Cretaceous Research (2001) **22,** 391–422
doi:10.1006/cres.2001.0264, available online at http://www.idealibrary.com on IDEAL®

Palaeoenvironment of the Cenomanian–Turonian transition at Eastbourne, England

***Gerta Keller, *Qi Han, †Thierry Adatte and ‡Stephen J. Burns**

**Department of Geosciences, Princeton University, Princeton NJ 08540, USA; email: gkeller@princeton.edu*
†Institut de Geologie, 11 Rue Emile Argand, 2007 Neuchatel, Switzerland
‡Department of Geosciences, University of Massachusetts, Box 35820 Amherst, MA 01003, USA

Revised manuscript accepted 3 April 2001

Lithology, stable isotopes and planktic foraminiferal analyses of the Eastbourne section at Gun Gardens (southeast England) reflect sea-level fluctuations and changing climatic and oceanographic conditions across the Cenomanian–Turonian transition. The δ^{13}C excursion began with a 1.8‰ positive shift in Plenus Marls Beds 1–3 (*R. cushmani* Zone), a trough in Bed 4, a second δ^{13}C shift of 0.8‰ in Bed 7 and a gradually decreasing plateau during deposition of the Ballard Cliff Member. Lithological variations, sharp erosion surfaces, bioturbation and increased detrital influx indicate that sea-level fluctuations, cooling and a marine regression accompanied the δ^{13}C excursion within the Plenus Marls, followed by warming and a major marine transgression in the upper part of the Plenus Marls and Ballard Cliff Member. Two faunal turnover phases coincided with the two-phased δ^{13}C excursion. Phase I in Bed 3 is marked by the extinction of the deeper dwelling planktic foraminifer *Rotalipora*, the origination of the thermocline dweller *Dicarinella*, dominance of the low oxygen tolerant *Heterohelix* species, and common surface dwellers *Guembelitria* and *Whiteinella*. This faunal turnover reflects a lower sea level, enhanced productivity and temporary expansion of the oxygen minimum zone associated with climate cooling and increased upwelling. Phase II near the top of the Plenus Marls (Beds 7–8) is marked by the temporary disappearance of about 50% of the species, increased abundance of surface dwellers and a shift to dominance of low-oxygen tolerant *Heterohelix* species globally. This faunal turnover may reflect increased primary productivity and a long-term expansion of the oxygen minimum zone associated with climate warming and a marine transgression. Faunal turnover phase II stratigraphically correlates with the global oceanic anoxic event in Italy (Bonarelli Level) and Tunisia (Bahloul Formation), whereas phase I correlates with the onset of organic-rich facies in the upper *R. cushmani* Zone of these regions. High resolution biostratigraphic correlation is based on planktic foraminifera and the subdivision of *Whiteinella archeocretacea* Zone into three subzones.

Key Words: Cenomanian–Turonian; Eastbourne; planktic foraminifera; stable isotopes; sea-level changes.

1. Introduction

The Cenomanian/Turonian boundary event (CTBE) in the Dover–Eastbourne region of England (Figure 1) has been documented by many studies based on geochemistry, mineralogy, and marine extinctions in various micro- and macrofossil groups. Nevertheless, there is still considerable controversy regarding the causes and effects of this event and its correlation globally. Perhaps the best agreement is among marine benthic and planktic fossil groups, all of which show major faunal turnovers in the Plenus Marls associated with the δ^{13}C excursion (e.g., Jarvis *et al.*, 1988; Hart *et al.*, 1993; Paul *et al.*, 1999). However, few studies have quantified these faunal turnovers or tied extinctions to specific environmental changes, such as changes in productivity, oxygen minimum zone, sea level or climate. Based on nannofossil diversity and abundance, Paul *et al.* (1994) and Lamolda *et al.* (1994) concluded that palaeoproductivity declined through the Plenus Marls and the δ^{13}C excursion, and based on faunal abundances and total organic carbon, Gale *et al.* (2000) inferred that surface water productivity dropped near the top of Plenus Marls Member. In contrast, Jarvis *et al.* (1988) concluded that increased upwelling and a widespread expansion of the oxygen minimum zone occurred at this time, whereas Jeans *et al.* (1991) concluded that palaeoproductivity remained normal, except for a major increase in Beds 3–5.

Although there is considerable disagreement regarding productivity across the CTBE, there is general agreement on the onset and duration of the δ^{13}C excursion in the Dover–Eastbourne sections where the excursion began in Plenus Marls Bed 1 and

0195–6671/01/040391+32 $35.00/0

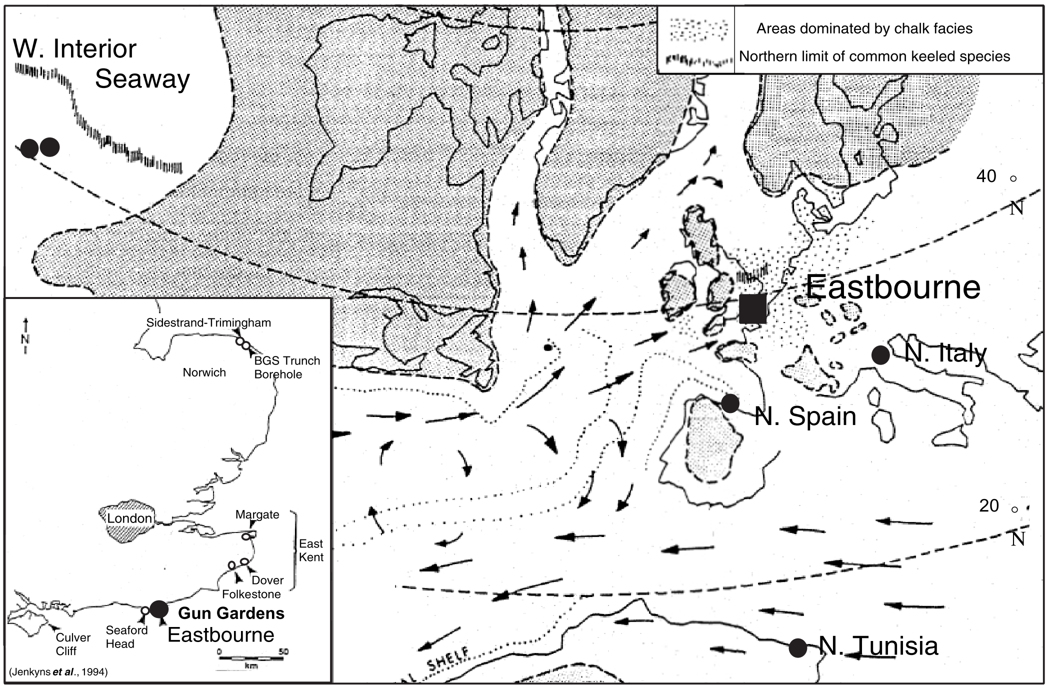
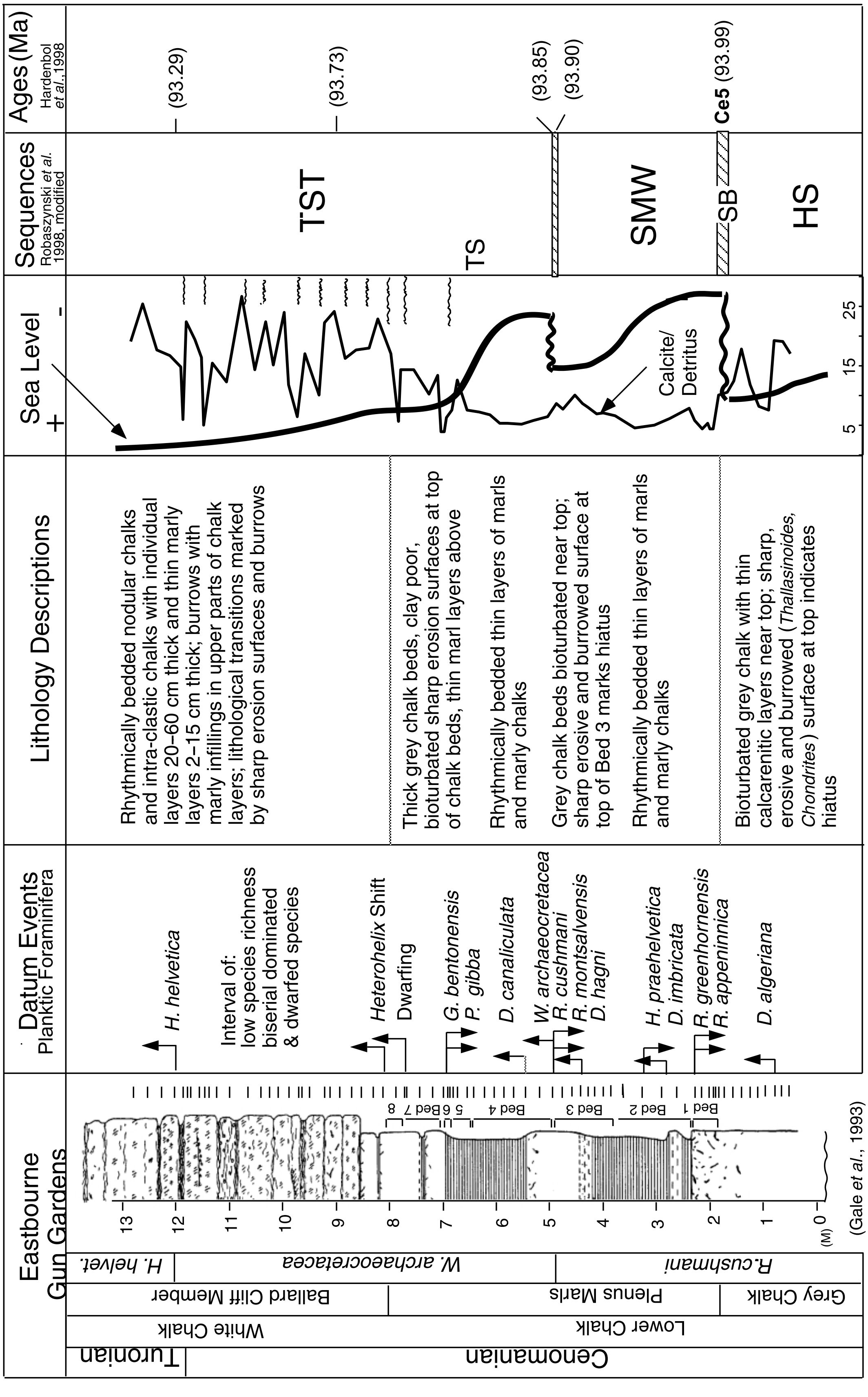


Figure 1. Palaeogeography and palaeoceanography of Eastbourne, England, and other sections discussed within northern low to middle latitudes during the Cenomanian–Turonian transition (reconstruction after Luyendyk *et al.*, 1972, Hart & Tarling, 1974 and Hart & Carter, 1975).

reached a maximum in Beds 7–8 (Jarvis *et al.*, 1988; Corfield *et al.*, 1990; Jeans *et al.*, 1991; Gale *et al.*, 1993; Paul *et al.*, 1994, 1999; Lamolda *et al.*, 1994; Jenkyns *et al.*, 1994). But the $\delta^{13}C$ records differ in details either owing to sample resolution, diagenetic overprints, or variations in the sediment accumulation records (e.g., Eastbourne sections are four times thicker than equivalent sections at Dover; Gale *et al.*, 1993). $\delta^{18}O$ records between Eastbourne and Dover also differ significantly (Jarvis *et al.*, 1988; Paul *et al.*, 1994, 1999; Mitchell *et al.*, 1997) and are generally interpreted as the result of diagenesis. Few authors offer climatic interpretations. Jeans *et al.* (1991) suggested a major cooling associated with a marine regression and increased terrigenous influx. Lamolda *et al.* (1994) inferred a sea-level regression at the base of the Plenus Marls followed by gradual recovery and a cooling in Beds 4–8. Other workers hold that deposition of the Plenus Marls occurred during climatic warming and a major marine transgression (e.g., Jenkyns, 1980; Arthur *et al.*, 1987; Jarvis *et al.*, 1988; Uličný *et al.*, 1993; Hallam & Wignall, 1999).

This report examines the palaeoenvironmental conditions across the Cenomanian–Turonian transition at Gun Gardens, Eastbourne, based on high resolution (15–20 cm sample intervals), quantitative, planktic foraminiferal biostratigraphy and faunal turnovers, stable isotope analysis, total organic carbon, lithological variations and detrital influx. The aim is to evaluate changes in climate, sea level, terrigenous flux, productivity and oxygen levels, and the response to these conditions by planktic foraminiferal faunas. Planktic foraminifera are excellent environmental indicators owing to their sensitivity to physical and chemical variations both vertically in the water column and across latitudes. This study examines their response to: (1) the Cenomanian/Turonian boundary event in terms of species extinctions and relative abundance changes; (2) the depth stratification of species based on biogeographic distribution and published monospecific stable isotope data; (3) the strength of the oxygen minimum zone based on the relative abundance of low-oxygen tolerant species; (4) palaeoproductivity based on the relative abundance of surface water dwellers and low-oxygen tolerant species, as well as carbon isotope data; (5) potential causes and effects of species dwarfism. (6) In addition, we propose a refinement in the current planktic foraminiferal biozones, particularly the subdivision of the *Whiteinella archaeocretacea* Zone into three subzones, that significantly improves correlation of the critical $\delta^{13}C$ excursion interval, ocean anoxic events (OAEs), species extinctions, timing of sea-level fluctuations and productivity events across latitudes.



Rhythmically bedded nodular chalks and intra-clastic chalks with individual layers 20–60 cm thick and thin marly layers 2–15 cm thick; burrows with marly infillings in upper parts of chalk layers; lithological transitions marked by sharp erosion surfaces and burrows

Thick grey chalk beds, clay poor, bioturbated sharp erosion surfaces at top of chalk beds, thin marl layers above

Rhythmically bedded thin layers of marls and marly chalks

Grey chalk beds bioturbated near top; sharp erosive and burrowed surface at top of Bed 3 marks hiatus

Rhythmically bedded thin layers of marls and marly chalks

Bioturbated grey chalk with thin calcarenitic layers near top; sharp, erosive and burrowed (*Thallasinoides, Chondrites*) surface at top indicates hiatus

Figure 2. Lithology, planktic foraminiferal datum events, calcite/detritus ratio, and sea-level curve of the Cenomanian–Turonian sequence at Gun Gardens, Eastbourne, England. Lithologic division after Gale *et al.* (1993); sea-level changes based on this study and Hardenbol *et al.* (1998). HS, highstand; SB, sequence boundary; TS, transgressive surface; SMW, shelf margin wedge; TST, transgressive system track.

Table 1. Relative per cent abundances of planktic foraminifera, C–T transition at Gun Gardens, Eastbourne (x, rare; 0, <1%).

Zones	*R. cushmani*																								*W. archaeocretacea*						
Subzones	*R. greenhornesis*			*D. algeriana*																					*G. bentonensis*						
Sample numbers	2	3	4	5	6	9	10	11	12	13	14	15	16	17	18	19	20	21	22	24	25	26	27	28	29	30	31	32	33	33	34
Sample depth (m)	0.5	0.7	0.8	1	1.1	1.6	1.8	1.9	1.9	2	2	2.2	2.3	2.6	2.9	3.3	3.7	3.9	4	4.3	4.4	4.6	4.8	4.9	5.2	5.5	5.7	5.9	6	6.2	6.4
Anaticinella multiloculata	0	1	1	x	x	0	0	x	x										x	0	0	0	x		9	2	7	8	11	5	8
Dicarinella algeriana			1				0								1	1	0	2	x	3	1	1	0	1	x	0	x	x	1	2	1
D. canaliculata																										1	x	0	1	x	0
D. hagni																						2	x	x	x	x	x	x	x	x	0
D. imbricata															0	x	x	x	x	0	1	5	0	1	1	x	x	x	x	1	1
Globigerinelloides bentonensis				0	x	x	x	1	1	2	2	1	1	1	3	x	2	2	0	x	1	x	x	1	1	x	x	0	1	1	1
G. ultramicra	5	10	5	4	5	4	5	14	14	20	13	14	11	12	9	4	5	7	7	11	4	7	4	10	21	8	4	7	3	2	5
Guembelitria cenomana	14	16	34	40	29	18	25	3	6	8	7	7	6	7	10	18	15	8	15	14	14	9	5	11	6	15	7	9	10	13	9
G. albertensis	2	1	4	3	4	1	2	1	1	1	1	1	2	1	1	1	2	1	1	2	1	2	2	1	3	1	3	1	1	2	1
Hedbergella delrioensis	5	10	11	13	11	7	12	3	9	4	2	4	3	9	4	8	9	6	9	7	6	4	10	4	6	2	3	3	1	2	2
H. planispira	23	16	11	15	18	27	15	29	15	9	11	11	9	11	3	4	5	12	11	12	13	14	14	17	15	26	19	31	12	20	19
H. simplex	4	5	1	3	2	1	1	x	3	2	4	1	2	3	2	x	1	1	0	1	1	2	1	x	x	0	0	x	3	x	1
Heterohelix moremani	22	19	19	17	20	21	14	2	3	12	12	15	19	17	32	38	37	24	13	16	21	27	18	25	15	23	29	16	22	27	18
H. reussi	1	5	3	1	1	4	3	x	1	1	1	0	1	1	1	2	2	6	7	4	1	2	1	3	2	2	11	10	4	6	2
H. praehelvetica			0	0							0				0	x															
Praeglobotruncana aumalensis	1	0	1	x	x	0	0	1	2	0	x	1	2	x	2	2	1	4	3	6	4	4	3	2	x	x	1	0	4	2	1
P. gibba																			0	x	x	3	x	0	1	0	x	x	1	x	1
P. stephani														1	0	x	x	1	0	0	1	0	x	0	0	x	x	x	x	x	x
Rotalipora appenninica	x		x			x		x			1	x	0																		
R. cushmani	1	x	0	x	0	x	x	x	1	1	1	0	x	x	1	0	x	0	x	x	0	x	x	x							
R. greenhornesis	x	x			x		0	x	x	x	1	x	x																		
R. montsalvensis	1		x		x	x	x	x	x	x	1	x	0	x	1	0	1	1	x	x	x	0	x	x							
Schackoina cenomana					0			0											1			1	0			0		0			
Whiteinella aprica	2	0	1	0	x	1	x	1	1	x	1	0	0	0											1	0	x	0	0	1	x
W. archaeocretacea	7	11	4	2	7	8	10	41	40	34	34	40	33	24	20	18	18	20	22	20	21	13	32	17	15	11	11	9	17	11	16
W. baltica	10	6	6	1	1	6	11	2	3	5	7	3	8	12	10	5	3	5	10	6	7	2	8	4	4	5	4	3	6	5	11
W. brittonensis	x		x	x	x	1	3	1	1	1	1	x	1	1	1	x	x	1	x	x	x	0	0	1	0	x	x	1	0	1	1
W. paradubia						0	x	x	x	0	1	x	x	0	1	x	0	0	x	x	0	1	0								
Total number counted	267	348	360	427	458	289	315	319	425	327	337	421	298	419	303	345	325	354	279	307	305	323	327	368	320	311	276	382	329	322	339

Table 1. (Continued).

