathysiphon spp.	12	6	4	8	3	5	4	32	4	1		9
Clavulinoides spp.	1											
Glomospirella spp.	2				2		1		2			
Haplophragmoides spp.	24	23	21	27	15	12	15	21	3	4	5	9
Hyperammina sp.				1								
Karrerulina horrida	4											
Karrerulina spp.	5	3	4	2	1	2	4	18		23	105	2
Marssonella oxycona						1						
Psammosphaera sp.					3							
Recurvoides spp.	14	28	10	49	12	3	6	38	9	8		6
Repmanina charoides	2	3	1		2		1		3			
Rhizammina spp.	3	3	2	5	1	2	3		5			3
Saccammina sp.	2	2	4	8		2	3		1			
Spiroplectammina spp.	1	1	1		3		4		2			
Spiroplectammina spectabilis	3	1	2			1						
Spiroplectinella esnaensis	1					1						
Subreophax sp.			2						1			1
Textularia spp.	2		2		2							
Trochamminids	15	42	26	39	23	20	22	38	17	5	95	26
Alabamina wilcoxensis	7	5	3	3	1		1		1			2
Angulogavelinella avnimelechi	5			7	3	20	17		7			2
Anomalinoides praeacutus	1	3	31	3	12	5	6		5			2
Anomalinoides aegyptiacus	3	5	17	5	15	8	9		2			14
Anomalinoides ammonoides	1		5	1	2	2	5		2			1
Anomalinoides midwayensis									2			
Anomalinoides rubiginosus		2			4		3		2			5
Anomalinoides zitteli	1	3						1	1			1
Anomalinoides spp.		2	6	2	4		6		2		1	4
Astacolus spp.		2	3		2		3					
Bulimina spp.		1				1						2
Bulimina midwayensis	1	2	2	3	2		2					1
Bulimina cf. *velascoensis*				1								
Cibicidoides cf. *hyphalus*				1								
Cibicidoides cf. *alleni*	2		5	13	5	3	5					
Cibicidoides cf. *dayi*				1								
Cibicidoides pharaonis		2	3	1	3	3	4					1
Cibicidoides pseudoacutus	1	9	7	2	7	16	10		20			18
Cibicidoides pseudoperlucidus	13	13	16	3	22	29	27	1	8			10
Cibicidoides proprius			7		2	4	3		3			4
Cibicidoides sp. A		1	1			2	1					2
Cibicidoides spp.	9	3	1	1	8	8	10	5	9			14
Coryphostoma spp.		1										
Coryphostoma cf. *midwayensis*			1									
Coryphostoma cf. *incrassata*					1							
Glandulina spp.	1		2			2	1					
Globobulimina spp.									1			1
Globocassidulina subglobosa	11	2	8	9	1				8			7
Guttulina spp.		1			1				1			
Globorotalites sp.				1								
Gyroidinoides beisseli	1	20	8	4	4	14	13		6			5
Gyroidinoides depressus	7	8	1	1	4	2	1		3			1
Gyroidinoides globosus		1		1	1		1					1
Gyroidinoides girardanus			2		1			1				1
Gyroidinoides spp.	1	13	2	1	1	3	4	1	3			
Laevidentalina spp.	11	12	8	5	10	15	18	4	4			21
Lagena spp.	2	3				5	6		1			2

