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Planktic foraminiferal turnover across the Paleocene–Eocene transition at DSDP Site 401, Bay of Biscay, North Atlantic

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Abstract

Planktic foraminifera across the Paleocene–Eocene transition at DSDP Site 401 indicate that the benthic foraminiferal mass extinction occurred within Subzone P 6a of Berggren and Miller (1988), or P5 of Berggren et al. (1995) and coincident with a sudden 2.0‰ excursion in $\delta^{13}\text{C}$ values. The benthic foraminiferal extinction event (BFEE) and $\delta^{13}\text{C}$ excursion was accompanied by a planktic foraminiferal turnover marked by an influx of warm water species (*Morozovella* and *Acarinina*), a decrease in cooler water species (*Subbotina*), a sudden short-term increase in low oxygen tolerant taxa (*Chiloguembelina*), and no significant species extinctions. These faunal changes suggest climatic warming, expansion of the oxygen minimum zone, and a well stratified ocean water column. Oxygen isotope data of the surface dweller *M. subbotina* suggest climate warming beginning with a gradual 0.5‰ decrease in $\delta^{18}\text{O}$ in the 175 cm preceding the benthic foraminiferal extinction event followed by a sudden decrease of 1‰ (4°C) at the BFEE. The $\delta^{13}\text{C}$ excursion occurred over 27 cm of sediment and, assuming constant sediment accumulation rates, represents a maximum of 23 ka. Recovery to pre-excursion $\delta^{13}\text{C}$ values occurs within 172 cm, or about 144 ka. Climate cooling begins in Subzone P 6c as indicated by an increase in cooler water subbotinids and acarininids with rounded chambers and a decrease in warm water morozovellids.

Keywords: planktic foraminifera; Paleocene–Eocene; DSDP Site 401; Bay of Biscay; biostratigraphy; paleoecology

1. Introduction

The Paleocene–Eocene transition has been studied by numerous workers to evaluate (1) climatic and environmental trends apparent in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ changes, (2) faunal turnovers in benthic and planktic foraminifera, (3) criteria for identifying the Paleocene/Eocene (P/E) boundary, and (4) sections with stratigraphically continuous records that may

be suitable as a Global Stratotype Section and Point (GSSP). The latter two goals have been hampered by the common presence of hiatuses (Aubry, 1995), carbonate dissolution and diachronous ranges of taxa in most sections and the lack of consensus among workers in identifying criteria for the P/E boundary. For instance, among planktic foraminifera, proposed P/E boundary criteria include the last appearance datum (LAD) of *Morozovella velascoensis* (Bolli, 1957) and the first appearance datum (FAD) of *Pseudohastigerina wilcoxensis* (Berggren et al., 1967),

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both datums appear to be diachronous across latitudes (King, 1990; Molina et al., 1992; Lu and Keller, 1993; Pardo et al., 1994, 1995). However, the proposed benthic P/E marker, the extinction of *Stensioiina beccariiformis*, appears to be isochronous and coincides with a major global $\delta^{13}\text{C}$ excursion in surface and deep waters (Thomas, 1989, 1990a,b; Kennett and Stott, 1991; Nomura, 1991; Pak and Miller, 1992; Lu and Keller, 1993; Speijer, 1994).

The benthic foraminiferal faunal turnover is marked by a major extinction event and decreased diversity in bathyal and abyssal species in the Atlantic and Caribbean (Schnitker et al., 1979; Tjalsma and Lohman, 1983; Boltovskoy and Boltovskoy, 1989), Indian Ocean (Sigal, 1974; Vincent et al., 1974; Nomura, 1991), Pacific Ocean (Miller et al., 1987, Pak and Miller, 1992), western Tethys (Ortiz and Keller, 1993; Ortiz, 1994, 1995) and Southern Indian Ocean (Thomas, 1990a; Katz and Miller, 1991). Tjalsma and Lohman (1983) reported a 50% disappearance among benthic foraminiferal species between planktic foraminiferal Zones P5 and P6a in the latest Paleocene and a similar rate of extinction was reported by Miller et al. (1987) between Zones P4 (late Paleocene) and P6b (earliest Eocene) at DSDP Site 577. In the southern Atlantic and Indian Oceans, between 30 and 40% of the deep-sea benthic foraminiferal taxa disappeared (Nomura, 1991; Thomas, 1989).

The planktic foraminiferal turnover across the P/E boundary has only been recently studied. Lu and Keller (1993) reported a major faunal turnover at the southern Indian Ocean ODP Site 738 and Canudo et al. (1995) observed this faunal event at Caravaca and Zumaya in Spain. In both studies it was found that this faunal turnover continues well after the benthic foraminiferal extinction event and $\delta^{13}\text{C}$ excursion (Molina et al., 1994), yet no major species extinctions occur. In Spain, this faunal turnover is variable in intensity between Zumaya and Caravaca (Canudo and Molina, 1992a; Canudo et al., 1995). In the southern Indian Ocean the faunal turnover spans the $\delta^{13}\text{C}$ excursion and benthic extinction and is marked by an invasion of tropical and subtropical species (i.e., acarininids and morozovellids), which displaced endemic cooler water taxa (i.e., subbotinids) during the maximum global warming. But, no net loss in taxic diversity was recorded by Kennett and Stott (1990), Stott and Kennett (1990) and Lu

and Keller (1993). The faunal turnover across the Subzone P 6a–P 6b interval (equivalent to P5–P6a of Berggren et al., 1995) is marked by the brief appearance of a unique compressed acarininid fauna during the $\delta^{13}\text{C}$ excursion at the equatorial Pacific DSDP Site 577 (Lu and Keller, 1995a,b), ODP Site 865 (Kelly et al., 1995), Alamedilla in southeastern Spain (Arenillas and Molina, 1996; Lu et al., 1996), the Negev sites in Israel (Lu et al., 1995), sections in Egypt (R.P. Speijer, 1994, pers. commun.) and the Kaurtakapy section in Kazakstan (Pardo and Keller, 1996, and unpub. data). These studies indicate that faunal, climatic and environmental changes across the P–E transition and $\delta^{13}\text{C}$ excursion were global, and that environmental conditions during the $\delta^{13}\text{C}$ excursion interval allowed the evolution of unique and short-lived morphotypes whose ranges and environmental implications are still unknown.

We report on the planktic foraminiferal turnover across the P–E transition at DSDP Site 401 in the Bay of Biscay, northeastern Atlantic. This section was previously studied by Saint-Marc (1991), and by Pak and Miller (1992) for benthic foraminifera and carbon and oxygen isotopic values of the benthic *Cibicidoides* spp. As a result of relatively low sample resolution across the $\delta^{13}\text{C}$ interval, Pak and Miller (1992) measured a $\delta^{13}\text{C}$ excursion of only 1‰, a relatively low value compared with other low or high latitude sites, suggesting that same low latitude regions responded more strongly than others. Our re-study of stable isotopes at higher sample resolution suggests, however, that the $\delta^{13}\text{C}$ excursion at Site 401 has the same magnitude as observed at all other sites. This study focuses on the planktic foraminiferal turnover, stable isotopic changes and their paleoecologic and climatic implications at Site 401 during the P–E transition.

2. Geological setting and methods

DSDP Site 401 is located in the western abyssal plain of the Bay of Biscay (47°25.65'N and 08°48.62'W, Fig. 1), at a paleobathymetry of about 2000 m which is analogous to the present depth of 2495 m (Montadert et al., 1979). The geologic setting of the Bay of Biscay is complex due to the opening of the North Atlantic and the convergent movement of the African and Iberian plates (Boillot

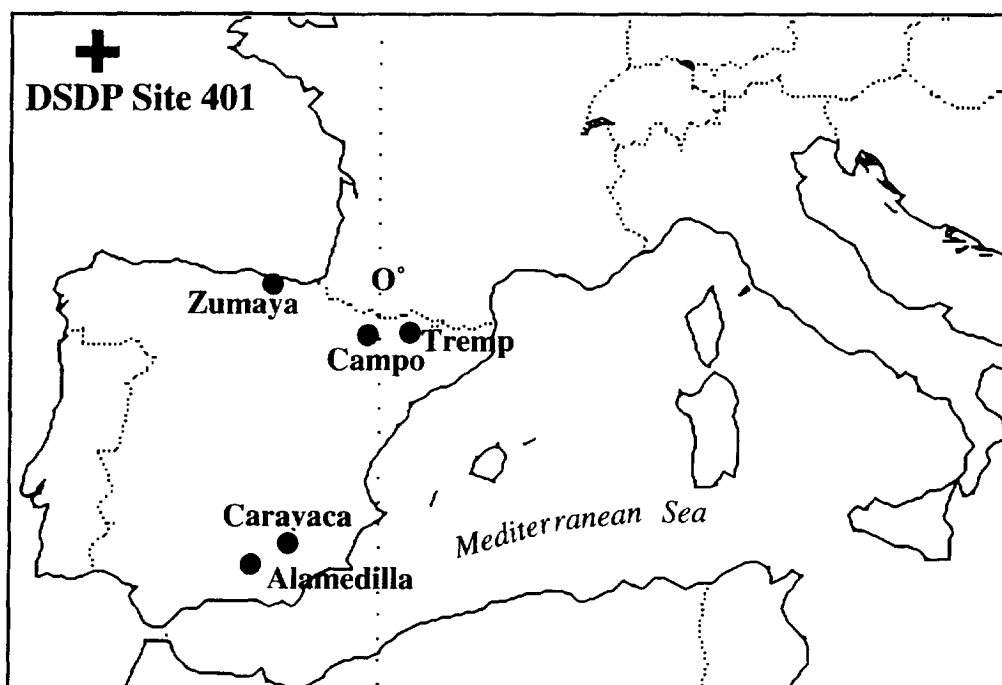


Fig. 1. Location map of DSDP Site 401.

et al., 1985). The opening steps of the Bay of Biscay remain unclear. However, during the early Paleogene the Bay of Biscay exhibited a general structure similar to today. Its extent was larger, entering the bay towards the East into the Pyrenees as a gap between the Iberian plate and France (Montadert et al., 1979; Boillot et al., 1985).

We sampled DSDP Site 401 cores 11 through 14 at 20 to 30 cm intervals across the benthic foraminiferal mass extinction, 50 to 70 cm intervals through the lower part of core 14 and the upper part of core 13, and 100 cm intervals through cores 11 and 12. A total of 49 samples were analyzed for this study. Core recovery was relatively good for this interval although section 6 of each core seems to be missing. However, the P–E transition is within core 14 section 3 and hence well within the recovered portion (Fig. 2). Samples were disaggregated in water. Each sample was cleaned with ultrasonic agitation during 10 to 15 s intervals and washed through a 63 μm sieve. The procedure was repeated until a clean foraminiferal residue was recovered. The final residue was dried in an oven below 50°C. Both planktic and benthic foraminifera have

well preserved morphologies and the original calcite shells seem to be only slightly recrystallized. This is evident in the generally clean test shells without sediment infilling (Plates I–IV) and the preservation of the original two layered inner wall structure (Plate II, 19).

Population counts for planktic foraminifera are based on representative random splits (using an Otto microsplitter) of 300 to 400 specimens from the 106 μm size fraction (Buzas, 1990). The 63 to 106 μm size fraction was also scanned, but was found to be impractical for quantitative studies due to the large number of juveniles. Specimens were picked from each sample and mounted on separate microslides for a permanent record and identified. The remaining sample was searched for rare species. Relative abundance data of planktic foraminifera are listed in Table 1. SEM photomicrographs of planktic foraminiferal specimens are shown in Plates I–IV.

3. Biostratigraphy

Various biostratigraphic schemes have been proposed for the late Paleocene to early Eocene interval.

Table 1
Relative abundance of planktic foraminifera at Site 401

CORE Unit	1 1					1 2					1 3					1 3									
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5					
SAMPLE (cm)	85-87	75-77	74-76	72-74	76-78	77-79	74-76	74-76	76-78	69-71	51-53	127-129	51-53	125-127	49-51	125-127	44-46	119-121	6-8	20-22	48-50	69-71	91-93	117-119	
<i>Subbotina hornibrooki</i>	9	7	11	28		2	5			x		x				1	3	6	5	6	6	6	7		
<i>S. eocaenica</i>	22	17		13	16	2	8	13	35	38	34	50	40	32	34	28	40	38	35	41	32	43	39	41	
<i>S. triangularis</i>	21	20	9	18	15	8	30	13	9	7	12	5	3	7	8	7	2	10	3	10	7	7	10	3	
<i>S. triloculinoides</i>																									
<i>S. velascoensis</i>																									
<i>S. finlayi</i>																							3	1	
<i>S. inaequispira</i>	2		35	6	11	7		3																	
<i>S. aff. 1 inaequispira</i>			6																						
<i>S. aff. 2 inaequispira</i>			3		2																				
<i>Morozovella aequa</i>																1	2	2	x	1	x	x	1	2	3
<i>M. occlusa</i>																	x								
<i>M. subbotinae</i>	x										4	6	30	26	19	24	22	11	18	22	13	8	15	8	
<i>M. velascoensis</i>																									
<i>M. angulata</i>																									
<i>M. acuta</i>																									
<i>M. crosswikensis</i>																									
<i>M. edgari</i>												x													
<i>M. gracilis</i>							17			6	5	1	1	10	12	6	1	4	6	1	5	7	1	5	
<i>M. marginodentata</i>															2										
<i>M. lensiformis</i>						2	x	6	26	10	7	x				x	6								
<i>M. lacerti</i>									2		2														
<i>M. formosa</i>		10		2	2	20	2	11	7	2	1*														
<i>M. aragonensis</i>	2	6		5	3	5		2*																	
<i>M. caucasica</i>	4	4																							
<i>Muricoglobigerina sp.</i>					x	2				3	3	2	1	1	1	6	2			x	3	2	x	3	
<i>M. soldadoensis</i>			2					x			4	11	3	3	3	8	2	11	6	4	8	6	6	3	
<i>M. chascaonana</i>									3	8		x	2	x				4	6	x	x	x	x	x	
<i>M. esnehensis</i>			1	2		7	4	8									2			x		1	x		
<i>M. mckannay</i>																									
<i>M. aequiensis</i>																									
<i>Acarinina acarinata</i>								7		9			3	3	2	3	x		1	x	3	2		1	
<i>A. triplex</i>							x	5	12	12	19	9	6	7	9	x			1					1	
<i>A. strabocella</i>								3				x			x				3		1	x		x	
<i>A. wilcoxensis</i>												3	2		3		1	x	2		x			1	
<i>A. cf. pentacamerata</i>																	1	1							
<i>A. spinuloinflata</i>	12	25	7	4	11	8	19	15	6	3	5								x	x					
<i>A. appressocamerata</i>	1		8	10	6	x	5	7	x		3														
<i>A. cuneicamerata</i>			10	12	3		1																		
<i>A. pentacamerata</i>	x	1	1	2		16																			
<i>A. bullbrookii</i>	20	3	1	10		5																			
<i>A. aspensis</i>			3																						
<i>A. decepta</i>			6																						
<i>Pianorotalites troelseni</i>		1				x												1		1	x	2	2	3	
<i>P. elongata</i>						1	2	x									x	x	x	x	1				
<i>Globorotaloides pseudoimitata</i>																	x							x	
<i>Paragloborotalia quadrilocula</i>		2					3										x	x	2	3	2	1		1	
<i>P. griffinae</i>	2	3		4	2																				
<i>Globanomalina ovalis</i>						x						x					x			x		2	2	x	4
<i>G. sp.</i>			x																						
<i>G. pseudochapmani</i>											1	x													
<i>Guembelitroides prolata</i>			3					x																	
<i>Pseudohastigerina wilcoxensis</i>	2	1	5		x		2		x		x	1	1	1											
<i>Chiloguembelina trinitatensis</i>																									
<i>Ch. wilcoxensis</i>											2	2	5	1	2	8		5	9	7	2	6	4		
<i>Ch. midwayensis</i>											6	5	1	1	3									3	
<i>Ch. crinita</i>															1				x						
<i>Ch. parallela</i>																	1	6	3	10					
<i>Zeauvigerina sp.</i>																									
TOTAL NUMBER COUNTED	307	344	326	326	345	333	329	330	342	336	332	347	358	344	319	335	286	376	297	344	344	323	323	372	

x- less than 1% * - conifer

Most of these schemes use the P-zonation proposed by Blow (1979) and later modified by various workers. As a result, the current P-zones differ significantly in both P-notation and identifying criteria as shown in Fig. 2. In this study we decided to use

the biostratigraphic zonation of Berggren and Miller (1988), rather than switch to the newer zonal scheme of Berggren et al. (1995), in order to facilitate correlation to other studies in the region which are based on the earlier zonation. To facilitate conversion to