Zones	*W. archaeocretacea*																								*H. helvetica*					
Subzones	*G. bentonensis*					*A. multiloculata*				*H. moremani*																				
Sample numbers	35	36	37	38	39	41	43	45	46	47	48	50	51	53	−15	−14	−13	−12	−11	−10	−9	−8	−7	−5	−2	−1	55	56	58	59
Depth (m)	6.5	6.7	6.8	6.9	6.9	7.2	7.7	7.9	8.1	8.3	8.5	8.9	9.1	9.5	9.7	9.7	9.7	9.7	9.9	10	10	10	11	11	12	12	12	12	13	13
Anaticinella multiloculata	10	10	15	17	14	5	1	13	4	2		1	x	2	5	5	6	10	4	x	5	0	2	4	2	3				
Dicarinella algeriana	0	1	x	x	2	1	2	1						2		x	x	3	0					1	x	x	3	x	2	
D. canaliculata					1									0				2	0					0	0	x		x		
D. hagni	0	x	x	0	2									1					0					0					x	x
D. imbricata	0	2	x	2	4	x	0							1	0	x	x	1	0					1	0	x	0	1		
Globigerinelloides bentonensis	0	0	0	1	0																									
G. ultramicra	3	2	6	27	7	4	8	9	7	4	17	9	1	3	6	2	1	3	0	5	7	0	1	x	2	1	x	x	4	x
Guembelitria cenomana	8	6	10	1	x	8	2	2	3			3	1	1	7	4	6	4	3	2	x	6	2	3	0	2	1	1	5	2
G. albertensis	2	2	1	0	0	3	1	2	2			2	4	5	3	2	1	2	0	0	3	4	1	6	2	x	x	4	1	3
Hedbergella delrioensis	3	4	2	3	1	5	1						0												0	1		1	1	0
H. planispira	10	16	16	34	38	9	27	5	23	17	22	30	19	25	21	25	20	18	21	36	19	42	33	29	26	52	67	31	25	22
H. simplex	2	x	0	x	0	1	13	19	6	11	28	3	1	x	6	6	3	5	8	3		4	10	1	1	1	0	3	10	x
Heterohelix moremani	22	14	27	2	6	25	16	8	40	38	6	35	43	37	18	9	8	17	28	37	35	35	42	36	53	19	5	26	32	29
Heterohelix cf. *moremani*	1	x	1	x	x	2	2	x	4	2	22	5	6	5	0	0	1	4	3	x	x	2	1	1	1	x	8	7	2	4
H. reussi	3	1	1	1	x	1	1	2	11	9	x	8	17	12	3	5	4	3	6	8	21	3	4	8	11	3	8	15	2	34
Helvetoglobotruncana helvetica																												x	x	
Praeglobotruncana aumalensis	1	2	1	1	1	2								x	0	x	1									3				
P. gibba	3	0	x	0	4																									
P. stephani	x	x	x	0	x	0	1	1							0	x	1													
Whiteinella aprica	0	2	0	x	2	0	0	1						2	3	0	1	x	1	x	2	x	x	1	x	2	0	4	2	0
W. archaeocretacea	18	24	15	8	15	22	7	17	1	2		1	3		5	30	20	9	5	3	2	0	3	1	0	3	2	3	4	
W. baltica	11	10	5	1	4	9	15	20	1	15	6	3	4	3	19	11	25	17	12	4	5	2	x	5	2	9	3	x	10	4
W. brittonensis	1	1	x	1	x	2								0	1	1	1	x	3	x	1	x	x	1	x	x	2	4	x	1
W. paradubia		1				0								1	x	x			1									1		x
Total number counted	325	294	314	351	360	320	215	106	182	47	18	237	275	305	283	287	269	202	232	229	243	226	164	269	340	232	238	194	255	271

2. Material and methods

A total of 77 samples spanning 13 m of sediments were collected across the Cenomanian–Turonian transition at the Gun Gardens section near Eastbourne with a sample spacing averaging 15–20 cm (Figure 2). Our section parallels that of Gale *et al.* (1993). For foraminiferal analysis, marly sediment samples were crushed to pea-sized pieces and disaggregated in a 20–40% solution of H_2O_2, agitated in an ultrasonic bath for several minutes, washed through a 63 µm sieve, and oven dried at 50°C. This procedure was repeated several times until clean planktic foraminiferal residues were obtained. Samples from marly chalk and chalks were processed using the freeze-thaw method (Slipper, 1996). Crushed samples were immersed in a supersaturated solution of Na_2SO_4, and dissociated by repeated (2–6 times) freezing and thawing followed by washing through a 63 µm sieve until relatively clean foraminiferal residues were obtained.

Foraminiferal preservation is relatively good for marly samples, but in more chalky lithologies small specimens are difficult to free from adhering carbonate, and even with repeated freeze-thaw cycles test chambers remained infilled with cement. All foraminiferal shells appear recrystallized. Quantitative foraminiferal analysis is based on representative sample splits of 250–350 specimens where available. The remaining residue for each sample was searched for rare species. A total of 31 planktic foraminiferal species were identified. Relative abundances of planktic foraminiferal species were estimated from counts of 250–350 specimens in the >63 µm sieve fraction (Table 1). The identification of species and classification of genera follows that of Robaszynski & Caron (1979), Caron (1985) and Wonders (1980).

Organic carbon analysis was conducted using a CHN Carlo-Erba Elemental Analyzer NA 1108 at the University of Neuchâtel. Total carbon was first measured on bulk samples (0.01–0.02 g). Total organic carbon (TOC) was determined after removing carbonate by acidification with hydrochloric acid (10%), assuming that dissolved organic matter in ancient sediments is nearly absent. The values obtained were compared with a standard reference sample. Analytical precision for a standard is ± 0.003% and reproducibility for the Cenomanian samples is 0.01% for bulk rocks (total carbon) and 0.02% for insoluble residues.

Stable isotope analyses were done on the bulk rock carbonate samples using the fine fraction <63 µm. Analyses were conducted at the stable isotope laboratory of the University of Bern, Switzerland using a VG Prism II ratio mass spectrometer equipped with a common acid bath (H_3PO_4). The results are reported relative to the VPDB standard reference material with a standard error of 0.1‰ for $\delta^{18}O$ and 0.05‰ for $\delta^{13}C$.

3. Lithology and sea level

The section at Gun Gardens is exposed in the seashore cliffs between Beachy Head and Eastbourne, Sussex, England, and is one of the most expanded Cenomanian–Turonian transitions in England (Jefferies, 1963; Jarvis *et al.*, 1988; Gale *et al.*, 1993; Lamolda et al., 1994; Paul *et al.*, 1999). The exposed section is about 13 m thick and consists of alternating chalk, marly chalk and rhythmically bedded marls. Chalks consist of clay-poor carbonates rich in microfossils (foraminifera, coccoliths, calcispheres) and macrofossils (inoceramids), whereas marls consist of clay-rich carbonates (or calcareous mudrocks) (Jefferies, 1963; Mortimore, 1986; Jarvis *et al.*, 1988; Jeans *et al.*, 1991; Gale *et al.*, 1993; Lamolda *et al.*, 1994; Paul *et al.*, 1999). Transitions from chalk to marly chalk are marked by burrowed sharp erosion surfaces and indicate repeated periods of erosion and/or non-deposition. Following Gale *et al.* (1993), we divide the sedimentary succession into three distinct units: the Grey Chalk Member (of the Lower Chalk Formation), the Plenus Marls Formation and the Ballard Cliff Member (=Melbourn Rock of Mortimore, 1986) of the White Chalk Formation (Figure 2). Gale *et al.* (1993) noted that the Gun Gardens section is at least four times as expanded as sections from the Dover/Folkestone region of East Kent and about 20 times as thick as the section at South Ferriby.

The lithological variations observed, including undulating erosional and burrowed surfaces, terrrigenous influx and fossil content, are indicative of sea-level changes. Periods of low sea levels generally coincide with high detrital influx (marls) and increased erosion and are predominantly associated with arid and/or cooler climatic conditions. Periods of high sea levels are generally characterized by increased carbonate production (chalks) and low detrital influx and these periods are predominantly associated with warm and humid climatic conditions (Jefferies, 1963; Pratt, 1984; Eicher & Diner, 1985; Paul *et al.*, 1999; Li *et al.*, 2000; Adatte *et al.*, unpubl. data).

The calcite/detritus ratio (quartz+feldspars+phyllosilicates) reflect sea-level changes with increased carbonate content indicative of deeper water environments (more distal source) and increased detritus (mainly clay, minor quartz and feldspar) indicative of shallower nearshore environments (Li *et al.*, 2000). At Eastbourne (Gun Gardens), marls and marly chalk deposition, with decreased calcite, increased phyllosilicates, quartz and feldspar, suggest low sea level episodes with increased erosion (Figure 2). In contrast, chalk deposition with increased calcite and decreased quartz and feldspar, reflects high sea levels. However, the overall carbonate dominance at Eastbourne implies an overall high sea level, correlative with the global sea-level transgression possibly associated with global tectonics (e.g., Haq *et al.*, 1987; Jeans *et al.*, 1991; Malartre *et al.*, 1998; Hallam & Wignall, 1999), although at Eastbourne, the overall sea-level transgression was interrupted by high frequency and amplitude sea-level falls.

At Gun Gardens, Eastbourne, the basal 1.8 m of the section (uppermost part of the Grey Chalk) consists of bioturbated grey chalk and may represent a moderately high sea level (Figure 2). Thin calcarenitic layers near the top and a sharp erosive and burrowed (*Thallasinoides*, *Chondrites*) surface indicates a hiatus and sea-level fall (see also Jeans *et al.*, 1991; Lamolda *et al.*, 1994) that has been identified as a sequence boundary (Figure 2; Robaszynski *et al.*, 1998). This interval is overlain by the 4.4-m-thick clay-rich Plenus Marls Formation that has been labelled by Jefferies (1963) as Beds 1–8, as also in this study. Beds 1, 2, 4 and 6 consist of rhythmically bedded thin layers of marls and marly chalks, whereas Beds 3, 5, 7 and 8 consist of thick grey chalk beds.

Sediment deposition during the Plenus Marls Formation reflects sea-level lowstand periods with increased erosion and accelerated detrital input (Figure 2; see also Jeans *et al.*, 1991; Lamolda *et al.*, 1994). For example, each chalk/marl couplet represents high/low sea levels with erosion or non-deposition at the transitions from high to low as noted by the sharp erosive and burrowed surfaces at the top of chalk Beds 3, 5, 7 and 8 (Jefferies, 1963). The maxima in detrital influx (calcite/detritus ratio, Figure 2) correspond to the rhythmically bedded thin marls and marly chalks in Beds 2 and 4 that may reflect sea-level falls overprinted by tectonic events. Since the detrital components (e.g., quartz, feldspar, and most of the phyllosilicates) in general do not represent a high relative amount of the total bulk rock, input from river runoff was not extensive. This suggests that terrestrial input during sea-level lowstands was controlled by erosion and physical weathering under cool to temperate climatic conditions. Near the top of the Plenus Marls (Beds 7–8), carbonate deposition increased and detrital influx decreased, marking a gradually rising sea level (Lamolda *et al.*, 1994; Gale, 1996), and the onset of a sea-level transgression.

The Plenus Marls are overlain by the Ballard Cliff Member (Gale, 1996) of which the lower 5 m sampled for this study consist of rhythmically bedded nodular chalks and intra-clastic chalks with individual layers 20–60 cm thick, and thin marly chalk beds 2–15 cm thick. Burrows with marly infillings are sometimes present in the upper part of the chalk layers and indicate that the rhythmic bedding is of primary sedimentary origin (Paul *et al.*, 1994). As in the Plenus Marls below, the transitions between different lithologies are generally marked by erosion surfaces, hiatuses, burrowed intervals, and rapid changes in the calcite/detritus ratio (Figure 2). In the Ballard Cliff Member, these rhythmic lithological transitions mark high frequency sea-level fluctuations, possibly associated with Milankovitch cycles (Gale, 1990, 1995; Lamolda *et al.*, 1994) during a sea-level high-stand period.

There is general agreement that the Plenus Marls were deposited during a sea-level regression followed by a transgression (Jefferies, 1963; Jeans *et al.*, 1991; Lamolda *et al.*, 1994), though Jarvis *et al.* (1988) argued for a transgression only. Jeans *et al.* (1991) argued that the sea-level regression was related to global cooling and high latitude glaciation, noting the presence of occasional dropstones, Jefferies' boreal faunas (Beds 4–6) and significantly more positive $\delta^{18}O$ values, suggesting cooler ocean temperatures. However, on a global scale, the Cenomanian/Turonian boundary event, characterized by its organic-rich facies and $\delta^{13}C$ excursion, is regarded as a warm climatic interval accompanied by a major sea-level transgression and ocean anoxia (Hancock & Kauffman, 1979; Hart, 1980a; Hancock, 1989; Hardenbol *et al.*, 1993; Uličný *et al.*, 1993). Uličný *et al.* (1993) argued that the CTBE was initiated by a rapid sea-level rise that continued through the peak $\delta^{13}C$ excursion after which the sea-level dropped. However, the evidence in support of this argument rests on sections that contain a major hiatus where most of the $\delta^{13}C$ excursion and the sea-level regression is missing, as evident by the absence of most of the planktic foraminiferal *W. archeocretacea* Zone, the upper part of the ammonite *M. geslinianum* Zone and all of the *N. juddii* Zone.

3.1. *Age control*

Age estimates for depositional and environmental events at Eastbourne can be calculated based on ages for various ammonite and planktic foraminiferal datum events extrapolated from the palaeomagnetic time scale and radiometric dates by Hardenbol *et al.* (1998) (Figure 3). For example, the last appearance

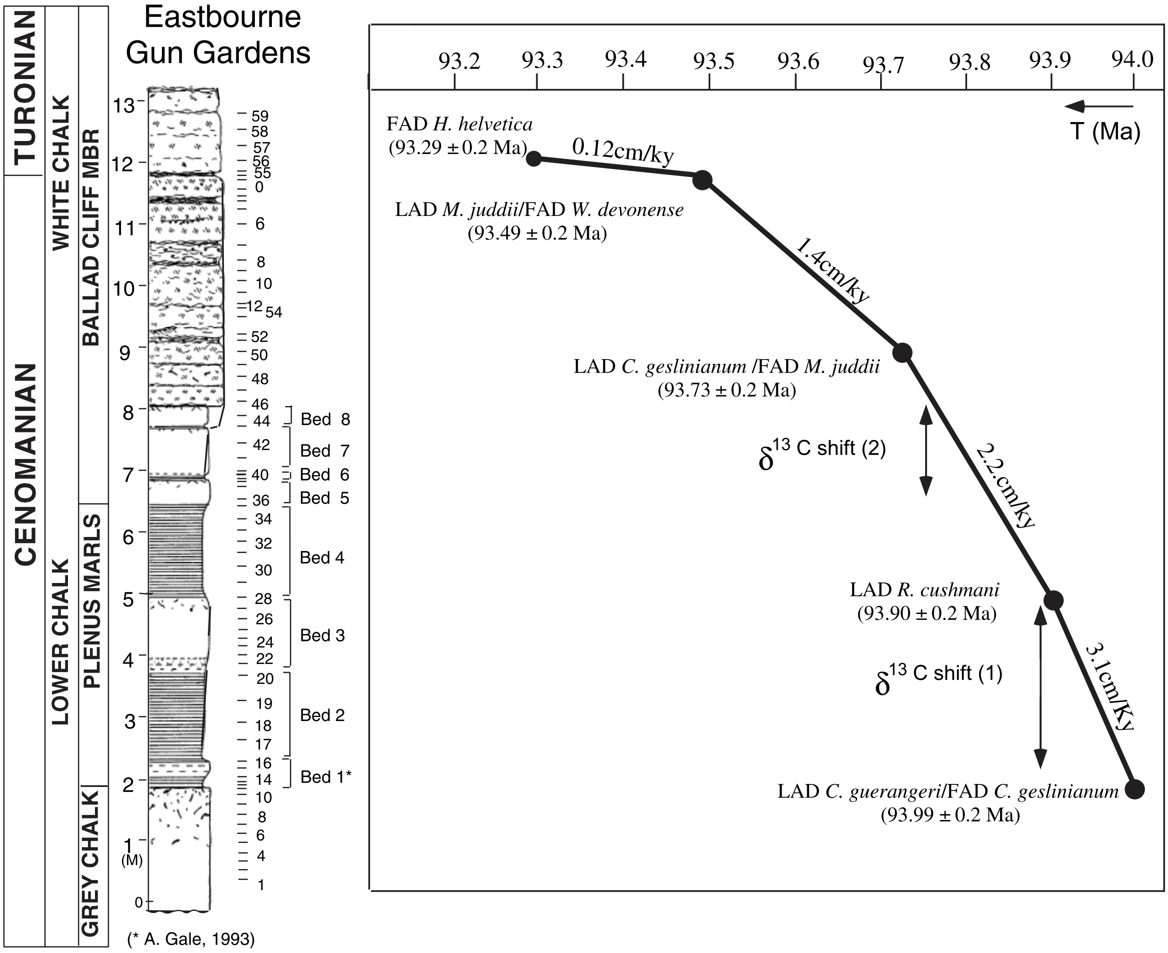


Figure 3. Sediment accumulation rates at Gun Gardens, Eastbourne, based on datum-event ages from Hardenbol *et al.* (1998). Note that there are two δ^{13}C excursions with estimated durations of 90 ky and 120 ky for the first and second respectively.

(LAD) of the ammonite *Calycoceras guerangeri* and first appearance (FAD) of *C. geslinianum* are dated at 93.99 ± 0.2 Ma, and at Eastbourne coincide with a sequence boundary (SB, Figure 2, and CE5 of Hardenbol *et al.*, 1998). The overlying shelf margin wedge (SMW) is laterally persistent and coincides with the first δ^{13}C excursion at Eastbourne (Figures 2, 3). The LAD of the planktic foraminifer *Rotalipora cushmani* dated at 93.90 ± 0.2 Ma is found at the top of Plenus Marls Bed 3 at an erosion surface and marks the top of the first δ^{13}C excursion. This interval spans about 90 ky and has a sediment accumulation rate of about 3.1 cm/ky (Figure 3).

Up-section, the LAD of *Calycoceras geslinianum* and FAD of *Neocardioceras juddii* are dated at 93.73 ± 0.2 Ma and coincide with the appearance of nodular chalk that reflects a sea-level highstand period (TST) that was initiated in the late *Metoicoceras geslinianum* and middle *W. archaeocretacea* zones (Beds 5–8; Figure 2). This sea-level transgression resulted in reduced terrigenous influx, as also reflected by reduced sedimentation rates (down to 2.2 cm/ky from 3.1 cm/ky; Figure 3) and widespread chalk deposition on basin margins. During the lower part of this interval δ^{13}C values decreased (trough in Beds 4–6), but reached maximum values at a second δ^{13}C excursion in the upper part (Beds 7–8; Figures 2, 3). Based on the above datum events and the sediment accumulation rate, the second δ^{13}C excursion occurred over about 120 ky (93.73–93.85 Ma).

The LAD of the ammonites *Neocardioceras juddii* and FAD of *Watinoceras devonense* that mark the Cenomanian/Turonian boundary are dated at 93.49 ± 0.2 Ma. Sediment accumulation rates were further reduced to 1.4 cm/ky (Figure 3) during the sea-level transgression of the Ballard Cliff Member, though this may partly be a result of erosion surfaces that mark the high frequency sea-level fluctuations during this period. Based on the above age estimates, sediment deposition from the base of the Plenus Marls to the C/T boundary occurred over a period of about 500 ± 0.4 ky. The FAD of the foraminifer *Helvetoglobotruncana helvetica* is dated at 93.29 ± 0.2 Ma and at Eastbourne occurs only 50 cm above the extinction of *N. juddii* and FAD of *W. devonense*. This indicates a short hiatus between these datum events.

4. Stable isotopes

4.1. *Oxygen isotopes*

Sediments at Eastbourne and Dover are diagenetically altered and therefore $\delta^{18}O$ values do not preserve seawater temperature signals (Jenkyns *et al.*, 1994; Mitchell *et al.*, 1997; Paul *et al.*, 1999). This is apparent in the overall similarity of $\delta^{13}C$ and $\delta^{18}O$ trends that indicate that diagenetic alteration obliterated the primary oceanographic $\delta^{18}O$ signal (Figures 4, 5). A test for diagenetic effects by Jenkyns *et al.* (1994) on bulk chalk samples of the Melbourn rock (Ballard Cliff Member in this study) showed that samples typically varied by 0.3‰ in $\delta^{13}C$ and up to 0.5‰ in $\delta^{18}O$ values. Paul *et al.* (1999) observed that since diagenetic cement preferentially concentrates in chalks, differential cementation between chalk and marl facies may have produced isotope oscillations in phase with lithologic variations. Mitchell *et al.* (1997) showed that isotopic values based on single recrystallized microfossils and cement samples indicate mixing lines between primary (oceanographic) compositions and (recrystallized) cements. As a result, $\delta^{18}O$ trends of single recrystallized foraminifera track $\delta^{13}C$ trends at Eastbourne. But the results of Mitchell *et al.* (1997) also show that diagenetic cement preferentially concentrates in pores of foraminifera and calcispheres, leaving the surrounding coccolith-rich sediments largely lacking in cement.

This means that bulk rock analyses, as in this study, provide more reliable palaeoceanographic signals when foraminiferal shells are recrystallized, as demonstrated by the fact that bulk rock $\delta^{13}C$ and $\delta^{18}O$ analyses do not track each other closely at Eastbourne, as shown by Paul *et al.* (1999) and this study (Figures 4, 5). Supported by lithologic and faunal changes, we interpret the major $\delta^{18}O$ trend as an oceanographic signal that indicates relatively cool conditions for the lower half of the Plenus Marls followed by warming for the upper part that continued through the deposition of the Ballard Cliff Member (Figure 4). This trend is similar to that observed in bulk rock data from Pueblo, Colorado, but differs from that of Oued Mellegue, Tunisia (Figure 4).