Table 1a Continued

	DBH 0	DBH 0.25	DBH 0.5	DBH 0.75	DBH 1	DBH 1.25	DBH 1.35	DBH 1.40	DBH 1.43	DBH 1.45	DBH 1.5	DBH 1.515
Lenticulina spp.	12	7	15	15	16	20	18	7	13			29
Loxostomoides applinae	6	10	10	22	18	18	19		7			5
Neoflabellina sp.			1									
Nuttallides sp.												1
Nuttallinella spp.		3	1		2							
Oolina spp.			1			1	2		1			
Oridorsalis plummerae	5	4	7		5	7	6					
Oridorsalis umbonatus		2			1				8			3
Oridorsalis sp.	4			1	2	1	2					
Osangularia spp.	1											
Praebulimina sp.				1	1				1			
Praebulimina cf. *reussi*	4		1									
Neobulimina farafraensis	8	9	4	31	2							3
Praeglobobulimina sp.		1							1			
Praeglobobulimina quadrata					1							
Pullenia jarvisi		2				1	1		3			
Nonion havanense	1	1	5			2	2					
Ramulina globulifera	1		1		2							
Rotamorphina cushmani				1		2	1					
Saracenaria sp.					1	1	1					
Siphogenerinoides sp.		1										1
Siphogenerinoides cf. *eleganta*	3		3									
Stensioeina beccariiformis		1							1			
Stillostomella sp.	5	2	1	4	1	2	4		1			3
Valvalabamina lenticula	6	3	6	1	3	3	2		3			3
Valvulineria scrobiculata	3		10	8	4	5	4		5			1
Total	231	278	289	294	244	259	284	167	183	41	206	230

diversity and heterogeneity of the assemblages increase towards the upper part of the CIE interval (upper part of DQB4 and DQB5; Fig. 2), where assemblages are dominated by calcareous foraminifera (87–95%), mainly by *Lenticulina* spp.

The local first occurrence of several species is recorded in the upper part of the CIE-interval (Fig. 1). Samples from the upper part of DQB 4 towards the top of the section contain up to 28–38% of buliminids (e.g. *Bulimina midwayensis*, *B. farafraensis*, *B. callahani*, *Loxostomoides applinae*, *Stainforthia* spp.) and *Lenticulina* spp., as well as other calcareous taxa that are common to abundant. Genus richness, diversity and heterogeneity of the assemblages increase in this interval, but they do not reach the pre-CIE values (Fig. 2).

Above the DQBeds, four levels (samples 5.5, 6.5, 7.5 and 8.5) are rich in pyritized foraminifera, and contain abundant agglutinated taxa (e.g. *Haplophragmoides*, trochamminids) and abundant buliminids (*Bulimina kugleri*, *Fursenkoina* spp. and *Globobulimina* spp.).

Palaeoenvironmental inferences

Upper Palaeocene

Benthic foraminiferal assemblages are diverse and consist of mixed infaunal and epifaunal morphogroups, suggesting intermediate trophic levels during the latest Palaeocene at Dababiya. They contain abundant specimens with large and heavily calcified tests, such as *Cibicidoides pseudoacutus* and *Cibicidoides pseudoperlucidus*, indicating that oxygen levels were high, and that oxygen deficiency at the sea floor prior to the IETM was confined to the shallowest (middle shelf) part of the basin in the Upper Nile Valley (Speijer and Wagner, 2002; Ouda and Berggren, 2003).

CIE interval (lowermost Eocene)

Dupuis *et al.* (2003) reported the presence of *Angulogavelinella avnimelechi* within the CIE-interval (up to sample DBH 3.4), but they suggested that these specimens are reworked, and that the extinction of *A. avnimelechi* occurred at the base of the CIE-

interval, as in other neritic sections in this part of the Tethys (e.g. Speijer *et al.*, 1995). Therefore, the extinction of *A. avnimelechi* was coeval with the main phase of extinction of deep-sea benthic foraminifera, and the extinction of *Stensioeina beccariiformis* (Thomas, 1998).

Some of the species whose last occurrence coincides with the P/E boundary in the nearby Gebel Aweina section, such as *Anomalinoides midwayensis* (Speijer and Schmitz, 1998), also occur as rare, poorly preserved, probably reworked specimens within the DQBeds.