Table 1 (continued)

CORE Section	1 4																																			
	1									2									3									4						5		
	SAMPLE (cm)																																			
SPECIES	5-7	18-20	42-44	72	92-94	119-121	148-150	0-2	22	44-46	72-74	92-94	119-121	145-147	0-2	22	42	72	95-97	122-124	18-20	69-71	120-122	20-22	68-70											
Subbotina hornibrooki	2	6	4	4	5	5	5	8	3	5	3	7	1	5	4	2	3	6	3	7	3	4	1	x	9											
S. eocaenica	42	46	37	38	38	34	29	33	43	32	40	42	43	38	29	50	36	34	37	47	44	45	34	7	6											
S. triangularis	6	7	5	3	5	16	11	5	9	7	7	9	10	7	8	7	3	2	2	10	6	5	6	4	2											
S. trilaculinoides																																				
S. velascoensis	1		2	1	4		2	2	3	2	2	2	2	2	x	1	2		x	3	5	1	4	50	38											
S. finlayi																																				
S. inaequispira																																				
S. aff. 1 inaequispira																																				
S. aff. 2 inaequispira																																				
Morozovella aequa	4	3	10	1	2	3	3	2	2	2	1	2	1	1	7	6	2	4	2	3	1	12	4	3												
M. occlusa	2	x	4	x	x	7	4	6	3	3	2	1	1	x	x	2	x	x	1	x	x	x	x	2	4											
M. subbotinae	12	16	12	14	14	12	8	11	11	10	9	9	10	11	15	4	15	14	20	7	20	8	11	3	3											
M. velascoensis																																				
M. angulata																																				
M. acuta																																				
M. crosswikensis																																				
M. edgari																																				
M. gracilis	3	x	5	9	4	1	3	1	1	4	2	x	2	2	4		x	7	4	3																
M. marginodentata																																				
M. lensiformis																																				
M. laceri																																				
M. formosa																																				
M. aragonensis																																				
M. caucasica																																				
Muricoglobigerina sp.	2	1	2	x	x	2	x	6	3	2	2	5	2	x	1	3	1	4	2	5	12	8	8													
M. soldadensis	4	2	3	3	2	7	16	1	7	10	6	9	5	5	5	4	6	5	2	4	5	8	7	4	6											
M. chascaonana	3																																			
M. esnehensis																																				
M. mckannay	1																																			
M. aguensis																																				
Acarinina acarinata	3	2	4	6	3	x	2	3	2	6	2	3	5	6	5	7	6	4	5	x	5	x	1	1												
A. triplex																																				
A. strabocella	x		1	1	1			x	x	2	1		x	2	3	2	x	3	3	x	1			x												
A. wilcoxensis	1	x																																		
A. cf. pentacamerata																																				
A. spinuloinflata																																				
A. appressocamerata																																				
A. cuneicamerata																																				
A. pentacamerata																																				
A. bulbrooki																																				
A. aspensis																																				
A. decepta																																				
Planorotalites troelseni	x		x		x		x		x		1		x		x		x		x		x		x		x											
P. elongata																																				
Globorotaloides pseudoimmitata																																				
Paragloborotalia quadricocula	2.		2	3	2	x	2	x	2	3	3	2	3		x		1	2	1	x	4	3	1	1	x											
P. grillinae																																				
Globanomalina ovalis	x	x		x			x		x				2	1	x	x		x		x		x														
G. sp.																																				
G. pseudochapmani																																				
Guembelitroides prolata																																				
Pseudohastigerina wilcoxensis																																				
Chilogaembelina trinitatis	3																																			
Ch. wilcoxensis	5	8		6	5	5	6	4		4	6	2		2		2		2		x		x		x												
Ch. midwayensis	6		5	6	5	1		x															x		x											
Ch. crinita																																				
Ch. parallela																																				
Zeauvigerina sp.																																				
TOTAL NUMBER COUNTED	333	333	335	322	341	345	371	335	342	354	340	327	326	328	355	319	331	333	340	334	328	313	341	337	337											

x- less than 1%

*- confer

the new zonation, we indicate the new zones in parentheses.

All zones and subzones were recognized at DSDP Site 401. We could not confirm the presence of Zone P4 that was noted by Saint-Marc (1991), because the index species *Planorotalites pseudomenardii* was not found. However, *Planorotalites troelseni* and

Planorotalites elongata which are morphologically very similar to *P. pseudomenardii*, are present in the lower part of core 14 (sections 4 and 5) and it is possible that the two species were misidentified. Moreover, $\delta^{13}\text{C}$ data (Fig. 7, Table 5) seem to support that the lower part of core 14 corresponds to Subzone P 6a, rather than Zone P 4 which com-

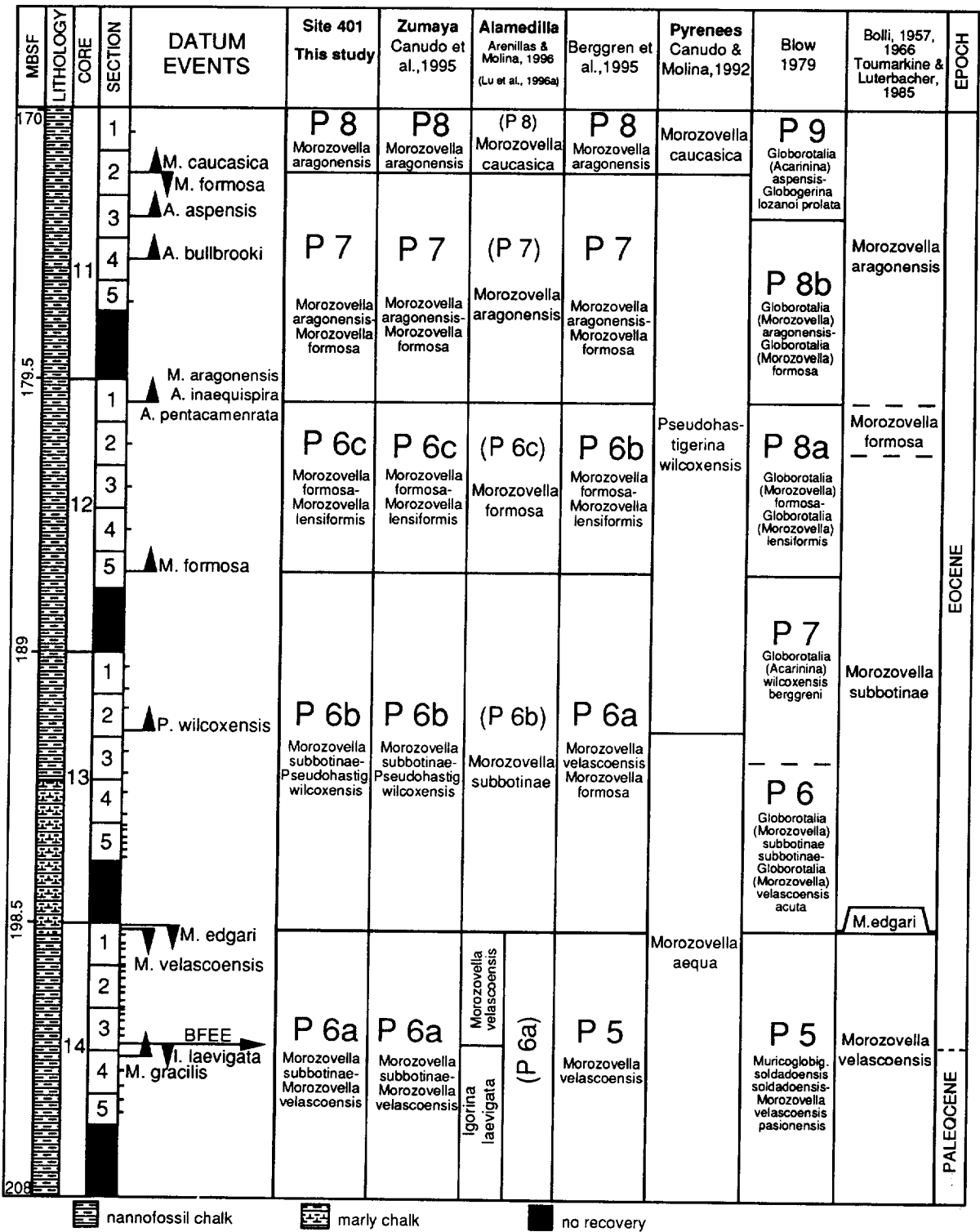


Fig. 2. Planktic foraminiferal biozonation and datum events of this study compared with other zonations commonly used for the Paleocene–Eocene transition. Dashed lines show zone boundaries which were not located at Site 401.

monly has much heavier values. Our study does not support the presence of a major hiatus in core 14 as suggested by Saint-Marc (1991).

The benthic mass extinction was reported between samples 14-3, 90–92 cm and 14-3, 110–112 cm (Pak and Miller, 1992), an interval corresponding to Subzone P 6a (equivalent to P5 in Berggren et al., 1995; Fig. 2). This is in agreement with the stratigraphic position of this extinction event in sections from Zumaya (Canudo et al., 1995; Ortiz, 1995), Caravaca (Ortiz and Keller, 1993; Ortiz, 1995), Alamedilla (Arenillas and Molina, 1996; Lu et al., 1996; Fig. 1), DSDP Site 577 (Lu and Keller, 1995a,b) and the Negev (Lu et al., 1995).

Fig. 2 compares various zonal schemes currently in use for Site 401 (this study), Zumaya (Canudo et al., 1995), the Pyrenean shallow water sections at Campo and Tremp (Canudo and Molina, 1992b) and Alamedilla (Arenillas and Molina, 1996; Lu et al., 1996) along with first appearance datums (FADs) and last appearance datums (LADs) of taxa used as zonal markers. Biostratigraphic analysis of these sections indicates the heterochrony between the LAD of *Morozovella velascoensis* and the FAD of *Pseudohastigerina wilcoxensis* at these locations. Thus, the FAD of *P. wilcoxensis* is in the upper part of Subzone P 6b at Site 401, within Subzone P 6b at Zumaya (Canudo et al., 1995), and in the lower part of Subzone P 6a at Caravaca (Canudo et al., 1995) and the Pyrenees (Canudo and Molina, 1992a,b; Molina et al., 1994). For this reason, these taxa are poor global markers for the P/E boundary. In the new biostratigraphic zonal scheme of Berggren et al. (1995) *P. wilcoxensis* is no longer used as an index species.

Morozovella subbotinae Zone (P 6):

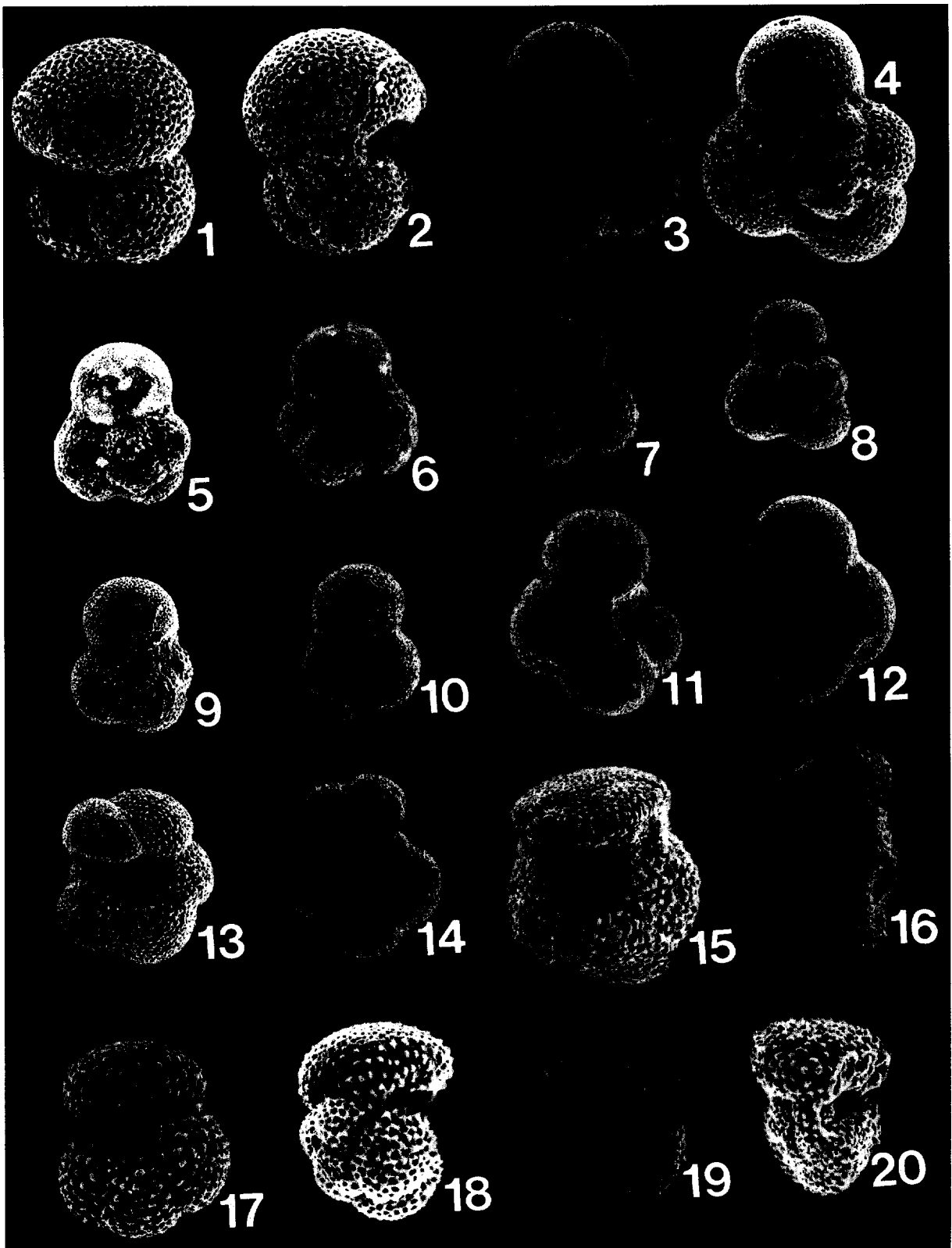
Originally proposed by Berggren (1969) and later updated by Berggren and Miller (1988), this zone defines the interval from the first appearance datum (FAD) of *M. subbotinae* (Plate III, 11 and 12) to the FAD of *Morozovella aragonensis* (Plate II, 15 and 16) and is subdivided into three subzones: P 6a, b and c. In the revision by Berggren et al. (1995), Subzone P 6a becomes Zone P5, and P6b and P 6c become P 6a and P 6b, respectively (Fig. 2). The entire original Subzone P 6 corresponds to the upper part of the *Globorotalia velascoensis* Zone of Bolli (1957),

the *Morozovella edgari* and *Morozovella subbotinae* Zones of Premoli Silva and Bolli (1973) and Zones P 6, P 7 and P 8a of Blow (1979; Fig. 2).

