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Age and paleoenvironment of the Cenomanian–Turonian global stratotype section and point at Pueblo, Colorado

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Abstract

Biostratigraphy and stable isotopes indicate that the global stratotype section and point (GSSP) at Pueblo contains an essentially complete sedimentary record across the global ocean anoxic event (OAE 2) and the Cenomanian–Turonian boundary. The OAE 2 $\delta^{13}\text{C}$ shift occurred over a period of about 90 ky and was accompanied by a major sea level transgression, which at its peak was marked by an incursion of oxygen-rich waters creating a benthic oxic zone that lasted about 100 ky. A mid-Cenomanian $\delta^{13}\text{C}$ shift, sea level transgression and faunal turnover occurred about 2 my before OAE 2. $\delta^{18}\text{O}$ values of the planktic foraminifer *Hedbergella planispira* and its relative abundance changes reveal cyclic variations in surface salinity due to alternating freshwater influx and marine incursions, whereas dominance by the low oxygen tolerant *Heterohelix* species indicates a well-developed oxygen minimum zone (OMZ) for most of the middle to late Cenomanian and early Turonian.

Profound faunal changes accompanied these oceanographic events, including the extinction of 30% of the species assemblage and an equal gain in evolutionary diversification, though the overall combined relative abundances of outgoing and incoming species were less than 2% and 4%, respectively, of the total assemblages. The faunal turnover began with the sea level transgression and rapid increase in $\delta^{13}\text{C}$ values, and accelerated with the influx of oxygen-rich deep water, increased water mass stratification and competition during the benthic oxic zone. The incursion of oxygen-rich deep waters at this time was also observed in Morocco and may represent a global event of a still unknown source.

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Keywords: Cenomanian–Turonian; Pueblo GSSP; paleoenvironment; planktic foraminifera

1. Introduction

During the late Cenomanian, the Western Interior Sea (WIS) was characterized by generally low sea levels, high terrigenous influx and low salinity, an

environment that supported few marine invertebrates or foraminifera (Kauffman, 1984; Cobban, 1985; Elder, 1985). Benthic foraminifera were generally rare (Eicher, 1969a) and low-diversity assemblages of planktic foraminifera persisted in the deepest parts of this seaway (Eicher and Diner, 1989; Leckie et al., 1998). During the late Cenomanian to early Turonian a major sea level transgression expanded the WIS (Greenhorn Sea) northward to the Arctic slope, transporting normal, saline, subtropical marine waters and

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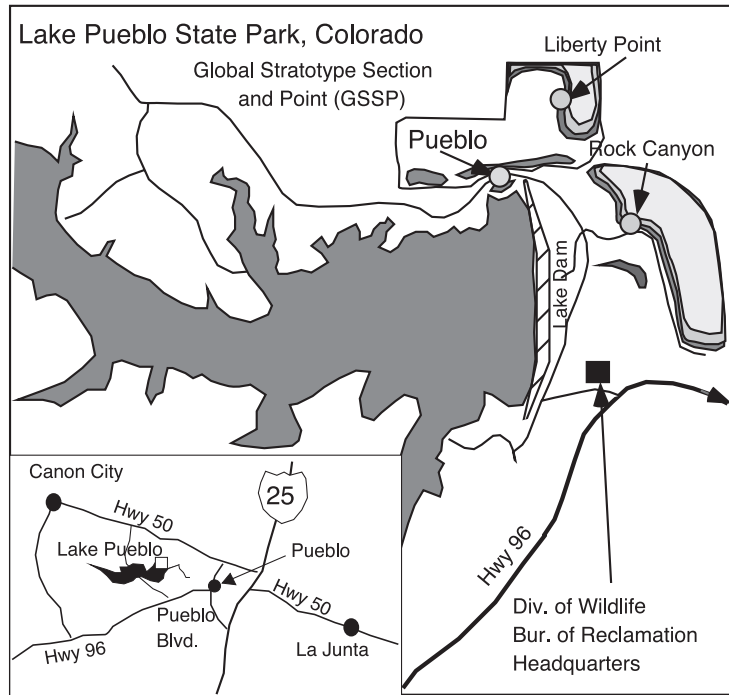


Fig. 1. Location of the Pueblo GSSP in the Rock Canyon Anticline area of Lake Pueblo State Park, Colorado. The section is exposed along the road on the lakeside.



Fig. 2. Outcrop of the Pueblo section exposed on the road along Lake Pueblo showing exposure of the Hartland Shale and Bridge Creek Limestone.

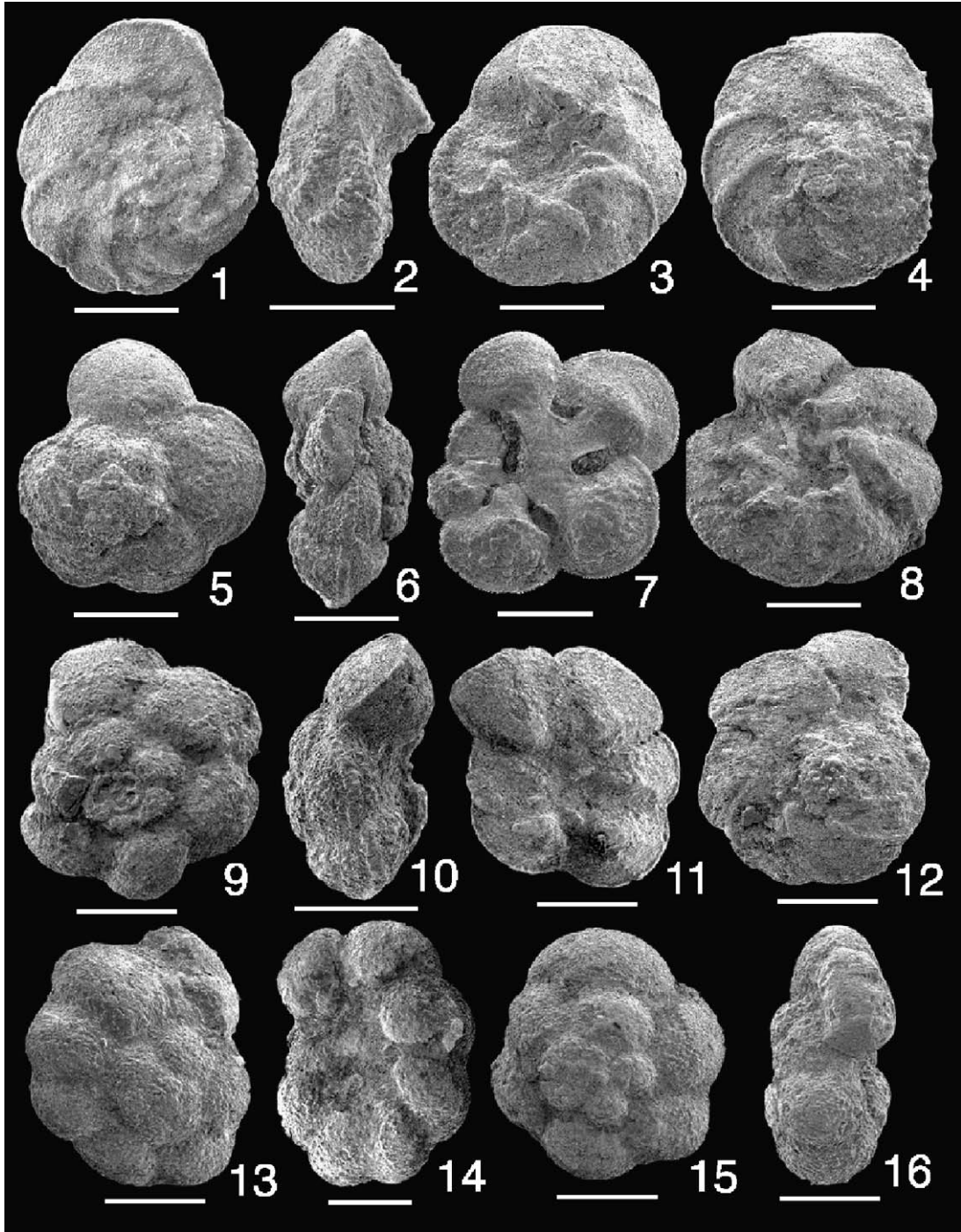


Plate 1. SEM illustrations of planktic foraminifera from the Pueblo GSSP, Colorado. All specimens are from the *R. cushmani* zone. Scale bar = 200 μm . Specimens 1–4: *R. greenhornensis* (Morrow). Specimens 5–7: *R. cushmani* (Morrow). Specimens 8 and 12: *R. deekei* (Franke). Specimens 9 and 11: *R. montsalvensis* Mornod. Specimens 13, 14, 15 and 16: *Rotalipora-A. multiloculata* transition.

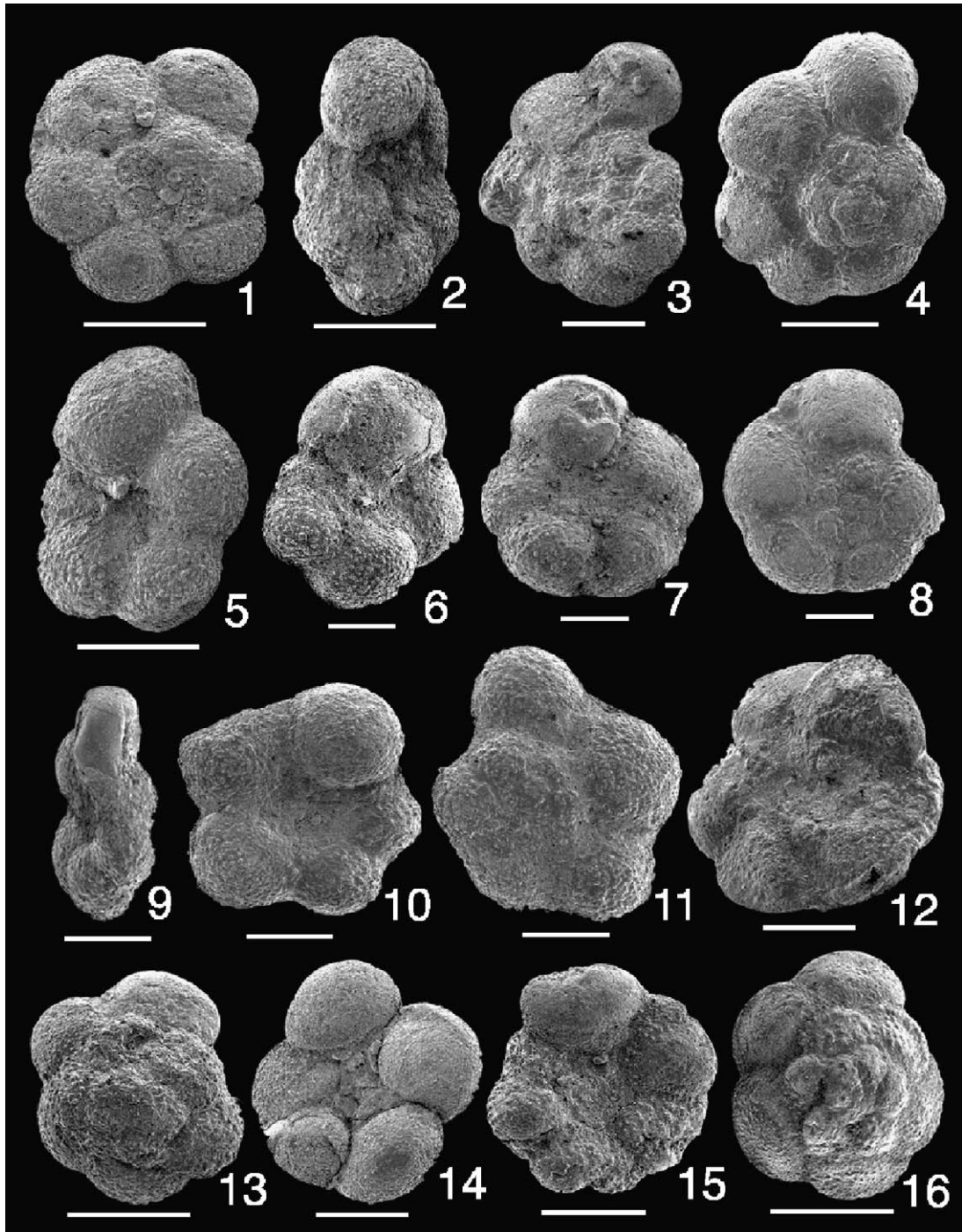


Plate 2. SEM illustrations of planktic foraminifera from the Pueblo GSSP, Colorado. All specimens from the *R. cushmani* zone. Scale bar = 100 μm for specimens 1–5, all others 200 μm . Specimens 1–5: *A. multiloculata* (Morrow), *A. multiloculata* subzone of *R. cushmani* zone. Specimens 6–8: *Praeglobotruncan aumalensis* (Sigal). Specimens 9–11: *P. stephani* (Gandolfi). Specimens 12–14, 15 and 16: *P. gibba* Klaus.

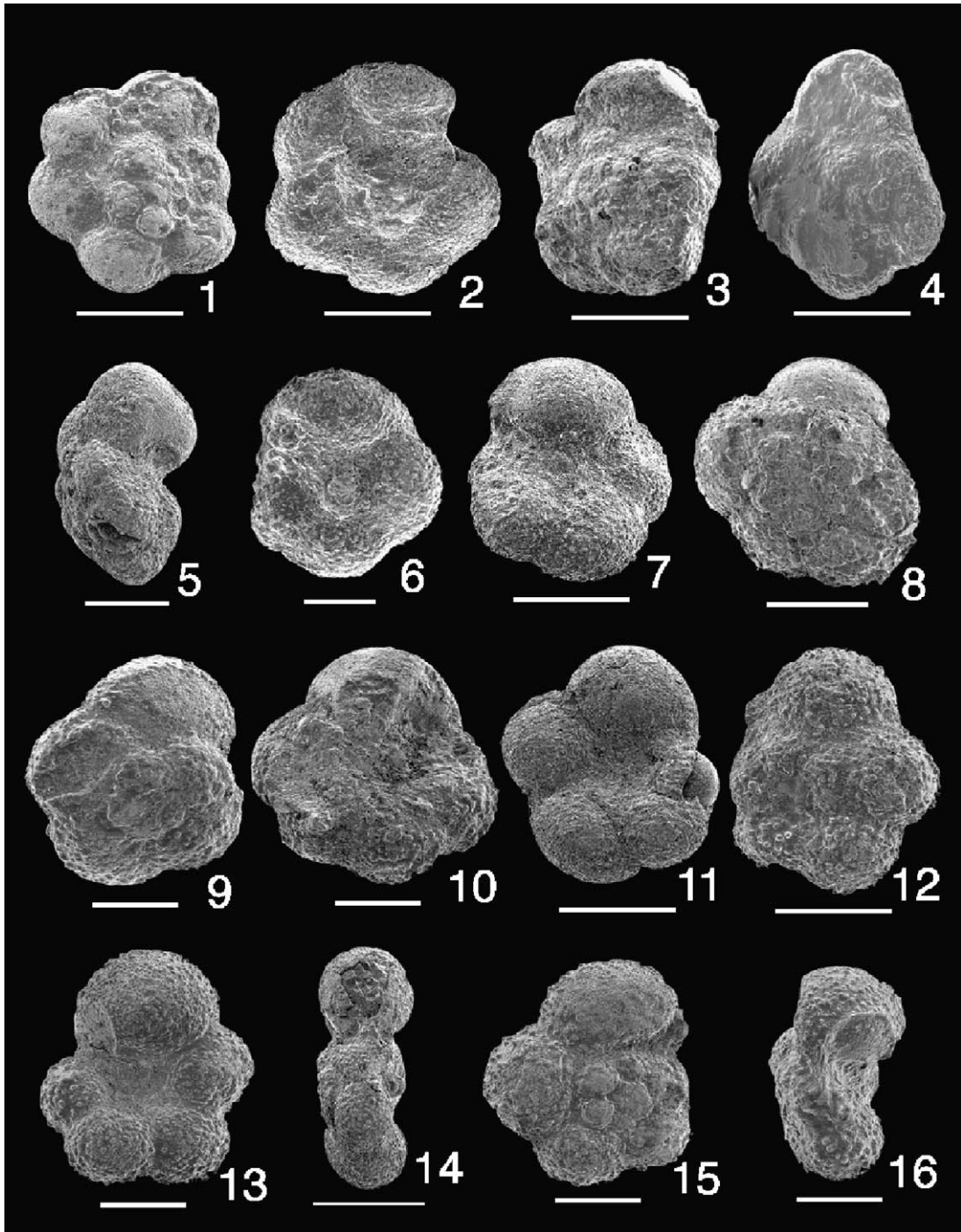


Plate 3. SEM illustrations of planktic foraminifera from the Pueblo GSSP, Colorado. Scale bar = 200 μm for specimens 1 and 2, all others 100 μm . Specimens 1 and 2: *P. praehelvetica* (Trujillo), upper *R. cushmani* zone. Specimens 3 and 4: *H. helvetica* (Bolli), base *H. Helvetica* zone (Bed 89, Pueblo). Specimens 5–7: *P. inornata* (Bolli), upper *R. cushmani* zone. Specimens 8 and 11: *D. algeriana* (Caron), upper *R. cushmani* zone. Specimens 9 and 10: *D. imbricata* (Mornod), lower *W. archaeocretacea* zone. Specimens 12–14, 15 and 16: *Whiteinella archaeocretacea* Pessagno, lower *W. archaeocretacea* zone, *D. hagni* subzone.