In the lowermost part of the CIE (lower part of DQB 1), the acme of agglutinated foraminifera and the absence of planktic foraminifera may have been caused by intense dissolution, which has been observed to occur at the beginning of the CIE-interval across the world (Ortiz, 1995; Thomas and Shackleton, 1996; Thomas, 1998). The absence of calcareous foraminifera not only at Dababiya but also at the nearby Qreiya section (Ouda and Berggren, 2003) may be related to the release of methane and

Table 1b Benthic foraminiferal species counts in lower Eocene samples from Dababiya. PYR = Pyritized tests. For considerations on relative abundance of branching foraminifera (e.g., *Bathysiphon*, *Rhizammina*), we divided the number of pieces by 4, considering that on average about four pieces are representative of one specimen.

	DBH 1.59	DBH 1.75	DBH 2	DBH 2.5	DBH 3.25	DBH 3.5	DBH 3.75	DBH 4	DBH 4.25	DBH 4.5	DBH 4.75	DBH 5	DBH 5.5	DBH 6	DBH 6.5	DBH 7	DBH 7.5	DBH 8	DBH 8.5	DBH 9
Ammodiscus spp.	1											1				1	2	2		10
Bathysiphon spp.	4		2			8	3						5	3	3	10	6			2
Bathysiphon spp. PYR						3								4	4	3				
Bolivinopsis sp.																				2
Clavulinoides spp.				7	3			1		1										3
Gaudryina cf. *ellisorae*				29				10	10	10		1	3	3		1				1
Gaudryina sp. A			3	27		3		12	12	12			2	2						
Gaudryina sp. juvenile			2	15				10	10					1	2					
Gaudryina spp.				13			1	24	12				1	1						
Glomospirella spp.	6					1		2								1				1
Haplophragmoides spp.		2				1		2				1	3	3						1
Karreriulina spp.	10	58	46	20				2			1									
Psammosphaera sp.						1		3						4	4					
Pseudoclavulina sp.								1												
Recurvoides spp.	5	4		6				3	2	1		27			11					9
Repmanina charoides						1						3	3							
Repmanina charoides PYR												2	2							
Rhizammina spp.				1							2	2			1	2				
Sigmoilopsis sp.					1															
Spiroplectammina spp.						2						2								
Spiroplectinella esnaensis	1		2	1		3		10	2	2	1	2	1		9	1	1		1	10
Subreophax sp.	1											1		1						
Trochamminids	40	340	265	36	243	28	22	5	2	4	30	26	112	13	11	39	88		6	
Trochamminids PYR					3	3					18	14		17		29	52			
Vulvulina mexicana				1			3	1	2	9	5			1			17			
Alabamina wilcoxensis						3	1	3		13	9				2					
Anomalinoides acutus				3				3		5			1							1
Anomalinoides praeacutus				5	10			4	2	5	12	6	2	15	1		2			7
Anomalinoides ammonoides								2			1	2	2	1						1
Anomalinoides midwayensis					1															
Anomalinoides rubiginosus								1	2		1		1							
Anomalinoides sp. A				2				6	1	2				3			1			4
Anomalinoides sp. B								55	17											
Anomalinoides zitteli			1	2		5	4	44	37	29	31	38	9		24		1	5		36
Anomalinoides spp.						3	1							1						3
Astacolus spp.																1				
Bandyella sp.													12							
Bulimina spp.															12					
Bulimina callahani				4				2				2	5	1			1	1	3	4
Bulimina farafraensis				1				7	6				1							2
Bulimina kugleri PYR								1		5	5			21		8	6			
Bulimina midwayensis								1	3	3	3	3	4		3	3	19		45