Morozovella subbotinae/Morozovella velascoensis Subzone (P 6a):

Concurrent range subzone defined by the FAD of *M. subbotinae* at the base and the LAD of *M. velascoensis* at the top (Berggren and Miller, 1988; Plate III, 15 and 16). Subzone P 6a corresponds to Zones P5 of Blow (1979) and Berggren et al. (1995), and *M. velascoensis* of Bolli (1957, 1966) and Toumarkine and Luterbacher (1985). At Site 401 Subzone P6a has a thickness of 641 cm. Berggren and Miller (1988) found the first appearance of *P. wilcoxensis* in the upper part of Subzone P 6a. Canudo and Molina (1992a,b) used this taxon as zonal marker in the Pyrenees. This FAD, however, seems diachronous occurring in the upper part of P 6b at Site 401, as also observed in other locations (e.g., King, 1990; Molina et al., 1992; Lu and Keller, 1993; Pardo et al., 1994, 1995; Canudo et al., 1995). In the revised zonal scheme of Berggren et al. (1995) *P. wilcoxensis* is eliminated as zonal marker and Subzone P 6a becomes Zone P 5 based on the last appearance of *P. pseudomenardii* at the base and the last appearance of *M. velascoensis* at the top (Fig. 2).

The benthic foraminiferal extinction event (BFEE) is within Subzone P 6a at Site 401 (between 110–112 cm and 95–97 cm of core 14, section 3, based on our observations and that of Pak and Miller, 1992). There is no equivalent faunal turnover in planktic foraminifera, though an assemblage change is present within the upper part of Subzone P6a, marked by the disappearance of *Subbotina triloculinoides*, *Subbotina finlayi* and *Morozovella angulata* below, *Igorina laevigata* at the BFEE, and *Muricoglobigerina aquiensis* and *Zeauvigerina sp.* above the BFEE (Fig. 3, Tables 2 and 4). Apart from these 6 disappearances, 13 species appear (i.e., originations or re-appearances) out of a total of 34 species, or about 38%, at or above the BFEE horizon (e.g., *Morozovella angulata*, *M. crosswickensis*, *M. edgari*, *Muricoglobigerina chascanona*, *M. esnehenensis*, *M. mckannai*, *Acarinina strabocella*, *A. cf. pentacamerata*, *Planorotalites elongata*, *Globorotaloides pseudoimitata*, *Globanomalina ovalis*, *Chiloguembelina wilcoxensis*, *C. midwayensis*; Fig. 3). Another 3



species appear after the BFEE (e.g., *Muricoglobigerina aquiensis*, *Chiloguembelina crinita* and *Zeauvigerina* sp.; Fig. 3 and Tables 2 and 4). We emphasize that many of these taxa are not evolutionary FADs or LADs, but may represent regional and/or ecological first or last occurrences and/or preservational bias. However, we are unable to evaluate the latter in these relatively well preserved assemblages. We suspect that at Site 401 the species turnover may include many pseudoextinctions and pseudoevolutions as a result of local environmental conditions. This is suggested by previous studies which indicate that the Subzone P 6a

planktic foraminiferal turnover is generally small (see Lu and Keller, 1993, 1995a,b).

Morozovella subbotinae–*Pseudohastigerina wilcoxensis* Subzone (P 6b)

Partial range subzone originally defined by the concurrence of *Morozovella subbotinae* and *Pseudohastigerina wilcoxensis* (Plate IV, 9–11) with the LAD of *M. velascoensis* at the base and the FAD of *M. formosa* at the top (Berggren and Miller, 1988). At Site 401 Subzone P 6b has a thickness of 757 cm and corresponds to zones P6 and P7 of Blow (1979), and the short *Morozovella edgari* Zone plus part of *Morozovella subbotina* Zone of Bolli (1957, 1966) and Toumarkine and Luterbacher (1985). As noted earlier, the FAD of *P. wilcoxensis* (at Site 401 in the upper part of P 6b, Fig. 2) is diachronous and the original definition of Berggren and Miller (1988) for Subzone P 6b can not be applied. At Site 401 we thus identify Subzone P 6b by the LAD of *M. velascoensis* at the base and the FAD of *M. formosa* at the top, using the same criteria as Berggren et al. (1995) for their redefined Zone P6a.

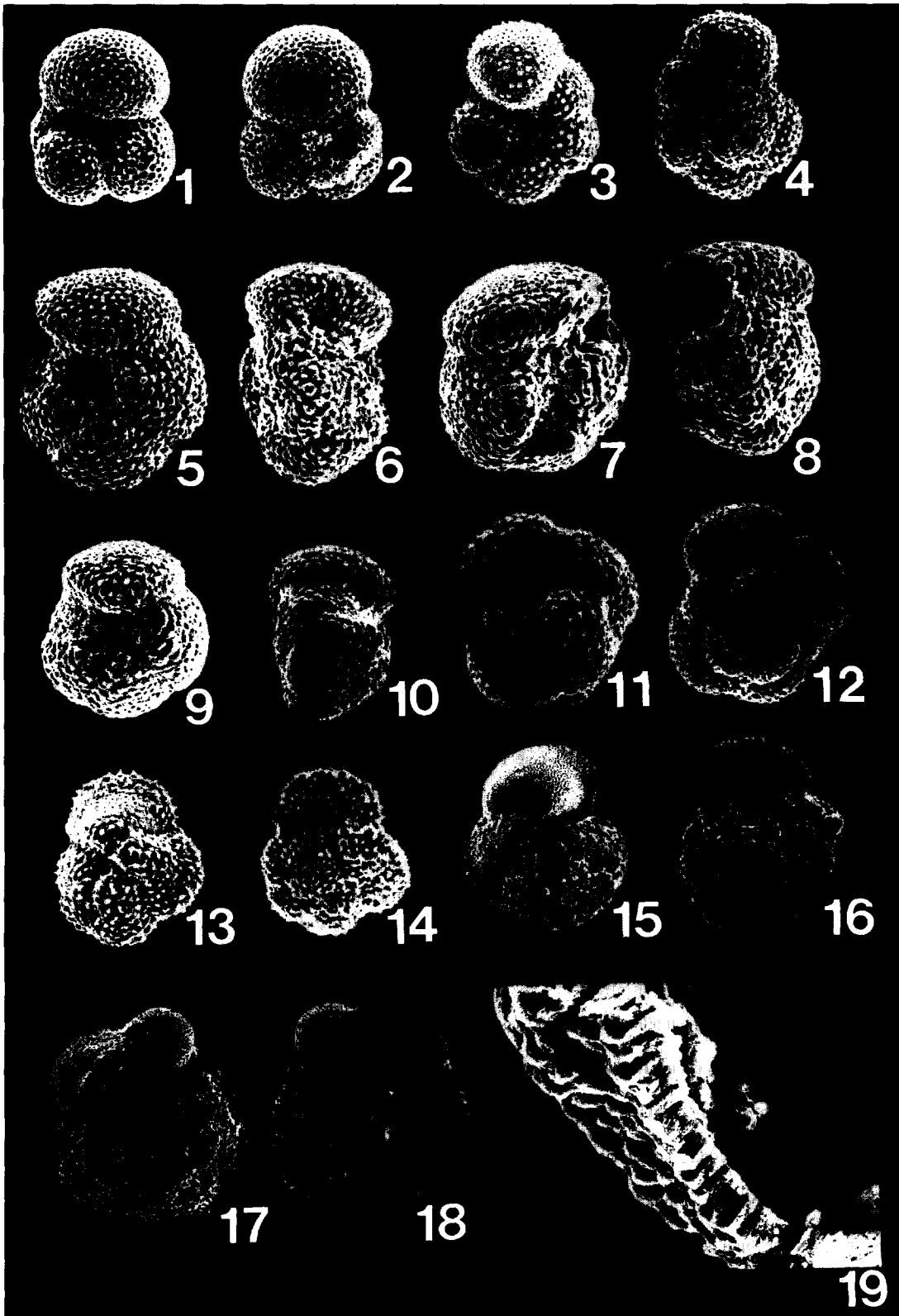
Seventeen species or 46% of the taxa disappear within Subzone P 6b (e.g., *Subbotina velascoensis*, *Morozovella aequa*, *M. occlusa*, *M. subbotinae*, *M. acuta*, *M. edgari*, *M. marginodentata*, *Muricoglobigerina mckannay*, *Acarinina wilcoxensis*, *A. cf. pentacamerata*, *Globorotaloides pseudoimitata*, *Chiloguembelina trinitatensis*, *Chiloguembelina wilcoxensis*, *Chiloguembelina midwayensis*, *Chiloguembelina crinita* and *C. parallela*; Fig. 3). Seven species or 19% first appear in Subzone P 6b (e.g., *Morozovella marginodentata*, *M. lensiformis*, *M. lacerti*, *Acarinina appressocamerata*, *Globanomalina pseudochapmani*, *Pseudohastigerina wilcoxensis* and *Chiloguembelina parallela*; Fig. 3). Montadert et al. (1979) suggested the presence of a hiatus between samples 123–128 cm, in core 13, section 4. Our study indicates the abrupt disappearance and appearance of *C. trinitatensis* and *C. parallela*, respectively, at this interval which seems to support a short intra-zonal (P 6b) hiatus.

Morozovella formosa–*Morozovella lensiformis* Subzone (P 6c):

Partial range subzone defined by the concurrence of the nominate species and marked by the FAD of

Plate I

1. *Subbotina eocenica* (Terquem), umbilical view, ×200, core 14, 2, 119–121.
2. *Subbotina eocenica* (Terquem), lateral view, ×200, core 14, 2, 119–121.
3. *Subbotina inaequispira* (Subbotina), umbilical view, ×200, core 11, 3, 74–76.
4. *Subbotina inaequispira* (Subbotina), dorsal view, ×200, core 11, 3, 74–76.
5. *Subbotina inaequispira* (Subbotina), umbilical view, ×200, core 11, 3, 74–76.
6. *Subbotina inaequispira* (Subbotina), dorsal view, ×200, core 11, 3, 74–76.
7. *Subbotina* aff. *inaequispira* 2, umbilical view, ×120, core 11, 3, 74–76.
8. *Subbotina* aff. *inaequispira* 2, dorsal view, ×120, core 11, 3, 74–76.
9. *Subbotina* aff. *inaequispira* 1, umbilical view, ×120, core 11, 3, 74–76.
10. *Subbotina* aff. *inaequispira* 1, dorsal view, ×120, core 11, 3, 74–76.
11. *Guembelitroides prolata* (Bolli), umbilical view, ×120, core 11, 3, 74–76.
12. *Guembelitroides prolata* (Bolli), dorsal view, ×120, core 11, 3, 74–76.
13. *Acarinina aspensis* (Colom), umbilical view, ×120, core 11, 3, 74–76.
14. *Acarinina aspensis* (Colom), dorsal view, ×120, core 11, 3, 74–76.
15. *Acarinina spinuloinflata* (Bandy), umbilical view, ×200, core 11, 2, 75–77.
16. *Acarinina spinuloinflata* (Bandy), lateral view, ×200, core 11, 2, 75–77.
17. *Acarinina acarinata* (Subbotina), umbilical view, ×300, core 14, 2, 119–121.
18. *Acarinina acarinata* (Subbotina), lateral view, ×300, core 14, 2, 119–121.
19. *Acarinina triplex* (Subbotina), umbilical view, ×200, core 13, 5, 117–119.
20. *Acarinina triplex* (Subbotina), lateral view, ×200, core 13, 5, 117–119.



Morozovella formosa at the base and the FAD of *Morozovella aragonensis* at the top (Berggren and Miller, 1988). The same datum events define the age equivalent Subzone P 6b in the revised zonal scheme of Berggren et al. (1995). Subzone P 6c spans 444 cm at Site 401. This subzone corresponds to Subzone P 8a of Blow (1979) and the upper part of the *Morozovella subbotinae* plus *Morozovella formosa* Zones of Bolli (1957, 1966) and Toumarkine and Luterbacher (1985).

Six species (or 25%) disappear within Subzone P 6c (e.g., *Acarinina acarinata*, *A. triplex*, *A. strabocella*, *Morozovella gracilis*, *M. lacerti* and *Muri-*

coglobigerina chascanona), and three species (or 12.5%) first appear (e.g., *Subbotina inaequispira*, *Acarinina cuneicamerata*, *Guembelitroides prolata*; Fig. 3).

Morozovella aragonensis/*Morozovella formosa* Zone (P 7):

This zone defines the interval between the FAD of *Morozovella aragonensis* (Plate II, 15 and 16) and LAD of *Morozovella formosa* in both the Berggren and Miller (1988) and Berggren et al. (1995) zonal schemes. Zone P 7 spans 584 cm at Site 401, and corresponds to Subzone P 8b plus the lower part of Zone P 9 of Blow (1979), the lower part of *Morozovella aragonensis* of Bolli (1957, 1966) and Toumarkine and Luterbacher (1985). Originally proposed by Bolli in 1966, this zone was later redefined by Berggren (1969) as *Globorotalia formosa* Zone (P 7) with the same name.