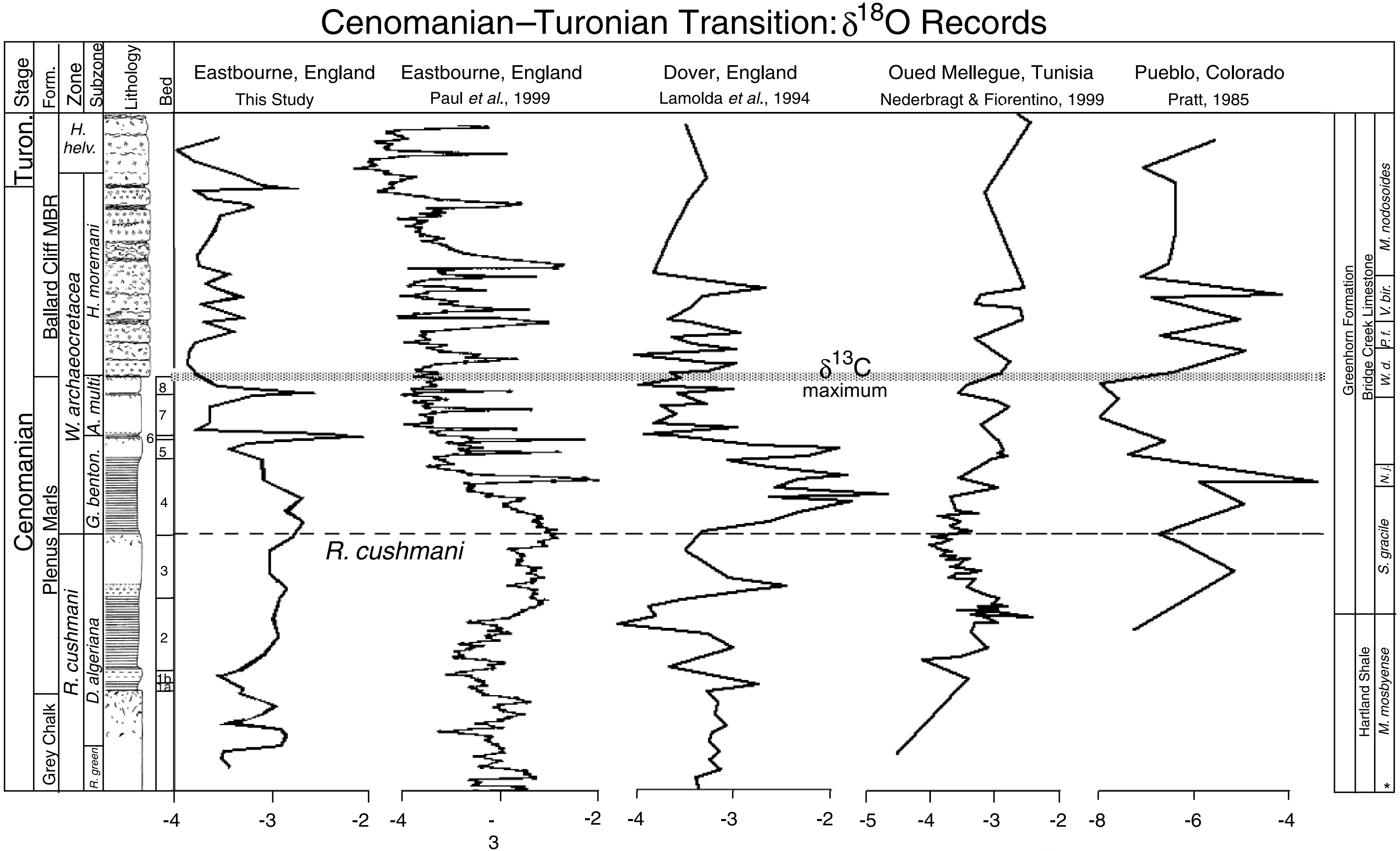
4.2. *Carbon isotopes*

In contrast to $\delta^{18}O$, $\delta^{13}C$ values are little affected by recrystallization processes because pore waters have low concentrations of carbon (Magaritz, 1975; Brand & Veizer, 1980; Schrag *et al.*, 1995). Thus, neither bulk rock nor foraminiferal shell $\delta^{13}C$ values should be significantly compromised by diagenetic alteration. This is demonstrated by the fact that the $\delta^{13}C$ record of single recrystallized foraminifera at Eastbourne by Mitchell *et al.* (1997) closely tracks the $\delta^{13}C$ records based on bulk rocks by Paul *et al.* (1999) and this study (Figure 5). The global stable isotope record across the Cenomanian/Turonian boundary in marine sediments shows a positive $\delta^{13}C$ excursion that is generally interpreted as a primary oceanographic signal reflecting enhanced organic carbon burial during a major OAE (e.g., Jenkyns, 1980; Scholle & Arthur, 1980; Arthur *et al.*, 1987; Jenkyns *et al.*, 1994; Accarie *et al.*, 1996). The Eastbourne and Dover sections show similar broad excursions, as can be observed in Colorado (Pratt & Threlkeld, 1984), Tunisia and elsewhere (Accarie *et al.*, 1996; Nederbragt & Fiorentino, 1999) (Figure 5), indicating that the $\delta^{13}C$ record reflects a primary oceanographic signal.

The $\delta^{13}C$ excursion reached peak values at the top of the Plenus Marls. Pre-excursion values average about 2.8‰ in the Grey Chalk, then gradually increased at the base of the Plenus Marls (Bed 1) to a peak of 4.75‰ in the middle of Bed 3 (first $\delta^{13}C$ shift). In Bed 4 $\delta^{13}C$ values decreased to about 4.3‰ (4.1‰ and 3.9‰ in the data sets of Paul *et al.*, 1999, and Lamolda *et al.*, 1994, respectively), rising gradually in the upper part of Bed 4 and through Beds 5 and 6. The second $\delta^{13}C$ shift reached a maximum of 5.3‰ in Beds 7–8 (Bed 8 in Paul *et al.*, 1999). Above this interval in the Ballard Cliff Member, $\delta^{13}C$ values plateau, though slightly declined to about 4.5‰ (Figure 5). The small scale cyclical oscillations observed in this interval (Ballard Cliff Member) may be largely as a result of lithological changes (Ditchfield & Marshall, 1989; Paul *et al.*, 1999).

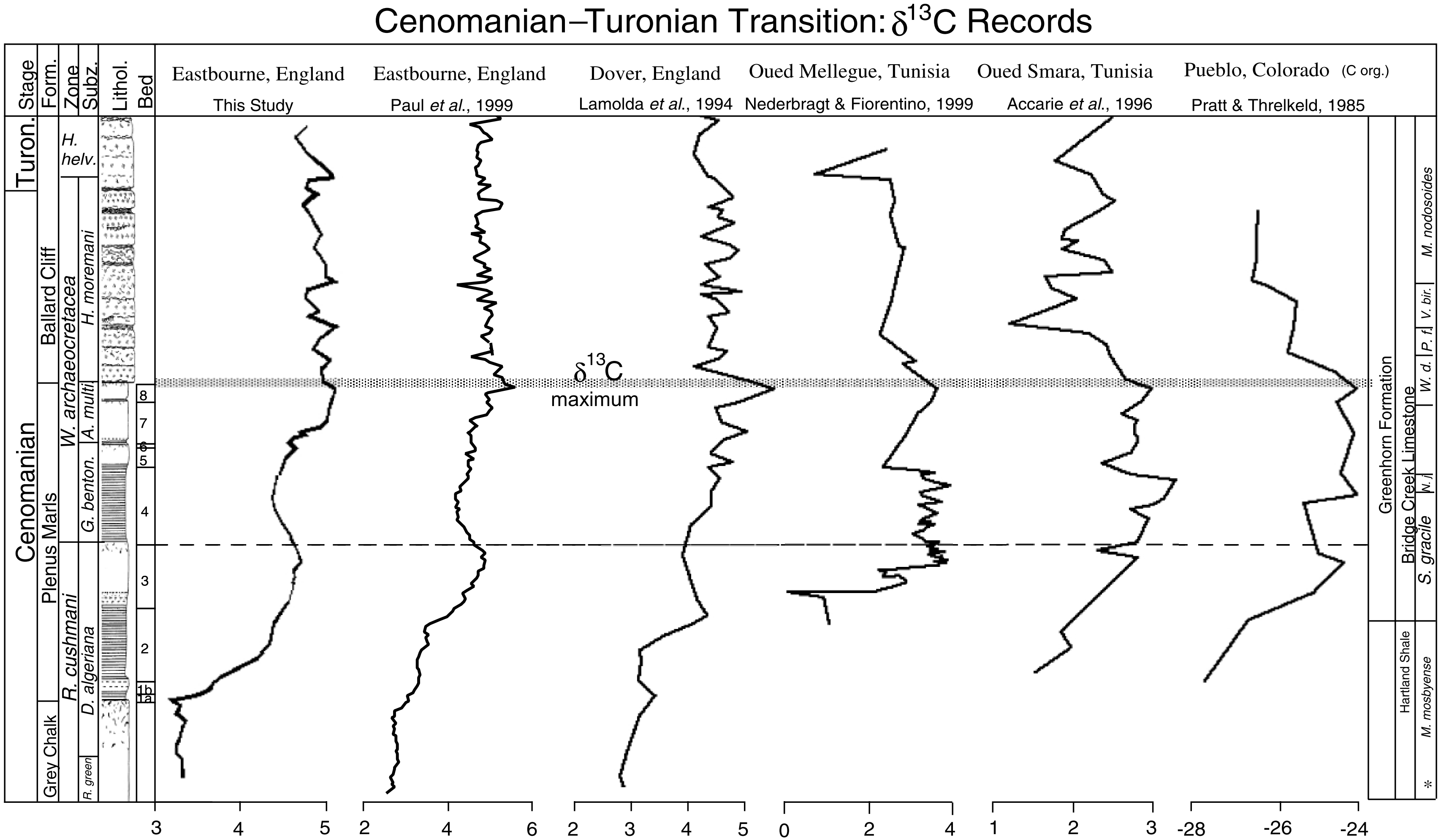
4.3. *$\delta^{13}C$ excursion and oceanic anoxic event*

The positive $\delta^{13}C$ excursion in whole rock carbonates observed at Eastbourne and documented globally in Cenomanian–Turonian transitions is generally attributed to enhanced marine productivity and preservation of organic matter (e.g., Arthur et al., 1987; Jenkyns *et al.*, 1994; Accarie *et al.*, 1996; Leckie *et al.*, 1998). In low to middle latitudes, black organic-rich facies represent an oceanic anoxic event (OAE) correlative with the CTBE, though the OAE and $\delta^{13}C$ excursion may not be coeval, as observed earlier by



* Correlation is based on ammonite zones and $\delta^{13}C$ by Gale *et al.*, 1993

Figure 4. Summary stratigraphical successions of bulk-sediment oxygen isotope ratios at Eastbourne, Dover, Tunisia, and of organic carbon at Pueblo, Colorado, USA. The two oxygen isotope records from Eastbourne differ significantly from that of Dover, particularly in the upper part of the Plenus Marls, suggesting a diagenetic overprint and/or variations owing to the much more condensed sequence at Dover. Correlation lines are based on the extinction of *Rotalipora cushmani* (dashed line) and the maximum $\delta^{13}C$ excursion and *Heterohelix* shift (shaded line).



* Correlation is based on ammonite zones and $\delta^{13}C$ by Gale *et al.*, 1993

Figure 5. Summary stratigraphical successions of bulk-sediment carbon isotope ratios at Eastbourne, Dover, Tunisia and of organic carbon at Pueblo, Colorado, USA. Note the similarity in the $\delta^{13}C$ excursion at all localities. Correlation lines are based on the extinction of *Rotalipora cushmani* (dashed line) and the maximum $\delta^{13}C$ excursion and *Heterohelix* shift (shaded line).

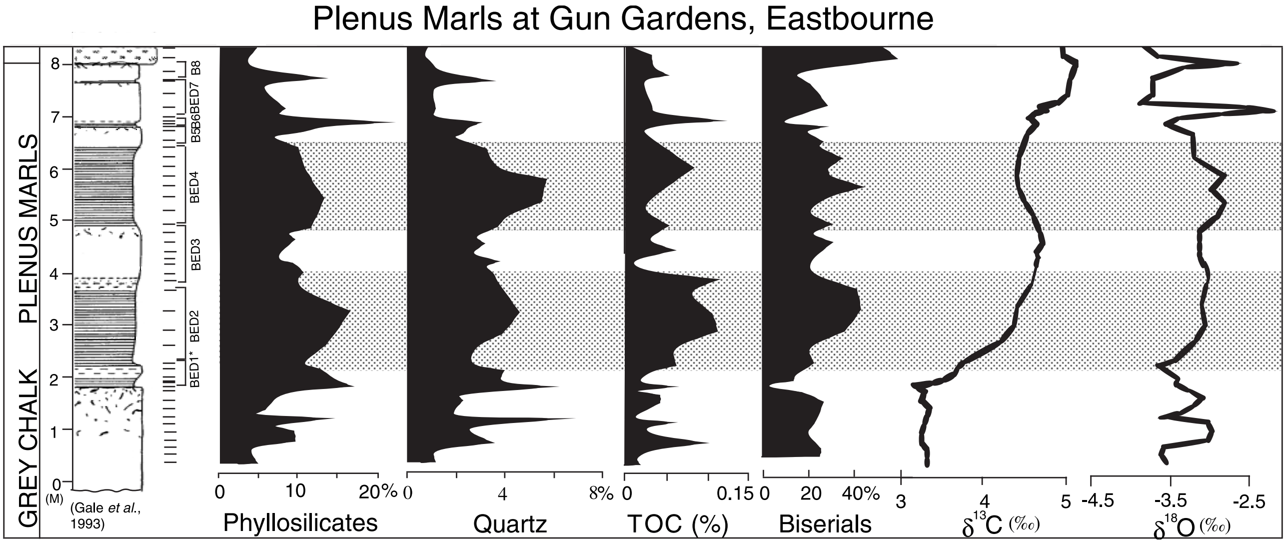


Figure 6. Lithological log, terrestrial influx (quartz), total organic carbon (TOC), relative abundance of low-oxygen tolerant biserial species and carbon isotopes at Gun Gardens, Eastbourne. The high relative abundance of biserial species correlates with enhanced TOC and high δ^{13}C values.

Hilbrecht (1986), Hilbrecht *et al.* (1986) and Hart & Leary (1989). This is also evident from biostratigraphic correlations between Eastbourne and sections in Italy and Tunisia. At Eastbourne where no OAE is present (total organic carbon TOC <0.1%; Figure 6), the δ^{13}C excursion begins at the base of the Plenus Marls in the upper *R. cushmani* Zone. In Tunisia the OAE is within the lower part of the *W. archaeocretacea* Zone, but the δ^{13}C excursion begins in the *R. cushmani* Zone coincident with the first organic-rich facies (Hardenbol *et al.*, 1993; Accarie *et al.*, 1996; Nederbragt & Fiorentino, 1999). Similarly in Italy the OAE, identified as the Bonarelli Level, is within the lower *W. archaeocretacea* Zone (Luciani & Cobianchi, 1999), which we correlate with the *A. multiloculata* Subzone and possibly also the *G. bentonensis* Subzone at Gun Gardens, Eastbourne. But the first major organic-rich facies is below the Bonarelli Level within the upper *R. cushmani* Zone (no stable isotope data available for this section). These data suggest that the δ^{13}C shift is synchronous world wide (e.g., Schlanger *et al.*, 1987; Jenkyns *et al.*, 1994; Accarie *et al.*, 1996), but that the OAE, or zone of maximum organic enrichment, when present, may have developed well after the onset of the δ^{13}C excursion.

The global extent of the δ^{13}C excursion indicates an increase in the global burial rate of organic carbon. In the Plenus Marls, organic carbon is very low, with 0.1% in marls and less than 0.02% in chalks (Figure 6), though Lamolda *et al.* (1994) and Paul *et al.* (1994) attributed the δ^{13}C excursion to increased rates of organic carbon burial, arguing that the alternative, increased primary productivity, is not supported by estimated coccolith accumulation rates. Similarly, Gale *et al.* (2000) attributed the decrease in total organic carbon from 0.21% in Bed 6 to 0.05% in Bed 7, and concurrent decreases in nannoplankton and foraminiferal abundances, to a drop in surface water productivity. However, inferring rates of primary productivity based on marine plankton is fraught with difficulties, as evident from the fact that the opposite conclusion may be argued based on planktic foraminifera.

For example, the relative abundance of biserial species (*Heterohelix*) covaries with TOC, with maximum values in marl layers. Small *Heterohelix* species, such as *H. moremani* and *H. reussi* that dominated during the CTBE, were low-oxygen tolerant and thrived within the oxygen minimum zone (Boersma & Premoli Silva, 1989, 1991; Kroon & Nederbragt, 1990; Keller, 1993; Barrera & Keller, 1994). A relative abundance increase in these species would therefore indicate an expansion of the oxygen minimum zone, which is normally associated with increased surface productivity and the depletion of oxygen in subsurface waters as a result of oxidation of organic carbon (Hart & Ball, 1986). It may, therefore, be argued that a high abundance of biserial species indirectly reflects high primary productivity. This would suggest a significant increase in primary productivity, at least in the marl layers of the Plenus Marls (notably Beds 2 and 4; Figure 6) and a major increase in the overlying Ballard Cliff Member where biserial species dominate (see below). The inferred increased

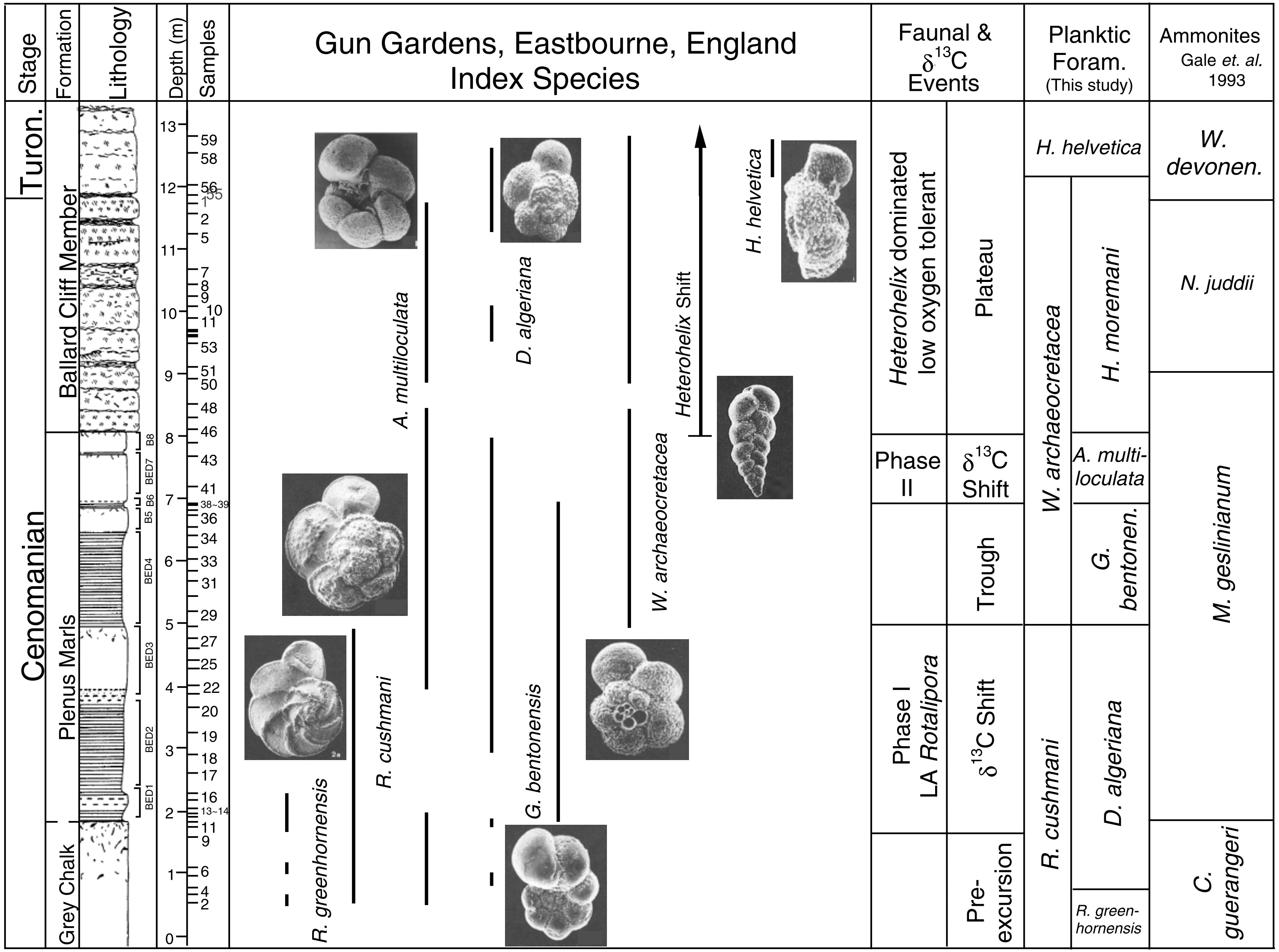
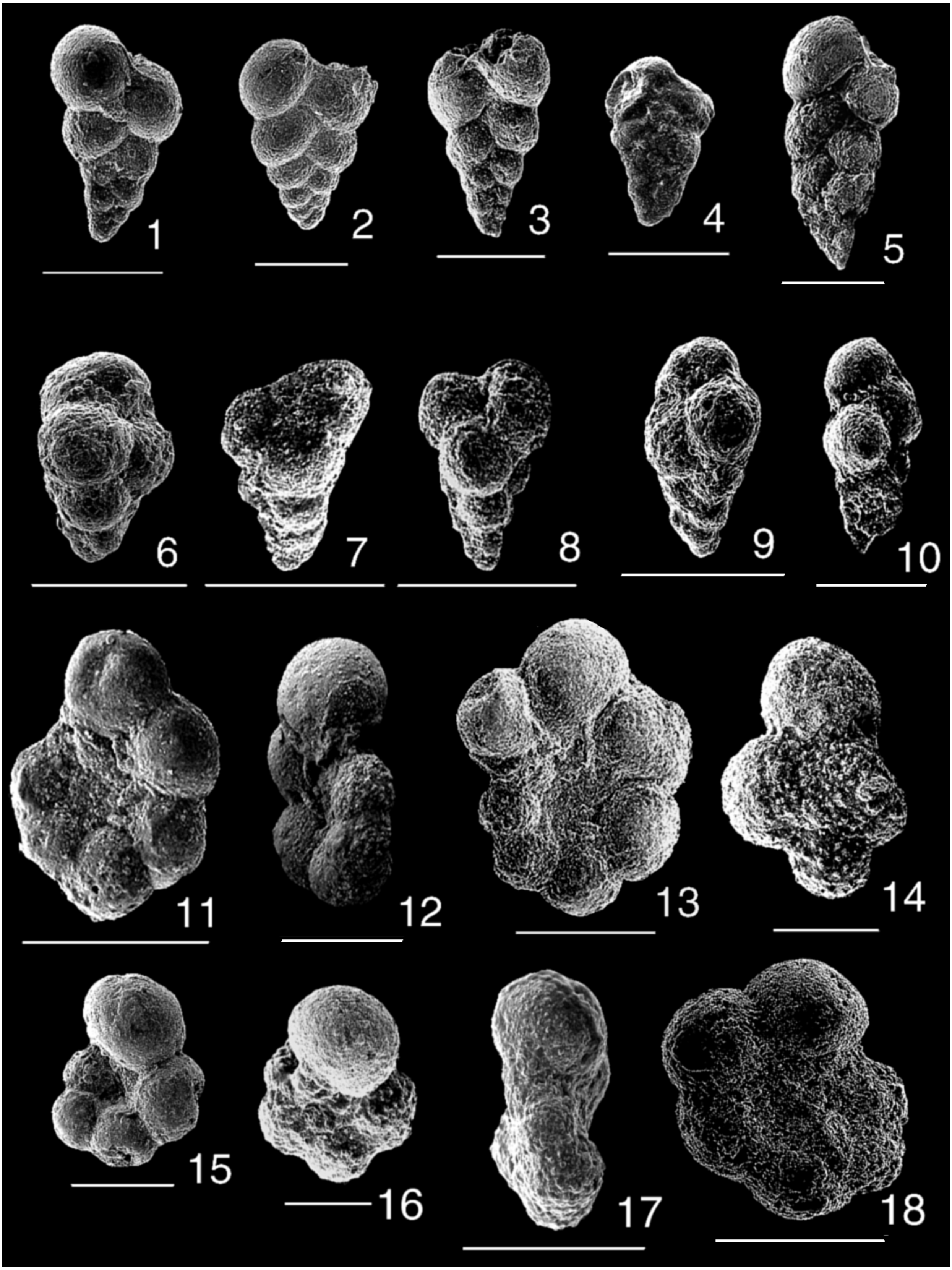


Figure 7. High resolution correlation scheme for the Cenomanian–Turonian transition based on planktic foraminiferal index species, faunal and δ^{13}C events at Gun Gardens, Eastbourne. The planktic foraminiferal *Whiteinella archaeocretacea* Zone is here subdivided into three subzones, which greatly enhance correlation of the CTBE across latitudes (SEM illustrations from Caron, 1985).