Table 1b Continued

	DBH 1.59	DBH 1.75	DBH 2	DBH 2.5	DBH 3.25	DBH 3.5	DBH 3.75	DBH 4	DBH 4.25	DBH 4.5	DBH 4.75	DBH 5	DBH 5.5	DBH 6	DBH 6.5	DBH 7	DBH 7.5	DBH 8	DBH 8.5	DBH 9
Bulimina tuxpamensis									1											
Cibicidoides decoratus									1											
Cibicidoides pharaonis		11	25	10	16	12		2				2	1	23		3				23
Cibicidoides pseudoacutus				3		2								1				2		2
Cibicidoides pseudoperlucidus	1	1	2	1				1			4		1							
Cibicidoides proprius	1		2	2	8								1							
Cibicidoides sp. A		6	7	7				2	4				3		1					3
Cibicidoides spp.	1	6	1	1		2		4	7				2		3	4				
Cibicidoides succedens		11	4	4		11		7				5	1		3		2			1
Coryphostoma spp.												1		1						
Chilostomella sp.															2		1			
Fursenkoina spp.						6					13		16	1		1	32			
Glandulina spp.												3								
Globobulimina spp.		2		2		2					3	4	4	6	3		40			3
Globocassidulina subglobosa		2	2			1						2	1	1	2					
Guttulina spp.					1						1		1	1						
Gyroidinoides beisseli	1		1		1	2					4	4	2	2	3					2
Gyroidinoides depressus					5	2					5	3	2		2					
Gyroidinoides girardanus			2													1				
Gyroidinoides spp.				2						2	2	1	2		2	3				
Laevidentalina colei				8	5	8					8	13	1	2			3			10
Laevidentalina spp.	2	1		1																
Lagena spp.		3		1						1		2	5				1			1
Lenticulina spp.	11	32	94	83	97	104	94	60			11	63	108	18	71	14		94		
Lenticulina spp. PYR														1	1	3				
Loxostomoides applinae	1	3	2	6	13	4	13	1			4	15	9	3	1	1	3			
Loxostomoides applinae PYR												3	3			7				
Hemirobulina pachygaster											1									
Hemirobulina sp.	6	3										4	3			1	1			1
Nodosaria longiscata	1	2	4	3	3	5		5			6	19	3	1	1					11
Nodosariids	2	2	11	6	4	5		4			7	7	5		2	3				3
Nonionella spp.	1										3		3	3		8				
Oridorsalis plummerae		13	20	6	6	7	24	1			6	6	13		13	8		17		
Oridorsalis umbonatus	2			3	3	2	13				24	24	2		2	7		7		
Oridorsalis sp.											2		2							
Osangularia plummerae		1	4	5	5	12	24				8	8	16		2	2		9		
Osangularia spp.	1																			
Pleurostomella sp.	1																	1		
Praebulimina sp.	1					1														
Praeglobobulimina quadrata											3									
Pullenia jarvisi																				
Pyramidulina latejugata-paupercula	1	4		2		1		3			2	5	1			1		4		3
Pyramidulina semispinosa				2							3	3	2		2					

Table 1b Continued

	DBH 1.59	DBH 1.75	DBH 2	DBH 2.5	DBH 3.25	DBH 3.5	DBH 3.75	DBH 4	DBH 4.25	DBH 4.5	DBH 4.75	DBH 5	DBH 5.5	DBH 6	DBH 6.5	DBH 7	DBH 7.5	DBH 8	DBH 8.5	DBH 9
Pyramidulina sp. F LeRoy 1953							3		1			6		2		3			2	
Rotamorphina cushmani							1		1											
Siphogenerinoides sp.			1																	
Siphogenerinoides cf. *eleganta*					2		1	3	2			3		3	3	2				
Siphonodosaria annulifera						15	9	7	12		2	4	4	4	2			1	4	11
Stainforhia sp. 1 Speijer 1994							1	2						2						
Stillostomella alexanderi							1	1	1	1	1	1								
Tappanina selmensis								1				1								
Trifarina esnaensis								3	3					2						
Turrilina brevispira						1	1	1	1						1				1	3
Uvigerina spp.										1										1
Valvalabamina lenticula						1	1	2	2	1										1
Valvulineria scrobiculata				3	15	20	15	20	20	17	1	14	3	10	8	9	6	22
Valvulineria cf. *scrobiculata*						4	5		1		1		2	2		1		
Total	73	402	319	4	60	57	310	343	320	389	337	418	138	321	250	344	118	207	281	394

the increase in its oxidation product CO_2, reacting to HCO_3^- and thus causing strong $CaCO_3$ dissolution during the early stage of warming (Dickens *et al.*, 1997; Thomas, 1998). The occurrence of severe dissolution at such shallow depths, however, is not expected by carbon cycle modelling (e.g. Dickens *et al.*, 1997; Zachos *et al.*, in press).