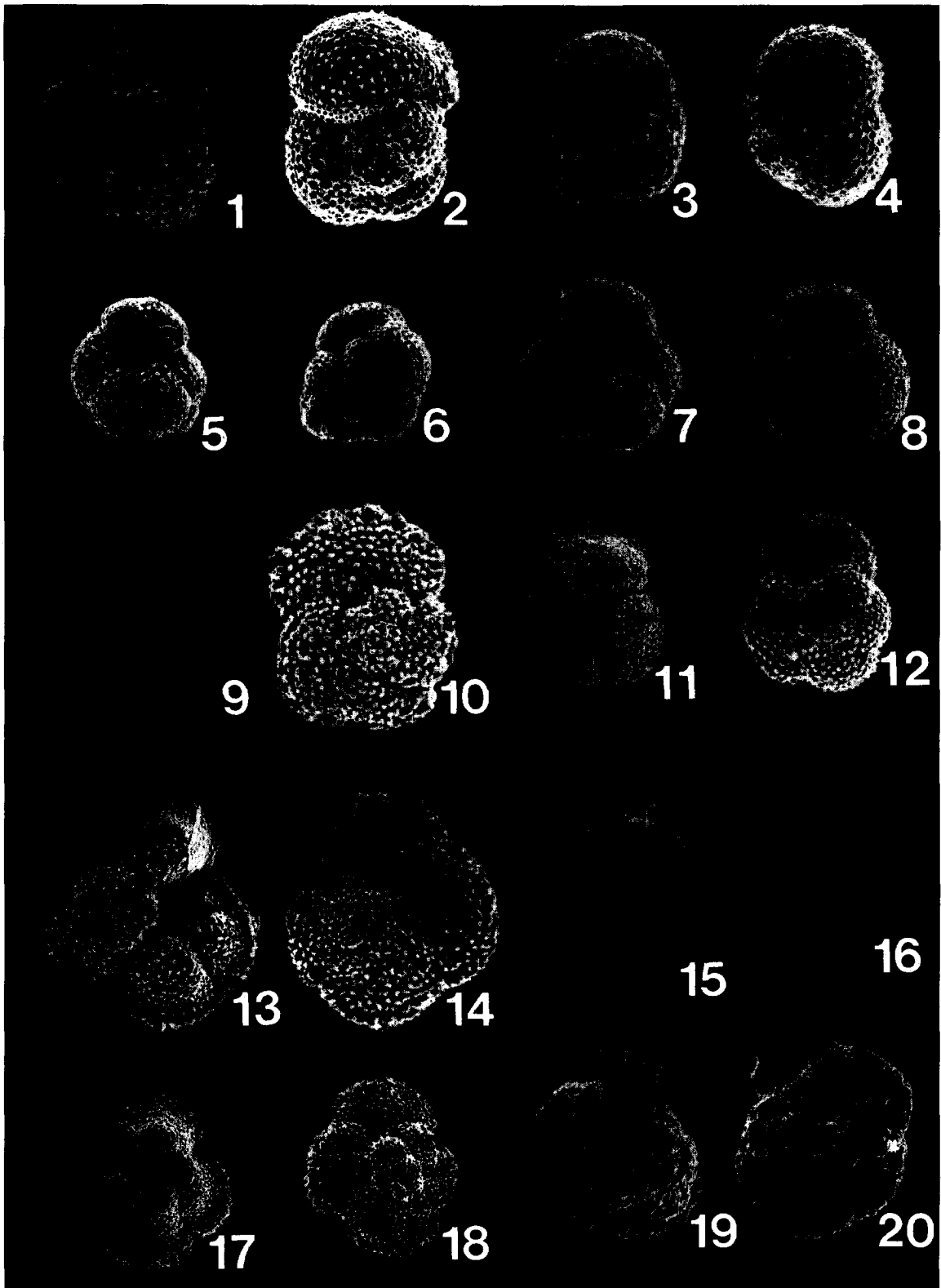
Twelve out of a total of 24 species or morphotypes (or 50%) disappear in Zone P 7 at DSDP Site 401 (e.g., *Subbotina* aff. 1 *inaequispira*, *S.* aff. 2 *inaequispira*, *Muricoglobigerina* sp., *M. soldadoensis*, *M. esnehensis*, *Acarinina cuneicamerata*, *A. aspensis*, *A. decepta*, *Planorotalites troelsenii*, *P. elongata*, *Paragloborotalia quadrilocula* and *Guembelitroides prolata*), and eight species or morphotypes (or 33%) first appear within Zone P 7 (e.g., *Morozovella aragonensis*, *Subbotina* aff. 1 *inaequispira*, *S.* aff. 2 *inaequispira*, *Acarinina pentacamerata*, *A. bullbrooki*, *A. aspensis*, *A. decepta*, *Paragloborotalia griffinae*; Fig. 3).

Morozovella aragonensis Zone (P 8):

Partial range zone defined by the LAD of *Morozovella formosa* at the base and FAD of *Planorotalites palmerae* at the top (see also Berggren et al., 1995). Zone P 8, and spans at least 142 cm at Site 401 (from core 11, section 2, 74 cm to the top of the section). Saint-Marc (1991) placed this interval in Zone P 9; however, we could not confirm the presence of *Subbotina palmerae*, the index species of P 9. Zone P 8 corresponds to the *Globorotalia aragonensis* Zone of Bolli (1957). The correlation of this zone with the biostratigraphic zonation of Blow (1979) is difficult due to taxonomic problems with *G. aragonensis*, *A. aspensis* and *A. pentacamerata*. At DSDP Site 401 *Morozovella caucasica* appears within Zone P 8.

Plate II

1. *Subbotina triangularis* (White), umbilical view, ×200, core 14, 2, 119–121.
2. *Subbotina triangularis* (White), dorsal view, ×200, core 14, 2, 119–121.
3. *Acarinina pentacamerata* (Subbotina), umbilical view, ×200, core 11, 2, 75–77.
4. *Acarinina pentacamerata* (Subbotina), dorsal view, ×200, core 11, 2, 75–77.
5. *Acarinina decepta* (Martin), umbilical view, ×200, core 11, 2, 75–77.
6. *Acarinina decepta* (Martin), lateral view, ×200, core 11, 2, 75–77.
7. *Acarinina bullbrooki* (Bolli), umbilical view, ×200, core 11, 2, 75–77.
8. *Acarinina bullbrooki* (Bolli), lateral view, ×200, core 11, 2, 75–77.
9. *Acarinina appressocamerata* (Blow), umbilical view, ×120, core 11, 2, 75–77.
10. *Acarinina appressocamerata* (Blow), lateral view, ×120, core 11, 2, 75–77.
11. *Muricoglobigerina soldadoensis* (Brönniman), umbilical view, ×200, core 14, 1, 118–120.
12. *Muricoglobigerina soldadoensis* (Brönniman), dorsal view, ×200, core 14, 1, 118–120.
13. *Morozovella gracilis* (Bolli), umbilical view, ×200, core 14, 2, 119–121.
14. *Morozovella gracilis* (Bolli), dorsal view, ×200, core 14, 2, 119–121.
15. *Morozovella aragonensis* (Nutall), umbilical view, ×120, core 11, 2, 75–77.
16. *Morozovella aragonensis* (Nutall), dorsal view, ×120, core 11, 2, 75–77.
17. *Morozovella caucasica* (Glaessner), umbilical view, ×120, core 11, 2, 75–77.
18. *Morozovella caucasica* (Glaessner), dorsal view, ×120, core 11, 2, 75–77.
19. Cross-section of the calcitic test of a *Morozovella* specimen, ×750.



4. Paleocene/Eocene boundary problem

There are currently no uniformly accepted criteria for placing the P/E boundary, although various stratigraphic horizons have been proposed. For example, Bolli (1957) proposed the top of the *Morozovella velascoensis* Zone, Hottinger and Schaub (1960) the top of the Ilerdian stage, Berggren et al. (1967) the FAD of *Pseudohastigerina wilcoxensis*, Martini (1971) the base of the nannofossil NP 10 Zone, Pomerol (1975) the base of the Ilerdian stage, Berggren et al. (1985) the base of the Ypresian stage,

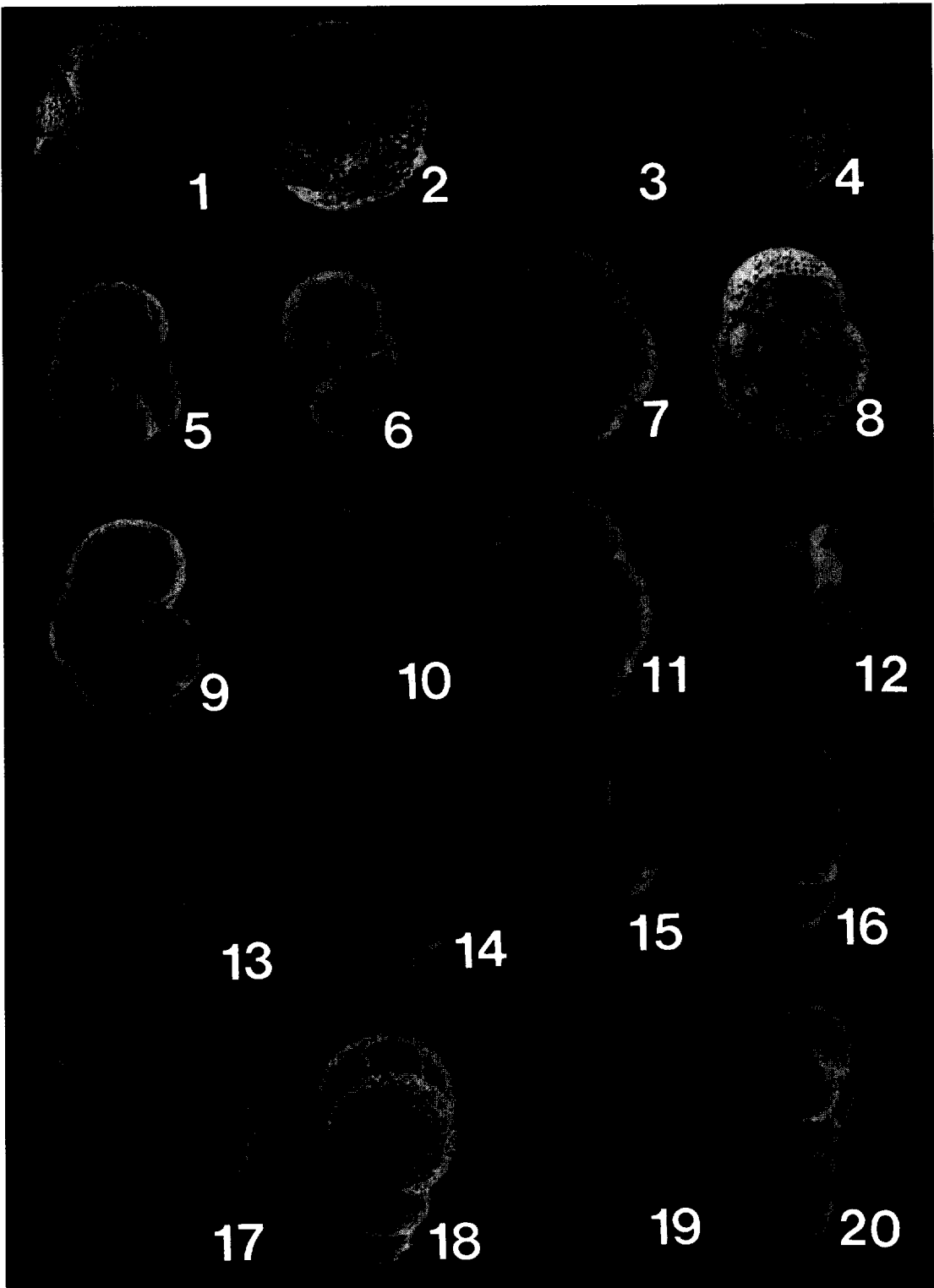
Plate III

1. *Muricoglobigerina* sp., umbilical view, $\times 200$, core 14, 2, 119–121.
2. *Muricoglobigerina* sp., dorsal view, $\times 200$, core 14, 2, 119–121.
3. *Muricoglobigerina* sp., umbilical view, $\times 300$, core 14, 1, 118–120.
4. *Muricoglobigerina* sp., dorsal view, $\times 300$, core 14, 1, 118–120.
5. *Muricoglobigerina chascanona* (Loeblich and Tappan), umbilical view, $\times 200$, core 14, 1, 118–120.
6. *Muricoglobigerina chascanona* (Loeblich and Tappan), dorsal view, $\times 200$, core 14, 1, 118–120.
7. *Muricoglobigerina aquiensis* (Loeblich and Tappan), umbilical view, $\times 200$, core 14, 1, 118–120.
8. *Muricoglobigerina aquiensis* (Loeblich and Tappan), dorsal view, $\times 200$, core 14, 1, 118–120.
9. *Morozovella aequa* (Cushman and Renz), umbilical view, $\times 120$, core 14, 4, 18–20.
10. *Morozovella aequa* (Cushman and Renz), dorsal view, $\times 120$, core 14, 4, 18–20.
11. *Morozovella subbotinae* (Morozova), umbilical view, $\times 200$, core 14, 4, 18–20.
12. *Morozovella subbotinae* (Morozova), dorsal view, $\times 200$, core 14, 4, 18–20.
13. *Morozovella acuta* (Toulmin), umbilical view, $\times 200$, core 14, 2, 120–122.
14. *Morozovella acuta* (Toulmin), dorsal view, $\times 200$, core 14, 2, 120–122.
15. *Morozovella velascoensis* (Cushman), umbilical view, $\times 200$, core 14, 4, 18–20.
16. *Morozovella velascoensis* (Cushman), umbilical view, $\times 120$, core 14, 2, 119–121.
17. *Morozovella marginodentata* (Subbotina), umbilical view, $\times 120$, core 13, 5, 117–119.
18. *Morozovella marginodentata* (Subbotina), dorsal view, $\times 120$, core 13, 5, 117–119.
19. *Morozovella caucasica* (Glaessner), umbilical view, $\times 120$, core 11, 2, 75–77.
20. *Morozovella caucasica* (Glaessner), dorsal view, $\times 120$, core 11, 2, 75–77.