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

productivity in the marl layers of the Plenus Marls is associated with cooler temperatures, lower sea-levels, increased detrital influx, including terrestrial organic matter, which may have boosted primary productivity, and probably enhanced upwelling.

5. Biostratigraphy

The Late Cretaceous, including the Cenomanian–Turonian (C–T) transition, is stratigraphically defined by ammonite and inoceramid zones which provide reliable age determinations for regional correlations (e.g., Cobban, 1984; Gale *et al.*, 1993; Bengtson, 1996; Gale, 1996). At Eastbourne and elsewhere the Cenomanian–Turonian is recognized by: the *Calycoceras guerangeri* Zone in the Grey Chalk, the *Metoicoceras geslinianum* Zone, which spans the Plenus Marls and basal 1 m of the Ballard Cliff Member, and the *Neocardioceras juddii* Zone, which spans the lower part of the Ballard Cliff Member up to 12 m from the base of the section at Gun Gardens. However, neither inoceramid bivalves nor ammonites have a worldwide distribution across the C–T transition, which makes global correlations difficult (Cobban, 1984; Elder, 1987; Hancock, 1989; Kennedy & Cobban, 1991; Hardenbol *et al.*, 1993; Jenkyns *et al.*, 1994). In contrast, microfossils, such as planktic foraminifera and calcareous nannofossils, are widespread and offer excellent global correlation tools (Hart & Ball, 1986; Jarvis *et al.*, 1988; Hart & Leary, 1989; Paul *et al.*, 1999). This study uses planktic foraminifera to determine the biozonation and correlates the foraminiferal zones at the Gun Gardens section, with the ammonite zones of Gale *et al.* (1993) of the same section (Figure 7). The *Whiteinella archaeocretacea* Zone, is subdivided into three new subzones that yield improved correlation for the δ^{13}C excursion. Stratigraphically important species are illustrated in Figures 8–10.

Rotalipora cushmani Total Range Zone

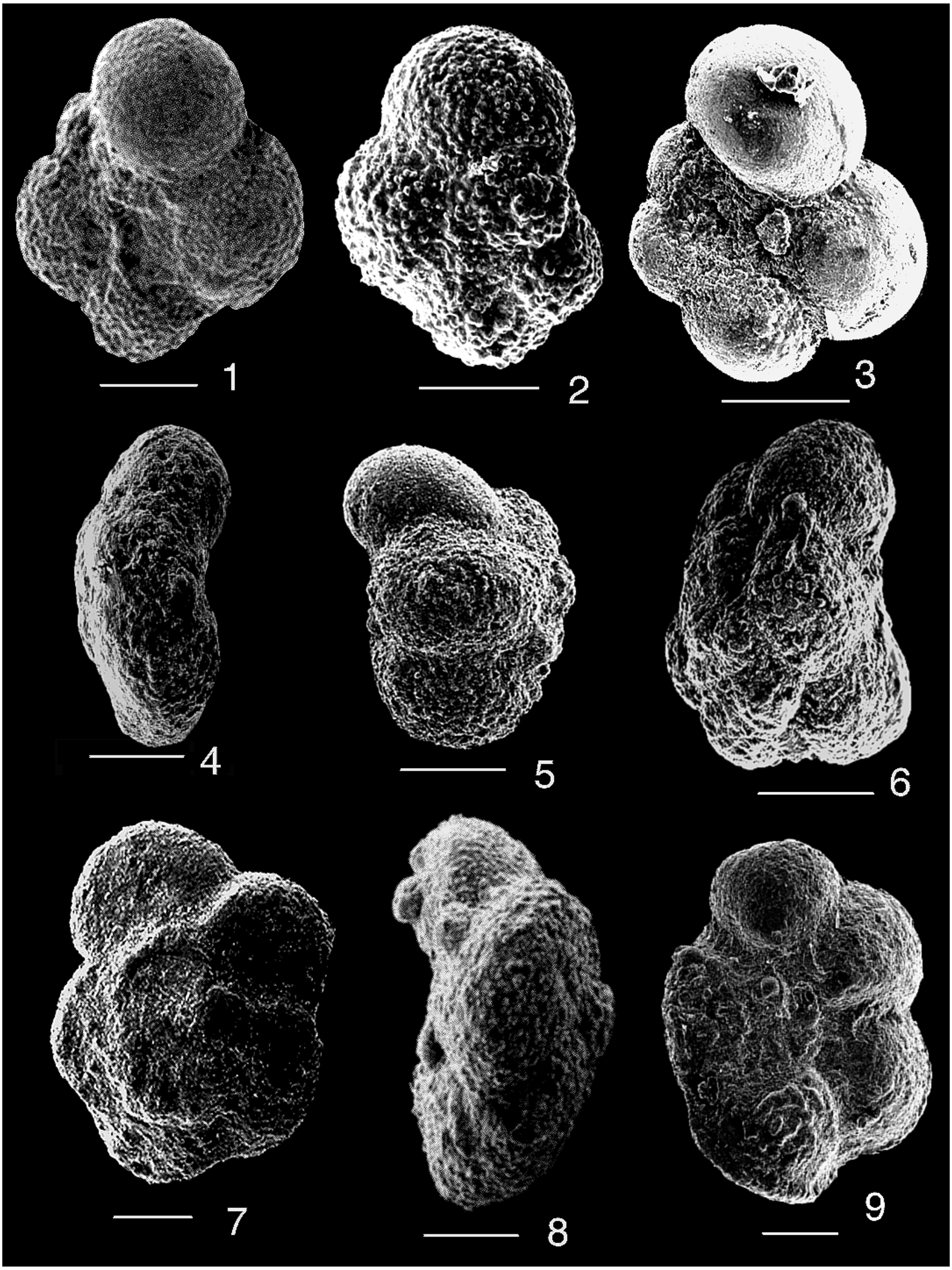
The *Rotalipora cushmani* Zone is defined by the total range of *R. cushmani* (Morrow). The base of this zone was not sampled at Gun Gardens. The extinction of *R. cushmani* marks the last representative of this genus, and at Gun Gardens coincides with the last appearance (LA) of *Rotalipora montsalvensis* at the top of Bed 3 and is nearly coincident with the top of the first δ^{13}C shift (Figure 7). Since this interval is also marked by a sharp erosion surface, the top ranges of these species may be truncated, although many studies have shown that the extinction of *R. cushmani* may be synchronous globally and precedes the ocean anoxic event (OAE 2) (e.g., Carter & Hart, 1977; Hart & Bigg, 1981; Hilbrecht & Hoefs, 1986; Jarvis *et al.*, 1988; Hart, 1996; Hilbrecht *et al.*, 1996; Lamolda *et al.*, 1997; Paul *et al.*, 1999). At Gun Gardens, the extinction of *R. cushmani* falls within the middle of the *Metoicoceras geslinianum* ammonite Zone. The base of the *M. geslinianum* Zone coincides with the upper *R. cushmani* Zone at the base of Bed 1 (Figure 7).

The genus *Rotalipora* is very rare and restricted to the base of the Gun Gardens section. *Rotalipora appenninica* (Renz) and *R. greenhornensis* (Morrow) disappeared simultaneously at the top of Bed 1 of the Plenus Marls and near the base of the δ^{13}C excursion (Figures 7, 10). The disappearance of *R. greenhornensis* seems to be synchronous with the records in other European sections (Hart & Ball, 1986; Jarvis *et al.*, 1988; Hart & Leary, 1991; Hart, 1996; Lamolda *et al.*, 1997; Paul *et al.*, 1999). This species extinction precedes the appearance of keeled *P. gibba* and double keeled *D. imbricata* (Figures 7, 9). *Rotalipora cushmani* and *R. montsalvensis* disappear at the top of bed 3 of the Plenus Marls and mark the extinction of the keeled genus *Rotalipora*, coincident with the top of the first δ^{13}C shift. Note that in this study we follow Robaszynski & Caron (1979) in distinguishing *R. montsalvensis* from *R. cushmani* by the not fully developed keel.

Rotalipora greenhornenesis Subzone

This subzone marks the interval from the first appearance (FA) of *R. cushmani* to the FA of *Dicarinella algeriana*. At Gun Gardens, *D. algeriana* is present in

Figure 8. Scanning electron micrographs of stratigraphically important biserial, triserial and planispiral planktic foraminifera at Gun Gardens, Eastbourne. Scale bars represent 100 µm. 1–3, *Heterohelix reussi* (Cushman), sample Eb57, *H. helvetica* Zone. 4, *Heterohelix* cf. *moremani*, sample Eb 31, *G. bentonensis* Subzone. 5, *Heterohelix moremani* (Cushman), sample Eb 31, *G. bentonensis* Subzone. 6–8, *Guembelitria cenomana* (Keller), sample Eb 30, *G. bentonensis* Subzone. 9–10, *Guembelitria albertensis* (Stelck & Wall), sample Eb 7, *H. moremani* Subzone. 11–13, *Globigerinelloides ultramicra* (Subbotina), sample Eb 5, *D. algeriana* Subzone. 14, *Hedbergella simplex* (Morrow), sample Eb 6, *D. algeriana* Subzone. 15–16, *Hedbergella delrioensis* (Carsey), sample Eb 3, *R. greenhornensis* Subzone. 17–18, *Hedbergella planispira* (Tappan), sample Eb 32, *G. bentonensis* Subzone.


1
2
3
4
5
6
7
8
9

the Grey Chalk Member (sample 4), although the first continuous occurrence begins in Plenus Marls Bed 2, just above the last appearances of *Rotalipora greenhornensis* and *R. appenninica* (Figure 7). Similar first and last appearances of *D. algeriana* and *R. greenhornensis* were reported from northern Spain (Lamolda *et al.*, 1997) and Tunisia (Nederbragt & Fiorentino, 1999). This suggests that the juxtaposition of these two species is a useful biostratigraphic marker within the *R. cushmani* Zone and marks the base of *D. algeriana* Subzone.

Although in northern Italy and the US Western Interior, *R. greenhornensis* is reported to range to the top of the *R. cushmani* Zone (Douglas, 1969; Eicher, 1969; Eicher & Diner, 1985; Leckie, 1985; Luciani & Cobianchi, 1999). This may be a result of either local variations in its range, or range truncation of *R. cushmani* because of a condensed interval or short hiatus particularly in the shallow Western Interior Seaway. However, biogeographic differences in species ranges at different latitudes are common. For example, several more temperate and cooler water species of the *Whiteinella* group (e.g., *W. aprica*, *W. baltica*, *W. paradubia*, Figure 8; see also Lamolda *et al.*, 1997) first appear earlier in the *R. greenhornensis* Subzone or near the base of the *D. algeriana* Subzone in the northern transitional zone than in the warmer environment of the Tethys Ocean to the south (Luciani & Cobianchi, 1999).

Dicarinella algeriana Subzone

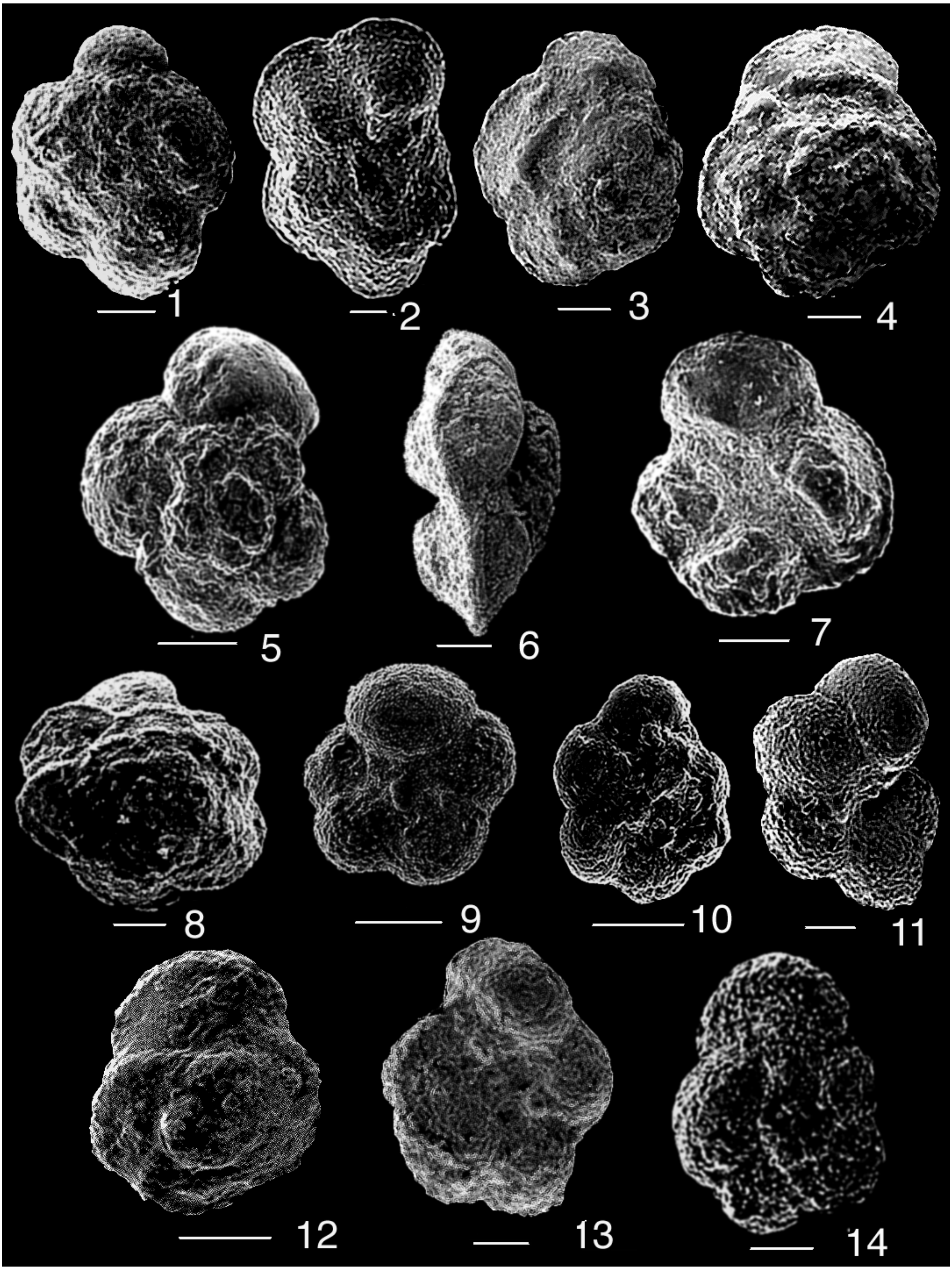
This subzone ranges from the FA of *D. algeriana* to the extinction of *R. cushmani* and all rotaliporids coincident with the top of the first $\delta^{13}C$ shift (Figure 7). *Rotalipora greenhornensis* and *R. appenninica* disappear in the lower part of this subzone (top of Plenus Marls Bed 1) followed by the LA of *Helvetoglobotruncana praehelvetica* and the FA of *D. imbricata* (Figures 10, 11). At the top of the subzone, *D. hagni* and *W. archaeocretacea* first appear near the extinction of *R. cushmani* at Gun Gardens as well as at localities in northern Spain (Lamolda *et al.*, 1997), northern Italy (Luciani & Cobianchi, 1999) and Tunisia (Nederbragt & Fiorentino, 1999). At Gun Gardens the juxtaposition of first and last appearances of these four species coincides with an erosion surface and suggests truncated species ranges (Figure 11), though the similar stratigraphic occurrences of these species in Spain, Italy and Tunisia indicate that this hiatus (though possibly present in all sections) is likely to be short.

At Gun Gardens, the first of two positive shifts in $\delta^{13}C$ values (1.8‰ increase) occurs in the *D. algeriana* Subzone (Figures 5, 7). This global positive shift in $\delta^{13}C$ values provides an important stratigraphic marker for the *D. algeriana* Subzone. Hedbergellids and guembelitrids significantly decreased coincident with the rise in $\delta^{13}C$ values, but *Whiteinella aprica* is abundant in this interval. *Whiteinella baltica* is common, but *W. brittonensis* (Loeblich & Tappan) and *W. paradubia* (Sigal) are rare. *Whiteinella brittonensis* differs from *W. aprica* by its higher spiral chambers (Figure 9). *Whiteinella paradubia* is characterized by the highest spiral chambers among the three *Whiteinella* species. The recognition of *Guembelitria albertensis* (Stelck & Wall) is based on its more slender shape as compared with *G. cenomana* (Keller) (Figure 8).

All species of the genus *Helvetoglobotruncana* are rare at the Gun Gardens section (Figure 12). *Helvetoglobotruncana praehelvetica* (Trujillo), which disappears in the Plenus Marls, is generally regarded as the ancestor of *H. helvetica* (Bolli), which first appears at the top of the Ballard Cliff Member. In the intervening interval neither of these morphotypes is present, which suggests adverse ecological conditions (low oxygen) for these taxa. *Helvetoglobotruncana praehelvetica* morphologies are distinguished from *H. helvetica* by a thicker body in side view and thinner keels. *Praeglobotruncana aumalensis* (Sigal) and *P. stephani* (Gandolfi) have similar species ranges as well as morphologies, except that the latter has a more obviously raised keel on the spiral side. Both *P. aumalensis* and *P. stephani* are absent above the C/T boundary, but this may be a result of their sporadic occurrence and poor preservation rather than extinction. *Helvetoglobotruncana praehelvetica*, *R. greenhornesis* and *R. appenninica* are only sporadically present in the Grey Chalk and lower part of the Plenus Marls.

Double-keeled morphotypes of the genus *Dicarinella* are also generally few to rare at Gun Gardens, but suggest recovery of deeper dwellers

Figure 9. Scanning electron micrographs of stratigraphically important whiteinellid planktic foraminifera at Gun Gardens, Eastbourne. Scale bars represent 100 µm. 1–3, *Whiteinella baltica* (Douglas & Rankin), sample Eb 18, *D. algeriana* Subzone. 4, *Whiteinella aprica* (Loeblich & Tappan), sample Eb 16, *D. algeriana* Subzone. 5, *Whiteinella brittonensis* (Loeblich & Tappan), sample Eb 18, *D. algeriana* Subzone. 6, *Whiteinella paradubia* (Sigal), sample Eb 17, *D. algeriana* Subzone. 7–9, *Praeglobotruncana gibba* (Klaus), sample Eb 18, *D. algeriana* Subzone.