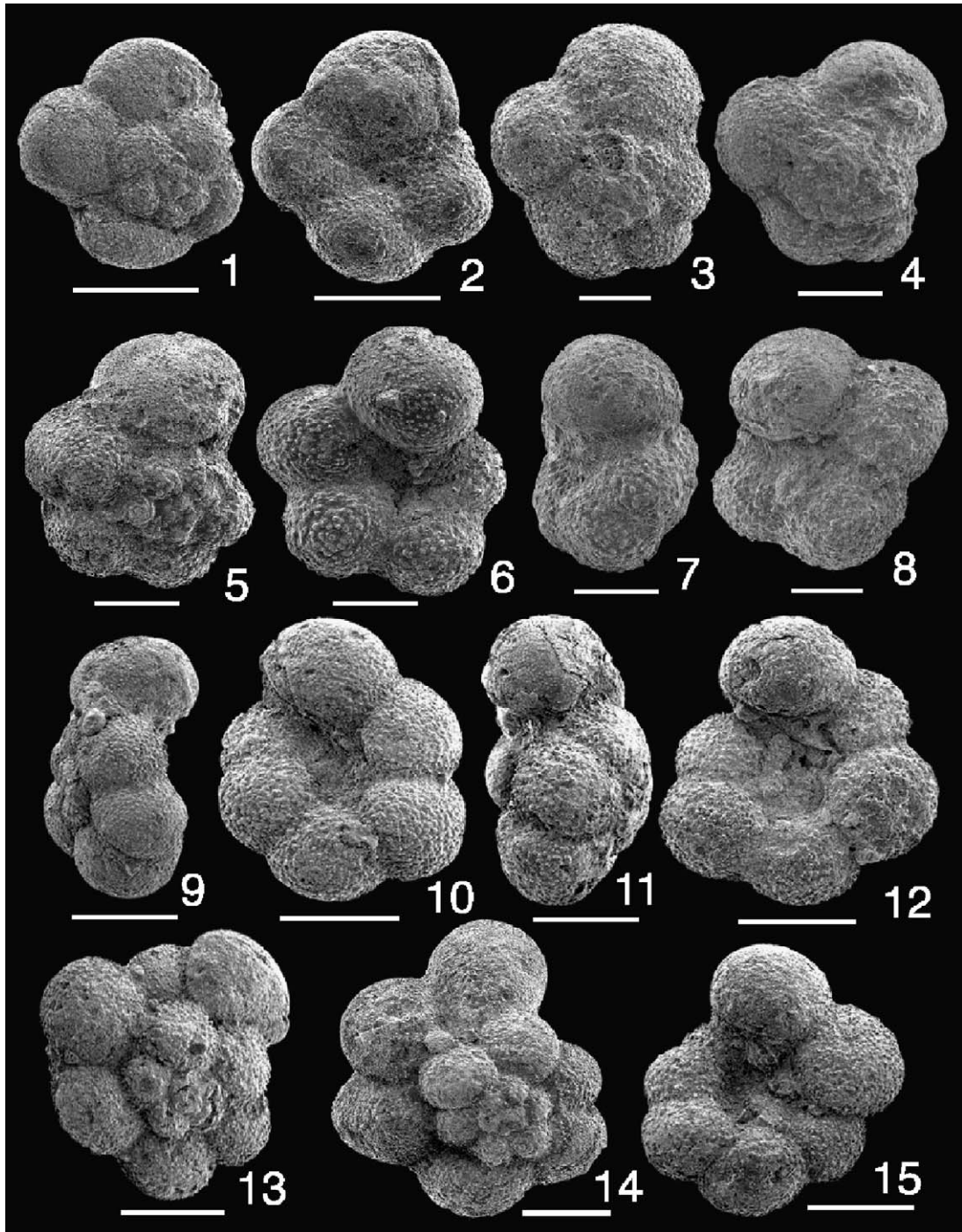


Plate 4. SEM illustrations of planktic foraminifera from the Pueblo GSSP, Colorado. Scale bar = 100 μm , specimens 1–9; 200 μm for specimens 10–15. Specimens 1 and 2: *W. archaeocretacea* Pessagno, lower *W. archaeocretacea* zone, *D. hagni* subzone. (Specimens 3, 4, 7, 8): *W. baltica* Douglas and Rankin, *R. cushmani* zone. (Specimens 5, 6, 9): *W. aprica* (Loeblich and Tappan), *W. archaeocretacea* zone, *H. moremani* subzone. Specimens 10–14 and 15: *W. brittonensis* (Loeblich and Tappan), *R. cushmani* zone.

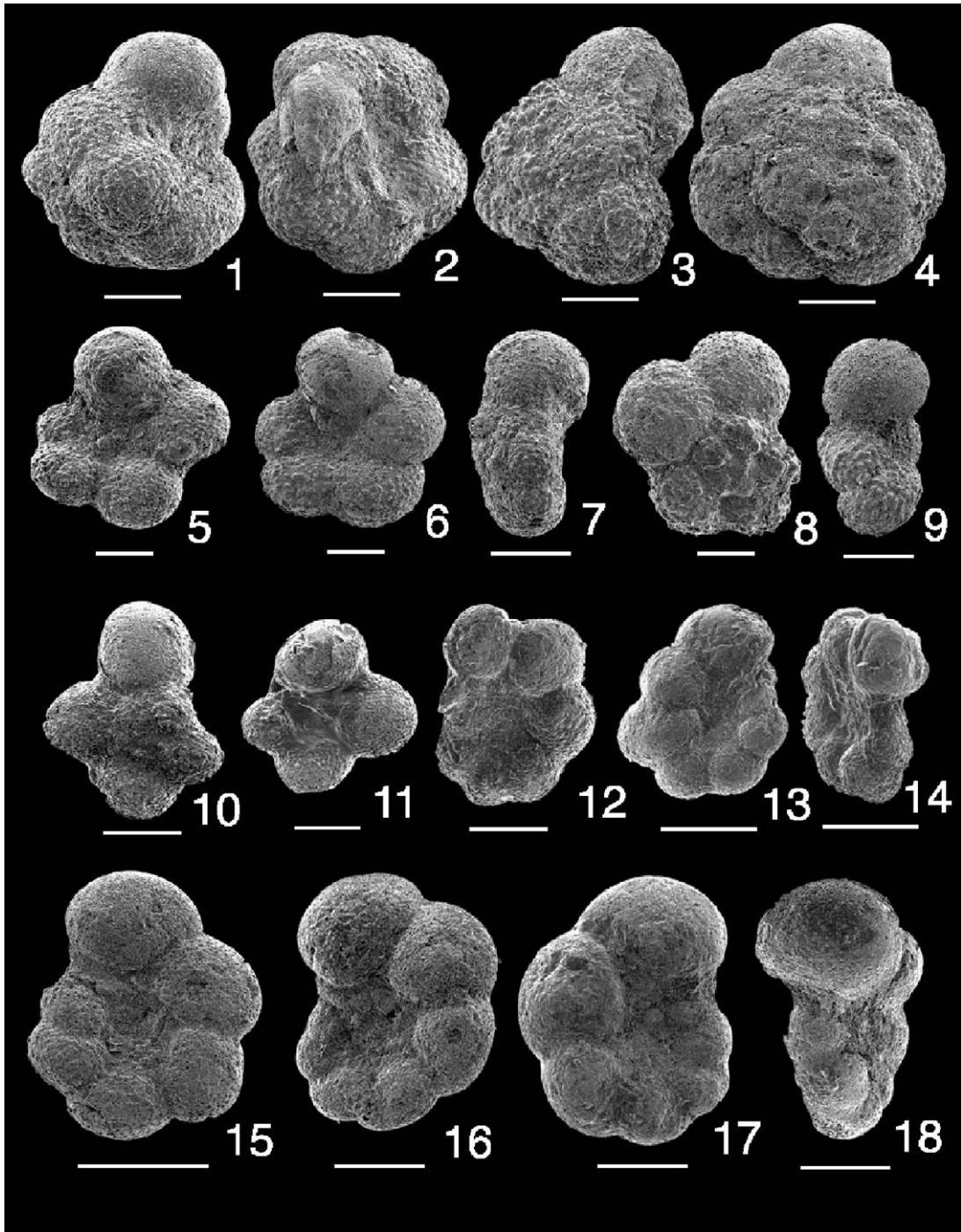


Plate 5. SEM illustrations of planktic foraminifera from the Pueblo GSSP, Colorado. Scale bar = 100 μm . Specimens 1–4: *W. paradubia* (Sigal), upper *R. cushmani* zone. Specimens 5–9: *H. delrioensis* (Carsey), *R. cushmani* zone. Specimens 10 and 11: *H. simplex* (Morrow), *R. cushmani* zone. Specimens 12–14: *G. ultramicra* (Subbotina). Specimens 15–18: *G. bentonensis* (Morrow), *W. archeocretacea* zone, *G. bentonensis* subzone.

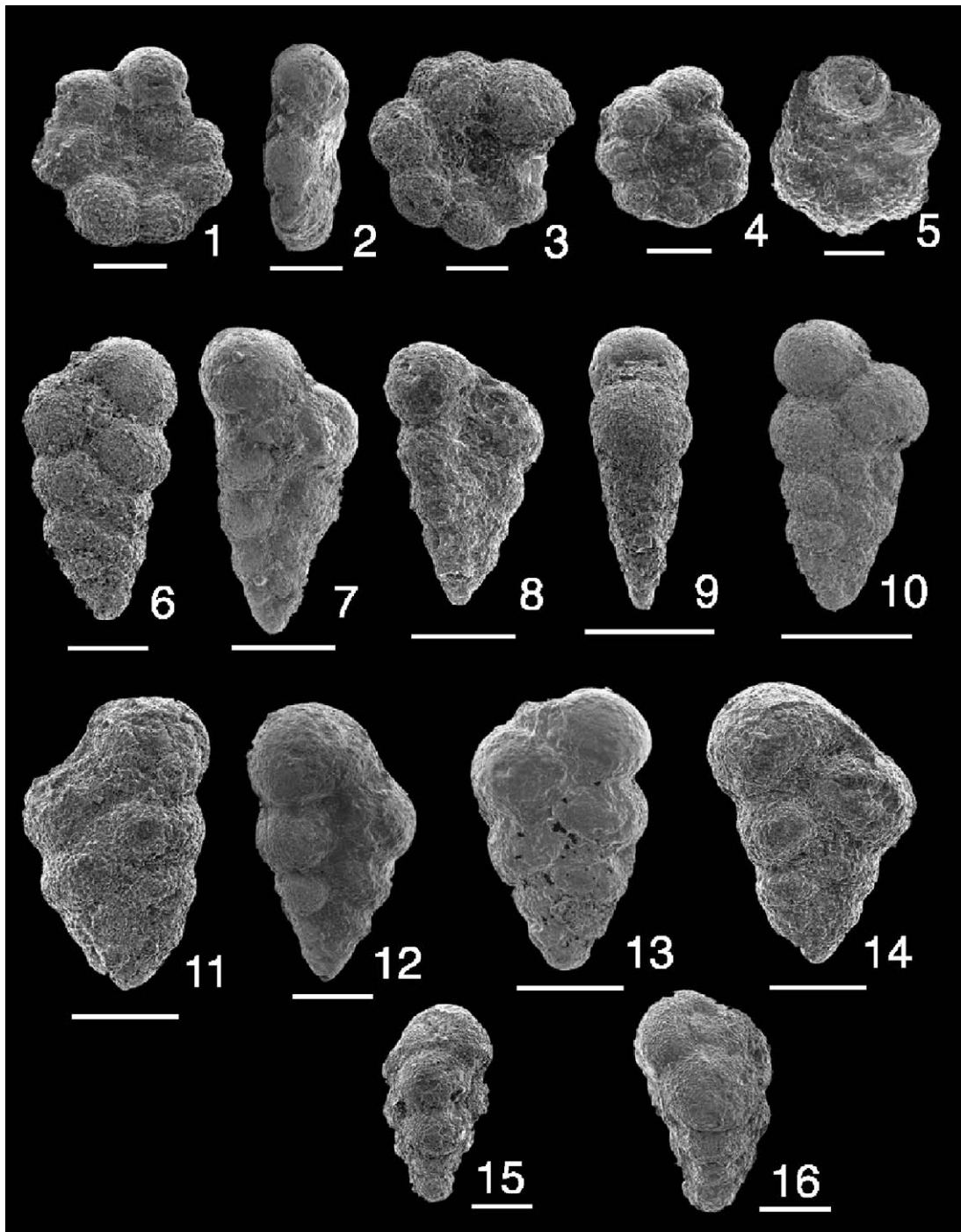


Plate 6. SEM illustrations of planktic foraminifera from the Pueblo GSSP, Colorado. Scale bar = 100 μm for specimens 1–614, *R. cushmani* zone. Scale bar = 50 μm for specimens 15 and 16, *W. archaeocretacea* zone. Specimens 1–5: *H. planispira* (Tappan). Specimens 6 and 7: *Heterohelix* cf. *moremani* (morphotype with compressed chambers). Specimens 8–10: *H. moremani* (Cushman). Specimens 11–14: *H. reussi* (Cushman). Specimens 15 and 16: *G. cenomana* (Keller).

their biotas (Kauffman, 1984; Caldwell and Kauffman, 1993; Leckie et al., 1998). With the onset of this transgression during the latest Cenomanian, bottom water conditions abruptly improved as observed by the establishment of diverse warm water mollusk and calcareous benthic foraminiferal assemblages (“benthic zone” of Eicher, 1969b). A positive excursion in $\delta^{13}\text{C}$ values of organic carbon marks a major increase in productivity, the onset of low oxygen conditions and a major turnover in planktic foraminifera (Elder, 1985). These events have been studied extensively and summarized by Pratt et al. (1993) and Leckie et al. (1998).

The Cenomanian–Turonian transition is exposed along the Rock Canyon Anticline to the north and northeast of Lake Pueblo State Park, Colorado (USA), with well-known outcrops in the Rock Canyon, Pueblo and Liberty Point localities (Fig. 1). The best and most easily accessible outcrops are exposed along a railroad cut and nearby road cut at the Pueblo locality (Fig. 2). In this area of the Rock Canyon Anticline, the Cenomanian–Turonian boundary Stratotype Section and Point (GSSP) has been designated (Kennedy and Cobban, 1991, Kennedy et al., 2000, official designation expected in 2003).

We collected and examined the road cut sequence at Pueblo, which spans 15 m of Cenomanian and 3.5 m of lower Turonian sediments (Fig. 1). This section was analyzed as reference point for comparison with sections in Europe and North Africa. Our study focused on (1) high-resolution age control based on planktic foraminiferal biostratigraphy, (2) paleoecology of planktic foraminiferal species based on quantitative abundance data and carbon and oxygen isotope variations recorded in the monospecific planktic foraminifer *Hedbergella planispira* (as reported in Keller et al., *in press*), and (3) evaluation of faunal turnovers based on depth stratification of species and implied changes in water mass stratification.

2. Methods

A total of 100 samples were collected and analyzed at 10 cm intervals in the changing lithologies of the Bridge Creek Limestone, and at 20–25 cm intervals in the more monotonous shales of the

Hartland Shale Member. For foraminiferal analysis shale, marly limestone and bentonite samples were processed for small (38–63 μm) and larger (>63 μm) size fractions by standard methods (Keller et al., 1995). Both size fractions were analyzed quantitatively based on representative splits of 150–250 specimens per sample for biostratigraphic and environmental analyses. Species from each sample split were picked, identified and mounted on microslides for a permanent record and illustrated by SEM (Plates 1–6). The remaining sample residues were examined for rare species.