Table 2

Number of species and first and last appearance datums of planktic foraminifera per sample at Site 401

Core	Sample	No. of species	No. of FAD	No. of LAD	% of FAD	% of LAD	Bio-zone
11	1, 85–87	13	0	0	0.00	0.00	P8
	2, 75–77	13	1	6	7.69	46.15	
	3, 74–76	15	0	5	0.00	33.33	P7
	4, 72–74	13	3	0	23.08	0.00	
	5, 76–78	13	2	1	15.38	7.69	
12	1, 77–79	15	3	3	20.00	20.00	
	2, 74–76	14	1	2	7.14	14.29	P6C
	3, 74–76	16	2	2	12.50	12.50	
	4, 76–78	9	0	2	0.00	22.22	
	5, 69–71	12	1	0	8.33	0.00	
13	1, 51–53	13	3	2	23.08	15.38	P6B
	1, 127–129	18	1	3	5.56	16.67	
	2, 51–53	13	0	0	0.00	0.00	
	2, 125–127	15	1	0	6.67	0.00	
	3, 49–51	19	0	4	0.00	21.05	
	3, 125–127	19	0	2	0.00	10.53	
	4, 44–46	18	1	0	5.56	0.00	
	4, 119–121	13	1	0	7.69	0.00	
	5, 06–08	18	0	1	0.00	5.56	
	5, 20–22	17	0	0	0.00	0.00	
14	5, 48–50	18	0	0	0.00	0.00	
	5, 69–71	19	0	0	0.00	0.00	
	5, 91–93	17	1	2	5.88	11.76	
	5, 117–119	18	0	0	0.00	0.00	
	1, 05–07	19	0	1	0.00	5.26	
	1, 18–20	17	0	2	0.00	11.76	
	1, 42–44	21	0	2	0.00	9.52	P6A
	1, 70–72	21	0	0	0.00	0.00	
	1, 92–94	21	0	0	0.00	0.00	
	1, 119–121	18	0	0	0.00	0.00	
BFEE	1, 148–150	20	0	0	0.00	0.00	
	2, 00–02	22	0	0	0.00	0.00	
	2, 20–22	20	0	0	0.00	0.00	
	2, 44–46	23	0	0	0.00	0.00	
	2, 72–74	24	0	2	0.00	8.33	
	2, 92–94	24	0	0	0.00	0.00	
	2, 119–121	19	0	0	0.00	0.00	
	2, 145–147	22	1	0	4.55	0.00	
	3, 00–02	29	0	0	0.00	0.00	
	3, 20–22	24	0	0	0.00	0.00	
3, 40–42	22	0	0	0.00	0.00		
3, 70–72	22	0	0	0.00	0.00		
3, 95–97	23	2	1	8.70	4.35		
3, 122–124	18	1	0	5.56	0.00		
4, 18–20	22	3	0	13.64	0.00		
4, 69–71	23	5	0	21.74	0.00		
4, 120–122	19	3	2	15.79	10.53		
5, 20–22	18	2	1	11.11	5.56		
5, 68–70	18	0	0	0.00	0.00		
Total No.			38	46			
Species mean		18.31					



Berggren and Miller (1988) the base of Chron 24, and Berggren and Miller (1989) the base of Benthic Biozone BB2.

Planktic foraminiferal researchers have placed the P/E boundary at the LAD of *Morozovella velascoensis*, which was assumed to be coincident with the FAD of *Pseudohastigerina wilcoxensis* (Bolli, 1957; Toumarkine and Luterbacher, 1985; Berggren and Miller, 1988). But there are problems with this criterion. For example, *M. velascoensis* is common in tropical waters but not in colder environments, whereas the FAD of *P. wilcoxensis* appears to be diachronous (Molina et al., 1992; Canudo et al., 1995),

and does not coincide with the FAD of *M. velascoensis* (e.g., this study; King, 1990; Pardo et al., 1994, 1995).

The level of the major extinction event in benthic foraminifera, which is coincident with negative excursions in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope values measured in benthic and planktic foraminifera, appears to be globally synchronous (Thomas, 1989, 1990a,b; Kennett and Stott, 1990, 1991; Pak and Miller, 1992; Lu and Keller, 1993, 1995a,b; Canudo et al., 1995). Moreover, in their study Pak and Miller (1992) compared the BFEE and isotopic excursion of DSDP Site 401 and DSDP Site 577 in the Pacific Ocean, DSDP Site 690 in the Antarctic Ocean and DSDP Site 702 in the South Atlantic, and concluded that this extinction event is indeed globally synchronous and coincident with the isotopic excursion. They also observed that this isotopic excursion occurred 1 m.y. prior to the LAD of *M. velascoensis*. For these reasons, the benthic foraminiferal extinction event (BFEE) and the isotopic excursion are excellent potential global markers for the Paleocene/Eocene boundary event (Molina et al., 1996). A possible planktic foraminiferal marker species for the BFEE may be the LAD of *Igorina laevigata* (*Igorina pusilla* sensu Lu et al., 1996), as noted by Arenillas and Molina (1996) in the Alamedilla section of southeastern Spain. At Site 401 rare *Igorina laevigata* specimens are present and disappear also at the BFEE. If this extinction datum can be confirmed globally, the LAD of *I. laevigata* is another potential event marker along with the isotopic excursion and benthic extinction.

5. Faunal turnover

5.1. Patterns of species richness and abundance

The faunal turnover observed at Site 401 confirms observations from sections in Spain at Alamedilla (Arenillas and Molina, 1996; Lu et al., 1996), Zumaya and Caravaca (Canudo et al., 1995), as well as Site 577 (Lu and Keller, 1995a,b). At Site 401 planktic foraminiferal assemblages are indicative of a middle to high latitude environment, as shown by the low species richness and high abundance of subbotinids (50%), as well as muricoglobigerinids and acarininids with few chambers in the last whorl of the test (3, $3\frac{1}{2}$ and 4 chambers; Premoli Silva

Plate IV

1. *Morozovella crosswikensis* (Olsson), umbilical view, $\times 300$, core 14, 2, 119–121.
2. *Morozovella crosswikensis* (Olsson), dorsal view, $\times 300$, core 14, 2, 119–121.
3. *Morozovella acuta* (Toulmin), umbilical view, $\times 120$, core 14, 2, 75–77.
4. *Morozovella acuta* (Toulmin), dorsal view, $\times 120$, core 14, 2, 75–77.
5. *Globanomalina ovalis* Haque, umbilical view, $\times 300$, core 14, 2, 119–121.
6. *Globanomalina ovalis* Haque, lateral view, $\times 300$, core 14, 2, 119–121.
7. *Paragloborotalia* sp., umbilical view, $\times 300$, core 14, 2, 119–121.
8. *Paragloborotalia* sp., dorsal view, $\times 300$, core 14, 2, 119–121.
9. *Pseudohastigerina wilcoxensis* (Cushman and Ponton), umbilical view, $\times 200$, core 11, 2, 75–77.
10. *Pseudohastigerina wilcoxensis* (Cushman and Ponton), lateral view, $\times 200$, core 11, 2, 75–77.
11. *Pseudohastigerina wilcoxensis* (Cushman and Ponton), umbilical view, $\times 300$, core 11, 2, 75–77.
12. *Planorotalites elongata* (Glaessner), umbilical view, $\times 300$, core 14, 2, 119–121.
13. *Planorotalites elongata* (Glaessner), umbilical view, $\times 300$, core 13, 5, 69–71.
14. *Planorotalites elongata* (Glaessner), dorsal view, $\times 300$, core 13, 5, 69–71.
15. *Chiloguembelina crinita* (Glaessner), frontal view, $\times 200$, core 14, 2, 119–121.
16. *Chiloguembelina crinita* (Glaessner), lateral view, $\times 200$, core 14, 2, 119–121.
17. *Chiloguembelina wilcoxensis* (Cushman and Ponton), frontal view, $\times 200$, core 13, 5, 117–119.
18. *Chiloguembelina wilcoxensis* (Cushman and Ponton), lateral view, $\times 200$, core 13, 5, 117–119.
19. *Chiloguembelina trinitatis* (Cushman and Renz), frontal view, $\times 300$, core 14, 2, 119–121.
20. *Chiloguembelina trinitatis* (Cushman and Renz), lateral view, $\times 300$, core 14, 2, 119–121.

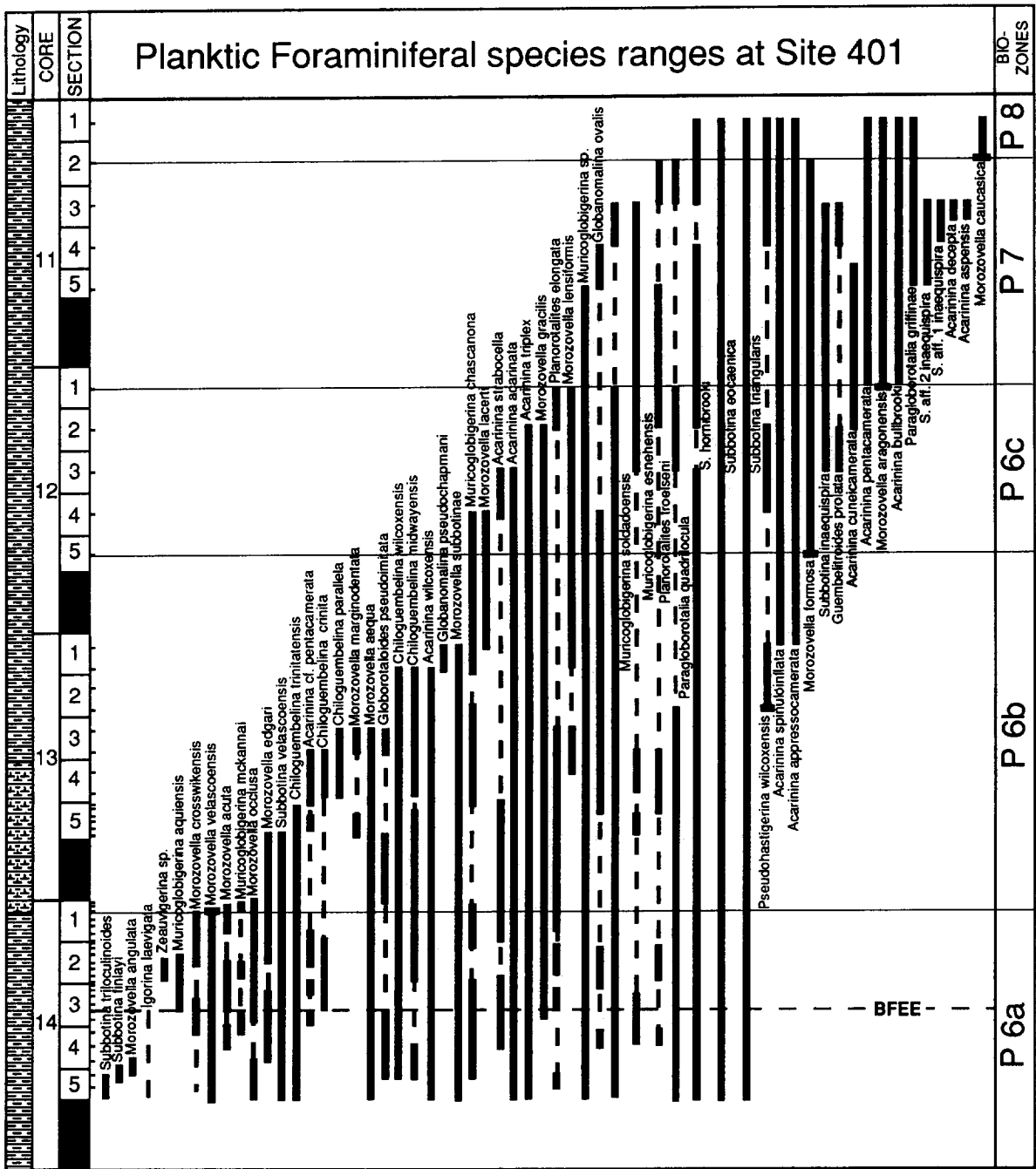


Fig. 3. Planktic foraminiferal species ranges during the latest Paleocene and early Eocene at DSDP Site 401. Note that no major extinctions coincide with the benthic foraminifera mass extinction (identified in the figure as BFEE).

Table 3
Number of species and first and last appearance datums of planktic foraminifera per genus at Site 401

Genera	No. species	Appearances	Disappearances
<i>Subbotina</i>	9	3	5
<i>Morozovella</i>	15	10	13
<i>Igorina</i>	1	0	1
<i>Muricoglobigerina</i>	6	4	6
<i>Acarinina</i>	12	9	8
<i>Planorotalites</i>	2	1	2
<i>Globorotaloides</i>	1	1	1
<i>Paragloborotalia</i>	2	1	1
<i>Globanomalina</i>	2	2	2
<i>Guembelitroides</i>	1	1	1
<i>Pseudohastigerina</i>	1	1	0
<i>Chiloguembelina</i>	5	4	5
<i>Zeauvigerina</i>	1	1	1
Total number	58	38	46

and Boersma, 1988; Lu and Keller, 1993). The low relative abundance of the warm water and low latitude morozovellids and acarininids with more than 4 chambers also suggests a cooler temperate environment for Site 401.

Fig. 3 shows that the P–E warming trend of Zone P 6 produced a low extinction rate in planktic foraminifera and a net increase, rather than net loss, of species. This pattern is similar to that observed in the Antarctic Ocean (Lu and Keller, 1993) and equatorial Pacific Ocean (Lu and Keller, 1995a,b). In the southern and northern latitudes, the faunal turnover is largely due to the in-migration of tropical–subtropical taxa from low latitudes and the resultant displacement of cooler water taxa (Stott and Kennett, 1990; Canudo and Molina, 1992a,b; Lu and Keller, 1993, 1995a,b). This also appears to be the case at Site 401 as shown in Fig. 4.

The dominant component at Site 401 are species of the cooler water genus *Subbotina* (Fig. 4a) with a total combined relative abundance of 45%. Although *Subbotina* species dominate, their diversity is low (6 species) with one species and two morphotypes (i.e., *S. inaequispira*; Plate I, 3–10) appearing in Subzone P 6c and Zone P 7, respectively, and three species disappearing in Subzones P 6a and P 6b (Fig. 4a, Table 3). Thus, the faunal turnover within the *Subbotina* group is marked by an overall reduction in species richness within Subzones P 6a and P 6b. The major change in subbotinids is observed in the

morphologic transition from *Subbotina velascoensis* to *S. eoacaenica* (Fig. 4a, Plate I, 1–2). However, this apparently sudden transition more likely represents a taxonomic problem than an evolutionary transition, and/or response to a pre-BFEE environmental change.

Species richness and relative abundances for the *Morozovella* and *Muricoglobigerina* groups are shown in Fig. 4b. Similar to the *Subbotina* group, there are no species extinctions or major faunal turnovers in these two genera across the BFEE interval. In fact, these two genera show high taxonomic richness throughout Subzone P 6a. Near the P 6a/P 6b boundary morozovellids show a high faunal turnover with six species disappearing, whereas only one *Muricoglobigerina* species disappeared.