1
2
3
4
5
6
7
8
9
10
11
12
13
14

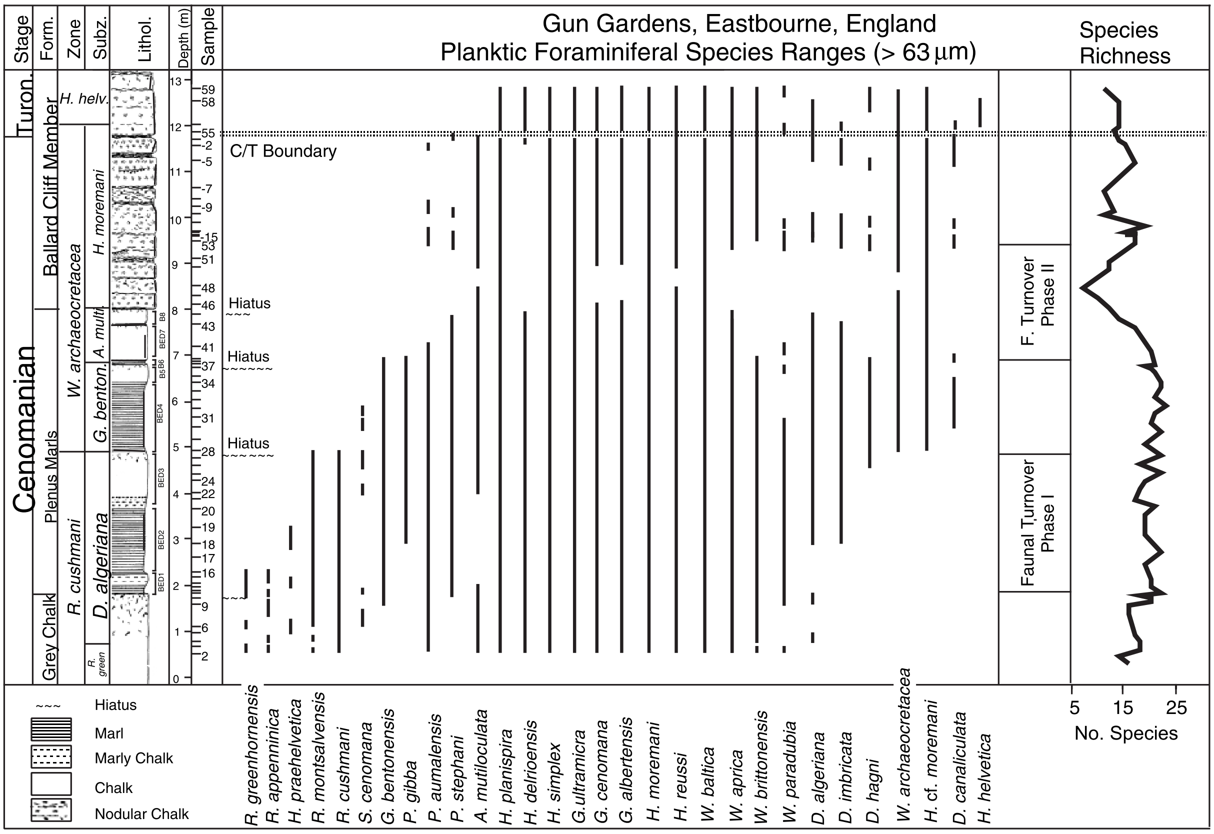


Figure 11. Planktic foraminiferal species ranges and species richness curve at Gun Gardens, Eastbourne. Note that species originations and extinctions are approximately equal through most of the Plenus Marls and the δ^{13}C excursion, but species richness decreased to a mere six species above the Plenus Marls owing to the temporary disappearances.

[e.g., *Dicarinella algeriana* (Caron), *D. imbricata* (Mornod), *D. hagni* (Scheibnerova) and *D. canaliculata* (Reuss), Figures 10–12]. Although all of these species range through the Ballard Cliff Member, their extreme rarity and temporary absence at Gun Gardens may reflect both the stressful low oxygen conditions (during the *H. moremani* Subzone) and the northern limit of their biogeographic range (Figure 1).

Comparison with ammonite zones at Gun Gardens indicates that the base of the *D. algeriana* Subzone is about 1 m below the base of the *Metoicoceras geslinianum* Zone of Gale *et al.* (1993). Stratigraphic and stable isotope correlations of Gun Gardens with the Pueblo, Colorado, section indicates that the *Metoicoceras geslinianum* Zone correlates with the *Siphonoceras gracile* Zone of Bengtson (1996). The top of the *R. cushmani* Zone and *D. algeriana* Subzone marks the middle of these ammonite zones.

Whiteinella archaeocretacea Zone

The *Whiteinella archaeocretacea* (Pessagno) Zone is defined as the interval from the last appearance of *Rotalipora cushmani* to the first appearance of *Helvetoglobotruncana helvetica* (Bolli). As noted above, the LA of *R. cushmani* coincides with an erosion surface and short hiatus at Gun Gardens (Figure 6).

Figure 10. Scaning electron micrographs of stratigraphically important keeled planktic foraminifera. Scale bars represent 100 µm. 1–2, *Rotalipora montsalvensis* (Mornod), sample Eb 18, *D. algeriana* Subzone. 3–4, *Rotalipora greenhornensis* (Morrow), sample Eb 18, *D. algeriana* Subzone. 5–7, *Rotalipora cushmani* (Morrow), samples Eb 18, Eb 5, *D. algeriana* Subzone. 8, *Dicarinella imbricata* (Mornod), sample Eb 26, *D. algeriana* Subzone. 9, *Dicarinella algeriana* (Caron), sample Eb 33, *G. bentonensis* Subzone. 10–11, *Anaticinella multiloculata* (Eicher), sample Eb 33, *G. bentonensis* Subzone. 12, *Dicarinella hagni* (Scheibnerova), samples Eb 32, 33, *G. bentonensis* Subzone. 14, *Helvetoglobotruncana helvetica* (Bolli), sample Eb 57, *H. helvetica* Zone.

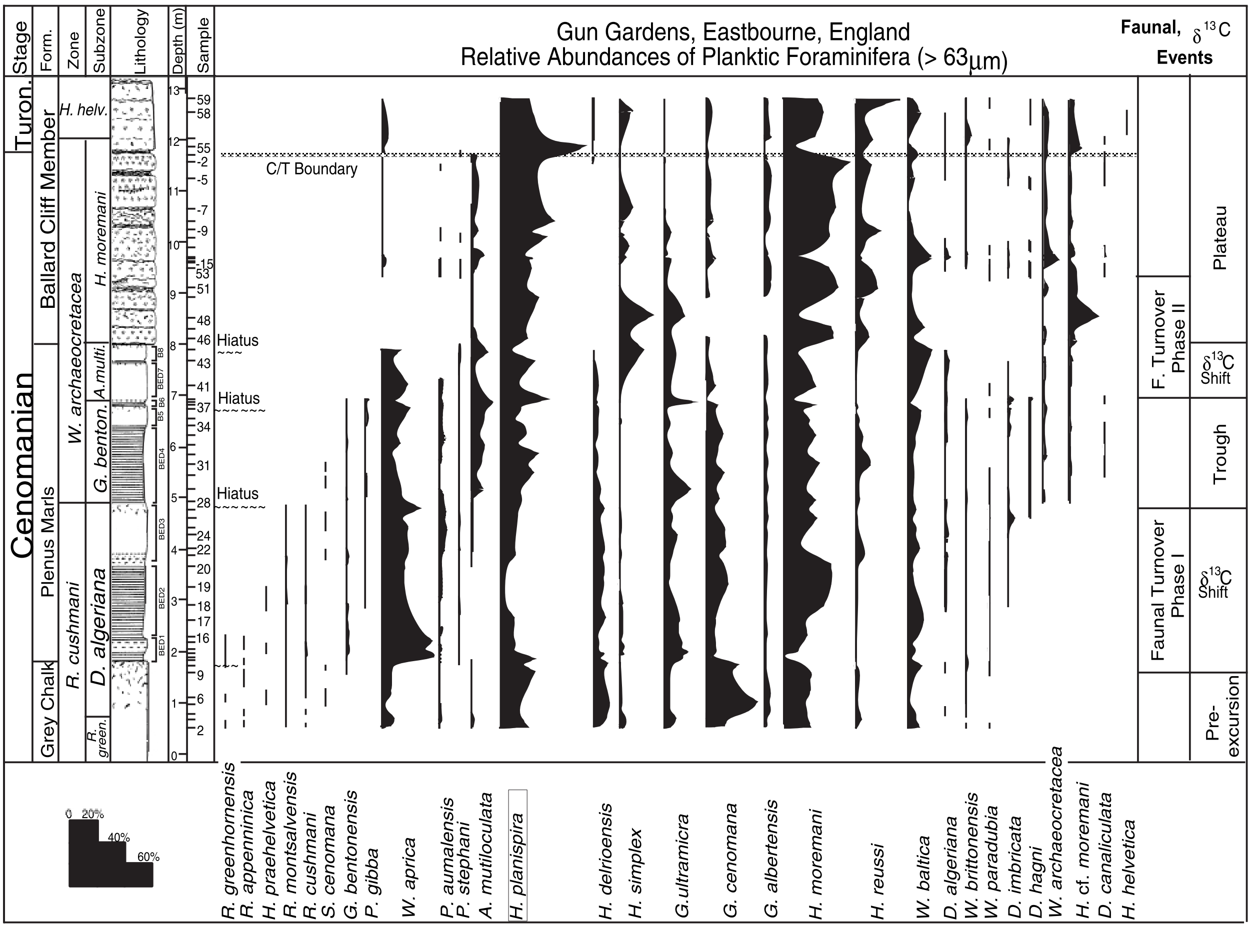


Figure 12. Relative species abundances of planktic foraminifera and δ^{13}C events at Gun Gardens, Eastbourne. All keeled species, which are subsurface dwellers, are relatively rare (total <2%). The faunal assemblages are dominated by surface dwellers (*Whiteinella, Hedbergella, Guembelitria*) and low-oxygen tolerant biserial taxa (*Heterohelix*).

Whiteinella archaeocretacea and a distinct biserial morphotype *H.* cf. *moremani* first appear at this hiatus. The top of the zone is about 20 cm above the base of the ammonite *Watinoceras devonense* Zone, which marks the C/T boundary (Figure 7). The *Whiteinella archaeocretacea* Zone can be subdivided into three subzones based on the LA of *Globigerinelloides bentonensis* and the *Heterohelix* shift as proposed herein.

Globigerinelloides bentonensis Subzone

The *G. bentonensis* Subzone is defined as the interval from the LA of *R. cushmani*, or the FA of *W. archaeocretacea* to the LA of *G. bentonensis*. At Gun Gardens, this interval corresponds with the lower third of the *W. archaeocretacea* Zone, spans Plenus Marls Beds 4–6 and coincides with the δ^{13}C trough between the two δ^{13}C shifts (Figures 5, 7). The disappearance of *G. bentonensis* in Bed 6 coincides with the disappearance of *Praeglobotruncana gibba*. However, an erosion surface and short hiatus in this interval suggests that the ranges of these species may be truncated (Figures 11, 12). However, this hiatus is likely to have been short since in northern Spain and Tunisia *G. bentonensis* also disappears in the lower third of the *W. archaeocretacea* Zone (Lamolda *et al.*, 1997; Nederbragt & Fiorentino, 1999). The range of this species in northern Italy is unclear because the interval of its occurrence is condensed and spans well into the Bonarelli Level, which is devoid of foraminifera (Luciani & Cobianchi, 1999). Paul *et al.* (1999) reported *G. bentonensis* as consistently present up to Bed 4 of the Plenus Marls, but noted a last occurrence in Bed 8, which we did not observe. At Gun Gardens, the *G. bentonensis* Subzone is dominated by a diverse assemblage of *Hedbergella planispira*, *Heterohelix moremani*, *Anaticinella multiloculata*, *Globigerinelloides ultramicra* and *Guembelitria cenomana* (Figures 8, 12). Dicarinellids (*D. algeriana*, *D. hagni*, *D. imbricata*) are rare, but consistently present.

Anaticinella multiloculata Subzone

This subzone defines the interval from the LA of *G. bentonensis* to the first appearance of abundant (>60%) *Heterohelix*, which represents a major long-term shift in planktic foraminiferal populations to biserial dominated assemblages. The subzone is also characterized by the disappearance of *P. gibba* near the base and the temporary disappearances of *W. aprica*, *P. aumalensis*, *H. delrioensis*, *D. algeriana*, *W. brittonensis*, *D. imbricata*, *D. hagni* and *D. canaliculata* (Figures 11, 12). These temporary species disappearances are accompanied by a second positive $\delta^{13}C$ shift of about 0.8‰ to maximum values of 5.3‰ at Gun Gardens (Figure 5). This second $\delta^{13}C$ shift appears to be characteristic of the $\delta^{13}C$ pattern across the C–T transition in England (Figure 5) and possibly globally (e.g., Accarie *et al.*, 1996; Paul *et al.*, 1999), and marks the *A. multiloculata* Subzone. This subzone spans chalk Beds 7 and 8 at the base of the Ballard Cliff Member at Gun Gardens (Figure 7). A sharp, burrowed, erosion surface marks the top of this subzone (top of Bed 8) and indicates a period of non-deposition or short hiatus. We correlate the *A. multiloculata* Subzone, and possibly the *G. bentonensis* Subzone, with the Bonarelli Level in Italy, as noted by Luciani & Cobianchi (1999).

The genus *Anaticinella*, represented by *Anaticinella multiloculata* (Eicher) in this study, appears about 1 m below the extinction of the genus *Rotalipora* (Figures 7, 10, 11). This planispiral species was once assigned to the non-keeled genus *Ticinella* owing to their morphological similarity. However, since the latter is limited stratigraphically to the Albian and latest Aptian, Eicher (1972) introduced the new genus *Anaticinella* to distinguish it phyletically as well as morphologically and biostratigraphically. Unfortunately, this genus was seldom reported and its occurrence seemed restricted to the United States where it was suggested to be an endemic genus of the interior seaway (Eicher, 1972; Leckie, 1985; Lamolda *et al.*, 1997). Leckie (1985) proposed that *R. cushmani* may have also given rise to the genus *Anaticinella* by losing its keel and occupying shallower waters in response to the expansion of the oceanic OMZ in the latest Cenomanian (see also Wonders, 1980). The occurrence of *A. multiloculata* at Gun Gardens indicates that this genus is not endemic to North America. At Gun Gardens, *A. multiloculata* co-occurs with *R. greenhornensis*, its suggested ancestor (Eicher, 1972), but also abruptly increases in relative abundance just above the extinction level of *R. cushmani*. This suggests that either of these *Rotalipora* species could have been the ancestor of *A. multiloculata* (Figure 10).

Heterohelix moremani Subzone

This subzone defines the interval from the first appearance of abundant *Heterohelix* to the FA of *Helvetoglobotruncana helvetica*. The shift to *Heterohelix*-dominated assemblages represents a major long-term shift in planktic foraminiferal populations. At Gun Gardens, the *Heterohelix* shift coincides with a sharp lithological change from chalk (Bed 8) to nodular chalk in the Ballard Cliff Member (Figures 2, 12). The *Heterohelix* shift appears to be global and has also been reported from Tunisia (Nederbragt & Fiorentino, 1999) and the US Western Interior Seaway where it has been used as powerful correlation tool (Leckie *et al.*, 1998) (Figure 13). The *H. moremani* Subzone is marked by the dominance of *Heterohelix* species, *H. moremani* and *H. reussi* at Gun Gardens and in northern Italy (Luciani & Cobianchi, 1999), *H. moremani* and *H. globulosa* in Tunisia (Nederbragt & Fiorentino, 1999), and undifferentiated heterohelicids in the US Western Interior Seaway (Leckie *et al.*, 1998; West *et al.*, 1998). A third biserial morphotype first appears at Gun Gardens coincident with the FA of *W. archaeocretacea* and LA of *R. cushmani*, and has been tentatively labelled *Heterohelix* cf. *moremani*. This species is similar to *H. moremani*, but less compressed, more slender and shorter, and bears a resemblance to *Zeauvigerina waiparaensis* of the late Maastrichtian and early Palaeocene (Keller, 1993).

Hedbergellids are common in the *H. moremani* Subzone, whereas keeled species are generally rare or absent (Figure 12). This subzone is also characterized by overall lower species richness, which is lowest at its base (down to six species; Figure 11) and marks the onset of a characteristic plateau with gradually decreasing $\delta^{13}C$ values at Gun Gardens, Pueblo, Kalaat Senan (Figure 5), and Menoyo, Spain (Paul *et al.*, 1994). At Gun Gardens, the *H. moremani* Subzone spans the first 4 m of the nodular chalk of the Ballard Cliff Member and roughly corresponds to the *N. juddii* ammonite Zone, though it begins 1 m below and ends about 20 cm above the *N. juddii* Zone (Figure 7).

Helvetoglobotruncana helvetica Zone

The total range of *Helvetoglobotruncana helvetica* defines this zone, which is generally regarded as marking the lowermost Turonian. The first appearance of the index species most closely approximates the FA level of the ammonite species *Watinoceras devonense* that was designated as defining the Cenomanian/Turonian boundary, and the section at the Rock Canyon Anticline near Pueblo that was

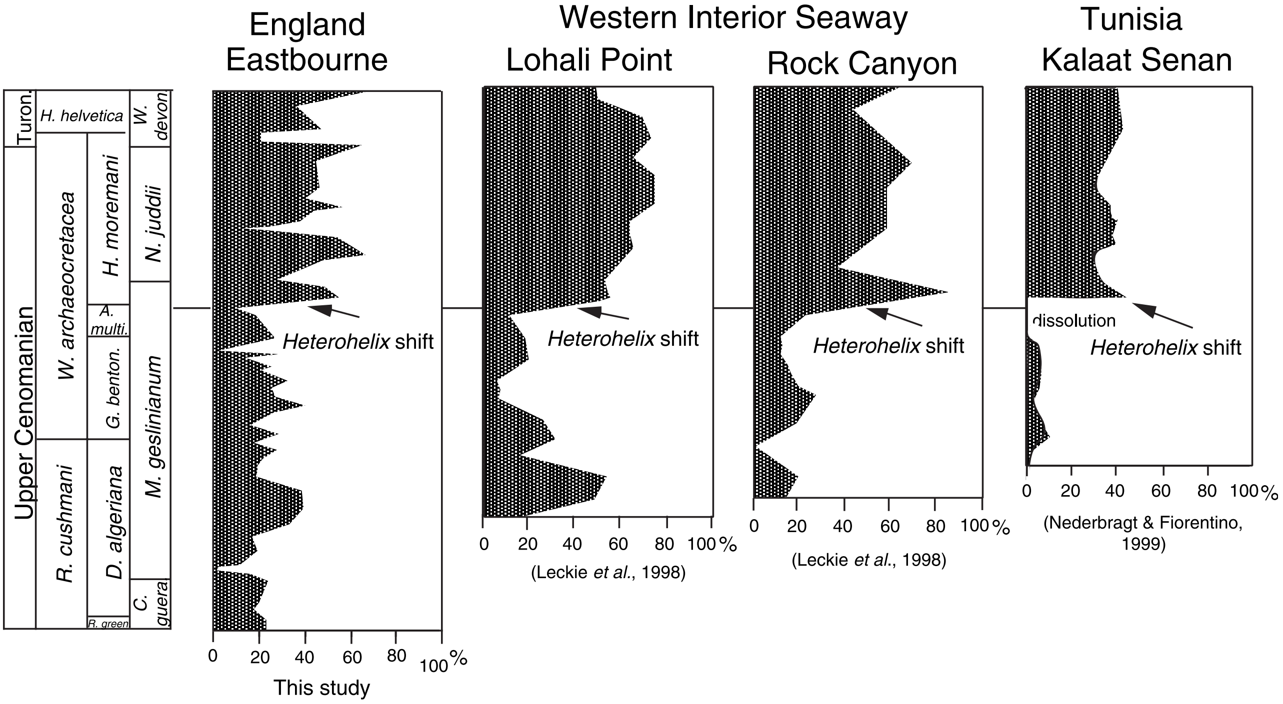


Figure 13. Relative abundances of *Heterohelix* at Gun Gardens, Eastbourne, Western Interior Seaway and Tunisia. At each locality there is a shift to *Heterohelix*-dominated assemblages which immediately follows the maximum $\delta^{13}C$ excursion and coincides with the temporary minimum in species richness and the onset of dwarfed species.

designated as the Global Boundary Stratotype Section and Point (GSSP) (Bengtson, 1996).

At Gun Gardens, the first appearance of *H. helvetica* is recorded at about 12 m above the base of the section and about 20 cm above the base of the *Watinoceras devonense* ammonite Zone (Figure 7). The rarity of *H. helvetica* at Gun Gardens and elsewhere leads to concerns of diachronous occurrences or different species concepts (Hart & Carter, 1975; Carter & Hart, 1977; Hart & Bigg, 1981; Hilbrecht, 1986; Hilbrecht *et al.*, 1986; Jarvis *et al.*, 1988). According to Carter & Hart (1977), the limit of the northern range distribution of this species is at palaeolatitude 40°N, or very near Gun Gardens, during the C–T transition (Figure 1). This suggests that the first appearance of *H. helvetica* at Gun Gardens may be diachronous and therefore not reliable as zonal marker. However, the correlation of biozones at Gun Gardens, with those of the Helvetic Zone (Alps) in Europe indicates that the first appearance of *H. helvetica* is at similar stratigraphic positions in these localities (Hilbrecht *et al.*, 1992). At the Pueblo, stratotype section, comparison of the carbon isotope stratigraphy with that of Gun Gardens indicates that the FA of *H. helvetica* may occur slightly later (about 1 m above) at Pueblo (Gale *et al.*, 1993; Bengtson, 1996).