Foraminiferal preservation is relatively good in shale and marl samples, but difficult to free of adhering carbonate in more chalky lithologies. All foraminiferal shells show some degree of recrystallization. In general, shells of small species (hedbergellids, globigerinellids, guembelitrids and heterohelicids) are less recrystallized than shells of larger species that may be infilled with blocky calcite. The identification of species and classification of genera follows that of Robaszynski and Caron (1979), Caron (1985) and Eicher (1972).

3. Lithology

The collected Pueblo section from the Rock Canyon Anticline area forms a road cut at the northeastern end of Lake Pueblo (Figs. 1 and 2). At this locality about 18.5 m of gray shales, bentonites and tan-colored limestones of the Greenhorn Formation are exposed (Cobban, 1985; Elder and Kirkland, 1985). The Greenhorn Formation is divided into Hartland Shale and Bridge Creek Limestone Members. The Hartland Shale Member at this outcrop consists of 11.2 m of rhythmically bedded thin calcarenite or nodular calcarenite layers and 30 to 100 cm thick gray shale layers. Bentonite layers are common and vary from 1–2 to 20 cm thick (Fig. 3).

The Bridge Creek Limestone Member is about 6.5 m thick. A prominent 40–50 cm thick bioturbated micritic limestone (Bed 63) marks the base of the Bridge Creek Limestone and contains an upper Cenomanian ammonite assemblage of the *Metoiceras gselinianum* zone (Kennedy et al., 2000), and

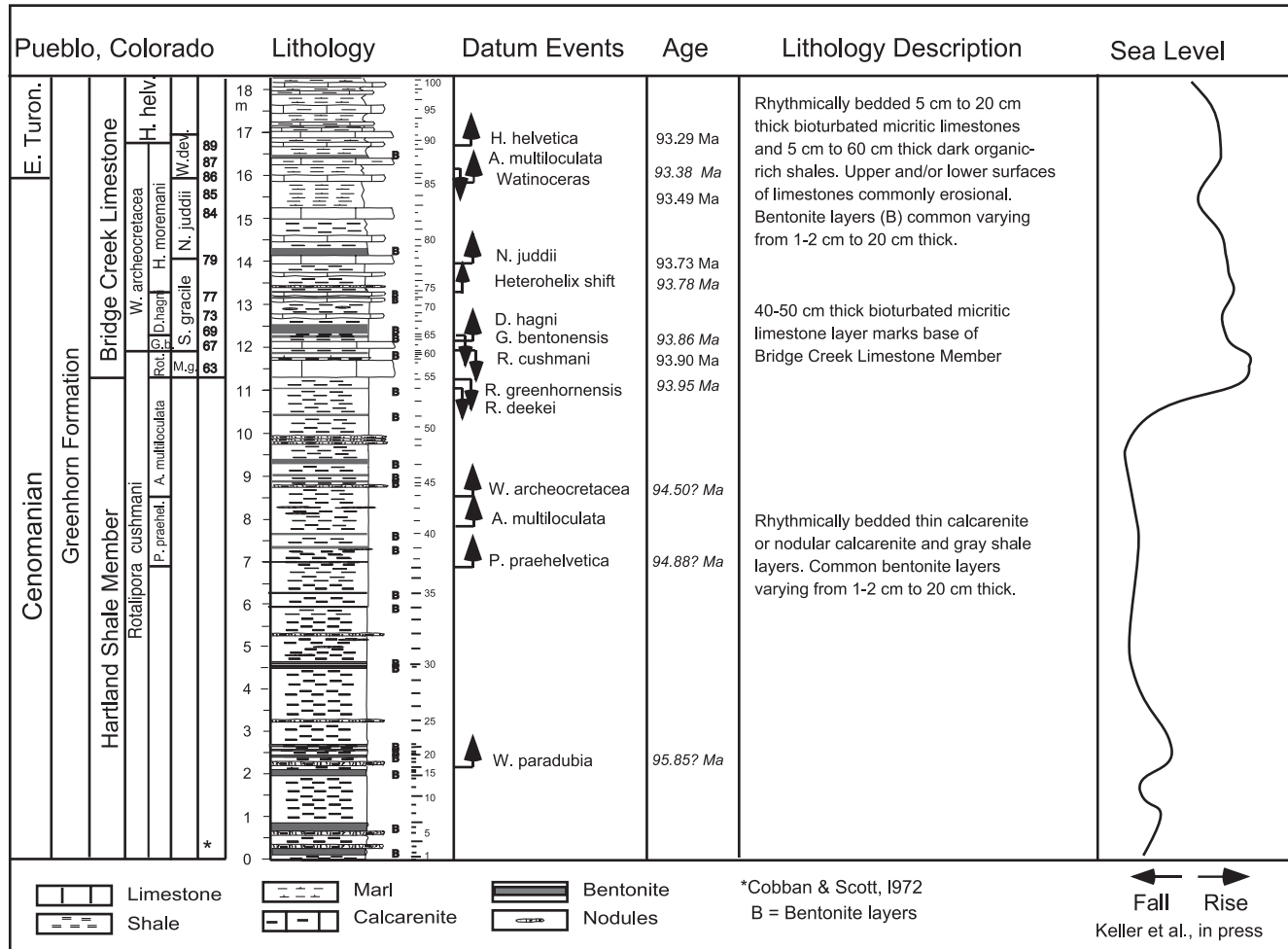


Fig. 3. Lithology, biostratigraphy, planktic foraminiferal and ammonite datum events of the Pueblo section in the Rock Canyon Anticline area of Lake Pueblo State Park, Colorado. Ages for datum events are from age/depth graph of Fig. 4. The sea-level curve is based on lithologic, mineralogical, paleontological and stable isotopic data discussed in Keller et al., in press. The larger sample ticks on the lithological column mark samples analyzed for this study; whereas shorter sample ticks mark additional limestone and bentonite (B) samples for geochemical and mineralogical analyses.

planktic foraminiferal assemblage indicative of the uppermost *Rotalipora cushmani* zone (Leckie, 1985; this study). Previous studies have identified this limestone facies as the main sea-level transgression near the end of the Cenomanian (Hancock and Kauffman, 1979; Kauffman, 1984; Sageman et al., 1998). Upsection, the lithology consists of rhythmically bedded 10–20 cm thick bioturbated micritic limestones alternating with 10–60 cm thick organic-rich dark shales (Figs. 2 and 3). Bentonite layers are common and of variable thickness ranging from 1–2 to 20 cm, similar to the underlying Hartland Shale Member. Prominent sediment layers of the Bridge Creek Limestone have been labeled as marker beds and in this study we follow the numbering system of Cobban and Scott (1972, Fig. 3).

Sea level changes for the Pueblo section have been inferred from paleontological, mineralogical and sedimentological investigations as well as stable isotopes (e.g., Hancock and Kauffman, 1979; Kauffman, 1984; Arthur et al., 1985; Pratt et al., 1993; Leckie et al., 1998; Keller et al., in press). The Hartland Shale was deposited in a shallow epicontinental sea in proximity to shoreline, which provided periodic freshwater influx and clastic debris during wet and humid climate conditions. A sea level rise and transgression occurred during the lower part of the Hartland Shale coincident with a $\delta^{13}\text{C}$ excursion that marks the mid-Cenomanian event (MCE) (Coccioni and Galeotti, 2003; Keller et al., in press). A major sea level transgression began near the top of the Hartland Shale and culminated in the Bridge Creek Limestone Bed 63 (Fig. 3), coincident with the $\delta^{13}\text{C}$ excursion that marks a global oceanic anoxic event (OAE 2) discussed below. Both sea level transgressions appear to have been eustatic (Hardenbol et al., 1998). A generally high though fluctuating sea level accompanied deposition of the Bridge Creek Limestone.

4. Age and depositional rates

The age of the Pueblo section is well constrained based on planktic foraminiferal and ammonite biostratigraphies, and details of the OAE 2 $\delta^{13}\text{C}$ excursion that indicate relatively continuous sediment deposition across the Cenomanian–Turonian (C–T)

transition. The stable isotope data is from Keller et al. (in press) and based on monospecific samples of the planktic foraminifer *H. planispira* from the same sample splits used for this study. Age estimates for species first and last appearances, $\delta^{13}\text{C}$ excursions, depositional and environmental events have been calculated based on ages of various ammonite and planktic foraminiferal datum events extrapolated from the paleomagnetic time scale and radiometric dates by Hardenbol et al. (1998) (Fig. 4, Table 1). Three $^{40}\text{Ar}/^{39}\text{Ar}$ ages determined from bentonite layers by Obradovich (1993) and Kowallis et al. (1995) are compatible with these dates. On the basis of the $^{40}\text{Ar}/^{39}\text{Ar}$ data, these workers estimated the CT boundary level at 93.3 ± 0.2 and 93.1 ± 0.3 Ma, respectively, as compared with 93.49 ± 0.2 Ma based on the first appearance of *Watinoceras devonense*, which is the preferred marker for the CT boundary, and 93.29 ± 0.2 Ma for the last appearance of *Helvetoglobotruncana helvetica*, the planktic foraminiferal marker species (Hardenbol et al., 1998; Kennedy et al., 2000).

Sedimentation rates calculated based on the age/depth plot for the Pueblo section indicate no major sedimentary breaks or discontinuities. From the base of the Bridge Creek Limestone Bed 63 to Bed 79, sediment accumulation rates average 1.23 cm/ky (1.11 cm/ky excluding bentonite layers), whereas in the upper part they average 0.87 cm/ky (0.75 cm/ky excluding bentonite layers), assuming that limestone and shale layers were deposited at roughly equal rates (Fig. 4). Based on cycle analysis, Meyers et al. (2001) concluded that there is a hiatus of about 25,000 years in the upper part of Bed 78, though no hiatus is apparent in outcrops or faunal analyses. This short hiatus does not significantly affect the sediment accumulation rate, nor change the slope of the age/depth curve.

Estimated sedimentation rates for the Bridge Creek Limestone by Elder and Kirkland (1985) average 0.5–1.0 cm/ky, by Scott et al. (1998) 0.9 cm/ky and by Sageman et al. (1998) 0.57 cm/ky. In comparison, the comparable interval at Eastbourne averages 2.4 cm/ky. The lower sediment accumulation rate at Pueblo is probably due to cyclic climate variations and periods of nondeposition between shale/limestone couplets (Sageman et al., 1998). Shale deposition occurred during humid wet periods accompanied by high sediment and freshwater influx. Limestone de-

Pueblo, Colorado (GSSP)

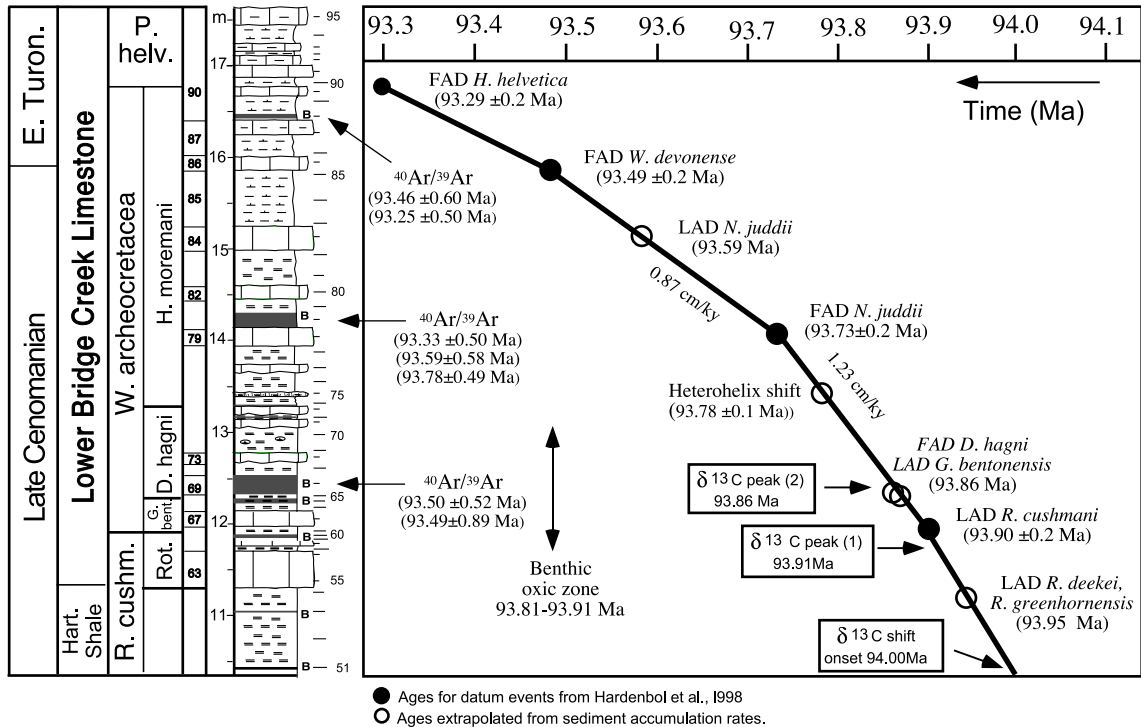


Fig. 4. Age/depth plot of the Pueblo section in the Rock Canyon Anticline area of Lake Pueblo State Park, Colorado, based on planktic foraminiferal and ammonite datum events from Hardenbol et al. (1998) and other datum events for which ages have been extrapolated from the age/depth and sediment accumulation rates. Calculated datum events are coeval at Pueblo and Eastbourne sections within errors of 10 to 20 ky, except for the last appearance of *G. bentonensis* for which a 50 ky difference occurs due to the condensed interval in Bed 68 at Pueblo. $^{40}\text{Ar}/^{39}\text{Ar}$ ages for bentonite layers are from Obradovich (1993) and Kowallis et al. (1995).

position occurred during more arid periods accompanied by reduced sedimentary influx and increased production of biogenic carbonate (foraminiferal tests, coccoliths, invertebrates; Keller et al., in press). These dilution/productivity cycles have been interpreted as obliquity and precession cycles, respectively (Sage-man et al., 1998).

Meyers et al. (2001) estimated that overall sedimentation rates for the Hartland Shale average 2.7 cm/ky. Sedimentation appears to have been significantly lower, about 0.5 cm/ky, for the top 10 m of the Hartland shale, which is estimated to span a 2 my interval between the $\delta^{13}\text{C}$ shifts of the mid-Cenomanian event (MCE) and late Cenomanian OAE 2 (Coccioni and Galeotti, 2003). The lower sediment accumulation rate, compared with the Bridge Creek Limestone, may be due to lower biogenic productivity

in a shallower epeiric sea and nondeposition associated with cyclic sea level fluctuations.