Morozovellid populations can be divided into three different groups: (1) the ‘outgoing species’ group disappeared near the P 6a/P 6b boundary and includes *M. angulata*, *M. acuta*, *M. crosswikensis*, *M. velascoensis*, *M. occlusa* and *M. edgari* (Plates III and IV); (2) the ‘Paleocene survivors’ group thrives well into Subzone P 6b and includes *M. aequa* and *M. subbotinae* (Plate III); (3) the ‘incoming species’ group evolved and/or thrived in Zones P 6c and P 7 and includes *M. gracilis*, *M. marginodentata*, *M. lensiformis*, *M. lacerti*, *M. formosa*, *M. aragonensis* and *M. caucasica* (Plates II and III). Faunal turnovers in all three morozovellid groups seem related to ongoing climatic changes and in particular the maximum warming beginning at the BFEE and continuing through the upper part of P 6a and P 6b. This is suggested by the gradual replacement of species over time as well as major relative abundance fluctuations with 10 species appearing and 13 disappearing (Fig. 4b, Table 3). This faunal turnover trend is followed by cooling in P 6c to P 7 (Fig. 6) as suggested by the increased abundance and the appearance of cooler water subbotinids (*S. hornibrooki*, *S. inaequispira*) and the faunal turnover in morozovellids and muricoglobigerinids (Fig. 4b). Continued climatic cooling in Zones P 7 to P 8 is accompanied by the further reduction of morozovellids to two species (*M. aragonensis* and *M. caucasica*). Since the reduction in morozovellid species diversity is accompanied by the diversification of acarininids (both groups are surface dwellers), this may represent ecologic competition and displacement (Fig. 6). The same

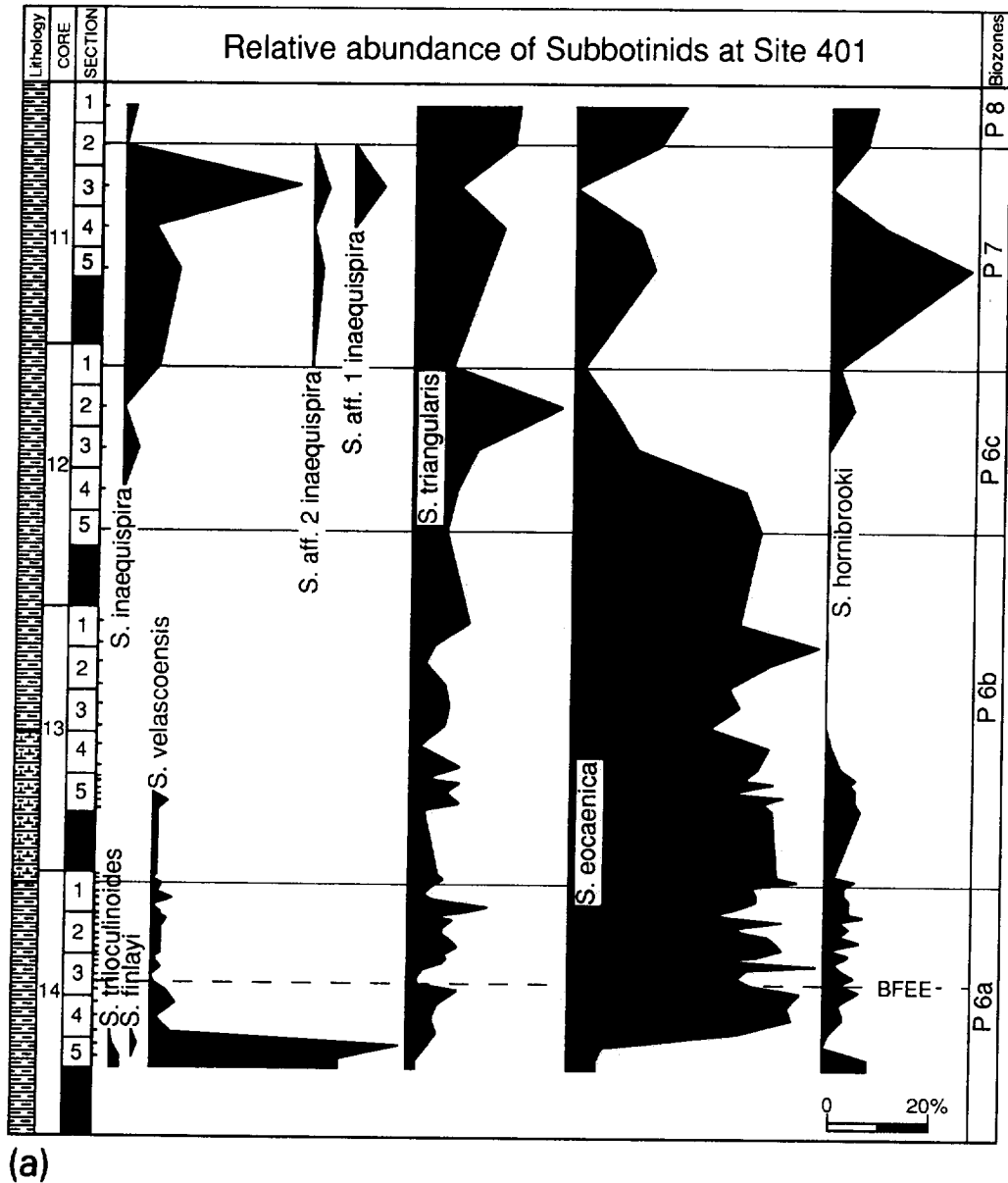
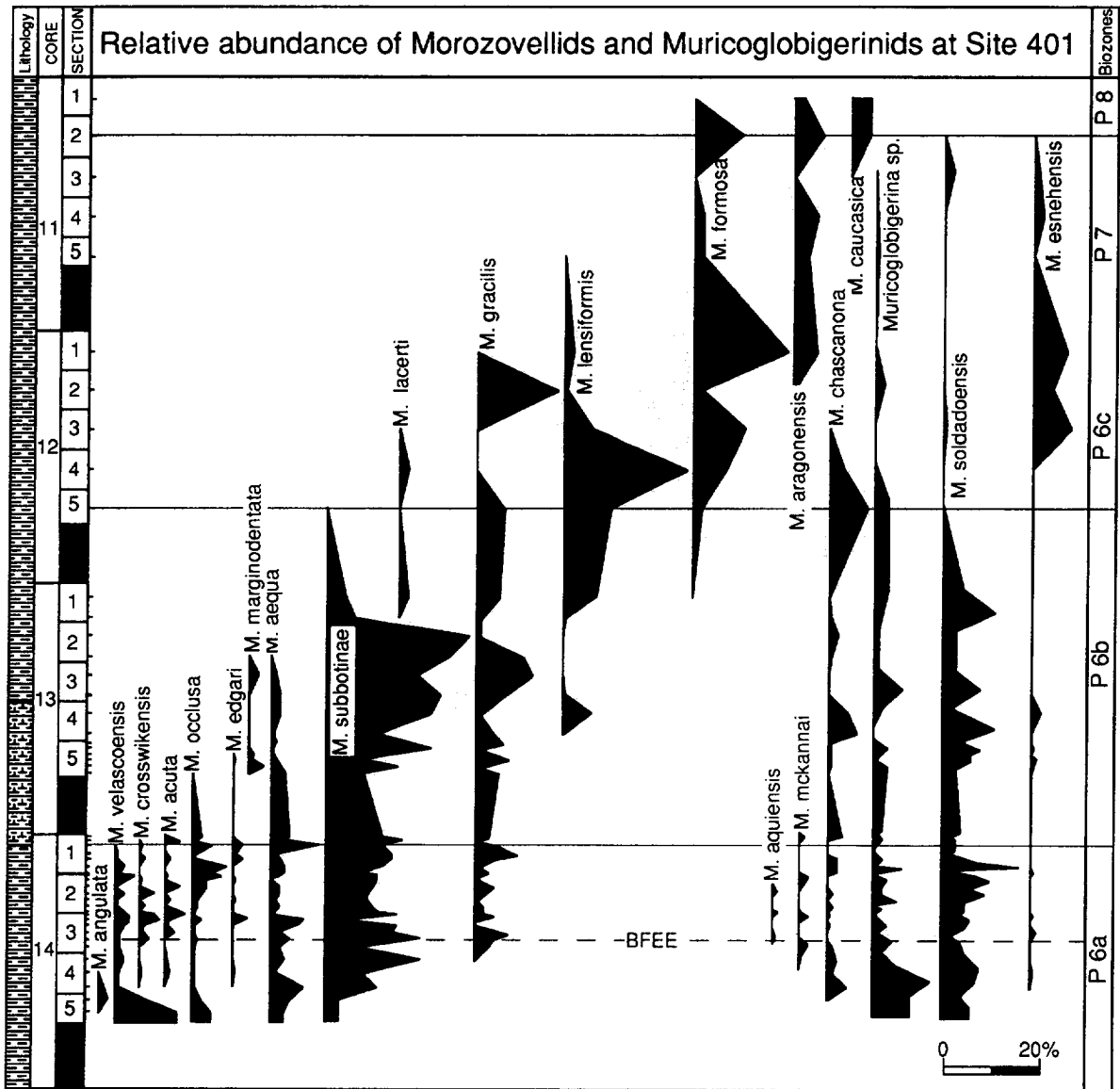


Fig. 4. (a) Relative abundance of subbotinids at Site 401.

pattern of morozovellids replaced by acarininids has been observed in Site 577 (Lu and Keller, 1995a,b) and Alamedilla (Arenillas and Molina, 1996; Lu et al., 1996). In contrast to morozovellids, muricoglobigerinid populations are relatively stable throughout this interval, though two species disappeared in the upper P 6a and near the P 6a/P 6b boundary and two disappeared in P 6c and P 7 (Fig. 4b, Table 3).

Fig. 4c shows the relative abundances of acarininids an other rothaliid and biserial taxa at Site 401. The genera *Planorotalites*, *Paragloborotalia*, *Globanomalina* and *Pseudohastigerina* are relatively stable in the P 6–P 7 interval, with only minor variations (Fig. 4c, Table 3), and only *Pseudohastigerina wilcoxensis* and *Paragloborotalia griffinae* range into Zone P 8. The genus *Acarinina*



(b)

Fig. 4 (continued). (b) Relative abundance of morozovellids and muricoglobigerinids at Site 401.

is common (Fig. 4c) although none of the species exhibit significant changes at the BFEE, or P 6a/P 6b boundary. A faunal turnover occurred in Subzone P 6b to P 6c, where 5 acarininid species disappear and 3 evolve. The major acarininid species turnover occurs in Zone P 7 (Fig. 4c), where 9 species appear and 8 species disappear (Table 3). Beginning in Zones P 7 and P 8, acarininids lead in species

richness and their diversification is correlative with the onset of major global cooling as seen in the stable isotopic signals (Kennett and Stott, 1990, 1991; Stott et al., 1990; Barrera and Hubber, 1991; Lu and Keller, 1993, 1995b).

Perhaps the most significant change is observed among chiloguembelinids. These biserial taxa (*Chiloguembelina* and *Zeauvigerina* genera, Fig. 4c)

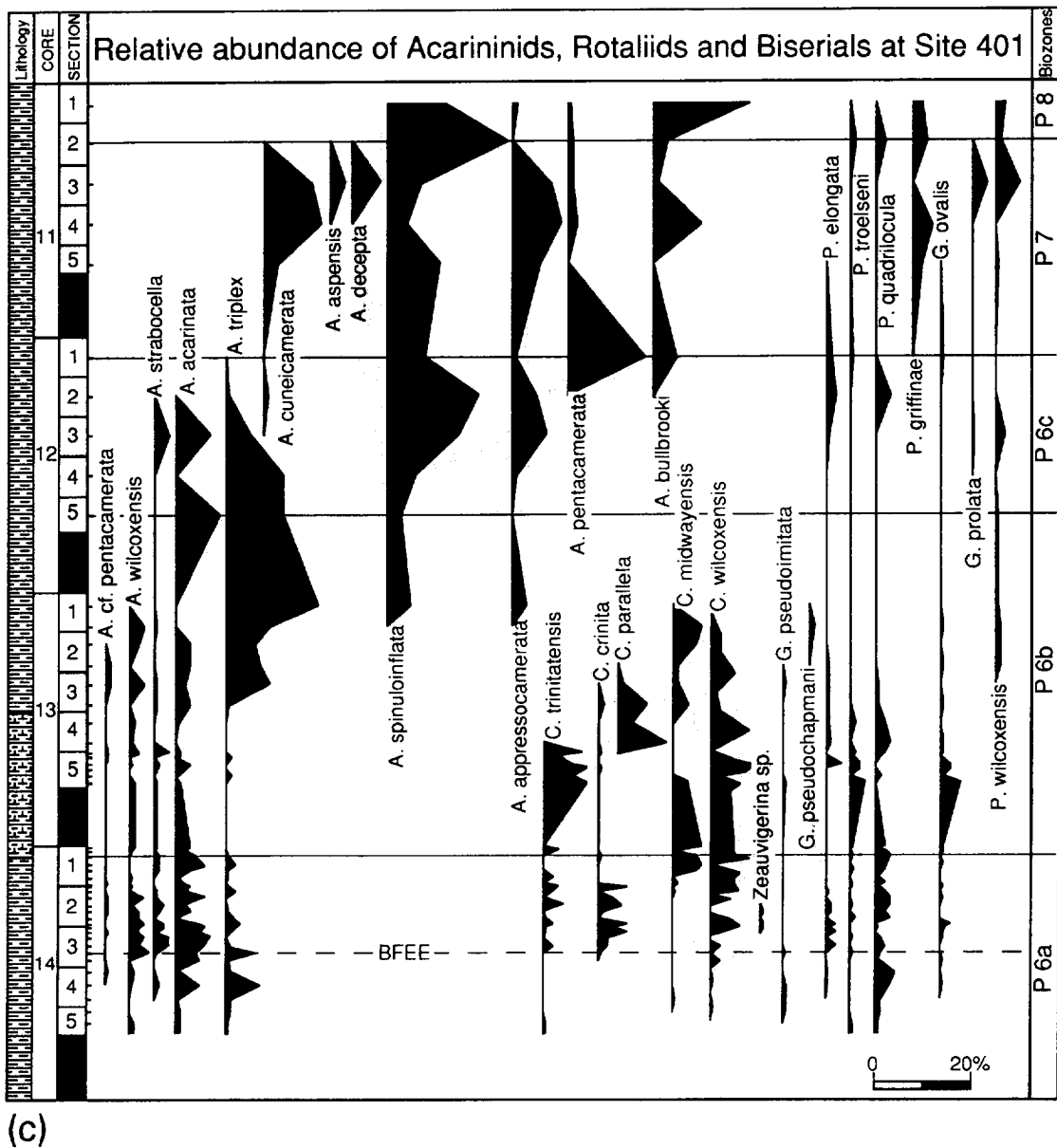


Fig. 4. (continued). (c) Relative abundance of acarininids, chiloguembelinids and other planktic foraminiferal genera at Site 401.

thrive in diversity and abundance beginning in Subzone P 6a near the BFEE and continue well into Subzone P 6b. Chiloguembelinids disappeared in the upper part of P 6b coincident with the onset of climate cooling (Kennett and Stott, 1990, 1991; Stott et al., 1990; Barrera and Hubber, 1991; Lu and Keller, 1993, 1995b).