6. Faunal turnover

6.1. *Cenomanian/Turonian Boundary Event (CTBE)*

The Cenomanian/Turonian Boundary Event occurred during deposition of the Plenus Marls at Gun Gardens, though the species-richness curve reveals little change because species disappearances nearly equal first appearances (Figure 11). But species census and relative abundance data reveal that this faunal turnover occurred in two phases that coincide directly with the two $\delta^{13}C$ shifts within the overall $\delta^{13}C$ excursion (see also Hart & Leary, 1991; Gale et al., 2000). During the first $\delta^{13}C$ shift in Plenus Marls Beds 2 and 3 (*D. algeriana* Subzone), four rotaliporid species and *H. praehelvetica* (*c.* 25%) disappeared and one new species (*D. imbricata*) appeared, but all of these species are rare (<2% of the total assemblage; Figure 12). However, dominant species show significant abundance changes during this interval. Hedbergellids [*H. planispira* Tappan, *H. delrioensis* (Carsey) and *H. simplex* (Morrow); Figure 8], and triserial species (*G. cenomana*) are abundant (20–40% each group) in the pre-excursion $\delta^{13}C$ interval, but declined to a minimum of 10–15% during the $\delta^{13}C$ shift. In contrast, biserial species thrived (*c.* 40%) and most other common species show only minor effects (Figure 12). Jarvis *et al.*

(1988) noted that several new macrofossil species appeared in this interval at Dover, Lamolda *et al.* (1994) documented a decline in calcareous nannofossil species, and Gale *et al.* (2000) noted a rapid faunal turnover near the base of the Plenus Marls Member.

There was a temporary recovery during the subsequent $\delta^{13}C$ trough (*G. bentonensis* Subzone, Plenus Marls Beds 4–6), with four new species and only one species disappearing (Figures 11, 12). Hedbergellids and *A. multiloculata* recovered in this interval, heterohelicids decreased, and most other common species remained unchanged (Figure 12). This interval is generally associated with the incursion of Jefferies' (1963) cool water boreal fauna.

The second faunal turnover coincides with the second $\delta^{13}C$ shift in the *A. multiloculata* Subzone; (Plenus Marls Beds 7–8; Figure 11). In this interval two species disappeared (*G. bentonensis*, *P. gibba*) and ten species temporarily disappeared. In the upper part of this subzone (Bed 8), hedbergellids recovered, though *W. aprica*, *A. multiloculata* and *G. cenomana* decreased and temporarily disappeared. Species richness census data mark this second faunal turnover with a temporary drop to as low as six species coincident with the second $\delta^{13}C$ shift (Bed 8 and base of Ballard Cliff Member, base *H. moremani* Subzone; Figure 11). A similar diversity decrease in this interval at Eastbourne and Dover was also observed in dinoflagellates that temporarily disappeared (Jarvis *et al.*, 1988), calcareous nannofossils (Jarvis *et al.*, 1988; Paul *et al.*, 1994; Lamolda *et al.*, 1994; Gale *et al.*, 2000), ostracods, and planktic and benthic foraminifera (Jarvis *et al.*, 1988; Paul *et al.*, 1999; Gale *et al.*, 2000).

Although the CTBE is marked by a major faunal turnover in two phases, the very few species extinctions and the rarity of species going extinct (<5% of the assemblages) indicate that no major mass extinction occurred in planktic foraminifera across the C–T transition in England, as also observed by Gale *et al.* (2000). Rather than a mass extinction as reported in low latitudes (Wonders, 1980; Leckie *et al.*, 1991; Tur, 1996), the observed pattern displays the selectivity of species extinctions related to environmental changes.

6.2. Heterohelix *shift and oxygen minimum zone*

The $\delta^{13}C$ plateau with gradually declining values through the Ballard Cliff Member and very low species diversity is the last phase of the CTBE faunal turnover. This interval is globally dominated by heterohelicids (*H. moremani*, *H. reussi*; Figure 8) and secondarily by hedbergellids (Leckie *et al.*, 1998; West *et al.*, 1998; Luciani & Cobianchi, 1999; Nederbragt & Fiorentino, 1999). At Eastbourne and in the US Western Interior Seaway, *Heterohelix* increased from 20 to over 60%, and in Tunisia from 10 to about 40% (Figures 10, 11).

Heterohelix species are interpreted as opportunistic and low-oxygen tolerant based on Late Cretaceous and Cenozoic studies (Boersma & Premoli Silva, 1989, 1991; Kroon & Nederbragt, 1990; Keller, 1993; Barrera & Keller, 1994). Across the Cretaceous–Tertiary transition *Heterohelix* (including *H. globulosa* and *H. moremani*) ranged into high latitudes where they dominated, replacing *Guembelitria* (Keller, 1993; Keller *et al.*, 1993; Pardo *et al.*, 1999). In low to middle latitudes these species thrived in well-stratified open marine settings with a well-developed oxygen minimum zone (Boersma & Premoli Silva, 1989; Keller, 1993, 1996; Resig, 1993; Keller *et al.*, 1993, in press). High abundances of *Heterohelix* species thus reflect an expanded oxygen minimum zone during the Cretaceous–Tertiary transition and these species are likely to have had similar environmental adaptations during the Cenomanian–Turonian transition.

There are several lines of evidence that support an expanded oxygen minimum zone coincident with the *Heterohelix* shift during deposition of the Ballard Cliff Member. Biotic evidence for high surface productivity and a major expansion of the oxygen minimum zone is seen in the very low species richness in planktic foraminifera (Figure 11), dwarfing of planktic foraminifera (see below), near absence of deeper dwellers (Table 1), dominance of *Heterohelix* (Figure 13), and the relatively high abundance of surface dwellers (*Hedbergella* and *Whiteinella*). In addition, ostracods and benthic foraminifera also decreased in diversity, size and abundance and are interpreted as the result of reduced oxygen levels (Jarvis *et al.*, 1998; Paul *et al.*, 1999). As noted above, increased surface productivity and an expanded oxygen minimum zone may also have occurred during marl deposition in Beds 2 and 4 of the Plenus Marls, as suggested by the increased abundance of *Heterohelix* and slight increase in total organic carbon (Figure 6). But unlike the Ballard Cliff interval, deposition of the Plenus Marls occurred during a lower sea level or a sea-level regression and possibly cooler temperatures and increased upwelling.

The interpretation of an expanded oxygen minimum zone associated with the $\delta^{13}C$ excursion in the Dover–Eastbourne region remains somewhat controversial because of the absence of organic-rich sediments. Jarvis *et al.* (1988) argued that since deposition of organic-rich sediments is controlled by rates of organic matter production, water depth and bulk sediment accumulation rates, they are not directly related to seawater oxygenation levels. For example, in many modern high-productivity upwelling areas (e.g., Gulf of California; Calvert *et al.*, 1992) no organic-rich sediments accumulate. Jeans *et al.* (1991) argued that the very low total organic carbon content within the Plenus Marls and Ballard Cliff Member may be owing to oxidization by bacteria during early diagenesis. They suggested that the higher primary productivity in the chalk facies is linked to greater availability of soluble Fe as a result of higher temperatures and greater oxidation of organic matter within the water column, both of which would lower the oxygen concentration in the water column. But on the basis of nannofossil abundance and diversity, Lamolda *et al.* (1994) argued for a progressive decline in productivity through the Plenus Marls, with a weak recovery to about one-half of the initial values in the overlying Ballard Cliff (Melbourn Rock), whereas Gale *et al.* (2000) argued for a primary productivity drop near the top of the Plenus Marls Member. The results of this study, including the heterohelicid abundance pattern, are more in keeping with those of Jarvis *et al.* (1988) and Jeans *et al.* (1991), suggesting a moderate increase in surface productivity and expansion of the oxygen minimum zone during deposition of the Plenus Marls, associated with a sea-level regression. A major productivity increase during deposition of the Ballard Cliff chalks is associated with warming and a sea-level transgression.

6.3. *Dwarfism and nutrient-rich environments*

All planktic foraminiferal species with simple morphologies (biserial, triserial, planispiral, and trochospiral) show a marked decrease in overall size beginning in Bed 8 and continuing through the Ballard Cliff Member. Similar size changes were reported for benthic and planktic foraminifera by many other workers (e.g., Phleger & Souter, 1973; Hart & Bigg, 1981; Perez-Cruz & Machain-Castillo, 1990; Koutsoukos *et al.*, 1990; Kaiho & Hasegawa, 1994; Leckie *et al.*, 1998; Luciani & Cobianchi, 1999; Paul *et al.*, 1999), as well as for ostracods, ammonites and bivalves (Harries, 1993; Paul *et al.*, 1999). The cause for dwarfism is still somewhat controversial. Paul & Mitchell (1994) argued that food shortage favoured species that reproduced before they starved. But Lipps (1979) and MacLeod *et al.* (2000) contended that dwarfing is generally associated with nutrient-rich environments which favours populations that can utilize resources fastest by rapid reproductive rates and early sexual maturation.

Size reductions of benthic and planktic species are generally observed across the K–T transition, where in low latitudes they coincide with the negative $\delta^{13}C$ shift, high TOC and low-oxygen conditions. Surface productivity is generally low amid nutrient-rich waters as a result of the mass extinction of all tropical and subtropical species. However, ecological opportunist survivor species, such as *Heterohelix globulosa* and *Guembelitria cretacea*, thrived (Brinkhuis & Zachariasse, 1988; Keller, 1988, 1989; Barrera & Keller, 1990; Luciani, 1997; Keller *et al.*, 1998). In high latitudes, size reductions are also associated with high TOC, low oxygen, and nutrient-rich waters. But at most a very small (<1‰) $\delta^{13}C$ excursion occurred and surface productivity remained relatively high among endemic high-latitude survivor species (e.g., *H. globulosa*, *Zeauvigerina waiparaensis*, *Guembelitria cretacea*; Keller, 1993; Keller *et al.*, 1993; Barrera & Keller, 1994; Pardo *et al.*, 1999). At the Cenomanian–Turonian transition high surface productivity as a result of increased upwelling and/or organic carbon influx because of sea-level changes and reduced oxygen may have been the likely cause for the observed dwarfing.

6.4. *Depth assemblages and water-mass stratification*

The evolution, diversification and extinction of planktic foraminifera are generally associated with stratification of the water column, variations in the trophic structures, vertical temperature and density gradients, and associated ecologic niche differentiation (Be, 1977; Lipps, 1979; Hart, 1980b; Wonders, 1980; Caron & Homewood, 1983; Hallock *et al.*, 1991; Leckie *et al.*, 1998; Li & Keller, 1998). Fundamentally important in maintaining planktic foraminiferal communities is stratification of the upper water column, which is affected by seasonal changes in the thermocline that in turn affects nutrient availability, nutrient cycling, productivity, reproduction and predation. Diversity of planktic foraminifera is proportional to the water-mass stratification, with highest diversity within a stable, stratified water column with normal salinity and nutrient waters, and year-round temperature gradients that provide a variety of ecological niches and a stable nutrient supply (Lipps, 1979; Leckie *et al.*, 1998; Hallock *et al.*, 1991).

The type of ecological niches occupied can be inferred from the diversity and relative species abundances, morphologies of species and biogeographic distributions. Complex morphotypes (e.g., keeled and highly ornamented species) generally occupy deeper oligotrophic environments, exist in assemblages with high species diversity but generally low species abundances, have larger morphologies, and prefer low and middle latitude open marine environments. Simpler morphotypes (e.g., little surface ornamentation, thin test walls) generally occupy the surface mixed layers (above thermocline), or shallow waters with generally unstable and/or eutrophic conditions, have small test sizes, low species diversity and often high species abundances, and predominate in higher latitudes, upwelling regions, shallow epicontinental seas and nearshore areas (Hart, 1980a, b; Caron & Homewood, 1983; Leckie, 1987; Keller, 1988, 1996; Li & Keller, 1998). At times of environmental extremes, these regions are inhabited by ecological opportunists, such as the small, thin-walled, triserial *Guembelitria*, biserial *Heterohelix* and trochospiral *Hedbergella* morphotypes. For example, during the K/T crisis, *Guembelitria* thrived in shallow marginal marine environments where they were most abundant in low to middle latitudes and probably tolerant of both salinity and oxygen variations (Keller, 1996; Abramovich *et al.*, 1998; Keller *et al.*, in press). In the modern ocean *Guembelitria* survives in upwelling areas of the northern Indian Ocean (Kroon & Nederbragt, 1990). *Heterohelix* ranged more widely into high latitudes and thrived in well-stratified open marine settings with a well-developed oxygen minimum zone (Boersma & Premoli Silva, 1989, 1991; Keller, 1993, 1996; Keller *et al.*, 1993; Resig, 1993; Pardo *et al.*, 1999). Similar habitats may have been occupied by these morphotypes during the Cenomanian/Turonian crisis.

Across the Cenomanian–Turonian transition, ecological opportunists also dominated in surface waters and consisted of the triserial *Guembelitria*, the biserial *Heterohelix* and trochospiral *Hedbergella* (Figure 8). Leckie *et al.* (1991, 1998) suggested that all of these preferentially inhabited shallower nearshore environments (see also Hart & Ball, 1986), although *Guembelitria* appears to have preferred somewhat warmer marginal marine environments with normal nutrient flux, as suggested by their maximum abundance at Gun Gardens prior to the $\delta^{13}C$ excursion, and they are most abundant in low to middle latitudes (Leckie *et al.*, 1998). *Heterohelix* ranged more widely into higher latitudes and also thrived in a well-stratified water column with a well-developed oxygen minimum zone (Eicher, 1969; McNeil & Caldwell, 1981; Leckie *et al.*, 1991, 1998). Whiteinellids also thrived in shallow marginal marine settings. However, all of these species are also common in the open ocean.

Depth habitats can also be inferred from $\delta^{13}C$ and $\delta^{18}O$ ranking of well-preserved test calcite from individual species. Although for the Cenomanian–Turonian interval such data are still scarce, they provide a glimpse of temperature-related depth habitats that are generally consistent with those inferred from morphology and biogeographic distributions. *Hedbergella* (*H. planispira*, *H. delrioensis*, and *H. simplex*) and *Whiteinella* (*W. archaeocretacea*) have consistently heavier carbon and lighter oxygen isotopic values than rotaliporid species. This indicates that they are surface dwellers in a thermally stratified ocean (Norris & Wilson, 1998; Price *et al.*, 1998), although Norris & Wilson (1998) asserted that in the low latitude open ocean *Hedbergella* (e.g., *H. simplex* and *H. delrioensis*) grew within thermocline waters, thus contradicting the conclusion reached by Price *et al.* (1998). When challenged by Price & Hart (1999), they conceded that their isotopic data are inconclusive and show enough scatter to warrant further testing in other localities (Norris & Wilson, 1999). The disagreement between these two studies may be a result of the small database and hedbergellid palaeoecology.

Hedbergellids are opportunistic species which Leckie *et al.* (1988, p. 107) labelled the 'weeds' of the mid-Cretaceous ocean, thriving in great abundances in both open marine and epicontinental settings (see also Premoli Silva & Sliter, 1995). They may have thrived in either thermocline or surface waters, as suggested by the wide range of temperature-related habitats (Price *et al.*, 1998) and, particularly in shallow marginal seas, they may have adapted to low salinity and high nutrient conditions. At Eastbourne, as well as in the US Western Interior Seaway, *Hedbergella*, *Whiteinella* and *Heterohelix* groups are the major components of the 'shallow water fauna' and in this study we group them as ecological opportunist 'surface dwellers' (Table 1), though we realize that further studies are needed across latitudes in both open ocean and marginal marine settings to determine the variations in the life habitats of these species.

Globigerinelloides, a planispiral morphotype, and *Shackoina* are generally present in low abundances and disappear shoreward (Leckie *et al.*, 1998), preferring more open marine settings as also observed across the K–T transition. We consider them as having lived below the surface mixed layer, but above keeled morphotypes. Keeled morphotypes, *Rotalipora, Dicarinella*, *Praeglobotruncana*, and *Helvetoglobotruncana* (Figure 10) are diagnostic of low to middle latitude open marine and normal stratified water masses where they occupied waters within or below the thermocline, as suggested by their consistently

Table 2. Depth ranking of late Cenomanian–early Turonian planktic foraminifera based on environmental inferences (morphology, biogeographic distribution) and stable isotopic data.

Surface assemblage (Surface mixed layer)	Intermediate assemblage (Thermocline)	Deep assemblage (Below thermocline)
*Hedbergella delrioensis**	*Shackoina cenomana*	*Rotalipora cushmani**
Hedbergella planispira	*Globigerinelloides bentonensis*	*R. greenhornensis*
*Hedbergella simplex**	*Anaticinella multiloculata*	*R. appenninica*
(Ecological opportunists, surface dwellers in shallow marginal settings)		*R. montsalvensis*
	Praeglobotruncana gibba	*Helvetoglobigerina helvetica*
	P. aumalensis	*Helvetoglobigerina praehelvetica*
*Whiteinella archeocretacea**	*P. stephani*	
Whiteinella aprica	*Dicarinella canaliculata*	
Whiteinella baltica	*Dicarinella algeriana*	
Whiteinella brittonensis	*Dicarinella imbricata*	
Whiteinella paradubia	*Dicarinella hagni**	
Guembelitria cenomana		
Guembelitria albertensis		
(Ecological opportunists, abundant in marginal marine settings, thrived in high-stress, high-nutrient environments)		
Heterohelix moremani		
Heterohelix reussi		
Heterohelix cf. *moremani*		
(Ecological opportunists, low-O_2 tolerant, thrived in oxygen minimum zone. Most abundant in well-developed oxygen minimum zone, but also common in surface mixed layer, though below *Guembelitria* and *Hedbergella*)		

*Depth ranking based on stable isotope depth ranking.

heavier oxygen and lighter carbon isotopic values (Jeans *et al.*, 1991; Price *et al.*, 1998; Norris & Wilson, 1998). A similar depth profile for globotruncanids was observed in the Maastrichtian (Premoli Silva & Sliter, 1995; D'Hondt & Arthur, 1995; Li & Keller, 1998). We tentatively rank keeled morphotypes as deeper water dwellers living below the thermocline, except for *Dicarinella* and *Praeglobotruncana* which may have been thermocline dwellers (Table 2).

In well-preserved foraminiferal tests, the δ^{13}C and δ^{18}O profiles reflect different depth habitats within a normally stratified water column where the δ^{13}C is controlled by phytoplankton production and subsequent oxidation as organic carbon settles through the water column, and δ^{18}O is controlled by the water temperature (Corfield *et al.*, 1990; Jeans *et al.*, 1991). Stable isotope ranking of the species measured thus indicates that the relatively small, thin-walled and little ornamented hedbergellids (*H. delrioensis*, *H. simplex*) and whiteinellids (*W. archaeocretacea*) were surface dwellers, whereas the larger, heavily ornamented and thick-walled keeled species *Rotalipora cushmani* and *Dicarinella hagni* were deeper water dwellers that probably lived within or below the thermocline layer consistent with depth habitats inferred from biogeographic species distributions (Table 2).