The age/depth plot and sediment accumulation rates at Pueblo provide age estimates for foraminiferal datum events and oceanographic events marked by the $\delta^{13}\text{C}$ excursion (Fig. 4). A similar age/depth plot for the Eastbourne section (Keller et al., 2001) has been used to cross-calibrate ages for the two-peaked $\delta^{13}\text{C}$ shifts, the *Heterohelix* shift, and the last appearance data (LAD) of *G. bentonensis*, *Rotalipora deekei* and *Rotalipora greenhornensis*. The ages of these datum events in these two sections are comparable within error margins of 0.01 to 0.02 my, except for *G. bentonensis* where ages differ by 50 ky as a result of a condensed interval at the top of Bed 68 at Pueblo (Table 1). This condensed interval is also evident by the juxtaposition of the first appearance datum (FAD)

Table 1

(a) Relative percent abundance of the middle to late Cenomanian planktic foraminifera in the Hartland Shale Member at Pueblo, Colorado

Biozones	<i>R. cushmani</i>																				
Subzones																					
Sample	1	4	7	10	13	16	19	22	24	25	26	27	28	30	31	32	33	34	35	36	37
Depth (cm) from section base	0	30	85	145	195	215	245	260	300	325	355	395	420	450	495	540	570	595	625	660	685
<i>A. multiloculata</i>																x	x		x		
<i>Anaticinella</i> cf. <i>multiloculata</i>																					
<i>Dicarinella algeriana</i>																					
<i>D. hagni</i>																					
<i>D.</i> cf. <i>imbricata</i>																					
<i>D. imbricata</i>																					
<i>Globigerinelloides bentonensis</i>		2			x	x	x	x						1				x		x	x
<i>G. ultramicra</i>			1	x		1				x											
<i>Gümbelitra cenomana</i>																					
<i>G. albertensis</i>																					
<i>Hedbergella delrioensis</i>	20	27	31	x		10	11	6		8			1	10	1	3	x		1	1	2
<i>H. planispira</i>	66	18	35	40	67	34	50	22	35	6	63	40	55	31	40	36	48	21	27	33	58
<i>H. simplex</i>		5				4	4					x	1	2	3		x	1	x		2
<i>Heterohelix moremani</i>	5	5	5	4	2	3	8	6	3	7	2	x	1	3	3	3	x	x	3	3	1
<i>H. reussi</i>	4	18	15	56	27	41	9	56	44	76	28	45	33	34	50	46	40	65	55	44	24
<i>H. sp. A</i>								x	1				x	10		4	1		4	4	
<i>H. sp. B</i>													x			x	1	2	1	3	
<i>Praeglobotruncana aumalensis</i>		5				x	x			1		x		x	x		x		2	x	2
<i>P. gibba</i>		x	x		x	1	1		3		x	x			x	x	x		x	x	
<i>P. inornata</i>																					
<i>P. praehelvetica</i>																					
<i>P. stephani</i>		4	2	x		3	2	1	6			3	2	3		x	1	3	1	2	
<i>Rotalipora cushmani</i>									x			x	x	x		x	x	x	x	1	x
<i>R. deekei</i>																					
<i>R. greenhornensis</i>											x	x	1	x	1	x	x		1	x	x
<i>R. montsalvensis</i>						x	1	x	x		x	x	2			x	x				x
<i>Whiteinella aprica</i>																					
<i>W. archaeocretacea</i>																					1
<i>W. baltica</i>	4	14	11		4	2	13	5	7	1	2	2	2	1	2	1	3	4	4	7	9
<i>W. brittonensis</i>	x	x	x	x	x	x	x	x	x		3	2	x	1	x	x	2	x	1		x
<i>W. paradubia</i>		x?				x	x	x	x		x	x		x	x	x	1	2	x		x
Total specimens counted	156	195	172	223	172	215	150	229	161	166	215	260	211	265	189	208	273	186	213	257	183

(continued on next page)

Table 1 (continued)

(b) Relative percent abundance of late Cenomanian planktic foraminifera in the Hartland Shale Member at Pueblo, Colorado

Biozones	<i>R. cushmani</i>																		<i>W. archeocretacea</i>								
Subzones	<i>P. praehelvetica</i>									<i>A. multiloculata</i>									<i>Rotalipora extinct.</i>			<i>G. bentonensis</i>			<i>D. hagni</i>		
Sample	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	57	59	60	61	63	64	65	67	69	
Depth (cm) from section base	715	740	765	795	825	855	875	885	895	930	975	985	1020	1050	1075	1100	1125	1175	1180	1185	1190	1210	1225	1230	1260	1280	
<i>A. multiloculata</i>				1	x	x	x				x		x	x	1	2		x		x							
<i>Anaticinella</i> cf. <i>multiloculata</i>	x																			x		x					
<i>Dicarinella algeriana</i>																3	2		1	8	7	x	x		x	x	
<i>D. hagni</i>																						x	x				
<i>D. cf. imbricata</i>																		x	x	x							
<i>D. imbricata</i>																					x			x			
<i>Globigerinelloides bentonensis</i>	1	4	2	4	2	x	x	3	x	6	9	6	2	5	3	5	8	6	7	4	2	4	x				
<i>G. ultramicra</i>		1		x			x	2	1		1	1	x		1	3	2	5		1	12	5	4	12	x	2	
<i>Gümbelitra cenomana</i>		x						1										2	9	2	3	8	11	3	2	10	
<i>G. albertensis</i>																			2			4	1	2	x	5	
<i>Hedbergella delrioensis</i>	3	19	7	2	8	7			2	2			4	4	7	4		3		15	11	7	9	7	5	4	
<i>H. planispira</i>	49	27	22	29	34	13	28	40	51	27	10	16	17	19	29	23	25	15	44	39	41	36	22	38	39	35	
<i>H. simplex</i>	x	4	1	1	x	3	x	1	x	x	7	1	2	x	2	3	1	x		1	1	x	x			1	
<i>Heterohelix moremani</i>	1	4	5	4	1	7	1	4	5	2	7	6	5	4	2	5	6	12		1	1	1	9	2	8	3	
<i>H. reussi</i>	25	21	41	35	36	33	50	48	37	38	46	49	44	30	44	20	47	36	10	5	10	24	34	22	33	27	
<i>H. sp. A</i>	13	6	x	3	2	2	3	5	x	11	x			1		5											
<i>H. sp. B</i>	1	2	3	7	9	7	6	5	x	1	13	7	12	12	1	12	x					1					
<i>Praeglobotruncana aumalensis</i>		2	2			x				x			x	x	2	x	x	x	x		3		x				
<i>P. gibba</i>	2	2	1	x			x			x			x	x	x	x	x	x	1	1	1	x	x	x		x	
<i>P. inornata</i>	1	1	x	1			2				x	4		x	x	x	x	x	2	1	1						
<i>P. praehelvetica</i>	x			x	x												x	x	x	x	x						
<i>P. stephani</i>	x	1	x	1	1	3	3	x	x		x	9	5	6	2	6	x	x	2			1	1		x	x	
<i>Rotalipora cushmani</i>	x	x	x	x	x	3	x	x	x	x	1	x	1	x	3	1	x	x		x							
<i>R. deekei</i>														x		x											
<i>R. greenhornensis</i>	x	x	x	x		x	x	1	x	x	x	x	x	x			1										
<i>R. montsalvensis</i>	x	x	x	x	x	x																					
<i>Whiteinella aprica</i>																					x	2	x	3	x	x	
<i>W. archaeocretacea</i>										x	x		3	2	1	2	x	5	12	10	3	3	1	2	6	6	
<i>W. baltica</i>	1	5	11	4	4	13	5	4	x	6	3	4	3	9	1	3	2	8	8	7	2	x	5	5	4	6	
<i>W. brittonensis</i>	1	x	2	1	x	4	x	x		x		x	x		x	2			x	x	x				x	x	
<i>W. paradubia</i>			1	2	2	x	x	x	x		x	x	x	4	x		x	x		x	x	1	x	3	x	x	
Total specimens counted	159	257	184	251	181	185	125	182	210	211	229	144	224	188	216	239	188	170	169	288	183	315	185	226	215	247	

(c) Relative percent abundance of late Cenomanian to early Turonian planktic foraminifera in the Bridge Creek Limestone Member at Pueblo, Colorado

Biozones	<i>W. archeocretacea</i>										<i>H. helvetica</i>										
	<i>D. hagni</i>					<i>H. moremani</i>															
Subzones	<i>D. hagni</i>					<i>H. moremani</i>															
Sample	70	72	74	76	77	78	79	80	81	82	83	84	85	86	88	89	90	94	96	98	100
Depth (cm) from section base	1295	1320	1335	1355	1375	1400	1425	1445	1475	1500	1530	1555	1580	1600	1645	1665	1680	1735	1775	1800	1825
<i>A. multiloculata</i>		x	x			x	x	x		1		8	3	2							
<i>Anaticinella cf. multiloculata</i>							x									x	1				
<i>Dicarinella algeriana</i>			x			x			x				x	5	2	3	4	2	1	6	4
<i>D. hagni</i>		x							x	x											x
<i>D. cf. imbricata</i>	1										x					x					
<i>D. imbricata</i>						x		x		x								x	x		
<i>Globigerinelloides bentonensis</i>																					
<i>G. ultramicra</i>			2	2			3	x					1	x	x			1	x	1	
<i>Gümbelitra cenomana</i>	1	4	5	3		2	2	6		x	2			3	10	6	4	3	1		x
<i>G. albertensis</i>		2		1																	
<i>Hedbergella delrioensis</i>	3	5	2		3	2	2	2	2	1					4	1		1	4		x
<i>H. planispira</i>	3	34	22	23	26	34	35	39	35	19	22	3	6	9	9	8	15	14	3	6	5
<i>H. simplex</i>		2	1															x	x		
<i>Heterohelix moremani</i>	5	9	5	3	5	4	1	3	1	3	3	1	x	2		3	1		1	2	
<i>H. reussi</i>	8	29	41	67	65	53	45	42	55	60	60	51	61	64	61	48	48	63	56	46	71
<i>H. sp. A</i>	x		1						x	x	x	2	5	8	4	8	x	1	10	7	5
<i>H. sp. B</i>					x	1		1									x	4	1	3	3
<i>Helvetoglobotruncana helvetica</i>																	1	x		x	
<i>Praeglobotruncana aumalensis</i>		x	x			x	x	x	x	x	x				x	x	x	x	x	2	1
<i>P. gibba</i>	2	x	1			x	x		x	x		x		x	x				x		x
<i>P. inornata</i>																					
<i>P. praehelvetica</i>			1			x	x	x	1	x	x	x		2	x	2	x	1	1	x	
<i>P. stephani</i>	x		x			x	x			x	x										
<i>Rotalipora cushmani</i>																					
<i>R. deekei</i>																					
<i>R. greenhornensis</i>																					
<i>R. montsalvensis</i>																					
<i>Whiteinella aprica</i>	5	3	x			x	3	x	x	6	x	3	x	x	1	1	5	3	5	4	6
<i>W. archaeocretacea</i>	1	3	2		x	1	1	1	2	x	1	3	x	1	4	x	3	4	4	10	3
<i>W. baltica</i>	54	7	11	1		x	2	2		x	4	10	10	3	2	6	5	5	5	4	2
<i>W. brittonensis</i>	13	1	x		x	x	3	2	x	5	4	13	8	x	1	2	2	1	4	4	3
<i>W. paradubia</i>	x	x	x			x	1	1	x	x	x	3	3	x		x	x	x	1	2	x
Total specimens counted	110	208	266	99	310	249	179	259	209	183	183	78	173	181	165	203	196	196	201	195	197
Preservation	poor										poor										

Table 2

Ages for planktic foraminiferal and ammonite first (FAD) and last (LAD) appearance data, and $\delta^{13}\text{C}$ shifts at the Pueblo GSSP

<i>Helvetoglobotruncan helvetica</i> FAD	93.29 ± 0.2 Ma	Hardenbol et al. (1998)
<i>Watinoceras devonense</i> FAD	93.49 ± 0.2 Ma	Hardenbol et al. (1998)
<i>Neocardioceras juddii</i> LAD	93.49 ± 0.2 Ma	Hardenbol et al. (1998)
<i>Neocardioceras juddii</i> LAD	93.59 Ma	this study at Pueblo
<i>Calycoceras geslineanum</i> LAD	93.73 ± 0.2 Ma	Hardenbol et al. (1998)
<i>Neocardioceras juddii</i> FAD	93.73 ± 0.2 Ma	Hardenbol et al. (1998)
Heterohelix shift	93.78 ± 0.02 Ma*	this study
OAE 2 $\delta^{13}\text{C}$ peak (2) excursion max.	93.86 ± 0.05 Ma*	this study
<i>Globigerinelloides bentonensis</i> LAD	93.86 ± 0.05 Ma*	this study
<i>Dicarinella hagni</i> FAD	93.86 ± 0.05 Ma*	this study
<i>Rotalipora cushmani</i> LAD	93.90 ± 0.02 Ma*	Hardenbol et al. (1998)
OAE 2 $\delta^{13}\text{C}$ peak 1	93.91 ± 0.02 Ma*	this study
OAE 2 $\delta^{13}\text{C}$ excursion onset	94.00 ± 0.02 Ma*	this study
<i>Rotalipora greenhornensis</i> LAD	93.95 ± 0.02 Ma*	this study
<i>Rotalipora deekei</i> LAD	93.95 Ma	this study
<i>Whiteinella archeocretacea</i> FAD	94.50 Ma	this study
<i>Praeglobotruncana praehelvetica</i> FAD	94.88 Ma	this study
Mid-Cenomanian $\delta^{13}\text{C}$ shift (MCE)	95.71 Ma	this study
<i>Whiteinella paradubia</i> FAD	95.85 Ma	this study

Asterisks mark datum events at Pueblo that have been cross-correlated with Eastbourne, England. Error margins reflect uncertainty between these two sections.

of *Dicarinella hagni* and peak 2 of the $\delta^{13}\text{C}$ excursion. The ages for datum events calculated by Hardenbol et al. (1998) also indicate good agreement with Eastbourne, except for *H. helvetica* which appears earlier at Eastbourne possibly because this species is diachronous and/or the evolutionary transition from *praehelvetica* to *helvetica* is difficult to determine (Table 2).

5. Biostratigraphy

The Cenomanian–Turonian transition in the Western Interior is stratigraphically defined by ammonite

and inoceramid zones, which provide reliable regional correlations and have been discussed in various publications (e.g., Cobban and Scott, 1972; Cobban, 1985; Elder, 1985; Kennedy and Cobban, 1991). Biostratigraphic correlation based on planktic foraminifera has received little attention due to the scarcity or low diversity of microfossils in these mostly very shallow Western Interior marine sequences. Early studies by Eicher (1969a,b, 1972) formed the critical groundwork for foraminiferal biostratigraphy and paleoecology, whereas Leckie (1985, 1989) and Leckie et al. (1998) significantly advanced the paleoclimatic and paleoceanographic applications. This study documents the planktic foraminiferal species ranges and applies the standard planktic foraminiferal biozones (Robaszynski and Caron, 1979) to achieve global integration of the Pueblo GSSP, and incorporates Keller et al.'s (2001) three-part subdivision of the *Whiteinella archeocretacea* zone to achieve a higher age resolution. Additional biomarkers are considered for subdivision of the *R. cushmani* zone, which after testing in other geographic regions may provide further biostratigraphic refinement and age control. The proposed planktic foraminiferal biostratigraphic scheme at Pueblo is shown in Fig. 5 along with the $\delta^{13}\text{C}$ excursion and ammonite zones. Species ranges and assemblages as well as the $\delta^{13}\text{C}$ excursion at Pueblo are very similar to those at Eastbourne and can be easily correlated (Paul et al., 1999; Keller et al., 2001).

5.1. *H. helvetica* zone

The first appearance (FA) of *H. helvetica* defines the base of this zone and is considered the planktic foraminiferal biomarker for the Cenomanian–Turonian (C/T) boundary. However, this species is a problematic biomarker and needs to be reevaluated. The problems are primarily due to the rarity of this species, potential diachronous occurrence, and identification and separation of the *H. helvetica* morphotype from its evolutionary ancestor *P. praehelvetica* (Hart and Bigg, 1981; Hilbrecht et al., 1986; Jarvis et al., 1988; Keller et al., 2001). At Pueblo, this species first appears in the shale above limestone Bed 90 about 75 cm above the FA of the ammonite *W. devonense* (Bed 86), which marks the C/T boundary, though transitional forms of *praehelvetica*–*helvetica* are present in Beds 85, 86 and 89. At Eastbourne the first appearance

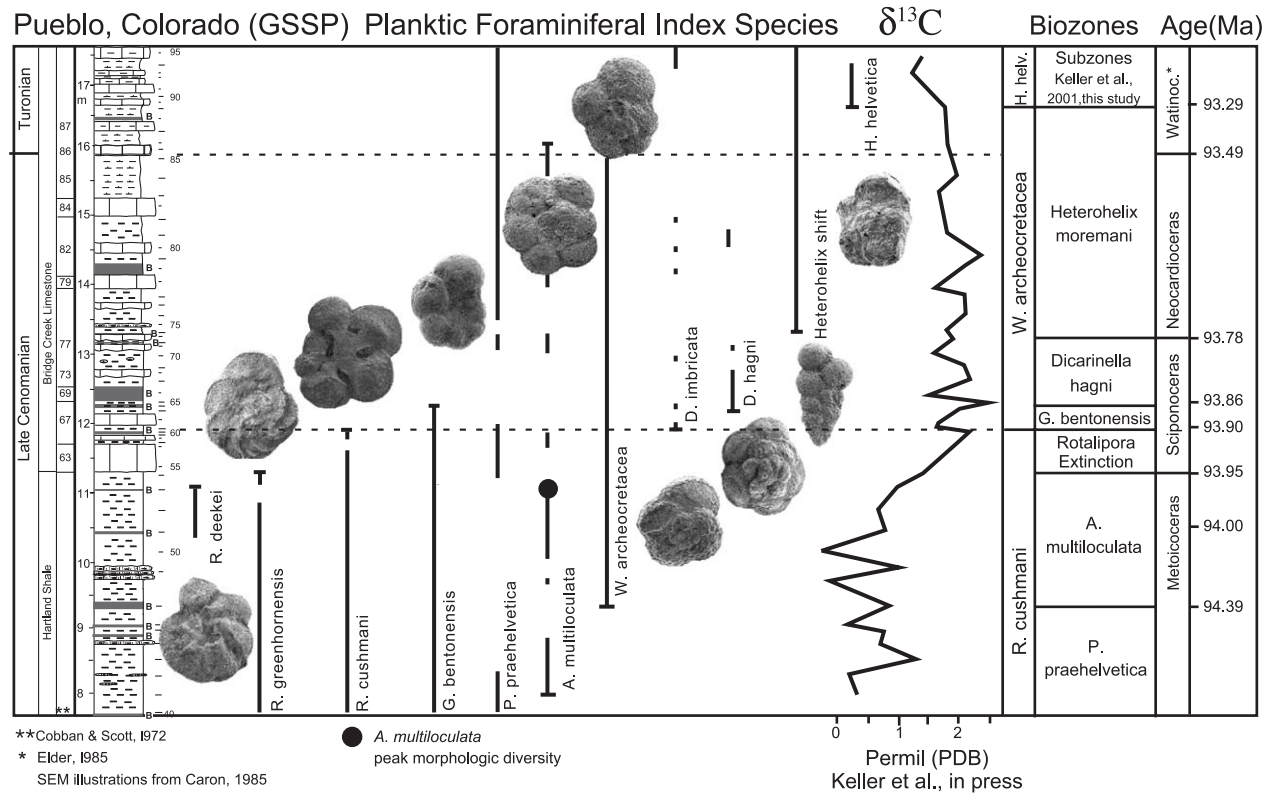


Fig. 5. High-resolution correlation scheme for the Cenomanian–Turonian transition based on planktic foraminifera and the carbon isotope curve of the planktic foraminifer *H. planispira* at the Pueblo GSSP. See Fig. 4 for ages of datum events.

of *H. helvetica* was observed 20 cm above the FA of *W. devonense* (Keller et al., 2001). The discrepancies in the observed first appearance of *H. helvetica* is largely due to the difficulty in finding a uniform criterion for determining the point at which the transition from *P. praehelvetica* to *H. helvetica* can be considered to have been completed. Such problems are commonly encountered for biomarkers based on evolutionary transitions in adaptation to changing environments and therefore can result in diachronous datum events.