The composition of the assemblages from the lower part of DQB 1 indicates a period of environmental stress: the abundance of trochamminids, *Haplophragmoides* and *Recurvoides* may be interpreted as an acme of taxa that tolerate low oxygen conditions as well as changes in the food supply (Sliter, 1975; Koutsoukos *et al.*, 1991; Ly and Kuhnt, 1994; Kuhnt *et al.*, 1996; Gooday, 2003). Opportunistic species of *Haplophragmoides* also peak in relative abundance in an interval with strong dissolution above the Palaeocene–Eocene extinction of benthic foraminifera in Spanish bathyal sections (Ortiz, 1995; Orue-Etxebarria *et al.*, 1996). The presence of dark laminated shales suggests oxygen deficiency during the early phase of the CIE. The strong decrease in the percentage of infaunal morphogroups might indicate oligotrophic conditions during this interval. We do not interpret the peak in agglutinated foraminifera as an indicator of sea-level fluctuations, but as a result of stressful conditions such as oxygen deficiency, carbonate dissolution, and changes in the food supply.

Higher in the section, the high percentages of acarininids (>95% of the planktic foraminiferal assemblages) and the near lack of other tropical–subtropical planktic foraminifera (e.g. large morozovellids) in DQB 2 (Fig. 2) suggest that the effects of the thermal maximum and the carbonate dissolution were not overwhelming during deposition of DQB 2, but may have returned during deposition of DQB 3.

The composition of benthic foraminiferal assemblages in the upper half of DQB 3 and the lower half of DQB 4, together with the high percentage of acarininids suggest oceanic environmental stress, probably related to low oxygen conditions, high temperature, moderate carbonate dissolution and high productivity in this area. We suggest that the IETM level in Dababiya mainly includes the first

Table 2 Habitat preferences of the most abundant calcareous (Corliss, 1985; Corliss and Chen, 1988) and agglutinated (Jones and Charnock, 1985) benthic foraminiferal taxa at Dababiya.

Epifaunal calcareous
Rounded trochospiral
Anomalinoides rubiginosus[1]
Plano-convex trochospiral
Angulogavelinella avnimelechi
Anomalinoides sp. B
Anomalinoides zitteli
Cibicidoides pharaonis
Gyroidinoides girardanus[1]
Valvalabamina lenticula
Valvulineria scrobiculata[2]
Biconvex trochospiral
Anomalinoides aegyptiacus[3]
Anomalinoides midwayensis
Anomalinoides praeacutus
Cibicidoides cf. *alleni*
Cibicidoides pseudoacutus
Cibicidoides pseudoperlucidus
Cibicidoides succedens
Oridorsalis plummerae[4]
Osangularia plummerae

Epifaunal agglutinated
A: Tubular or branching
Bathysiphon[5]
Rhizammina
Irregular
Trochamminids[6]

Infaunal calcareous
Cylindrical tapered
Bulimina callahani
Bulimina farafraensis
Bulimina kugleri
Bulimina midwayensis
Fursenkoina spp.
Globobulimina spp.
Hemirobulina spp.
Laevidentalinids
Neobulimina farafraensis
Nodosariids
Siphogenerinoides eleganta
Siphonodosaria annulifera
Stainforthia spp.
Flattened tapered
Loxostomoides applinae
Spherical/globose
Globocassidulina subglobosa
Biconvex trochospiral:
Gyroidinoides beisseli[7]
Oridorsalis umbonatus[8]
Biconvex planispiral
Lenticulina spp.[9,10]