Species richness data are summarized in Fig. 5 which plots the total number of species (squares), the number of first appearances (circles) and last appearances (triangles) per sample. A small faunal change was identified by Lu and Keller (1995b) during the earlier late Paleocene interval at the boundary between P 3a and P 3b. Note that prior

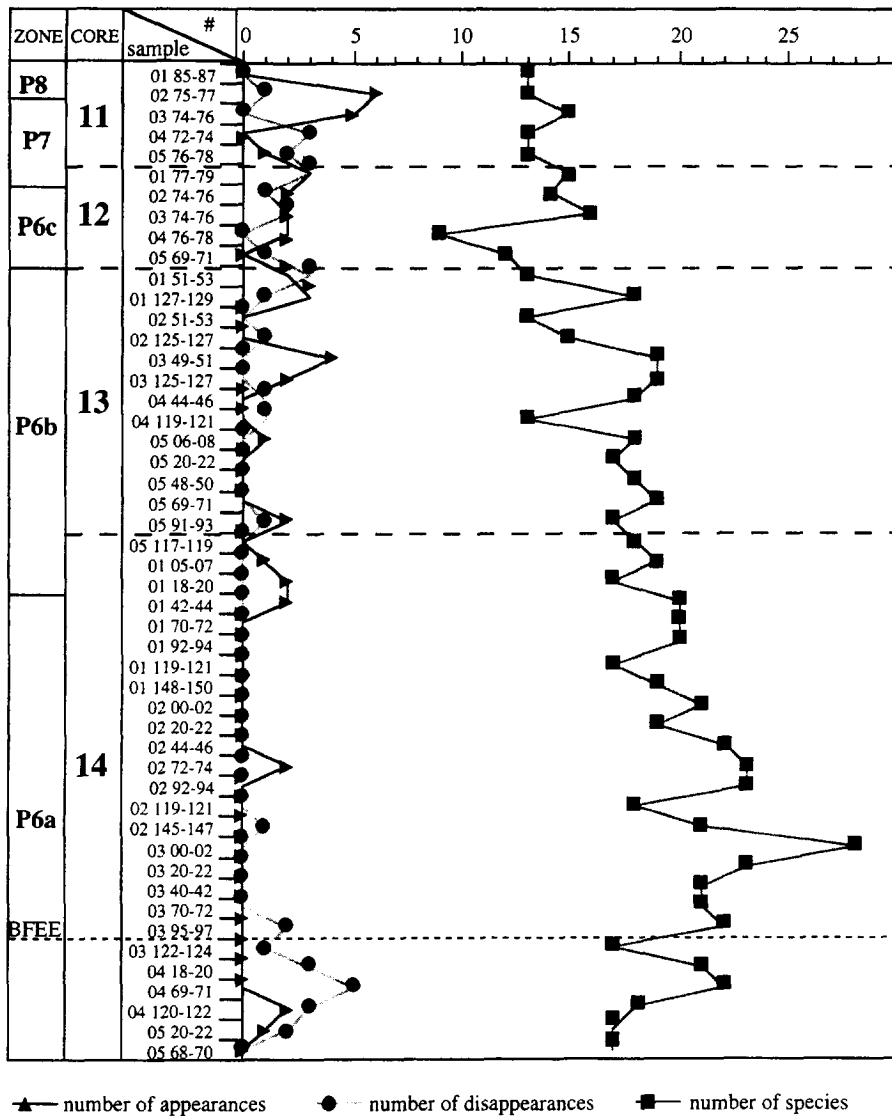


Fig. 5. Number of species and first and last appearances at Site 401. Note that not all first and last appearances represent evolution and extinction of species, but may be ecologically driven occurrences. Species numbers increase near the BFEE, remain high into the upper part of Subzone P 6b and decrease thereafter.

to the BFEE, there is a high planktic foraminiferal turnover with FADs (chilogaembelinids, morozovellids and muricoglobigerinids) and LADs (subbotinids), whereas after the BFEE in Subzone P 6a the turnover is low and the species richness reaches a maximum. The latter is coincident with maximum warming as documented in the stable isotope records of numerous sections worldwide (Kennett and Stott, 1990; Lu and Keller, 1993, 1995a,b; Canudo et

al., 1995). This maximum species richness in Subzone P 6a signals the major change among planktic foraminiferal populations associated with the P–E transition (see also Lu and Keller, 1993, 1995a,b). Planktic foraminiferal assemblages stabilize near the top of Subzone P 6a as also observed at Site 577 by Lu and Keller (1995a). Although the species turnover rate is slow during P 6a, the cumulative turnover is high (Table 4; Lu and Keller, 1995a)

Table 4
Number of species and first and last appearance datums of planktic foraminifera per zone at Site 401

Biozone	No. species	% Appearances	% Disappearances	% Total turnover
P6a pre BFMEE	34	38.2	8.8	47
P6a at BFMEE	34	0	2.9	2.9
P6a post BFMEE	34	8.8	5.8	14.6
P6b	37	18.9	45.9	64.8
P6c	24	12.5	25	37.5
P7	24	33.3	50	83.3
P8	11	9.1	0	9.1

with chiloguembelinids declining in abundance and disappearing. Upsection in Subzones P 6b and P 6c the morozovellid/acarininid ratio changes from a morozovellid-dominated to a acarininid-dominated fauna. In the lower part of P 7 species richness decreases (from 18 to 14 species) due to disappearances among morozovellids and muricoglobigerinids and appearances among acarininids. This rearrangement is likely the result of climatic cooling as suggested by oxygen isotope data (Kennett and Stott, 1990, 1991; Stott et al., 1990; Barrera and Hubber, 1991; Lu and Keller, 1993, 1995b) and leads to the local disappearance of subtropical species. Lu and Keller (1995a) identified a third faunal turnover at this interval in Site 577 which culminates in Zones P 8–P 9.

Table 4 shows the percentage of appearances and disappearances and the sum of both as a measure of the total turnover in each zone at DSDP Site 401. Note that, similar to ODP Site 738 (Lu and Keller, 1993), species richness is low in P 6a (see Table 2) with an average of 18 species present in each sample. However, since a total of 34 species is encountered in P 6a, the low average of 18 species in individual samples is likely a function of small sample size (10 cm³), rarity of some taxa, and the Signor–Lipps effect. The fact that planktic assemblages at similar latitudes (e.g., Caravaca, Zumaya and DSDP Site 577, Canudo and Molina, 1992a,b; Canudo et al., 1995; Lu and Keller, 1995a,b) generally average 25 species, supports this conclusion. Alternatively, Site 401 may have lower species diversity because this locality reflects cooler water temperatures.

5.2. Environmental implications

Planktic foraminiferal species live at restricted water depths (e.g., euphotic zone, thermocline) and

at different latitudes (tropical, temperate, cool). Their habitats can be inferred by shell morphology and $\delta^{18}\text{O}$ signals (Shackleton et al., 1985; Boersma and Premoli Silva, 1988, 1989; Premoli Silva and Boersma, 1988; Corfield and Cartledge, 1991; Lu and Keller, 1993, 1995a). Thus, environmental information can be gained from species assemblages and their changing populations. Surface water dwellers have generally lighter $\delta^{18}\text{O}$ and heavier $\delta^{13}\text{C}$ values and thermocline or deep dwellers have heavier $\delta^{18}\text{O}$ and lighter $\delta^{13}\text{C}$ values. Thus, *Morozovella* and *Acarinina* species have heavier (more positive) $\delta^{13}\text{C}$ values and lighter (more negative) $\delta^{18}\text{O}$ values, indicating that they lived in the surface mixed layer. In contrast, species of *Subbotina*, *Chiloguembelina* and *Planorotalites* have lighter $\delta^{13}\text{C}$ and heavier $\delta^{18}\text{O}$ values and are considered to have lived at thermocline or deeper depths (Shackleton et al., 1985; Corfield, 1987; Lu and Keller, 1993, 1995b; Canudo et al., 1995; D'Hondt et al., 1994). Isotopic analysis at DSDP Site 577 indicates that *Subbotina* and *Chiloguembelina* species lived near or at thermocline depths, whereas *Planorotalites* species lived at greater depths (Lu and Keller, 1995b). In Fig. 6 relative abundances of species are grouped by genera.

Based on these data, the relative abundances of genera (see Fig. 6) provide indications of changes in temperature or water-mass stratification. For instance, prior to the BFEE and $\delta^{13}\text{C}$ excursion, morozovellids are the dominant surface dwellers and subbotinids the dominant thermocline dwellers. Acarininids increased in the 1 m below the $\delta^{13}\text{C}$ excursion and BFEE (*A. acarinata*, *A. wilcoxensis*, *A. strabocella*, *A. cf. pentacamerata*, *A. triplex*; Fig. 4c), as also observed at Zumaya (Canudo et al., 1995) and Alamedilla (Arenillas and Molina, 1996; Lu et al., 1996). A short-term incursion of com-

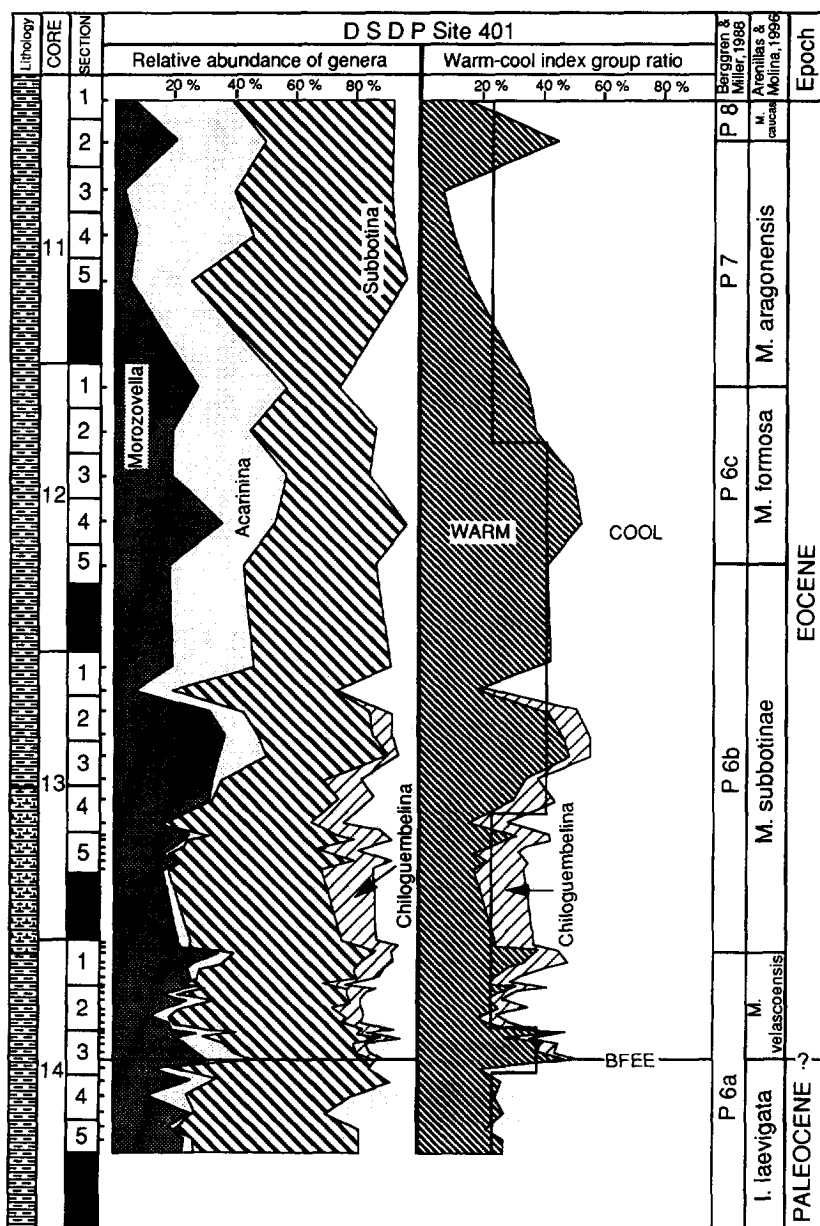


Fig. 6. Relative abundances of planktic foraminifera grouped by genera. Note climatic warming suggested by increased acarininids and chiloguembelinids near the BFEF and the $\delta^{13}C$ excursion. Cooling trend is indicated by decreased morozovellids and increased subbotinids and acarininids with rounded chambers in P 6c. Solid line marks average value for cool vs. warm water species which reflect climatic changes.

pressed acarininids (i.e., *A. bergrenni*, *A. sibaiyaensis*, *A. africana*) has been observed at Alamedilla (Lu et al., 1996), and is possibly present in the Antarctic Ocean Site 690 where they were labelled as small morozovellids by Stott and Kennett (1990). These

morphotypes are also present in the Negev (Lu et al., 1995), ODP Site 865 (Kelly et al., 1995) and Kazakstan (Pardo and Keller, 1996). At Site 401, these morphotypes have been grouped with the morphologically similar taxa *A. acarinata* and *A. cf. pen-*

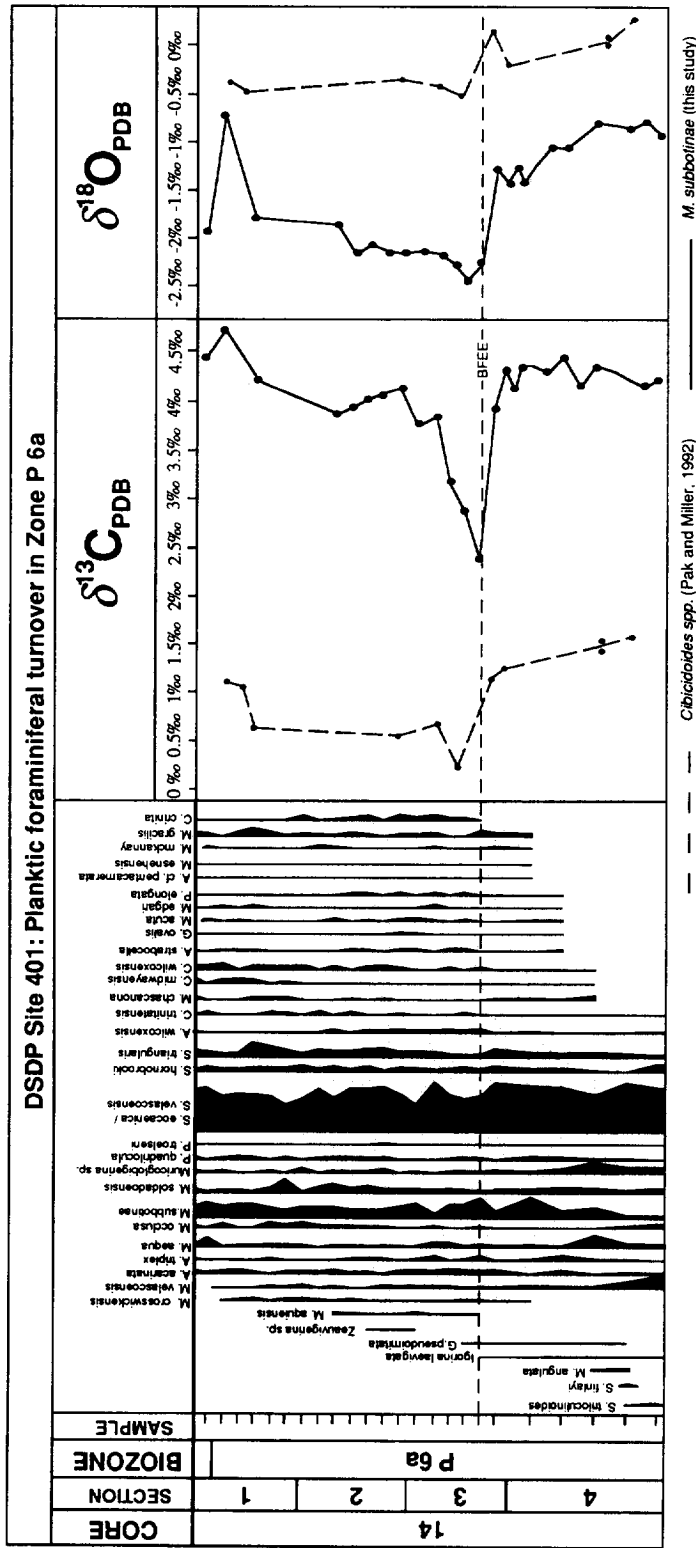


Fig. 7. Stable isotopes and planktic foraminiferal species abundances at DSDP Site 401. Note that $\delta^{13}C$ excursion occurred over a 27 cm interval which represents 23.6 ka. No significant faunal turnover occurred in planktic foraminifera at this time.

tacamerata, because of taxonomic problems (e.g., *A. acarinata*, *A. pseudotopilensis*, *A. berggreni* and *A. wilcoxensis*). Acarininids reach peak abundance during the BFEE and $\delta^{13}\text{C}$ excursion and decrease thereafter.