5.2. *Heterohelix moremani* subzone (93.29–93.78 Ma)

This subzone defines the interval from the first appearance of *Heterohelix* dominated assemblages (*Heterohelix* shift) after the initial OAE 2 $\delta^{13}\text{C}$ excursion to the FA of *H. helvetica*. This *Heterohelix* shift has previously been used as correlation tool in the US WIS by Leckie et al. (1998), but it also marks an interval of global heterohelicid dominance (*H. moremani* and *H. reussi*) in the *W. archeoretacea* zone after the $\delta^{13}\text{C}$ excursion reached its peak (Figs. 5 and 6, Nederbragt and Fiorentino, 1999; Keller et al., 2001). The *Heterohelix* shift is a reliable global

biomarker that reflects the expansion of the oxygen minimum zone after the major sea level transgression and $\delta^{13}\text{C}$ excursion. At Pueblo, the onset of the *Heterohelix* shift occurs 50 cm below Bed 79, near the base of the ammonite *Neocardioceras* zone.

5.3. *Dicarinella hagni* subzone (93.78–93.86 Ma)

This subzone defines the interval from the last appearance (LA) of *Globigerinelloides bentonensis* to the *Heterohelix* shift (Fig. 5). In addition, *D. hagni* first appears just prior to the extinction of *G. bentonensis*. At Pueblo, this subzone forms the upper part of the benthic oxic zone and spans from Bed 68 to Bed 78. Note that the *D. hagni* subzone replaces the *A. multiloculata* subzone of Keller et al. (2001), because examination of the Pueblo section revealed that the acme of development of *A. multiloculata* is in the upper *R. cushmani* zone.

5.4. *Globigerinelloides bentonensis* subzone (93.86–93.90 Ma)

This subzone defines the interval from the extinction of *R. cushmani* to the extinction of *G. bentonen-*

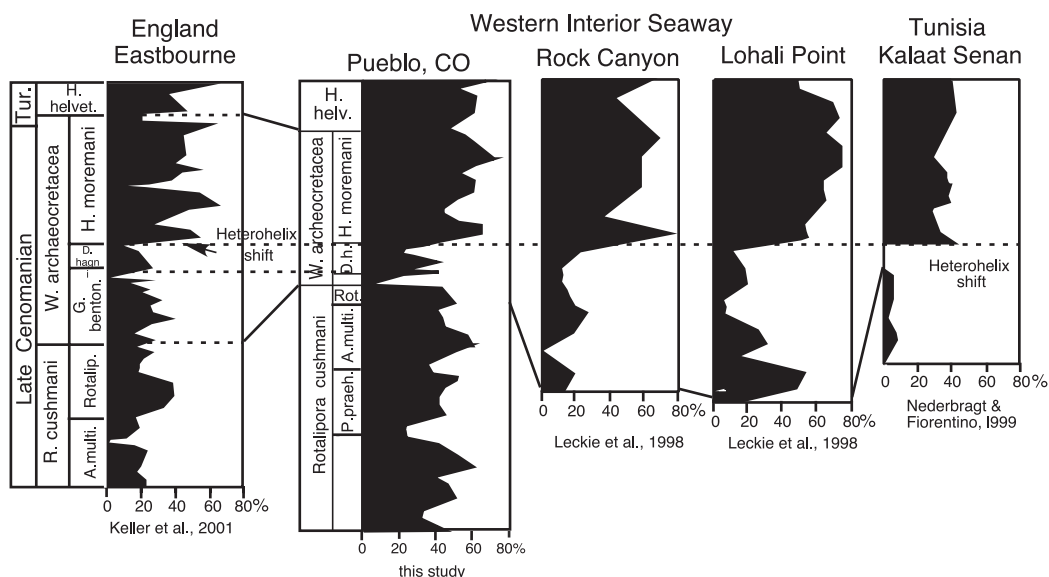


Fig. 6. Relative abundances of *Heterohelix* at Eastbourne, England, Pueblo, Lohali Point and Rock Canyon in Lake Pueblo State Park, and Kalaat Senan, Tunisia. At each locality, there is a shift to *Heterohelix*-dominated assemblages which follows the $\delta^{13}\text{C}$ shift and benthic oxic zone. The *Heterohelix* is an excellent biomarker for global correlations.

sis. The interval spans Beds 66 to 68 and corresponds to the trough between the first and second $\delta^{13}\text{C}$ peaks at Pueblo and Eastbourne (see also Keller et al., 2001).

5.5. *Rotalipora* extinction subzone (93.90–93.94 Ma)

This subzone spans the interval of extinction of the genus *Rotalipora* and is marked by the extinctions of *R. greenhornensis* and *R. deekei* at the base and *R. cushmani* at the top (Fig. 5). In addition, this subzone corresponds to the interval of $\delta^{13}\text{C}$ excursion and sea level transgression at both Pueblo and Eastbourne and is correlative with the *M. geslinianum* zone.

5.6. *Anaticinella multiloculata* subzone (93.94–94.50? Ma)

This subzone marks the interval from the FA of *W. archeocretacea* to the LA of *R. greenhornensis*. The nominate taxon is most abundant at the top of this zone and near the onset of the $\delta^{13}\text{C}$ excursion (Fig. 5). In this interval, *A. multiloculata* peaks in morphologic diversity showing gradations from its ancestor *R. greenhornensis* to *A. multiloculata* by losing its keel and inflating chambers, probably in adaptation to a shallower subsurface habitat in the lower photic zone (see Appendix, Eicher, 1972). The last occurrence of *R. greenhornensis* was observed at the same stratigraphic interval at Eastbourne (Keller et al., 2001).

5.7. *Praeglobotruncana praehelvetica* subzone (94.50–94.88? Ma)

This subzone spans the interval from the FA of *P. praehelvetica* to the FA of *W. archeocretacea* (Fig. 5).

6. Planktic foraminiferal turnovers

During the late Cenomanian to early Turonian at Pueblo planktic foraminifera experienced a major faunal turnover associated with the OAE 2 positive $\delta^{13}\text{C}$ excursion and major sea level transgression (e.g., Eicher, 1969a; Leckie, 1985; Leckie et al., 1998; West et al., 1998). A smaller faunal turnover occurred earlier in the *R. cushmani* zone and is also associated

with a positive $\delta^{13}\text{C}$ excursion and sea level transgression termed the mid-Cenomanian event (MCE) (Coccioni and Galeotti, 2003). The nature of these faunal turnovers can be evaluated based on species richness and relative species abundances.

At the base of the Pueblo section prior to the MCE $\delta^{13}\text{C}$ excursion, only seven species are consistently present and four show sporadic occurrences. During and immediately after the $\delta^{13}\text{C}$ shift, six species appeared, including *Praeglobotruncana aumalensis*, *Whiteinella paradubia*, *Heterohelix* sp. A (a large morphotype with inflated chambers), *R. cushmani*, *R. greenhornensis* and *R. montsalvensis* (Fig. 7). The absence of the latter three deeper dwelling *Rotalipora* species prior to the MCE may be ecological and related to the shallow environment at Pueblo. In the 4 m above this interval, species richness gradually increased to a maximum of 20 species between 7 and 8 m with the appearance of *P. inornata*, *P. praehelvetica*, *A. multiloculata* and *Guembelitra*, but decreased again below the OAE 2 $\delta^{13}\text{C}$ shift (Fig. 7).

With the onset of the major OAE 2 $\delta^{13}\text{C}$ shift and marine transgression that spans the top of the Hartland Shale and base of the Bridge Creek Limestone, four *Rotalipora* species disappeared (*R. montsalvensis*, *R. deekei*, *R. greenhornensis*, *R. cushmani*) followed by *G. bentonensis* and *Praeglobotruncana inornata* resulting in a loss of about 30% (Fig. 7). In the same interval and immediately following the *Rotalipora* extinction six species appeared (*Dicarinella algeriana*, *D. imbricata*, *D. hagni*, *W. archeocretacea*, *W. aprica* and *G. albertensis*, Fig. 7). This faunal turnover thus results in no net loss in species diversity. Relative species abundances indicate that both outgoing and incoming species were rare and endangered species and thus a minor components of the total planktic foraminiferal population with <2% and <4%, respectively. No significant change in species diversity is observed above the OAE 2 $\delta^{13}\text{C}$ shift. However, a sharp drop in species richness is observed in the lower part of the *H. moremani* subzone, Bed 78 of the Bridge Creek Limestone, coincident with maximum *Heterohelix* abundance. This event was also observed at the same stratigraphic interval at Eastbourne (Keller et al., 2001) and appears to be associated with a global expansion of the oxygen minimum zone.

Relative species abundances, dominant species groups, size and morphology yield further clues to

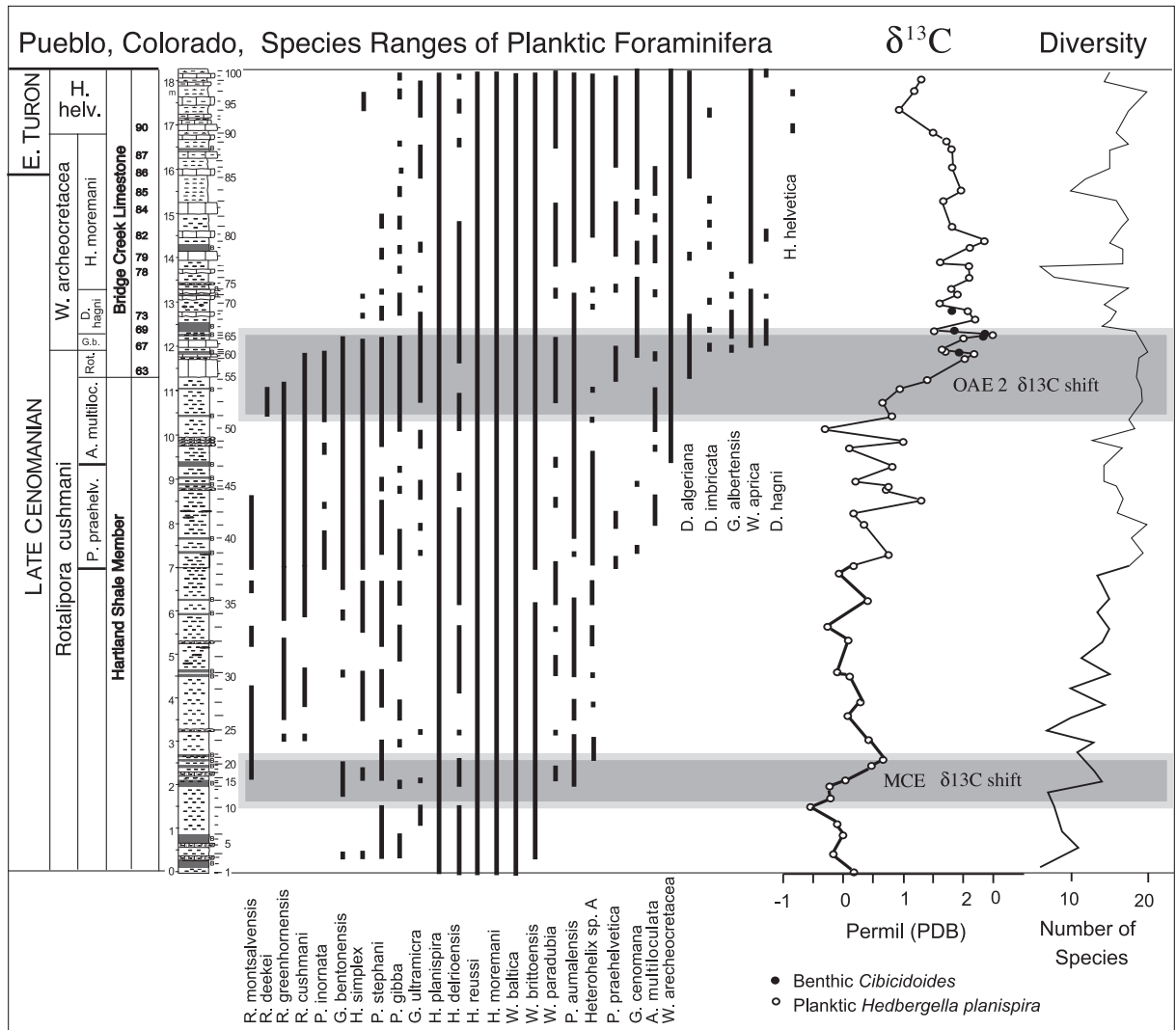


Fig. 7. Species ranges of planktic foraminifera, species richness and the $\delta^{13}\text{C}$ curve at Pueblo, Colorado. Note that species extinctions and originations are about equal and there is no net loss in diversity during the OAE 2 $\delta^{13}\text{C}$ shift. A sharp drop in species richness to seven species in the lower part of the *H. moremani* subzone is also observed at this stratigraphic interval at Eastbourne (Keller et al., 2001) and is associated with maximum *Heterohelix* abundance and intensified oxygen minimum zone. A smaller $\delta^{13}\text{C}$ shift and faunal turnover occurred during the middle Cenomanian.

the nature and degree of stress conditions during these faunal turnovers. For example, species in high stress environments documented from the early Danian globally and restricted environments of the late Maastrichtian tend to be morphologically smaller by up to 50% or more as a result of early sexual maturation and high reproductive rates (Keller, 1993, 2002; MacLeod et al., 2000; Abramovich et al., 2003). For this reason, the

small size fraction (38–63 μm) was investigated at Pueblo to assess the presence of small species (e.g., *Guembelitra*, *Globigerinella*, *Hedbergella*, *Heterohelix*) and quantify relative abundances. The results reveal a constant dominance of biserial species (~80%) and a smaller component of hedbergellids (Fig. 8). Guembelitrids appear only at the time of maximum $\delta^{13}\text{C}$ values after the OAE 2 $\delta^{13}\text{C}$ shift and