Infaunal agglutinated
C1: Elongate multilocular
Gaudryina spp.
Karrerulina spp.
Spiroplectinella esnaensis

Table 2 Continued

Flattened trochospiral:
Haplophragmoides[11,12]
Streptospiral
Recurvoides[13]

[1]Widmark and Malmgren (1992); [2]Speijer and Schmitz (1998); [3]Speijer and Wagner (2002); [4]Widmark and Speijer (1997); [5]Peryt *et al.* (1997); [6]Galeotti *et al.* (2004); [7]Alegret *et al.* (2001); [8]Rathburn and Corliss (1994); [9]Corliss (1991); [10]Thomas and Shackleton (1996); [11]Kuhnt *et al.* (1996); [12]Kaminski *et al.* (1999); [13]Kuhnt and Kaminski (1993).

250 cm above the P/E boundary, i.e. DQB 1, 2, 3, and the lower half of DQB 4 (Fig. 2).

Upper part of the CIE interval and above the DQBeds (lower Eocene)

Indicators of a high food flux and/or low oxygenation at the sea floor, such as buliminids and *Lenticulina* spp., make up 28–38% of the assemblages from DQB 4 towards the top of the section. Buliminids in the present oceans tolerate reduced oxygen concentrations, but their high relative abundance is thought to be mainly caused by an abundant food supply, not by low oxygenation (Fontanier *et al.*, 2002; Gooday, 2003; Alegret and Thomas, 2004). Moreover, the increased percentages of infaunal morphogroups indicate an increase in the nutrient flux to the sea floor. We thus infer moderate to high productivity rather than low oxygen levels in the sea bottom waters from the upper part of the CIE-interval (DQB 4) towards the top of the section.

The four pyrite-rich levels above the DQBeds contain low-diversity assemblages with abundant agglutinated taxa (e.g. *Haplophragmoides*, trochamminids) and numerous high-food indicators such as buliminids. These data suggest that the moderate trophic conditions recorded from the upper part of the CIE interval towards the top of the section were occasionally interrupted by periods of high productivity and/or low oxygen conditions at the sea floor. Similar dysoxic and eutrophic conditions were documented by Speijer and Schmitz (1998) in the nearby Gewel Aweina section (Egypt), and related to periods of upwelling that persisted for at least 1 Myr after the P/E boundary.

Conclusions

Benthic foraminifera from Dababiya Quarry (Egypt) indicate an outer shelf depth of deposition during the late Palaeocene and early Eocene. Benthic foraminiferal assemblages exhibit a major faunal turnover across the IETM that may be linked to carbonate dissolution, low dissolved oxygen levels at the sea floor and a high organic flux. The extinction of *Angulogavelinella avnimelechi*, among other species, occurs at the base of the CIE, and thus may be correlated to the main phase of extinction of benthic foraminifera in the deep sea.

Severe carbonate dissolution occurred in the lowermost part of the CIE (DQB 1). In this interval there is an acme of agglutinated foraminifera, which suggests that there may have been a lack of oxygen as well as changes in the food supply to the sea floor; the strong decrease in the percentage of infaunal morphogroups suggests oligotrophic conditions during the earliest phase of the CIE. Carbonate dissolution related to release and oxidation of methane during the earliest phase of warming is a plausible hypothesis to account for the presence of dissolution levels in the lowermost Eocene in Dababiya and in other sections across the world, although the very large depth range over which dissolution occurred is difficult to explain (Dickens *et al.*, 1997; Thomas, 1998; Zachos *et al.*, in press).

Composition of the benthic foraminiferal assemblages suggests moderate to high productivity and increased levels of dissolved oxygen towards the upper part of the CIE and afterwards. The environmental and faunal recovery was occasionally interrupted by periods of environmental stress at the sea floor, as inferred from four levels located above the DQBeds.

Acknowledgements

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