7. Discussion

7.1. Faunal changes

The climate, sea level and productivity fluctuations during deposition of the Plenus Marls and Ballard Cliff Member strongly influenced marine plankton and benthos leading up to what is commonly known as the Cenomanian/Turonian Boundary Event. However, the Plenus Marls and Ballard Cliff Member show no major species extinctions in planktic foraminifera and the faunal turnovers are largely a consequence of enhanced oxygen and nutrient fluctuations in a marginal marine setting. Our study provides few data on the Grey Chalk Formation, though peak abundance (*c.* 50%) of triserial *Guembelitria* and relatively low δ^{13}C values suggest a shallowing or restricted marginal marine environment. At the base of the Plenus Marls (Bed 1) peak abundance of the

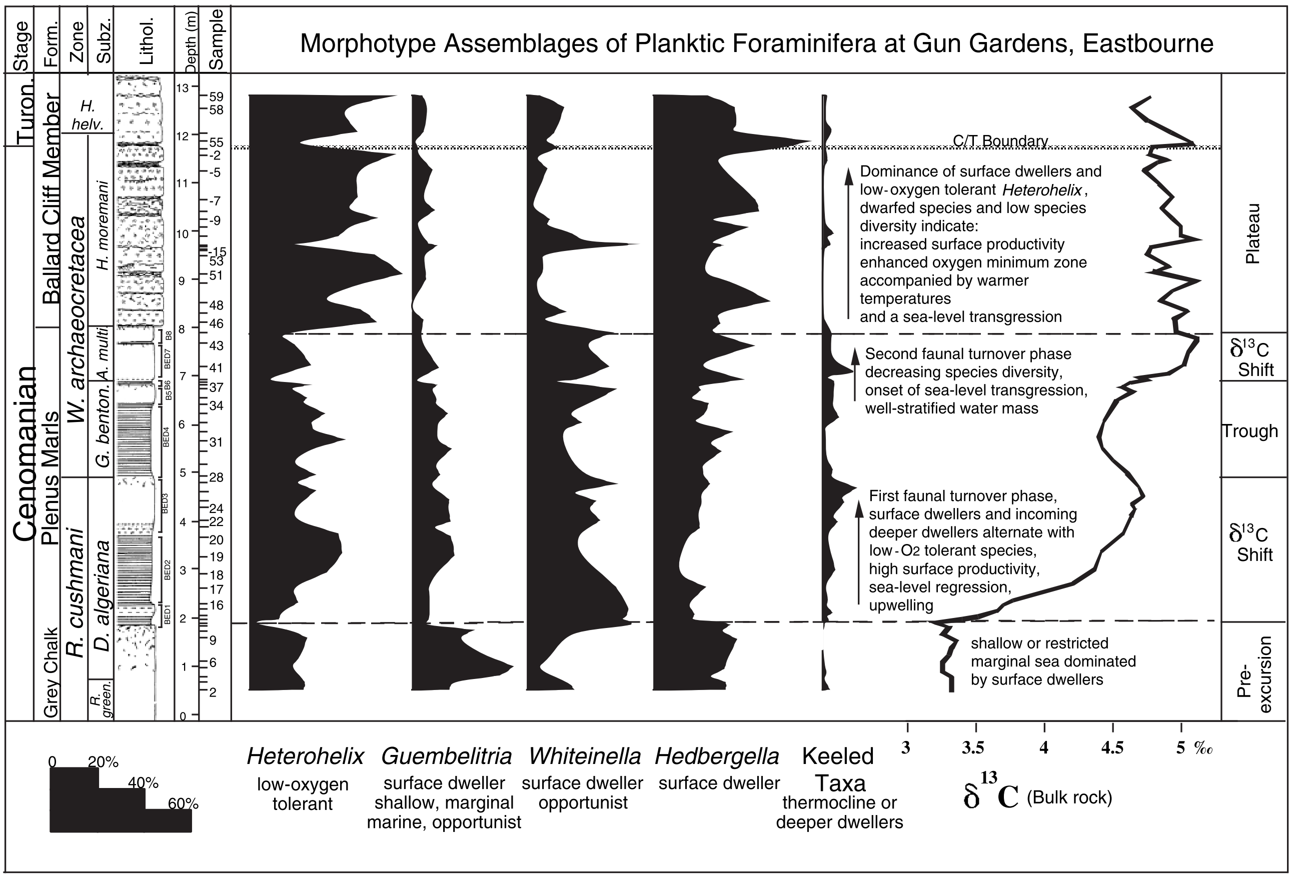


Figure 14. Relative species abundances of planktic foraminiferal morphotype assemblages and the $\delta^{13}C$ record at Gun Gardens, Eastbourne. Low-oxygen tolerant *Heterohelix* dominates at times of peak $\delta^{13}C$ values along with an increased abundance in surface dwellers.

opportunistic *Whiteinella* species accompany the positive $\delta^{13}C$ excursion and reflect increased surface productivity. The decrease in surface dwellers and increase in abundance of low oxygen tolerant *Heterohelix* species in Bed 2 mark the first faunal turnover phase (Phase I, Figure 14) and suggests the expansion of the oxygen minimum zone amid a shallowing sea.

Throughout deposition of the Plenus Marls the surface dweller *Whiteinella* and low-oxygen tolerant *Heterohelix* alternate in dominance suggesting repeated fluctuations in oxygen concentrations of subsurface waters, though overall surface productivity remained generally high, as suggested by the combined dominance of surface dwellers *Hedbergella* and *Whiteinella*. The relative abundance increase of keeled taxa in chalk Beds 3, 5 and 7, coincident with decreased *Heterohelix* abundances, suggest a well-stratified water mass and reduced oxygen minimum zone. The second faunal turnover phase (Phase II, Figure 14) is characterized by a temporary decrease in species diversity of *c.* 50% near the top of Plenus Marls Beds 7–8 coincident with a shift to *Heterohelix* dominance, the onset of dwarfed species, the second $\delta^{13}C$ excursion, a warming trend and rising sea level. Relatively low species diversity and dominance of *Heterohelix* in the Ballard Cliff chalks indicate high surface productivity and an expanded oxygen minimum zone accompanied by warm temperatures and a marine transgression.

7.2. Sea level and climate changes

Lithological and stable isotope variations at Eastbourne during the late Cenomanian and earliest Turonian indicate major climate and sea-level changes. Deposition of the Plenus Marls occurred in a shallowing sea punctuated by two sea-level drops, as indicated by repeated marl/chalk facies, detrital influx, erosion surfaces, and bioturbation (Figure 15). Hancock (1989) suggested that sea levels were broadly falling throughout Europe and the US Western Interior Basin at the time of Plenus Marls

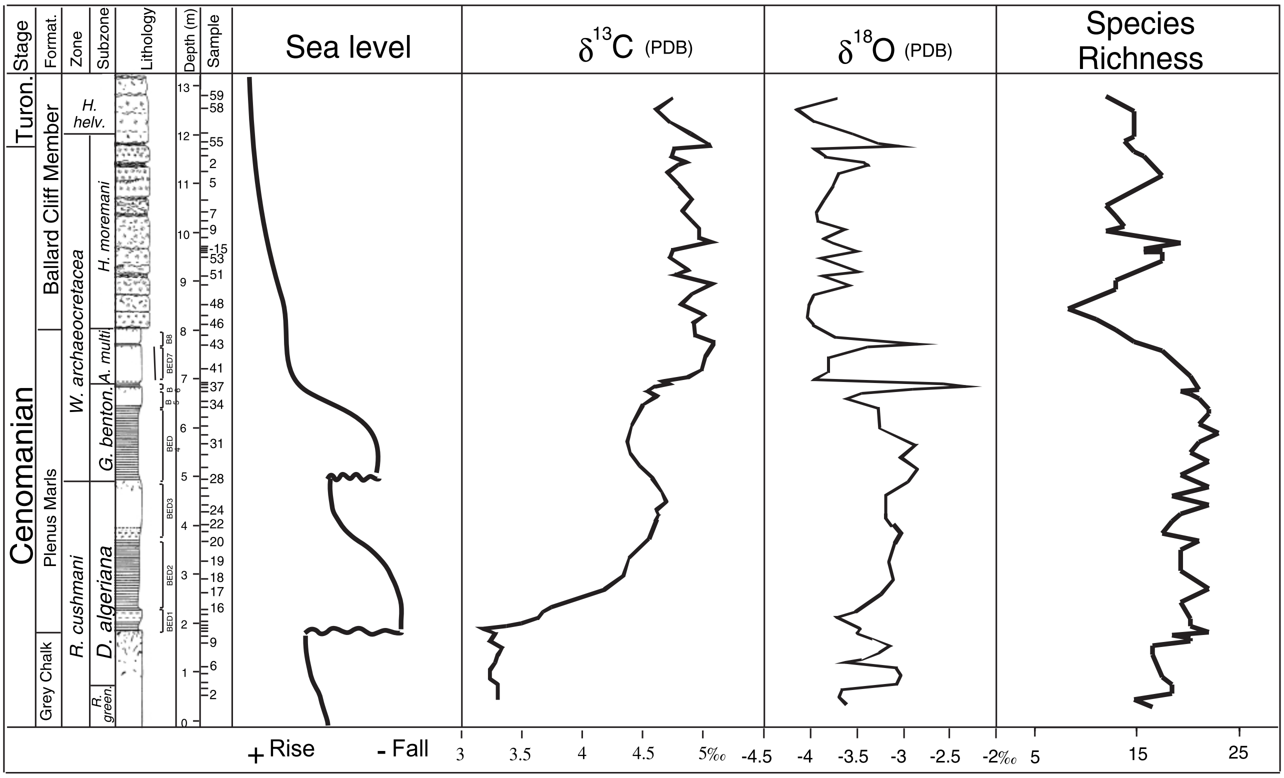


Figure 15. Summary diagram of sea-level changes, $\delta^{13}C$, $\delta^{18}O$ and species richness at Gun Gardens, Eastbourne. A sea-level regression, accompanied by fluctuating sea levels and erosion, is associated with the onset of the $\delta^{13}C$ excursion, possibly cooler temperatures, and relatively high species richness. The maximum $\delta^{13}C$ excursion coincides with a sea-level transgression, warmer temperatures, enhanced oxygen minimum zone and decreased species diversity.

deposition. The major regression phase began at the base of the Plenus Marls and was accompanied by a 1.8‰ increase in $\delta^{13}C$ values that reached a maximum in Bed 3.

A warming trend associated with a gradually rising sea level began in the upper part of the Plenus Marls and continued through the Ballard Cliff Member, accompanied by the second positive $\delta^{13}C$ excursion of 0.8‰ in Bed 7, predominantly chalk deposition, higher productivity, and an expanding oxygen minimum zone (Figure 15), though alternating chalks, thin marl beds and erosion surfaces indicate that the transgression was accompanied by high frequency sea-level fluctuations. A sea-level transgression superimposed over rhythmically fluctuating sea levels and cyclic sedimentary processes is well documented globally for the late Cenomanian and into the early Turonian (e.g., Arthur *et al.*, 1987; Robaszynski *et al.*, 1998). These rhythmic lithological changes are generally attributed to Milankovitch cycles (De-Boer & Wonders, 1981; Barron *et al.*, 1985; Arthur *et al.*, 1996; Sageman *et al.*, 1997). At Gun Gardens, the rhythmic sedimentation is also thought to be a result of orbital forcing, with each pair of beds representing the precession cycle (20 ka) (Berger & Loutre, 1989; Gale, 1990, 1995, 1996; Paul *et al.*, 1994, 1999).

A sea-level regression, accompanied by cooling and possibly ice rafting during the late Cenomanian coincident with the positive $\delta^{13}C$ excursion, is not consistent with current models for the OAE, which call for opposite conditions: global warming, increased low latitude deep-water production and a marine transgression across the Cenomanian/Turonian boundary (Arthur *et al.*, 1987, 1996; Schlanger *et al.*, 1987; Pratt *et al.*, 1993; Leckie *et al.*, 1998). Based on geochemical and faunal analyses of the Plenus Marls at Dover, Jeans *et al.* (1991) proposed the contrary scenario of global cooling, a sharply lower sea level possibly as a result of glaciation, a widespread marine regression, increased influx of terrestrially derived silicate and organic matter, and the development of anoxia in poorly ventilated basins. Our investigation is in substantial agreement with this scenario for deposition of the Plenus Marls, though deposition of the Ballard Cliff chalks is more consistent with current models of global warming. The Cenomanian–Turonian transition at Eastbourne is characterized by both a marine regression accompanied by cooling and a positive $\delta^{13}C$ excursion (Beds 1–3), and a major global warming, sea-level transgression, and a second positive $\delta^{13}C$ excursion (Beds 7–8).

8. Conclusions

1. The $\delta^{13}C$ excursion at Eastbourne began during the late Cenomanian (*D. algeriana* Subzone of *R. cushmani* Zone) and consists of a 1.8‰ positive excursion in Beds 1 through 3 of the Plenus Marls, a trough in Bed 4, a second excursion of 0.8‰ in Bed 7 and a gradually decreasing plateau during deposition of the Ballard Cliff Member.
2. Lithological variations, detrital influx, bioturbation and sharp erosion surfaces between chalk/marl lithologies indicate sea-level fluctuations during regression and transgression phases. A marine regression, or generally low but fluctuating sea level accompanied the $\delta^{13}C$ excursion between Plenus Marls Beds 1–4. This interval was followed by the onset of a major marine transgression, but was also accompanied by high frequency sea-level fluctuations that continued through the chalk deposition of the Ballard Cliff Member.
3. Planktic foraminifera indicate that the Cenomanian–Turonian transition is characterized by two major faunal turnover phases. Phase I (Beds 1–3) is marked by the extinction of *Rotalipora*, the first appearance of *Dicarinella*, and increased surface productivity (abundant *Whiteinella*), followed by reduced oxygen concentrations in subsurface waters (abundant *Heterohelix*) associated with the first positive $\delta^{13}C$ shift, increased terrigenous influx including organic matter, and a marine regression or low, fluctuating sea level.
4. Faunal turnover Phase II (Beds 7–8) is marked by increased surface productivity (dominance of *Hedbergella* and *Whiteinella*), followed by the temporary disappearance of over 50% of the species, the onset *Heterohelix* dominance and dwarfed species, expansion of the oxygen minimum zone, maximum $\delta^{13}C$ excursion, warmer temperatures and a major marine transgression.
5. The faunal turnover of Phase II and second $\delta^{13}C$ excursion correlate with the organic-rich Bonarelli Level of Italy and Bahloul Formation of Tunisia (near the base of the *W. archeocretacea* Zone). However, the organic-rich facies below these horizons correlate with the onset of the $\delta^{13}C$ excursion, the lower part of the Plenus Marls (upper *R. cushmani* Zone, *D. algeriana* Subzone), the first extinction phase and expansion of the oxygen minimum zone in Bed 3 and possibly also Bed 4 of the Plenus Marls.
6. *Heterohelix* species are low-oxygen tolerant and increased abundance reflects an enhanced oxygen minimum zone. The *Heterohelix* shift to biserial dominated assemblages coincides with the maximum $\delta^{13}C$ excursion and marks a change to an expanded oxygen minimum zone.
7. The onset of species dwarfism, or significantly smaller species sizes, associated with the maximum $\delta^{13}C$ excursion coincided with high surface productivity and an enhanced oxygen minimum zone, and may reflect early sexual maturation.
8. The subdivision of the planktic foraminiferal *W. archaeocretacea* Zone into three subzones enables correlation of the different phases of the CTBE.

Acknowledgements

We thank Andy Gale for sharing his knowledge and expertise of the Gun Gardens section, M-P. Bolle for help in sampling the section, and Chris Paul for permission to use his stable isotope date from Eastbourne. This study was supported by the Swiss National Funds FN 2100-043450.96/1 and FN 8220-028367.96/1.

References

Abramovich, S., Almogi-Labin, A. & Benjamini, C. 1998. Decline of the Maastrichtian pelagic ecosystem based on planktic foraminifera assemblage change: implications for the terminal Cretaceous faunal crisis. *Geology* **26**, 63–66.

Accarie, A., Emmanuel, L., Robaszynski, R., Baudin, F., Amédro, F., Caron, M. & Deconinck, J. 1996. Carbon isotope geochemistry as stratigraphic tool. A case study of the Cenomanian/Turonian boundary in central Tunisia. *Comptes Rendus de l'Académie des Sciences Paris,* **322**, *Serie IIa*, 579–586.

Arthur, M. A., Schlanger, S. O. & Jenkyns, H. C. 1987. The Cenomanian–Turonian Oceanic Anoxic Event, II. Palaeoceanographic controls on organic-matter production and preservation. In *Marine petroleum source rocks* (eds Brooks, J. & Fleet, J. A.), *Geological Society, London, Special Publication* **26**, 401–420.

Arthur, M. A., Slingerland, R. & Kump, L. R. 1996. A new hypothesis for the origin of limestone/marlstone couplets in deposits of the Cretaceous Western Interior Sea of North America. *Geological Society of America*, *Abstracts with Programs* **28** (7), 65.

Barrera, E. & Keller, G. 1990. Foraminiferal stable isotope evidence for gradual decrease of marine productivity and Cretaceous species survivorship in the earliest Danian. *Paleoceanography* **5**, 867–890.

Barrera, E. & Keller, G. 1994. Productivity across the Cretaceous-Tertiary boundary in high latitudes. *Geological Society of America, Bulletin* **106**, 1254–1266.

Barron, E. J., Arthur, M. A. & Kauffman, E. G. 1985. Cretaceous rhythmic bedding sequences: a plausible link between orbital variations and climate. *Earth and Planetary Science Letters* **72**, 327–340.

Bé, A. W. H. 1977. An ecological, zoogeographic and taxonomic review of Recent planktonic foraminifera. In *Oceanic micropaleontology 1* (ed. Ramsay, A. T. S.), pp. 1–100 (Academic Press, London).

Bengtson, P. 1996. The Turonian stage and substage boundaries. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* **66** (Supplement), 69–79.

Berger, A. & Loutre, M. F. 1989. Pre-Quaternary Milankovitch frequencies. *Nature* **342**, 133.

Boersma, A. & Premoli Silva, I. 1989. Atlantic Paleogene biserial heterohelicid foraminifera and oxygen minima. *Paleoceanography* **4**, 271–286.

Boersma, A. & Premoli Silva, I. 1991. Distribution of Paleogene planktonic foraminifera—analogies with the Recent? *Palaeogeography, Palaeoclimatology, Palaeoecology* **83**, 29–48.

Brinkhuis, H. & Zachariasse, W. J. 1988. Dinoflagellate cysts, sea level changes and planktonic foraminifera across the Cretaceous-Tertiary boundary at El Haria, northwest Tunisia. *Marine Micropaleontology* **13**, 153–191.

Brand, U. & Veizer, J. 1980. Chemical diagensis of a multi-component carbonate system: 1, Trace elements. *Journal of Sedimentary Petrology* **50**, 1219–1236.

Calvert, S. E., Bustin, R. M. & Pedersen, T. F. 1992. Lack of evidence for enhanced preservation of sedimentary organic carbon in the oxygen minimum of the Gulf of California. *Geology* **20**, 757–760.

Caron, M. 1985. Cretaceous planktic foraminifera. In *Plankton stratigraphy* (eds Bolli, H. M., Saunders J. B. & Perch-Niesen, K.), 17–86 (Cambridge University Press, Cambridge).

Caron, M. & Homewood, P. 1983. Evolution of early planktonic foraminifers. *Marine Micropaleontology* **7**, 453–462.

Carter, D. J. & Hart, M. B. 1977. Aspects of mid-Cretaceous stratigraphical micropalaeontology. *Bulletin of the British Museum* (*Natural History*) *Geology* **29**, 1–135.

Cobban, W. A. 1984. Mid-Cretaceous ammonite zones, Western Interior, United States. *Bulletin of the Geological Society of Denmark* **33**, 71–89.

Corfield, R. M., Hall, M. A. & Brasier, M. D. 1990. Stable isotope evidence for foraminifera habitats during the development of the Cenomanian/Turonian oceanic anoxic event. *Geology* **18**, 175–178.

De Boer, P. L. & Wonders, A. A. 1984. Astronomically induced rhythmic bedding in Cretaceous pelagic sediments near Moria, Italy. In *Milankovitch and climate* (ed. Berger, A. L.), pp. 163–177 (Reidel Publishing Company, Dordrecht).

D'Hondt, S. & Arthur, M. A. 1995. Interspecies variation in stable isotope signals of Maastrichtian planktonic foraminifera. *Paleoceanography* **10**, 123–135.

Ditchfield, J. M. & Marshall, J. D. 1989. Isotopic variation in rhythmically bedded chalks: paleotemperature variation in the Upper Cretaceous. *Geology* **17**, 842–845.

Douglas, R. G. 1969. Upper Cretaceous biostratigraphy of northern California. *Proceedings, First International Conference on Planktonic Microfossils* (Geneva, 1967) **2**, pp. 126–152 (Leiden).

Eicher, D. L. 1969. Cenomanian and Turonian planktonic foraminifera from the western interior of the United States. *Proceedings, First International Conference on Planktonic Microfossils* (Geneva, 1967) **2**, pp. 163–174 (Leiden).

Eicher, D. L. 1972. Phylogeny of the late Cenomanian planktonic foraminifer *Anaticinella multiloculata* (Morrow). *Journal of Foraminiferal Research* **2**, 184–190.

Eicher, D. L. & Diner, R. 1985. Foraminifera as indicators of water mass in the Cretaceous Greenhorn sea, Western Interior. In *Fine-grained deposits and biofacies of the Cretaceous Western Interior Seaway—evidence of cyclic sedimentary processes* (eds Pratt, L., Kauffman, E. & Zelt, F.), *Society of Economic Paleontologists and Mineralogists, Field Trip Guidebook* **4**, 60–71.

Elder, W. P. 1987. Paleoecology of the Cenomanian-Turonian (Cretaceous) stage boundary extinctions at Black Mesa, Arizona. *Palaios* **2**, 24–40.

Gale, A. S. 1990. A Milankovitch scale for Cenomanian time. *Terra Nova* **1**, 420–425.

Gale, A. S. 1995. Cyclostratigraphy and correlation of the Cenomanian of western Europe. In *Orbital forcing timescales and cyclostratigraphy* (eds House, M. R. & Gale, A. S.), *Geological Society, London, Special Publication* **85**, 177–197.

Gale, A. S. 1996. Turonian correlation and sequence stratigraphy of the Chalk in southern England. In *Sequence stratigraphy in British geology* (eds Hesselbo, S. P. & Parkinson, D. N.). *Geological Society, London, Special Publication* **103**, 177–195.

Gale, A. S., Jenkyns, H. C., Kennedy, W. J. & Corfield, R. M. 1993. Chemostratigraphy versus biostratigraphy: data from around the Cenomanian-Turonian boundary. *Journal of the Geological Society, London* **150**, 29–32.

Gale, A. S., Smith, A. B., Monks, N. E. A., Young, J. A., Howard, A., Wray, D. S. & Huggett, J. M. 2000. Marine biodiversity through the Late Cenonmanian–Early Turonian: palaeoceanographic controls and sequence stratigraphic biases. *Journal of the Geological Society, London* **157**, 745–757.

Hallam, A. & Wignall, P. B. 1999. Mass extinctions and sea-level changes. *Earth Science Reviews* **48**, 217–250.