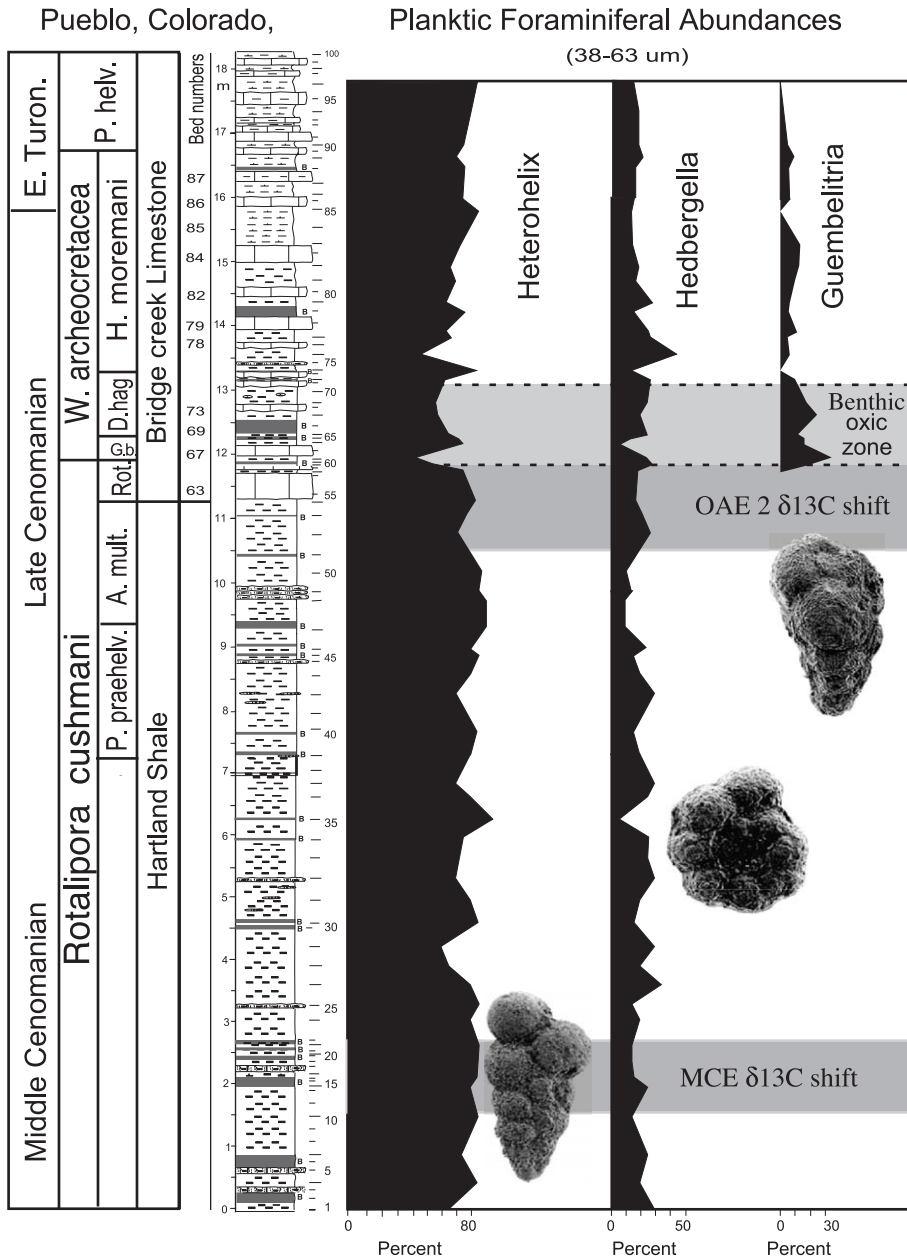


Fig. 8. Relative abundances of planktic foraminiferal species in the small size fraction (38–63 μm) at Pueblo. Note that low oxygen tolerant *Heterohelix* species (*H. reussi*, *H. moremani*) dominate (~80%) through most of the middle to late Cenomanian and early Turonian at Pueblo, suggesting that a well-developed OMZ was present most of the time. The opportunistic *Guembelitra* species appeared after at the onset of the benthic oxia zone, probably in response to upwelling and nutrient-rich surface waters.

coincident with a marked temporary decrease in heterohelicids (Fig. 8). This indicates that high stress conditions prevailed at Pueblo throughout the middle and

late Cenomanian, but that the maximum OAE 2 $\delta^{13}\text{C}$ excursion and sea level transgression provided the ecologic conditions for the opportunist *Guembelitra*.

Relative species abundances in the $>63 \mu\text{m}$ size fraction provide a more comprehensive assessment of the diversity and variations in foraminiferal habitats. This data set reveals faunal assemblages dominated by the same two species groups, *Heterohelix* and *H. planispira*, as in the smaller size fraction (Fig. 9). All other species are sporadically common (10–20%) or rare to few. This pattern reveals high stress conditions for the entire water column and suggests reduced water mass stratification, and variations in salinity, oxygen, temperature and nutrients. Examination of species habitats can provide information as to

the nature and probable cause of the high stress environment in the Western Interior Sea during the middle Cenomanian to early Turonian.

7. Planktic foraminiferal paleoecology

The evolution, diversification and extinction of planktic foraminifera are generally associated with stratification of the water column, variations in the trophic structure, vertical temperature and density gradients and the associated niche differentiation

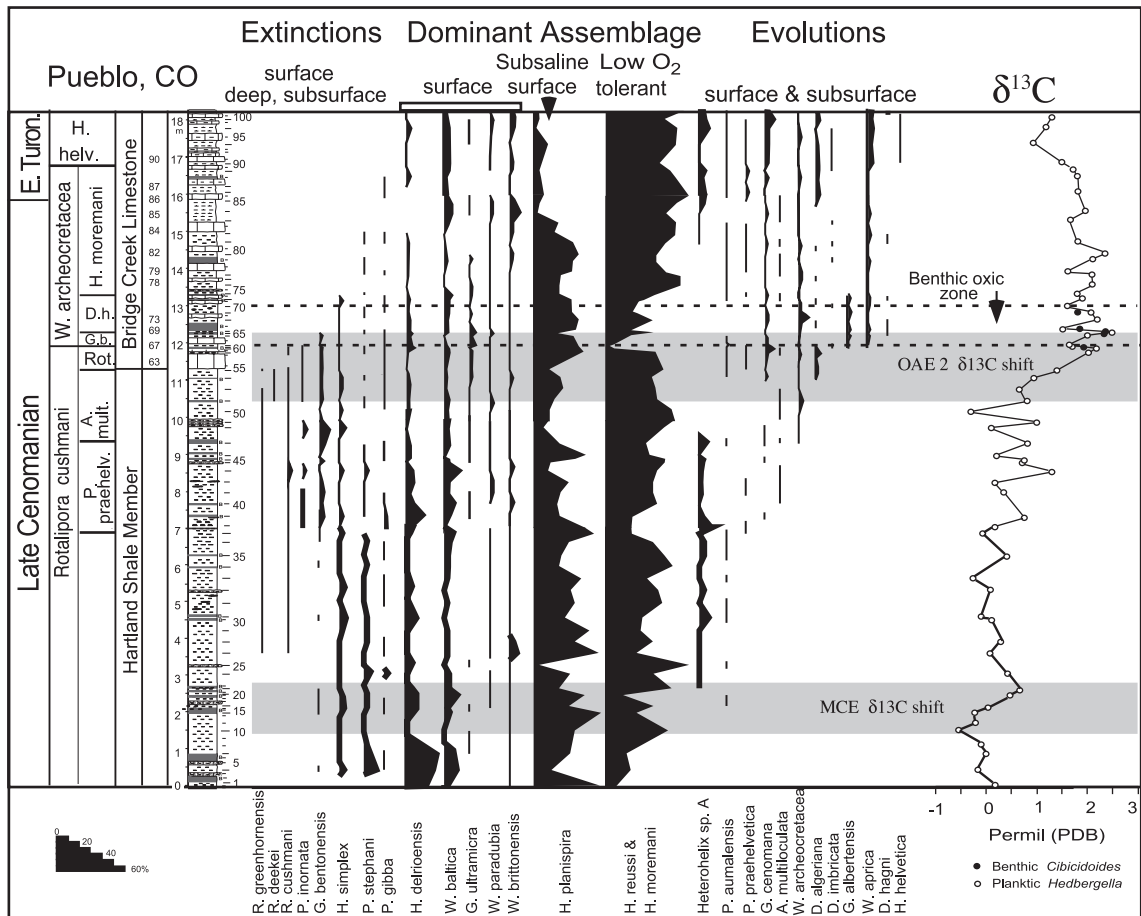


Fig. 9. Relative abundances of planktic foraminiferal species in the $>63 \mu\text{m}$ size fraction and the $\delta^{13}\text{C}$ curve of *H. planispira* at Pueblo, Colorado. Note that the assemblages are dominated by low oxygen tolerant *Heterohelix* and low salinity tolerant *H. planispira* reflecting a well-developed OMZ and low surface salinity due to freshwater influx. There are two $\delta^{13}\text{C}$ shifts, the OAE 2 and mid-Cenomanian event (MCE) and each is associated with a sea level transgression (see Fig. 3) and increased water mass stratification as indicated by reduced *Heterohelix* populations. Note that extinctions and originations of the OAE 2 faunal turnover affected only rare and endangered species whose combined relative abundances account for less than 2% and 4% of the total foraminiferal population, respectively.

(Lipps, 1979; Leckie et al., 1998; Price and Hart, 2002; Keller, 2002). Fundamentally important in maintaining diverse planktic foraminiferal communities is stratification of the upper water column, which is affected by seasonal changes in thermocline, nutrient cycling, and productivity. Species diversity is proportional to the water mass stratification, with highest diversity in a stable stratified water column with normal salinity and nutrients, and year-round temperature gradients that provide a variety of ecological niches and a stable nutrient supply.

Water mass stratification and the type of ecological niches occupied by different species can be inferred from the diversity and relative species abundances, morphologies of species, biogeographic distribution, and carbon and oxygen isotope ranking. Although stable isotopic ranking of species is the best single method to elucidate species depth habitats and has been successfully applied to Cretaceous species (e.g., Corfield et al., 1990; Norris and Wilson, 1998; Price and Hart, 2002; Abramovich et al., 2003), best results depend on excellent preservation, which is often difficult to find, and strong $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ gradients. Therefore, a combined approach integrating available isotopic, biogeographic and quantitative faunal data provides the most reliable results.

7.1. Deepwater dwellers—keeled species

Stable isotope ranking of large, complex, keeled and flattened morphotypes indicate that globotruncanids and rotaliporids generally occupied deeper oligotrophic habitats at or below thermocline depth during the late Cretaceous (e.g., Corfield et al., 1990; Price and Hart, 2002; Norris and Wilson, 1998; Abramovich et al., 2003). Faunal analysis indicates that these species are generally present in low abundances in high diversity species assemblages, suggesting adaptation in a stable and well-stratified water mass (Caron and Homewood, 1983; Leckie, 1987; Keller et al., 2001). In the Hartland Shale at Pueblo, keeled species are absent prior to the MCE $\delta^{13}\text{C}$ shift probably due to the shallow water environment. Above the MCE $\delta^{13}\text{C}$ shift keeled species are very rare (<1%) and include *R. greenhornensis*, *R. montsalvensis*, *R. deekei* and *R. cushmani* (Fig. 9, Plate 1). The rarity of rotaliporids can be

explained by the shallow water depth, low thermal gradients, reduced water mass stratification and well-developed oxygen minimum zone (OMZ) in the Western Interior Sea. All rotaliporids disappeared during the first phase of the OAE 2 $\delta^{13}\text{C}$ shift. Leckie (1985) suggested this might have been due to an expanding OMZ. However, the relative abundance of low oxygen tolerant heterohelicids remained relatively constant through the upper Hartland Shale and the extinction of the last rotaliporids actually coincided with a dramatic drop in heterohelicids indicating a strongly reduced OMZ, more oxygenated water column and increased water stratification (Fig. 9). This is also indicated by the presence of diverse benthic assemblages, including *Cibicidoides*, which mark the only interval with oxic bottom waters in the Pueblo section (benthic zone of Eicher, 1969b). The *Rotalipora* extinction is therefore more likely due to increased competition from evolving dicarinelids and praeglobotruncanids that accompanied increased water mass stratification.

7.2. Lower photic zone dwellers—weakly keeled species

This group is characterized by inflated chambers and weak or poorly developed keels and includes *A. multiloculata*, all praeglobotruncanids (e.g., *P. prae-helvetica*, *P. helvetica*, *P. inornata*, *P. aumalensis*, *P. stephani*), and some dicarinelids (*D. algeriana*, *D. hagni*, Fig. 9; Plates 1–3). These species may have descended from keeled morphotypes by inflating chambers and losing keels in response to adaptation to shallower and less oxygenated habitats (Eicher, 1972; Leckie, 1985). This interpretation gains support from isotopic analysis that indicates generally lighter $\delta^{18}\text{O}$ values for *P. stephani* than for *Rotalipora* species (Price and Hart, 2002), though the isotopic ranking of most other species has not yet been adequately documented.

Most of these adaptations were ultimately unsuccessful, as is evident with *P. inornata* and *A. multiloculata* that are reported extinct at the same time as *R. cushmani* (Eicher, 1972; Leckie, 1985), though we observed a recurrence of *A. multiloculata* in the upper *W. archeocretacea* zone at Pueblo and Eastbourne (*H. moremani* subzone, Fig. 9; Keller et al., 2001). Praeglobotruncanids fared little better, with

most species rare and sporadically present through the studied interval. We interpret these species as having occupied habitats in the lower photic zone but above the OMZ. In this ecologic niche, they would have thrived only at times when water mass stratification increased and the OMZ decreased. Such conditions prevailed only intermittently in the WIS and most notably immediately after the first phase of the OAE 2 $\delta^{13}\text{C}$ excursion with the appearance of oxygenated bottom water (oxic benthic zone), which favored the evolutionary diversification of dicarinelids (Fig. 9). Weakly keeled species fared little better in the more open sea environment at Eastbourne (Keller et al., 2001).

7.3. Oxygen minimum zone dwellers—heterohelicids

During the late Cretaceous heterohelicids thrived in low oxygen marine environments with well-developed oxygen minimum zones (OMZ) (Hart and Ball, 1986; Resig, 1993; Keller, 1993, 2002; Leckie et al., 1998). At Pueblo, this biserial group is dominated by *H. moremani* and *H. reussi*, with more restricted occurrences of *H. sp. A*, a large morphotype with globular chambers (Fig. 9, Plate 6). *Heterohelix reussi* and *H. moremani* dominated the faunal assemblages, averaging 40–50% in the Hartland Shale and 60–70% in the Bridge Creek Limestone, except for a short interval in the lower *W. archeoretacea* zone (subzones *G. bentonensis* and *D. hagni*). In the small size fraction (38–63 μm), *Heterohelix* species average 80% throughout the section, except for two brief intervals at the base of the *W. archeoretacea* zone (*G. bentonensis* subzone) and at the base of the *H. moremani* subzone (Fig. 8). This suggests that the OMZ was well developed during deposition of the Hartland Shale and Lower Bridge Creek Limestone, except for the interval of the benthic oxic event (Figs. 9 and 10).

Heterohelix abundances largely covary with $\delta^{18}\text{O}$ values. In general, high negative $\delta^{18}\text{O}$ values correspond to significantly reduced *Heterohelix* abundances in 86% of the time (19 out of 22 intervals), whereas high positive $\delta^{18}\text{O}$ values correspond to increased abundances 60% of the time (12 out of 20 intervals, Fig. 10). The lower correlation for positive $\delta^{18}\text{O}$ values occurs largely within the benthic oxic zone of OAE 2 and MCE. In addition, fewer isotope

data points in some intervals prevent point-by-point evaluation. Since highly negative $\delta^{18}\text{O}$ values reflect subsaline surface waters (Pratt, 1985; Pagani and Arthur, 1998; Keller et al., in press), this suggests that heterohelicids thrived at times of more normal marine salinity, but decreased during times of subsaline surface waters. However, at times of a more oxygenated water column and increased stratification, *Heterohelix* populations also decreased apparently due to a reduced OMZ.

This is apparent during OAE 2 where a major decrease in the *Heterohelix* population to <10% occurred following the sea level transgression and first peak in $\delta^{13}\text{C}$ shift (Fig. 11). The decrease in *Heterohelix* parallels a nearly 3‰ negative shift in $\delta^{18}\text{O}$ values and 1‰ shift in $\delta^{13}\text{C}$ values of the surface dweller *H. planispira* (Keller et al., in press). This interval also coincides with the first appearances of four planktic species (Figs. 7 and 9) and diverse benthic assemblages including *Cibicidoides* that mark the lower part of the “benthic zone” of Eicher (1969b) and Eicher and Worstell (1970). A likely interpretation is a well-oxygenated and stratified water column with a reduced OMZ probably due to upwelling of oxygen-rich deeper waters. The negative $\delta^{18}\text{O}$ values suggest increased freshwater runoff (Fig. 11). Species richness is generally high in the $\delta^{13}\text{C}$ shift interval and oxic zone (Fig. 7). Above this short oxic zone, a shift to *Heterohelix* dominance signals the return to an expanded OMZ, which is associated with a dramatic 2/3 drop in species richness. The same reduction in species richness at this time interval was observed at Eastbourne and suggests that this is a globally intensified OMZ event. A negative excursion in $\delta^{18}\text{O}$ values about 50 cm below the C–T boundary suggests a lower sea level and increased freshwater influx (Fig. 11).