Stable isotope data suggest that chiloguembelinids are thermocline dwellers and tolerant of low oxygen conditions (Boersma and Premoli Silva, 1988, 1989; Keller, 1993; Keller et al., 1993; Barrera and Keller, 1994). Chiloguembelinids are abundant from the BFEE and $\delta^{13}\text{C}$ excursion well into Zone P 6b (Figs. 4c and 6) and suggest the presence of a well-developed oxygen minimum zone during this interval. In the P 6a–P 6b interval their abundance increase seems to be linked to increased water-mass stratification and expansion of the oxygen minimum zone during maximum climate warming as also observed at Zumaya and Caravaca (Canudo and Molina, 1992a; Molina et al., 1994; Canudo et al., 1995). At the same time, subbotinids decreased during the $\delta^{13}\text{C}$ excursion and the BFEE and increased thereafter. Morozovellids increased in abundance from Zone P 6b through Zone P 6c correlative with a major increase in acarininids. Subbotinids decreased during this time, corresponding with the maximum global warming (Pak and Miller, 1992; Lu and Keller, 1993, 1995a,b).

This faunal turnover suggests climatic warming just after the BFEE and again in Subzone P 6b–c. Cooling is suggested in Zone P 7 with increased subbotinids and decreased morozovellids. These climatic trends are also reflected in the grouping of all warm water (morozovellids and acarininids) vs. cool water dwellers (e.g., subbotinids, muricoboglobigerinids, chiloguembelinids and acarininids with rounded chambers; Fig. 6). The same trans-P–E faunal pattern is apparent at the Alamedilla and Zumaya sections in Spain (Arenillas and Molina, 1996; Pardo et al., 1996, unpublished data). However, the temperature changes inferred from warm and cool water species do not always reflect temperatures inferred from $\delta^{18}\text{O}$ data at these sites. For instance, $\delta^{18}\text{O}$ data indicate maximum warming beginning at the BFEE and $\delta^{13}\text{C}$ excursion and continuing through P 6a. Foraminiferal data, however, suggest that the maximum warming contains a short-term cooling which begins shortly after the $\delta^{13}\text{C}$ excursion and lasts into the lower half of P 6b (Fig. 6). This short-term cool-

ing can also be observed at Alamedilla and Zumaya (Pardo et al., 1996, unpubl. data), and was marked by relative abundance changes in surface and thermocline dwellers particularly the presence of abundant chiloguembelinids (Fig. 6). The latter suggest a well developed oxygen minimum zone during this interval.

5.3. Paleocene–Eocene $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ excursion events

Pak and Miller (1992) analyzed the stable isotopic values of the benthic foraminifera *Cibicidoides* spp. at Site 401 and discovered a relatively small (<1‰) negative excursion at the BFEE. We re-analyzed Subzone P6 a at a higher sample resolution and measured the surface dweller *Morozovella subbotinae*. Both sets of data are shown in Fig. 7 and Table 5.

$\delta^{13}\text{C}$ values of *M. subbotinae* decreased by nearly 2‰ coincident with the BFEE, whereas $\delta^{13}\text{C}$ values

Table 5
 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values recorded at Subzone P 6a at Site 401

Sample DSDP 401	<i>Morozovella subbotinae</i>	
	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
14/1/18–20	4.41	–1.96
14/1/70–72	4.71	–0.73
14/1/119/121	4.18	–1.81
14/2/0–2	3.88	–1.84
14/2/44–46	3.95	–2.21
14/2/72–74	4.03	–2.09
14/2/92–94	4.04	–1.72
14/2/119–121	4.15	–2.18
14/2/145–147	3.77	–2.17
14/3/20–22	3.86	–2.19
14/3/40–42	3.16	–2.29
14/3/70–72	2.87	–2.41
14/3/95–97	2.32	–2.24
14/3/122–124	3.92	–1.29
14/3/143–145	4.31	–1.45
14/4/4–6	4.12	–1.26
14/4/18–20	4.37	–1.45
14/4/47–49	4.37	–1.24
14/4/69–71	4.29	–1.08
14/4/95–97	4.46	–1.1
14/4/120–122	4.14	–0.94
14/4/147–149	4.36	–0.81
14/5/0–2	4.3	–0.86
14/5/20–22	4.22	–0.87
14/5/45–47	4.16	–0.79
14/5/68–70	4.22	–0.94

of *Cibicidoides* spp. (Pak and Miller, 1992) decreased by only a 1‰. This difference is most likely due to the lower sample spacing of Pak and Miller (1992) which missed the critical interval (Fig. 7). Pak and Miller (1992) estimated that the $\delta^{13}\text{C}$ excursion occurred within 14 ka (or 20 cm) assuming a sedimentation rate of $1.36 \text{ cm}/10^3 \text{ yr}$; however, they provided no isotopic evidence in support of this estimate. Our isotopic analysis provides constraints for the $\delta^{13}\text{C}$ excursion interval; the excursion to minimum $\delta^{13}\text{C}$ values occurred within 27 cm (i.e., core-section: 14–3, 122–124 cm to 95–97 cm) or 22.6 ka. Our age estimate is based on average sediment accumulation rates of $1.19 \text{ cm}/10^3 \text{ yr}$ between two datums: the BFEE datum and the FAD of *M. aragonensis* at 54.80 Ma. and 52.92 Ma, respectively (Cande and Kent, 1992; Lu and Keller, 1995b; Lu et al., 1996). The sediment shows a CaCO_3 drop starting at the BFEE (Montadert et al., 1979; Saint-Marc, 1991) which could be caused either by dissolution or by an increase in the amount of terrigenous sediment influx. Since no major dissolution can be inferred from the preservation of the foraminifera tests, an increase in terrigenous sediment influx and therefore in the sedimentation rate is likely. Thus, the age estimates should be considered as maximum limits for the isotopic events. The difference in sedimentation rates between ours and that of Pak and Miller (1992) is due to their use of the Berggren et al. (1985) time scale (i.e., BFEE datum and the FAD of *M. aragonensis* at 57.56. and 55.67 Ma, respectively). Based on sedimentation rate of $1.19 \text{ cm}/10^3 \text{ yr}$, the $\delta^{13}\text{C}$ excursion occurred over 22.6 ka, whereas based on Pak and Miller's sedimentation rate ($1.36 \text{ cm}/10^3 \text{ yr}$) the $\delta^{13}\text{C}$ excursion occurred over $19.8 \times 10^3 \text{ yr}$. The entire $\delta^{13}\text{C}$ excursion (i.e., negative excursion until recovery to pre-excursion values) took place within 172 cm (i.e., from core 14, section 2, 143–145 cm to 119–121 cm), or a maximum of 144.5 ka (126.4 ka using Pak and Miller's sedimentation rate). This estimated duration for the $\delta^{13}\text{C}$ excursion is within error range of estimated durations of a few thousand years by Kennett and Stott (1991), 63 ka by Lu and Keller (1993) and 12 ka by Canudo et al. (1995). Thus, the global carbon change probably took place within a few thousand years and lasted less than 200 ka as earlier suggested by Kennett and Stott (1991), Lu et al. (1996), Thomas and Shackleton (1996).

Oxygen isotope values of surface waters show little or no changes at the $\delta^{13}\text{C}$ interval in tropical and subtropical regions, whereas in middle to high latitudes surface water temperature increased by 5° to 7°C (Stott, 1992; Pak and Miller, 1992; Lu and Keller, 1993, 1995a; Lu et al., 1996). The middle latitude locality of Site 401 shows surface warming of about 4° – 5°C as indicated by a 1‰ negative excursion in surface $\delta^{18}\text{O}$ values, accompanied by an increase in warm water species (Figs. 6 and 7). This warming trend continued at least up to the P 6 a/P 6b boundary. At the same time, benthic $\delta^{18}\text{O}$ values decreased, indicating a 2°C bottom water warming (Pak and Miller, 1992). However, these temperature values should be considered with caution because diagenesis is likely to have altered the original isotopic signal.

6. Discussion

During the Paleocene–Eocene transition climate reached the warmest temperatures of the Cenozoic, accompanied by the lowest average $\delta^{13}\text{C}$ values (Shackleton et al., 1985; Shackleton, 1986; Miller et al., 1987; Corfield and Shackleton, 1988; Kennett and Stott, 1990, 1991). Deep water temperatures rose between 10°C and 15°C , whereas surface water temperatures remained relatively stable in low latitudes, but increased 5°C to 7.5°C in Antarctic waters (Corfield and Shackleton, 1988; Kennett and Stott, 1990, 1991; Barrera and Hubber, 1991; Pak and Miller, 1992; Corfield and Cartlidge, 1991, 1992; Lu and Keller, 1993, 1995a,b; Bralower et al., 1995). These climatic changes associated with major changes in oceanic deep water circulation, a temporary absence of cold deep water formation in Antarctica and the production of warm saline deep waters in the Tethys region, are generally considered as possible causes for the isotope excursion and benthic foraminiferal mass extinction (Kennett and Stott, 1990, 1991; Pak and Miller, 1992; Lu and Keller, 1993; Lu et al., 1996). Other hypotheses suggest the reorganization of tectonic plates associated with increased volcanic and submarine hydrothermal activities, greenhouse warming due to increased CO_2 accompanied by warming of bottom water, and increased emission of H_2S along with decreased oxygen content, leading to a poisonous anaerobic environment for bottom dwellers (Stott and Kennett, 1990; Eldholm and Thomas, 1993).

Many workers support the idea that the main source of warm saline deep waters was the Tethys region (Kennett and Stott, 1990, 1991; Pak and Miller, 1992; Lu and Keller, 1993, 1995a,b; Canudo et al., 1995; Ortiz, 1995; Lu et al., 1996). This could explain the more abrupt planktic foraminiferal extinction at Caravaca or Alamedilla during the P–E transition as compared with Zumaya in northern Spain which is influenced by colder and well oxygenated Atlantic waters (Canudo et al., 1995; Ortiz, 1995; Arenillas and Molina, 1996; Pardo et al., 1996, unpublished data). At DSDP Site 401 the planktic foraminiferal turnover is more gradual than at Zumaya and also suggests a North Atlantic circulation regime. Despite duration differences between the Tethys and open ocean or North Atlantic provinces, current data indicate that the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic excursions across the P–E transition are isochronous worldwide.

At Site 401 the BFEE coincides with the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ negative excursions (Fig. 7), the abundance peak of warm water morozovellid and acarininid species and the appearance of low O_2 tolerant chiloguembelinids (Figs. 4 and 6). However, there is no significant change in species richness, or sudden change in relative species abundances through this interval as also noted at Caravaca, Alamedilla and Zumaya sections (Canudo et al., 1995; Arenillas and Molina, 1996; Lu et al., 1996; Pardo et al., 1996, unpublished data), as well as at Site 577 and 738 (Lu and Keller, 1993, 1995a,b). Through the latest Paleocene and early Eocene (Zones P 6a–P 8) planktic foraminifera changed gradually to reach maximum warming in the upper Subzone P 6a. From the upper Subzone P 6b through Zones P 7–P 8 planktic foraminiferal faunas show a cooling trend with decreased abundance of morozovellids, disappearance of chiloguembelinids and increased abundance of cooler water, rounded chambered acarininids. Similar turnovers have been observed at other sections (e.g., Zumaya, Caravaca, Alamedilla, Site 577, Site 738).

7. Conclusions

(1) There is no major planktic foraminiferal change coinciding with the BFEE and the $\delta^{13}\text{C}$ excursion at Site 401. Only *Igorina laevigata* disappears within the isotopic excursion interval.

(2) Planktic foraminifera change gradually in response to climatic changes. Surface water warming of -1‰ (4°C) occurs beginning at the $\delta^{13}\text{C}$ excursion (upper Subzone P 6a of Berggren and Miller, 1988, or P5 of Berggren et al., 1995) and continued into Subzone P 6b. This warming is accompanied by abundant warm water surface dwellers (morozovellids and acarininids) and the appearance of common low O_2 tolerant chiloguembelinids, whereas cooler water subbotinids decrease.

(3) Planktic foraminifera indicate climate cooling beginning in the upper part of Subzone P 6b and continuing through Zone P 8 as inferred from a decrease in warm surface dwellers (morozovellids), the disappearance of low O_2 tolerant chiloguembelinids, and increase in round chambered acarininids which suggests cooler surface waters.

(4) A 2‰ negative excursion in $\delta^{13}\text{C}$ occurs in surface waters at Site 401 similar to sections worldwide. This excursion is estimated to have occurred over a maximum of 23 ka and recovery to pre-excursion conditions occurred after a maximum of 144 ka. Within limits of dating based on average sediment accumulation rates, these durations are similar to estimates from other localities (e.g., Sites 690, 738, 577, 577a).

(5) $\delta^{18}\text{O}$ data suggest that at Site 401 temperatures remained warm well after $\delta^{13}\text{C}$ returned to pre-excursion values.

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