Hallock, P., Premoli Silva, I. & Boersma, A. 1991. Similarities between planktonic and larger foraminiferal evolutionary trends through Paleogene paleoceanographic changes. *Palaeogeography, Palaeoclimatology, Palaeoecology* **83**, 49–64.

Hancock, J. M. 1989. Sea-level changes in the British region during the Late Cretaceous. *Proceedings of the Geologists' Association* **100**, 565–594.

Hancock, J. M. & Kauffman, E. G. 1979. The great transgressions of the Late Cretaceous. *Journal of the Geological Society, London* **136**, 175–186.

Haq, B. U., Hardenbol, J. & Vail, P. R. 1987. Chronology of fluctuating sea levels since the Triassic. *Science* **235**, 1156–1167.

Hardenbol, J., Caron, M., Amedro, F., Dupuis, C. & Robaszynski, F. 1993. The Cenomanian-Turonian boundary in central Tunisia in the context of a sequence-stratigraphic interpretation. *Cretaceous Research* **14**, 449–454.

Hardenbol, J., Thierry, J., Farley, M. B., de Graciansky, P. C. & Vail, P. P. 1998. Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins. In *Mesozoic and Cenozoic sequence stratigraphy of European basins* (eds de Graciansky, P. C., Hardenbol, J., Jacquin, T. & Vail, P. P.), *SEPM* (*Society for Sedimentary Geology*) *Special Publication* **60**, 3–13.

Harries, P. J. 1993. Dynamics of survival following the Cenomanian-Turonian (Upper Cretaceous) mass extinction event. *Cretaceous Research* **14**, 563–583.

Hart, M. B. 1980a. The recognition of mid-Cretaceous sea-level changes by means of foraminifera. *Cretaceous Research* **1**, 289–297.

Hart, M. B. 1980b. A water-depth model for the evolution of the planktic Foraminiferida. *Nature* **286**, 252–254.

Hart, M. B. 1996. Recovery of the food chain after the Late Cenomanian extinction event. In *Biotic recovery from mass extinction events* (ed. Hart, M. B.), *Geological Society, London, Special Publication* **102**, 265–277.

Hart, M. B. & Ball, K. C. 1986. Late Cretaceous anoxic events, sea-level changes and the evolution of the planktonic foraminifera. In *North Atlantic palaeoceanography* (eds Summerhayes, C. P. & Shackleton, N. J.), *Geological Society of America, Special Publication* **21**, 67–78.

Hart, M. B. & Bigg, P. J. 1981. Anoxic events in the Late Cretaceous chalk seas of north-west Europe. In *Microfossils from Recent and fossil shelf seas* (eds Neale, J. W. & Brasier, M. D.), pp. 177–185 (Ellis Horwood, Chichester, for the British Micropalaeontological Society).

Hart, M. B. & Carter, D. J. 1975. Some observations on the Cretaceous Foraminiferida of southeast England. *Journal of Foraminiferal Research* **5**, 114–126.

Hart, M. B. & Leary, P. N. 1989. The stratigraphic and palaeoceanographic setting of the late Cenomanian "anoxic" event. *Journal of the Geological Society, London* **146**, 305–310.

Hart, M. B. & Leary, P. N. 1991. Stepwise mass extinctions: the case for the Late Cenomanian event. *Terra Nova* **3**, 142–147.

Hart, M. B., Dodsworth, P. & Duane, A. M. 1993. The Late Cenomanian Event in eastern England. *Cretaceous Research* **14**, 495–508.

Hart, M. B. & Tarling, D. H. 1975. Cenomanian palaeoceanography of the North Atlantic and possible mid-Cenomanian eustatic movements and their implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **15**, 95–108.

Hilbrecht, H. 1986. On the correlation of the Upper Cenomanian and Lower Turonian of England and Germany (Boreal and N-Tethys). *Newsletters on Stratigraphy* **15**, 115–138.

Hilbrecht, H., Arthur, M. A. & Schlanger, S. S. O. 1986. The Cenomanian-Turonian boundary event; sedimentary, faunal and geochemical criteria developed from stratigraphic studies in NW-Germany. In *Global bio-events; a critical approach* (eds Bhattacharji, S., Friedman, G. M., Neugebauer, H. J. & Seilacher, A.), **8**, 345–351.

Hilbrecht, H. & Hoefs, J. 1986. Geochemical and palaeontological studies of the $\delta^{13}C$ anomaly in Boreal and North Tethyan Cenomanian-Turonian sediments in Germany and adjacent areas. *Palaeogeography, Palaeoclimatology, Palaeoecology* **53**, 169–189.

Hilbrecht, H., Frieg, C., Troeger, K. A., Voigt, S. & Voigt, T. 1996. Shallow water facies during the Cenomanian–Turonian anoxic event; bio-events, isotopes, and sea level in southern Germany. *Cretaceous Research* **17**, 229–253.

Hilbrecht, H., Hubberten, H. W. & Oberhansli, H. 1992. Biogeography of planktonic foraminifera and regional carbon isotope variations: productivity and water masses in Late Cretaceous Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* **92**, 407–421.

Jarvis, I., Carson, G. A., Cooper, M. K. E., Hart, M. B., Leary, P. N., Tocher, B. A., Horne, D. & Rosenfeld, A. 1988. Microfossil assemblages and the Cenomanian-Turonian (late Cretaceous) oceanic anoxic event. *Cretaceous Research* **9**, 3–103.

Jeans, C. V., Long, D., Hall, M. A., Bland, D. J. & Cornford, C. 1991. The geochemistry of the Plenus Marls at Dover, England: evidence of fluctuating oceanographic conditions and of glacial control during the development of the Cenomanian-Turonian $\delta^{13}C$ anomaly. *Geological Magazine* **128**, 603–632.

Jefferies, R. P. S. 1963. Fauna and environment in the lowest Turonian (*Actinocamax plenus* Subzone) of the Anglo-Paris Basin. In *Problems in palaeoclimatology* (ed. Nairn, A. E. M.), pp. 600–608 (Wiley, London).

Jenkyns, H. C. 1980. Cretaceous anoxic events: from continents to oceans. *Journal of the Geological Society, London* **137**, 171–188.

Jenkyns, H. C. 1991. Impact of Cretaceous sea level rise and anoxic events on the Mesozoic carbonate platform of Yugoslavia. *American Association of Petroleum Geologists, Bulletin* **75**, 1007–1017.

Jenkyns, H. C., Gale, A. S. & Corfield, R. M. 1994. Carbon- and oxygen-isotope stratigraphy of the English Chalk and Italian Scaglia and its palaeoclimatic significance. *Geological Magazine* **131**, 1–34.

Kaiho, K. & Hasegawa, T. 1994. End-Cenomanian benthic foraminifera extinctions and oceanic dysoxic events in the northwestern Pacific Ocean. *Palaeogeography, Palaeoclimatology, Palaeoecology* **111**, 29–43.

Keller, G. 1988. Extinction, survivorship and evolution of planktic foraminifera across the Cretaceous-Tertiary boundary at El Kef, Tunisia. *Marine Micropaleontology* **13**, 239–263.

Keller, G. 1989. Extended Cretaceous/Tertiary boundary extinctions and delayed population change in planktic foraminifera from Brazos River, Texas. *Paleoceanography* **4**, 287–332.

Keller, G. 1993. The Cretaceous/Tertiary boundary transition in the Antarctic Ocean and its global implications. *Marine Micropaleontology* **21**, 1–45.

Keller, G. 1996. The Cretaceous-Tertiary mass extinction in planktonic foraminifera: biotic constraints for catastrophe theories. In *Cretaceous-Tertiary mass extinctions: biotic and environmental changes* (eds MacLeod, N. & Keller, G.), pp. 49–84 (W. W. Norton & Company, New York).

Keller, G., Barrera, E., Schmitz, B. & Mattson, E. 1993. Gradual mass extinction, species survivorship, and longterm environmental changes across the Cretaceous/Tertiary boundary in high latitudes. *Geological Society of America, Bulletin* **105**, 979–997.

Keller, G., Adatte, T., Stinnesbeck, W., Stüben, D., Kramar, U., Berner, Z., Li, L. & Salis Perch-Nielsen, K. 1998. The Cretaceous–Tertiary transition on the Saharan platform of southern Tunisia. *Geobios* **30**, 951–975.

Keller, G., Adatte, T., Stinnesbeck, W., Luciani, V., Karoui-Yaakoub, N. & Zaghbib-Turki, D. in press. Palaeoecology of the Cretaceous-Tertiary mass extinction in planktic foraminifera. *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Kennedy, W. J. & Cobban, W. A. 1991. Stratigraphy and interregional correlation of the Cenomanian–Turonian transition in the Western Interior of the United States near Pueblo, Colorado, a potential boundary stratotype for the base of the Turonian stage. *Newsletters on Stratigraphy* **24**, 1–33.

Koutsoukos, E. A. M., Leary, P. N. & Hart, M. B. 1990. Latest Cenomanian–earliest Turonian low-oxygen tolerant benthonic foraminifera: a case study from the Sergipe Basin (N. E. Brazil) and the western Anglo-Paris Basin (southern England). *Palaeogeography, Palaeoclimatology, Palaeoecology* **77**, 145–177.

Kroon, D. & Nederbragt, A. J. 1990. Ecology and paleoecology of triserial planktic foraminifera. *Marine Micropaleontology* **16**, 25–38.

Lamolda, M. A., Gorostidi, A. & Paul, C. R. C. 1994. Quantitative estimates of calcareous nannofossil changes across the Plenus Marls (latest Cenomanian), Dover, England; implication for the generation of the Cenomanian-Turonian boundary event. *Cretaceous Research* **15**, 143–164.

Lamolda, M. A., Gorostidi, A., Martinez, R., Lopez, G. & Peryt, D. 1997. Fossil occurrences in the upper Cenomanian–lower Turonian at Ganuza, northern Spain; an approach to Cenomanian/Turonian boundary chronostratigraphy. *Cretaceous Research* **18**, 331–353.

Leckie, R. M. 1985. Foraminifera of the Cenomanian-Turonian boundary interval, Greenhorn Formation, Rock Canyon Anticline, Pueblo, Colorado. In *Fine-grained deposits and biofacies of the Cretaceous Western Interior Seaway—evidence of cyclic sedimentary processes* (eds Pratt, L., Kauffman, E. & Zelt, F.), *Society of Economic Paleontologists and Mineralogists, Field Trip Guidebook* **4**, 139–150.

Leckie, R. M. 1987. Paleoecology of mid-Cretaceous planktonic foraminifera: a comparison of open ocean and epicontinental sea assemblages. *Micropaleontology* **33**, 164–176.

Leckie, R. M., Schmidt, M. G., Finkelstein, D. & Yuretich, R. 1991. Paleoceanographic and paleoclimatic interpretations of the Mancos Shale (Upper Cretaceous), Black Mesa Basin, Arizona. In *Stratigraphy, depostional environments, and sedimentary tectonics of the western margin, Cretaceous Western Interior Seaway* (eds Mations, J. D. & Eaton, J. G.), *Geological Society of America, Special Paper* **260**, 139–152.

Leckie, R. M., Yuretich, R., West, O. L. O., Finkelstein, D. & Schmidt, M. G. 1998. Paleoceanography of the southwestern Western Interior sea during the time of the Cenomanian-Turonian boundary (Late Cretaceous). In *Stratigraphy and paleoenvironments of the Cretaceous Western Interior Seaway, USA. SEPM (Society for Sedimentary Geoology), Concepts in Sedimentology and Paleontology* **6**, 101–126.

Li, L. & Keller, G. 1998. Diversification and extinction in Campanian–Maastrichtian planktic foraminifera of northwestern Tunisia. *Eclogae Geologicae Helvetiae* **91**, 75–102.

Li, L., Keller, G., Adatte, T. & Stinnesbeck, W. 2000. Late Cretaceous sea-level changes in Tunisia: a multi-disciplinary approach. *Journal of the Geological Society, London* **157**, 447–458.

Lipps, J. H. 1979. Ecology and paleoecology of planktic foraminifera. In *Foraminiferal ecology and paleoecology* (eds Lipps, J. H. *et al.*), *Society of Economic Paleontologists and Mineralogists, Short Course* **6**, 62–104.

Luciani, V. 1997. Planktonic foraminiferal turnover across the Cretaceous-Tertiary boundary in the Vajont valley (Southern Alps, northern Italy). *Cretaceous Research* **18**, 799–821.

Luciani, V. & Cobianchi, M. 1999. The Bonarelli Level and other black shales in the Cenomanian–Turonian of the northeastern Dolomites (Italy): calcareous nannofossil and foraminiferal data. *Cretaceous Research* **20**, 135–167.

Luyendyk, B. P., Forsyth, D. & Phillips, J. D. 1972. Experimental approach to the palaeocirculation of the oceanic surface waters. *Geological Society of America, Bulletin* **83**, 2649–2664.

Magaritz, M. 1975. Sparitization of pelleted limestone: a case study of carbon and oxygen isotopic composition. *Journal of Sedimentary Petrology* **45**, 599–603.

Malartre, F., Ferry, S. & Rubino, J.-L. 1998. Interactions climat-eustatisme-tectonique. Les enseignements et perspectives du Crétacé supérieur (Cénomanien-Coniacien). *Geodinamica Acta* (Paris) **11** (6), 253–270.

McNeil, D. H. & Caldwell, W. G. E. 1981. Cretaceous rocks and their foraminifera in the Manitoba Escarpment. *Geological Association of Canada, Special Paper* **21**, 439 pp.

MacLeod, N., Ortiz, N., Fefferman, N., Clyde, W., Schulter, C. & MacLean, J. 2000. Phenotypic response of foraminifera to episodes of global environmental change. In *Biotic response to global change: the last 145 million years* (eds Culver, S. J. & Rawson, P.), pp. 51–78 (Cambridge University Press, Cambridge).

Mitchell, S. F., Ball, J. D., Crowley, S. F., Marshall, J. D., Paul, C. R. C., Veltkamp, C. J. & Samir, A. 1997. Isotope data from Cretaceous chalks and foraminiferal environmental or diagenetic signals? *Geology* **25**, 691–694.

Mortimore, R. N. 1986. Stratigraphy of the Upper Cretaceous White Chalk of Sussex. *Proceedings of the Geologists' Association* **97**, 97–139.

Nederbragt, A. & Fiorentino, A. 1999. Stratigraphy and paleoceanography of the Cenomanian-Turonian boundary event in Oued Mellegue, northwestern Tunisia. *Cretaceous Research* **20**, 47–62.

Norris, R. D. & Wilson, P. A. 1998. Low latitude sea-surface temperatures for the mid-Cretaceous and the evolution of planktic foraminifera. *Geology* **26**, 823–826.

Norris, R. D. & Wilson, P. A. 1999. Low latitude sea-surface temperatures for the mid-Cretaceous and the evolution of planktic foraminifera: comment and reply. *Geology* **27**, 858.

Pardo, A., Adatte, T., Keller, G. & Oberhänsli, H. 1999. Paleoenvironmental changes across the Cretaceous-Tertiary boundary at Koshak, Kazakhstan, based on planktic foraminifera and clay mineralogy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **154**, 247–273.

Paul, C. R. C. & Mitchell, S. F. 1994. Is famine a common factor in marine mass extinctions? *Geology* **22**, 679–682.

Paul, C. R. C., Mitchell, S. F., Lamolda, M. A. & Gorostidi, A. 1994. The Cenomanian-Turonian Boundary Event in northern Spain. *Geological Magazine* **131**, 801–817.

Paul, C. R. C., Lamolda, M. A., Mitchell, S. F., Vaziri, M. R., Gorostidi, A. & Marshall, J. D. 1999. The Cenomanian-Turonian boundary at Eastbourne (Sussex, UK): a proposed European reference section. *Palaeogeography, Palaeoclimatology, Palaeoecology* **150**, 83–121.

Perez-Cruz, L. L. & Machain-Castillo, M. L. 1990. Benthic foraminifera of the oxygen minimum zone, continental shelf of the Gulf of Tehuantepec, Mexico. *Journal of Foraminiferal Research* **12**, 65–80.

Peryt, D. & Wyrwicka, K. 1991. The Cenomanian-Turonian anoxic event in SE Poland. *Cretaceous Research* **12**, 65–80.

Phleger, F. B. & Soutar, A. 1973. Production of benthic foraminifera in three East Pacific oxygen minima. *Micropaleontology* **19**, 110–115.

Pratt, L. M. 1984. Influence of paleoenvironmental factors on preservation of organic matter in the middle Cretaceous Greenhorn Formation, Pueblo, Colorado. *American Association of Petroleum Geologists, Bulletin* **68**, 1146–1159.

Pratt, L. M. & Threlkeld, C. N. 1984. Stratigraphic significance of $^{13}C/^{12}C$ ratios in mid-Cretaceous rocks of the Western Interior, U.S.A. In *The Mesozoic of middle North America* (eds Stott, D. F. & Glass, D. J.), *Canadian Society of Petroleum Geologists, Memoir* **9**, 305–312.

Pratt, L. M., Arthur, M. A., Dean, W. E. & Scholle, P. A. 1993. Paleoceanographic cycles and events during the Late Cretaceous in the Western Interior Seaway of North America. In *Cretaceous evolution of the Western Interior Basin of North America* (eds Caldwell, W. G. E. & Kauffman, E. G.), *Geological Association of Canada, Special Paper* **39**, 333–353.

Premoli Silva, I. & Sliter, W. V. 1995. Cretaceous planktonic foraminiferal biostratigraphy and evolutionary trends from the Bottacione section, Gubbio, Italy. *Palaeontographica Italica* **82**, 1–89.

Price, G. D., Selwood, B. W., Corfield, R. M., Clarke, L. & Cartlidge, J. E. 1998. Isotopic evidence for paleotemperatures and depth stratification of Middle Cretaceous planktonic foraminifera from the Pacific Ocean. *Geological Magazine* **135**, 183–191.

Price, G. D. & Hart, M. B. 1999. Low latitude sea-surface temperatures for the mid-Cretaceous and the evolution of planktic foraminifera: comment and reply. *Geology* **27**, 857.

Resig, J. M. 1993. Cenozoic stratigraphy and paleoceanography of biserial planktonic foraminifera, Ontong Java Plateau. *Proceedings of the Ocean Drilling Program, Scientific Results* **130**, 231–244.

Robaszynski, F. & Caron, M. 1979. Atlas de foraminifères planctoniques du Crétacé moyen (Mer Boreale et Tethys), première partie. *Cahiers de Micropaléontologie* **1**, 185 pp.

Robaszynski, F., Gale, A., Juignet, P., Amédro, F. & Hardenbol, J. 1998. Sequence stratigraphy in the Upper Cretaceous series of the Anglo-Paris Basin: exemplified by the Cenomanian Stage. In *Cenozoic and Mesozoic sequence stratigraphy of European basins. SEPM (Society for Sedimentary Geology) Special Publication* **40**, 363–386.

Sageman, B. B., Rich, J., Arthur, M. A., Birchfield, G. E. & Dean, W. E. 1997. Evidence for Milankovitch periodicities in Cenomanian–Turonian lithologic and geochemical cycles, Western Interior U.S.A. *Journal of Sedimentary Research, Section B: Stratigraphy and Global Studies* **67**, 286–302.

Schlanger, S. O., Arthur, M. A., Jenkyns, H. C. & Scholle, P. A. 1987. The Cenomanian–Turonian oceanic anoxic event. I. Stratigraphy and distribution of organic carbon-rich beds and the marine $\delta^{13}C$ excursion. In *Marine petroleum source rocks* (eds Brooks, J. & Fleet, J. A.), *Geological Society, London, Special Publication* **26**, 371–399.

Scholle, P. A. & Arthur, M. A. 1980. Carbon isotope fluctuations in Cretaceous pelagic limestones: potential stratigraphic and petroleum exploration tool. *American Association of Petroleum Geologists, Bulletin* **64**, 67–87.

Schrag, D. P., DePaolo, D. J. & Richter, F. M. 1995. Reconstructing past sea surface temperatures: correcting for diagenesis of bulk marine carbon. *Geochimica et Cosmochimica Acta* **59**, 2265–2278.

Slipper, I. J. 1996. Early Turonian Ostracoda: the Melbourne Rock fauna from Abbots Cliff, Dover, England. *Proceedings of the Second European Ostracologists' Meeting* (Glasgow, 1993), pp. 49–56 (British Micropaleontological Society, London).

Tur, N. A. 1996. Planktonic foraminifera recovery from the Cenomanian-Turonian mass extinction event, northeastern Caucasus. In *Biotic recovery from mass extinction events* (ed. Hart, M. B.), *Geological Society, London, Special Publication* **102**, 259–264.

Uličný, D., Hladiková, J. & Hradecká, L. 1993. Record of sea-level changes, oxygen depletion and the $\delta^{13}C$ anomaly across the Cenomanian-Turonian boundary, Bohemian Cretaceous Basin. *Cretaceous Research* **14**, 211–234.

West, O. L. O., Leckie, R. M. & Schmidt, M. 1998. Stratigraphy and paleoenvironments of the Cretaceous Western Interior Seaway, USA. *SEPM (Society for Sedimentary Geology), Concepts in Sedimentology and Paleontology* **6**, 79–99.

Wonders, A. A. H. 1980. Middle and Late Cretaceous planktonic foraminifera of the western Mediterranean area. *Utrecht Micropalaeontological Bulletin* **24**, 158 pp.