7.4. Subsaline surface dweller—*Hedbergella planispira*

Stable isotope ranking indicates that all *Hedbergella* species lived in surface or near-surface waters (Price and Hart, 2002), as also indicated by paleogeographic distribution and abundance patterns in open ocean and shallow epeiric sea environments (Hart and Bailey, 1979; Leckie, 1985; Hart, 1999). In the Western Interior Seaway, *H. planispira* alternately

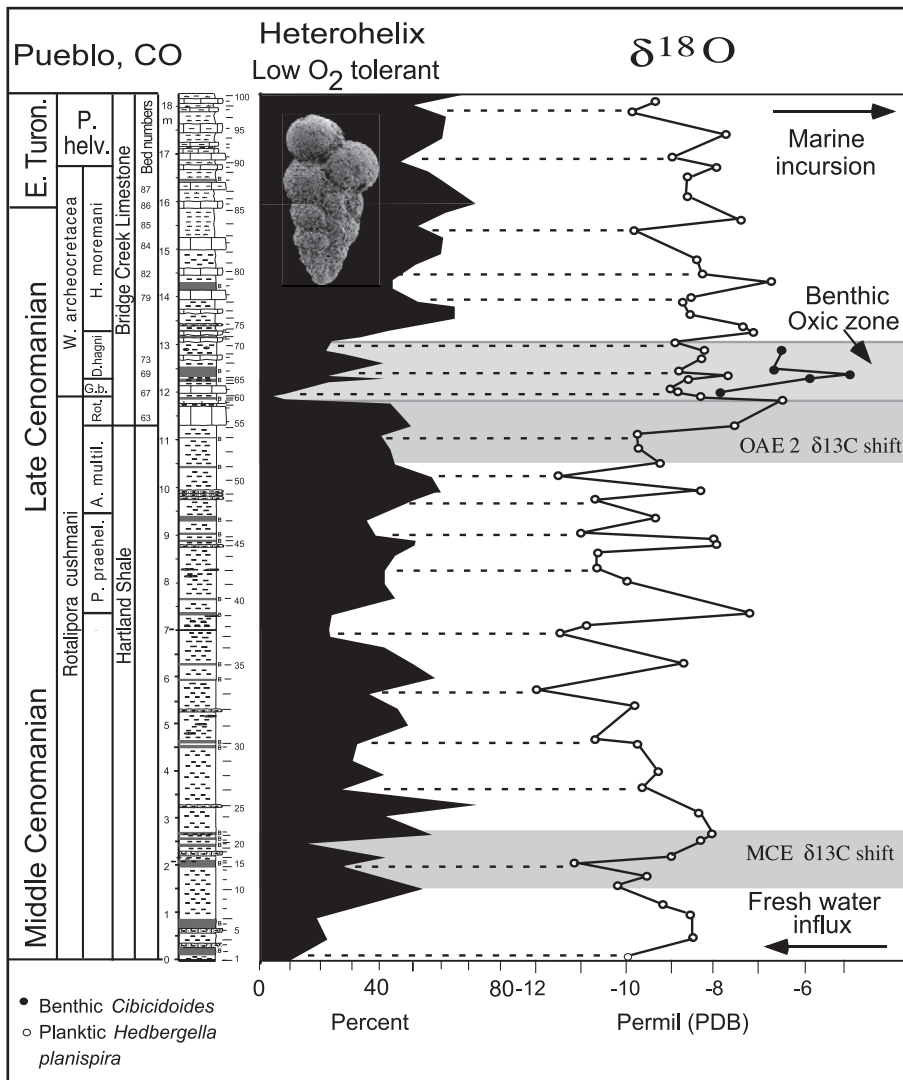


Fig. 10. Relative abundance of *Heterohelix* compared with the $\delta^{18}\text{O}$ curve of *H. planispira* at the Pueblo section. There is an 86% correlation between high negative $\delta^{18}\text{O}$ values and significantly reduced *Heterohelix* abundances, and a 60% correlation between high positive $\delta^{18}\text{O}$ values increased *Heterohelix*. The lower correlation occurs largely within the benthic oxidic zone of OAE 2 and MCE. These data indicate that heterohelicids thrived at times of more normal marine salinity and low oxygen, but decreased at times of sea level transgressions and the arrival of oxidic deeper waters.

dominates with low oxygen tolerant biserial species (Eicher, 1969b; Eicher and Worstell, 1970; Leckie, 1987). Assuming that *H. planispira* calcified its shell in equilibrium with seawater, similar to other planktic foraminiferal species (Corfield et al., 1990; Norris and Wilson, 1998; Price and Hart, 2002), the cyclic variations in $\delta^{18}\text{O}$ values of this surface dweller record alternating periods of more normal marine

salinity with freshwater influx in the WIS (Fig. 12). Hence, 2–4‰ negative $\delta^{18}\text{O}$ excursions reflect freshwater influx at times of humid and wet periods with high runoff, as supported by correlative peaks in detrital input, whereas positive $\delta^{18}\text{O}$ excursions reflect dry periods with low runoff, or marine incursions at times of rising sea levels (Pratt et al., 1993; Pagani and Arthur, 1998; Keller et al., in press).

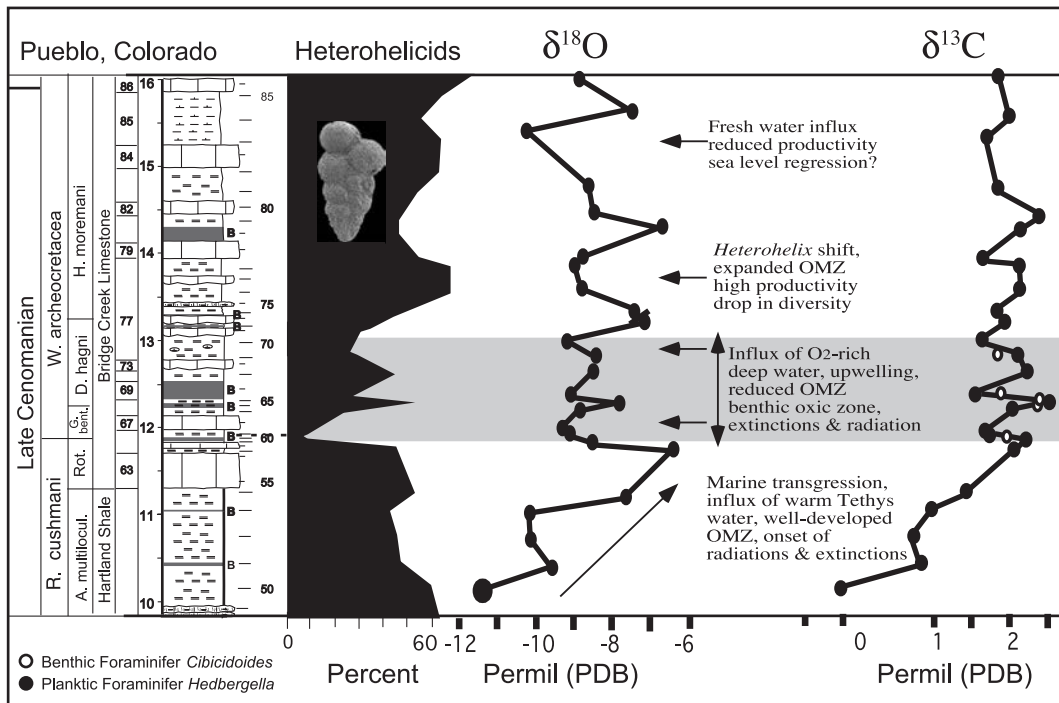


Fig. 11. *Heterohelix* abundance, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ across OAE 2 at Pueblo. The $\delta^{13}\text{C}$ shift is accompanied by a sea level transgression, which is followed by an influx of oxygen-rich deep water forming a benthic oxie zone, upwelling, increased water mass stratification and strongly reduced OMZ. Most extinctions and radiations take place in the benthic oxie zone.

Population abundances of *H. planispira* covary with the $\delta^{18}\text{O}$ signal of their shells. Relatively high population abundances of *H. planispira* correlate with 2–4‰ negative $\delta^{18}\text{O}$ excursions 91% of the time (20 out of 22 data points, Fig. 12) and suggest a high tolerance for subsaline surface waters. A similarly high correlation is observed between relatively low *H. planispira* abundances and positive $\delta^{18}\text{O}$ excursions, which indicate a low tolerance for more normal marine surface water salinity. *H. planispira* is thus an excellent proxy for surface salinity. However, this relationship does not hold at times when relative abundances of *H. planispira* drop below 15% and signal more normal surface salinity, as is the case in the *A. multiloculata* subzone and early Turonian (upper *H. moremani* to *H. helvetica* zones). There is also a notable exception in sample 79 where stable isotope values of a high *H. planispira* population (35%) indicate a positive $\delta^{18}\text{O}$ excursion (Fig. 12). The reason for this discrepancy is not clear.

7.5. Surface dwellers—normal marine salinity

7.5.1. Hedbergellids

As noted above, paleobiogeographic distribution patterns (Hart and Bailey, 1979; Leckie, 1985; Hart, 1999) and stable isotope ranking of *Hedbergella* species indicate that this group inhabited surface or near-surface waters during the middle to late Cenomanian (Corfield et al., 1990; Price and Hart, 2002). At Pueblo, the low relative abundances of *Hedbergella simplex* and *H. delrioensis*, as compared with *H. planispira*, indicates different habitats. *Hedbergella delrioensis* reached a maximum of 31% near the base of the section, but only intermittent peaks of 10% thereafter, whereas *H. simplex* is generally rare, but both species covary suggesting similar habitats (Fig. 12). Their peak abundances coincide with heavier $\delta^{18}\text{O}$ values, indicating a preference for normal marine salinity. These species are more abundant at Eastbourne where more normal marine conditions prevailed (Keller et al., 2001).

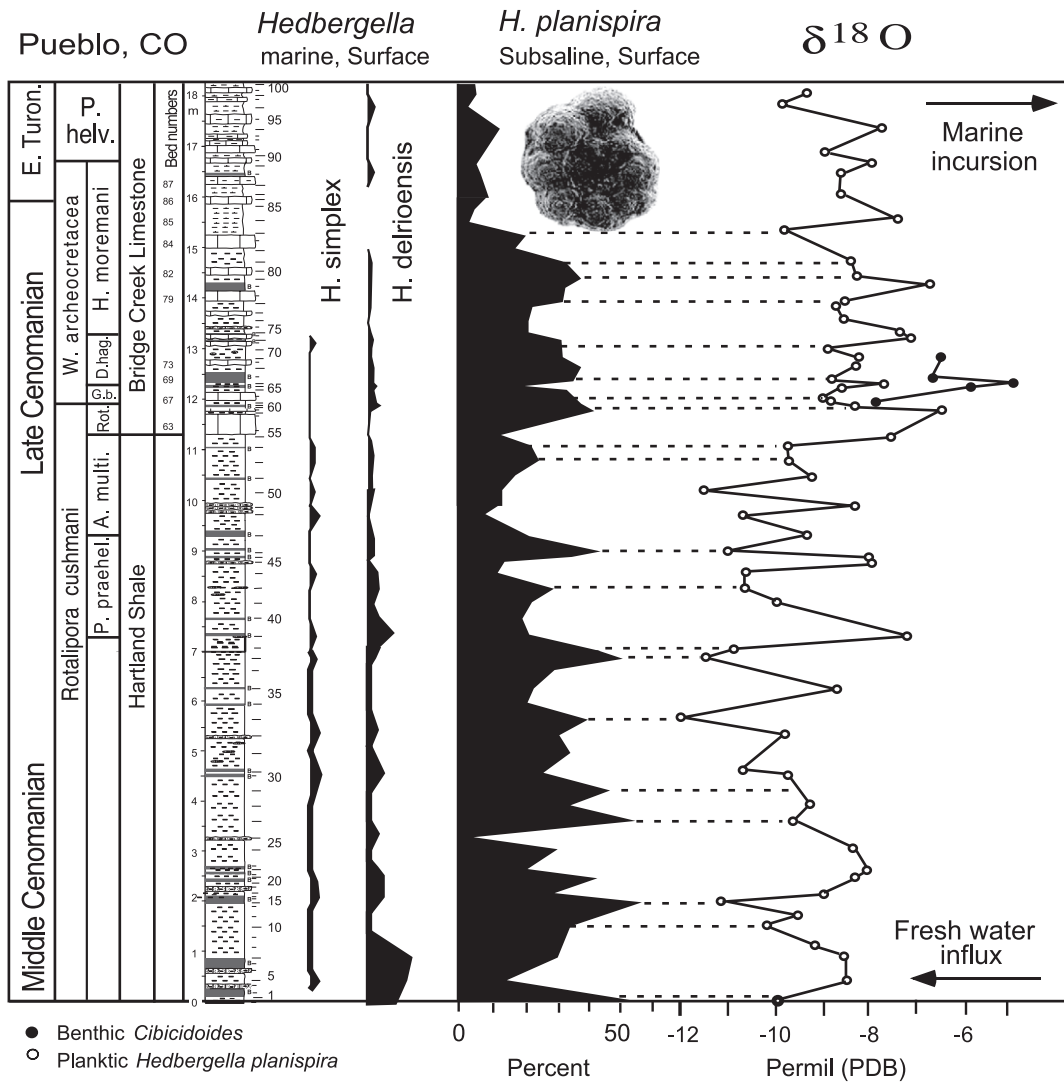


Fig. 12. Relative abundance of *H. planispira* compared with the $\delta^{18}\text{O}$ curve of this species at the Pueblo section. There is excellent (91%) correlation between relatively high *H. planispira* abundance and negative $\delta^{18}\text{O}$ excursions, which indicates that this species has a high tolerance for subsaline surface waters and can be used as proxy for low surface salinity. However, this relationship does not hold at times when relative abundances of *H. planispira* drop below 15% and signal more normal surface salinity. Other *Hedbergella* species show no tolerance for subsaline waters.

7.5.2. Globigerinellids

Globigerinelloides bentonensis and *Globigerinelloides ultramicra* thrived in surface waters in marginal or open marine environments. At Pueblo, *G. bentonensis* is rare in the lower part of the Hartland Shale examined, but increased to about 5% in the upper part of this unit and disappeared coincident with the OAE 2 $\delta^{13}\text{C}$ shift in the lower part of the Bridge Creek

Limestone, as also observed at Eastbourne (Fig. 9, Plates 5 and 6, Keller et al., 2001). *Globigerinelloides ultramicra* is also rare and sporadically present, reaching a maximum of 3% in the interval of the $\delta^{13}\text{C}$ excursion. In contrast, this species is relatively common at Eastbourne where it reached peak abundance of 20%, suggesting a preference for normal salinity (Keller et al., 2001).

7.5.3. *Whiteinellids*

The globular, large *Whiteinella* species are morphologically similar to the rugoglobigerinids of the Maastrichtian and may have occupied similar habitats in the lower part of the surface mixed layer, as suggested by stable isotope depth ranking (Norris and Wilson, 1998). At Pueblo, *Whiteinella* species are always present in low abundances (5–15%, Fig. 9; Plates 3–5), but *Whiteinella* abundance peaks coincide with decreased abundances of the low salinity tolerant *H. planispira*, suggesting a preference for normal marine salinity.

7.6. *Opportunists—eutrophic surface: Guembelitra*

Late Cretaceous *Guembelitra* species thrived in eutrophic surface waters of shallow marginal marine environments with variable salinities at times of severe ecological stress when few other species survived (e.g., Keller, 2002; Keller et al., 2002). Although *Hedbergella* and *Globigerinella* species also thrived in surface waters, there is no evidence that they occupied the same ecological niche with *Guembelitra* (Hart and Ball, 1986; Leckie et al., 1991; Keller et al., 2002). At Pueblo, *Guembelitra cenomana* and *G. albertensis* are absent in the shallow subsaline surface waters of the Hartland Shale in both the small (38–63 μm) and larger (>63 μm) size fractions, but they appeared in relatively low abundance during the sea level transgression and benthic oxic interval of OAE 2 (Figs. 8 and 9). The low abundance of heterohelicids in this interval and high $\delta^{13}\text{C}$ values suggest upwelling of oxic nutrient-rich waters, though surface waters appear to have remained subsaline, as suggested by a negative shift in $\delta^{18}\text{O}$ values and abundant *H. planispira*. This implies that late Cenomanian *Guembelitra* species have a preference for eutrophic surface waters and tolerate salinity variations, similar to late Maastrichtian and early Danian morphotypes.

8. Discussion

8.1. Faunal turnovers

The warm low latitude location of Pueblo in the Western Interior Sea during the middle and late

Cenomanian should in principle have fostered relatively high species diversity, but three factors worked against it: (a) relatively shallow water depth that reduced the ecologic niches available for deeper dwelling species, (b) variable salinity due to periodic freshwater influx, and (c) low oxygen condition associated with a well-developed oxygen minimum zone (OMZ). These factors significantly influenced, and for the most part reduced, ecologic niche availability for plankton communities in the WIS and the resultant assemblages reflect a complex interaction between salinity, oxygen, nutrients and depth. This can be seen in the abundance changes of the two dominant species, the low oxygen tolerant *Heterohelix*, which reflects changes in the oxygen minimum zone (Fig. 11), and the low salinity tolerant *H. planispira* (Fig. 12), which reflects freshwater influx.

Temperature also played a key role in limiting species habitats, but is not considered in this study because temperature estimates based on salinity influenced $\delta^{18}\text{O}$ data are not reliable. However, some inferences can be made based on cephalopod Sr and O isotope data by Cochran et al. (2003) who estimated a 10 °C increase in temperature (from ~ 13 to 23 °C) associated with a change from marine to brackish water in the WIS during the late Maastrichtian. If this estimate is correct and can be used as yardstick for similar conditions during the late Cenomanian, such major temperature changes at the frequencies indicated by $\delta^{18}\text{O}$ data would have severely limited plankton habitats throughout the studied interval. Perhaps this was the case at Pueblo where faunal assemblages are dominated by just two stress tolerant species (low oxygen and low salinity). Superimposed on these overall high stress conditions of the WIS are the two major oceanographic events MCE and OAE 2, which forced many ecologically specialized species to adapt or die out.

8.2. Mid-Cenomanian $\delta^{13}\text{C}$ event (95.71–95.80 Ma)

The mid-Cenomanian event (MCE) at Pueblo is characterized by a 1‰ positive $\delta^{13}\text{C}$ shift in the planktic foraminifer *H. planispira* in the lower *R. cushmani* zone. Near the onset of the $\delta^{13}\text{C}$ shift is a nearly 3‰ negative shift in $\delta^{18}\text{O}$ values that reflects freshwater influx. The subsequent $\delta^{13}\text{C}$ shift is ac-

accompanied by a positive 3.5‰ $\delta^{18}\text{O}$ shift that likely reflects a marine incursion and sea level transgression (Fig. 13, Keller et al., in press). Based on sediment accumulation rates, the $\delta^{13}\text{C}$ shift occurred over about 90 ky (95.71–95.80 Ma). A likely cause for this $\delta^{13}\text{C}$ shift is increased terrestrial input as suggested by high detrital and terrestrial organic matter (Keller et al., in preparation). The same oceanographic event has been identified from sections in Italy and southeastern England (Jenkyns et al., 1994; Coccioni and Galeotti, 2002). The MCE at Pueblo is associated with a significant faunal turnover, though not of the same magnitude as OAE 2 (Fig. 13). During the freshwater influx *H. planispira* dominates and reflects subsaline surface waters, whereas during the transgression *Heterohelix* dominates and indicates an expanded OMZ. Four species appeared before and two species after the peak *Heterohelix* abundance and transgression and inhabited surface (*Whiteinella*), subsurface (*Praeglobotruncan*, *Heterohelix* sp. A), and deeper waters (*Rotalipora*). There are no extinctions. This diversification reflects a deeper marine environment and increased water mass stratification

as a result of the sea level transgression. The appearance of *Rotalipora*, and possibly also the other species at Pueblo at this time, is likely due to transport from the western Tethys during the marine incursion, rather than evolutionary diversification. The three *Rotalipora* species (*R. cushmani*, *R. greenhornensis*, *R. montsalvensis*) are known to have evolved prior to the MCE (Coccioni and Galeotti, 2003).

8.3. Late Cenomanian OAE 2 $\delta^{13}\text{C}$ shift

The major features of the late Cenomanian global oceanic anoxia event (OAE 2) at Pueblo are a nearly 3‰ positive $\delta^{13}\text{C}$ shift in the uppermost *R. cushmani* zone accompanied by a positive 5.5‰ $\delta^{18}\text{O}$ excursion that reflects a major sea level transgression (Fig. 14). The likely cause for this $\delta^{13}\text{C}$ shift is increased productivity and enhanced preservation, as suggested by high organic matter of marine origin (Pratt et al., 1993; Keller et al., in press). Based on sediment accumulation rates the $\delta^{13}\text{C}$ shift occurred over about 90 ky (93.91–94.00 Ma) and has been

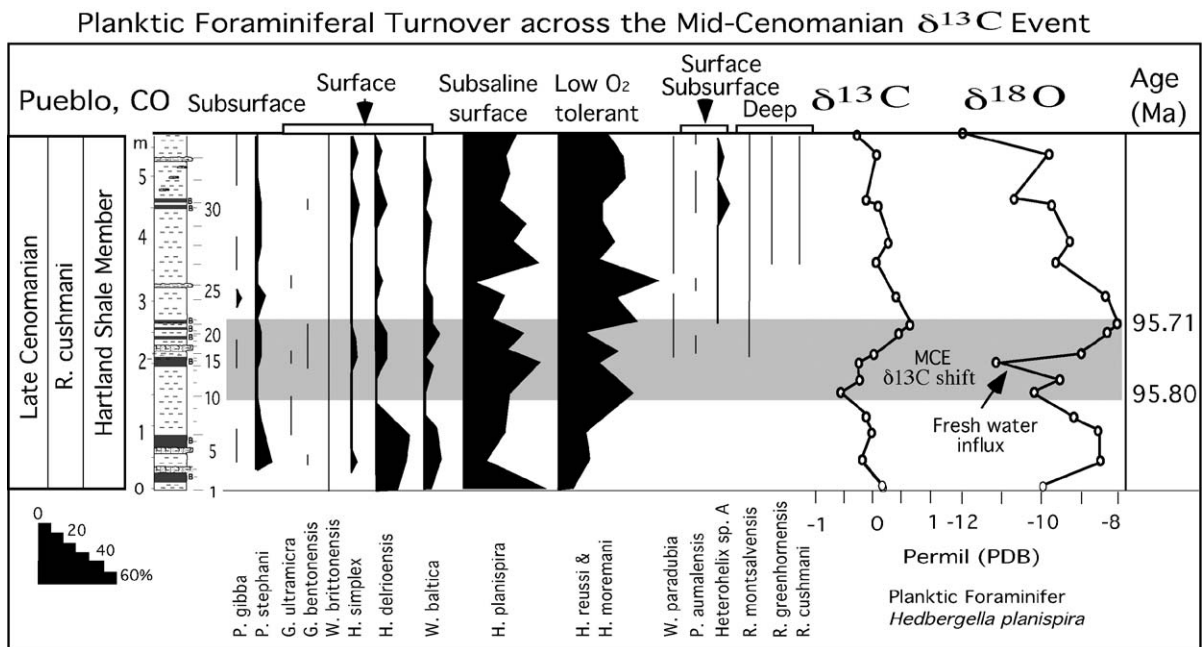


Fig. 13. The mid-Cenomanian $\delta^{13}\text{C}$ shift event (MCE) and faunal turnover at Pueblo, Colorado. A freshwater influx in the lower part of the $\delta^{13}\text{C}$ shift is followed by a marine transgression. No species extinctions occurred. The increased species diversity is partly due to originations in subsurface and surface waters and partly due to immigration of deeper dwelling *Rotalipora* species during the sea level transgression.

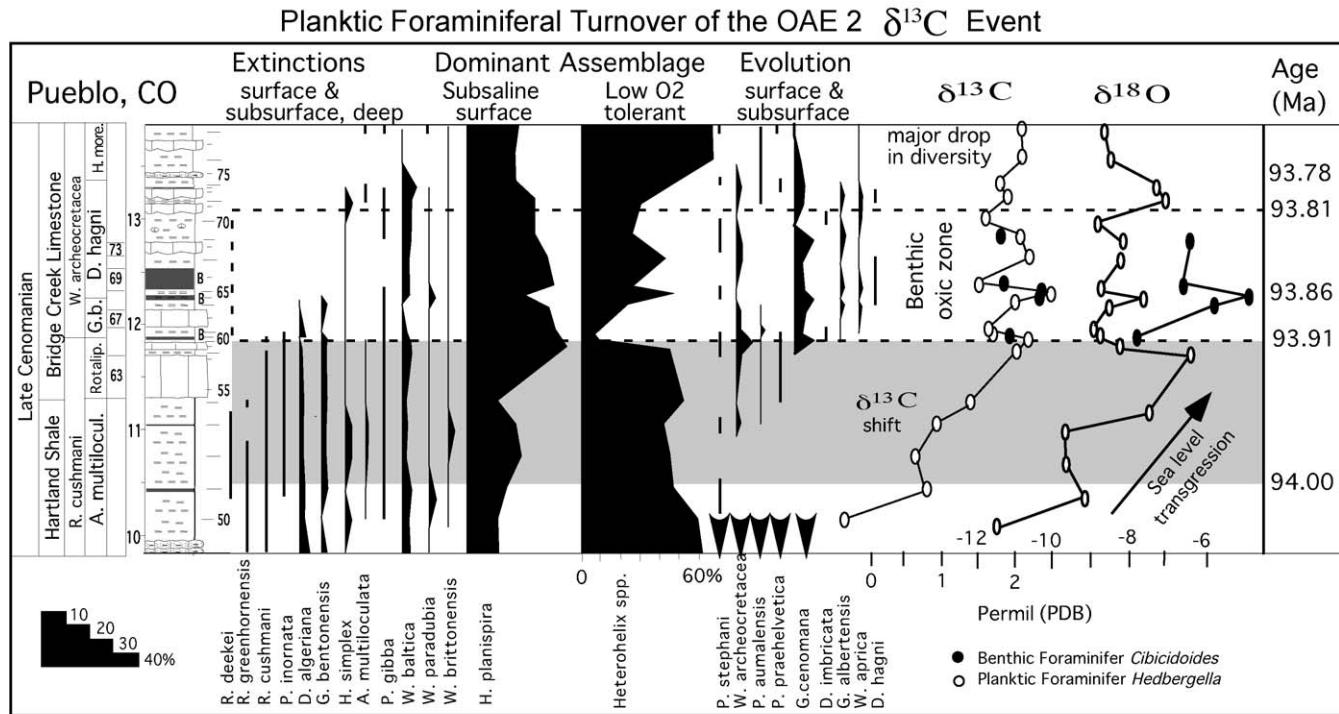


Fig. 14. The OAE 2 $\delta^{13}\text{C}$ shift and faunal turnover at Pueblo, Colorado. Species extinctions primarily occurred in subsurface and deeper waters, whereas originations occurred primarily in surface and subsurface waters. About 30% of the species disappeared and 30% originated, but their combined relative abundances are less than 2% and 4% of the total population, respectively. There is no net loss in diversity. The major faunal turnover occurs in the benthic oxic zone, whereas the lowest species diversity coincides with the return of dominant *Heterohelix* populations (*Heterohelix* shift) signaling an expanded OMZ.

recognized in late Cenomanian sequences globally. A major faunal crisis is associated with this environmental change at Pueblo. During the first phase of the $\delta^{13}\text{C}$ excursion (initiation to first peak, Fig. 14) two deeper dwelling *Rotalipora* species (*R. deekei*, *R. greenhornensis*) disappeared and one surface (*W. archeocretacea*) and two subsurface dwellers (*P. aumalensis*, *P. praehelvetica*) appeared. Further extinctions and evolutions occurred at the top of this interval and transition to the benthic oxic zone (Fig. 14). At this transition, the last deep dweller (*R. cushmani*) and a subsurface dweller (*P. inornata*) disappeared, followed by the temporary disappearance of several other subsurface dwellers (e.g., *P. aumalensis*, *P. praehelvetica*, *A. multiloculata*, *D. algeriana*, Plates 1 and 2). At the same time diversification occurred in surface (*Whiteinella aprica*, *G. albertensis*) and subsurface waters (*D. imbricata*, *D. hagni*), though one surface dweller (*G. bentonensis*) disappeared coincident with the peak $\delta^{13}\text{C}$ shift in the benthic oxic zone (93.86 Ma).

This faunal turnover indicates major changes in water mass stratification from surface to deep, and struggling populations trying to adapt to these changing conditions. The deeper water rotaliporids died out, though not before trying to adapt to living in shallower subsurface habitats by losing keels and inflating chambers for greater buoyancy. Such experiments in adaptations included *A. multiloculata* as well as early praeglobotruncanids and dicarinellids (Eicher, 1972). Only one surface dweller disappeared (*G. bentonensis*) and several new species evolved (mostly whiteinellids). This is not surprising since surface dwellers are more adapted to variable conditions, whereas subsurface and deep dwellers inhabit relatively stable habitats and adapt poorly to changing habitats.

What caused the change in water mass stratification and what was its nature? Clues can be obtained from the stable isotope record. After the first phase of the $\delta^{13}\text{C}$ shift and sea level transgression there is a rapid decrease in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (93.91 Ma, Fig. 14), coincident with the first diverse benthic assemblages (including *Cibicidoides*) indicating well oxygenated bottom waters. These oxic bottom waters and lower $\delta^{18}\text{O}$ values persisted for about 100 ky, though $\delta^{13}\text{C}$ values remained high and suggest high surface

productivity. The benthic oxic zone has been observed throughout the WIS (Eicher, 1969a,b; Eicher and Worstell, 1970; West et al., 1998) and may reflect an influx of oxygenated deeper water from the Tethys as a result of the sea level transgression. However, a benthic oxic zone at this interval is also observed in Morocco (Thomas Wagner, personal communication, 2002) and suggests a global event, though the actual source of this oxic deep water still needs to be investigated.

Upwelling of oxygen-rich waters is the likely cause for the weak oxygen minimum zone during the benthic oxic zone, as suggested by the strongly reduced *Heterohelix* populations. Surface water appears to have remained largely subsaline due to freshwater influx, as suggested by the 2.5‰ lower $\delta^{18}\text{O}$ values and high abundance of *H. planispira* (Fig. 14). However, the appearance of significant populations of the eutrophic surface opportunist *Guembeltria* (*G. cenomana*, *G. albertensis*) suggests that surface waters are nutrient enriched, probably due to upwelling. By 93.78 Ma, a major shift to *Heterohelix* dominated assemblages and rare low oxygen tolerant benthic assemblages mark the return of an expanded OMZ and dysoxic or anoxic bottom waters. This OMZ event is associated with a 2/3 drop in species diversity at both Pueblo and Eastbourne, indicating severely restricted habitats. In the early Turonian strongly reduced *H. planispira* populations reflect more normal marine surface salinity and increased abundance of deeper dwelling dicarinellids and praeglobotruncanids indicate a deeper marine environment.

9. Conclusions

1. The global stratotype section and point (GSSP) at Pueblo contains an essentially complete sedimentary record across the global ocean anoxic event (OAE 2) and the Cenomanian–Turonian boundary. Sediment accumulation rates average 1.23 cm/ky for the lower part and 0.87 cm/ky for the upper part of the Bridge Creek Limestone and about 0.5 cm/ky during deposition of the Hartland Shale Member.
2. A high-resolution biostratigraphic scheme is introduced that integrates the $\delta^{13}\text{C}$ shift and new

subdivisions of *W. archeocretacea* and *R. cushmani* zones; the same zonal subdivisions are coeval at Eastbourne.

3. *H. planispira* is a proxy for subsaline surface waters as indicated by covariance in negative $\delta^{18}\text{O}$ shifts (freshwater influx) and peak abundance in *H. planispira* populations. *Heterohelix*, a proxy for low oxygen waters, dominates at times of positive $\delta^{18}\text{O}$ shifts (incursion of more normal marine salinity) and is an indicator of the strengths of the oxygen minimum zone.
4. A benthic oxic zone begins after the maximum sea level transgression and OAE 2 $\delta^{13}\text{C}$ shift and persist for about 100 ky. Low *Heterohelix* abundance indicates a well-oxygenated water column, and the appearance of *Guembelitra* suggests nutrient-rich surface waters. These conditions can be explained by an influx of oxygenated deeper water from the Tethys and upwelling during the sea level transgression.
5. The OAE 2 faunal turnover, characterized by 30% species extinctions and 30% evolutionary diversification, results in no net loss in diversity and the combined relative abundances of outgoing and incoming species are less than 2% and 4%, respectively, of the total assemblages. This faunal turnover is related to a major sea level transgression, the influx of oxygen-rich bottom waters, increased productivity associated with a major positive excursion in $\delta^{13}\text{C}$ values. Lowest species diversity coincides with a shift to *Heterohelix* dominance that marks an expanded OMZ after the benthic oxic zone.
6. A mid-Cenomanian $\delta^{13}\text{C}$ shift and sea level transgression in the Hartland Shale (95.71–95.80 Ma) is associated with a significant faunal turnover, though not of the magnitude of OAE 2. The increased species diversity reflects the deeper marine environment and increased water mass stratification.

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