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1.5

Cretaceous palaeoceanographic events and abyssal agglutinated foraminifera

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ABSTRACT

Abundance and diversity of deep water agglutinated foraminifera reflect changes in oxygenation and temperature of deep water masses in the Cretaceous ocean since the Cenomanian/Turonian boundary. Major diversity crises are linked to palaeoceanographic events involving oxygen depleted deep water masses at the Cenomanian/Turonian boundary and in the lower Campanian. Overall species diversity is inversely related to the general trend of deep water palaeotemperatures. Abundance and diversity of deep-water agglutinated foraminifera therefore have potential as tracers of deep water circulation changes in the Cretaceous ocean.

INTRODUCTION

A special feature of late Cretaceous deep sea environments is the occurrence of palaeoceanographic events leading to oxygen depletion and the deposition of organic-rich sediments over vast areas of the abyssal realm. The causes and consequences of these global events at the Cenomanian/Turonian and Santonian/Campanian boundaries (Oceanic Anoxic Events 2 and 3 of Schlanger & Jenkyns, 1976 and Jenkyns, 1980) have been the subject of considerable discussion during the last decade (e.g. Arthur, 1979; Ginsburg & Beaudoin, 1990). General circu-

Table 3.1.

HOLE 398D	CORE																													
	SECTION																													
	INTERVAL (top)		54	54	54	53	53	53	53	53	53	53	53	53	53	53	53	52	52	52	52	52	52	52	51	51	51	51	51	51
	2	2	1	1	6	6	5	5	4	4	3	3	2	2	1	1	4	4	3	3	2	2	1	1	3	3	2	2		
	77	5	134	14	110	10	107	10	111	9	110	10	106	10	110	9	110	10	110	10	116	10	89	6	111	13	110	14		
<i>Ammodiscus cretaceus</i>					3	3	4	1		2		2		7			2	2	1	3	1	1?								
<i>Ammodiscus planus</i>					1								1																	
<i>Ammosph. pseudopauciloculata</i>																				3	9	5	7							
<i>Arenobulimina dorbignyi</i>																														
<i>Aschemonella carpathica</i>																														
<i>Clavulinoides eggeri</i>																														
<i>Clavulinoides subparisiensis</i>																														
<i>Dorothia crassa</i>																														
<i>Dorothia oxycona</i>																														
<i>Dorothia sp. 398</i>																														
<i>Dorothia sp. 41</i>																														
<i>Gaudryina pyramidata</i>																														
<i>Gaudryina sp.398</i>									4																					
<i>Glomospira charoides</i>	3	5	11	42	27	33	43	30	16	13	11	14	14	10	2	13	10	24	10	32	1	10	11	2	3	2		1		
<i>Glomospira gordialis</i>	1			4	9	1	3	2	2	5	2	6	6	6	8	2	1	2	2	3		2	2							
<i>Glomospira irregularis</i>	1			2		1			1	1	5	2	3			1	6	2		17	1	1								
<i>Glomospira serpens</i>				1			1	1					1	1			1	2		1										
<i>Glomospirella gaultina</i>																														
<i>Goesella rugosa</i>																														
<i>Bulbobaculites problematicus</i>					15	6		1																						
<i>Haplophragmoides aff. bulloides</i>					15	2	3								2?					3?		2								
<i>Haplophragmoides cf. concavus</i>																						2	4							
<i>Haplophragm. fraudulentus</i>																				1		1	2							
<i>Haplophragmoides herbichi</i>																	8	4	8	11	11	5	1							
<i>Haplophragm. perexplicatus s.l.</i>																					12									
<i>Haplophragmoides sp.1</i>																	2						1							
<i>Hormosina crassa</i>					2			1				2					1						1							
<i>Hormosina excelsa</i>						8	2			1																				
<i>Hormosina gigantea</i>										1																5	5	3		
<i>Hormosina ovuloides</i>																														
<i>Hormosina ovulum</i>																											3		9	
<i>Hyperammina subdiscreta</i>					9	7			2		1			1	3					1		2								
<i>Hyperammina-fragments</i>	1	1		2	1	1	10	7		1	2	3	11	9	9		5					8	1	2	2	10	4	2		
<i>Kalamopsis grybowskii</i>						2		1							2															
<i>Karriella conversa</i>					76	42	82	37	62	22	37	16	8	17	15	13	3	15	21	23	32	13	14							
<i>Karriella horrida</i>																										4		1		
<i>Labrospira pacifica</i>						13		1	1			1	4																	
<i>Matanzia varians</i>																														
<i>Paratrochamminoides sp.1</i>						1	1																							
<i>Paratrochamminoides sp.2</i>							1											1	1				1							
<i>Paratrochamminoides spp.</i>																														
<i>Plectrocurvodes / Recurvodes</i>					10	19	50	19	26	13	33	14	44	21	30	15	23	40	34	36	66	41	38	2		4	2	3		
<i>Pr.(?) cf. globigerinaeformis</i>					18	8		5	10	19		6			2			3	5	9	2	1								
<i>Praecyst. globigerinaeformis</i>						2																								
<i>Pseudobolivina munda</i>																		2		4	5	2	2							
<i>Reophax aff. dentaliformis</i>																		3		10	43	8	12							
<i>Reophax pilulifer</i>																														
<i>Rhabdammina sp. (quadratisch)</i>																														
<i>Rhabdammina spp.</i>																														
<i>Rhizammina indivisa</i>	2	1	50	50	10	18	8	9	16	18	8	9	8	2	1	13	15		33	5		34	3							
<i>Rzhakina epigona</i>																														
<i>Rzhakina inclusa</i>																														
<i>Saccammina placenta</i>							1																2							
<i>Saccammina placenta cf.</i>																		4	1		4									
<i>Saccammina sphaerica</i>																														
<i>Spiroplectammina dentata</i>																														
<i>Spiroplectammina cf. israelskyi</i>																														
<i>Spiroplectammina laevis</i>																														
<i>Spiroplectammina sp. (smooth)</i>																														
<i>Subreophax guttifer</i>																														
<i>Subreophax scalaris</i>						1																								
<i>Trochammina altiformis</i>						2				1	1				1															
<i>Trochammina bulloidiformis</i>																														
<i>Trochammina deformis</i>																														
<i>Trochammina gyroidinaeformis</i>						9	8	2	20		22	11	1	1	6	11	9	14	9	23	3	7	1	1			3			
<i>Trochammina spp.</i>																														
<i>Trochamminoides cf. dubius</i>																														
<i>Trochamminoides cf. proteus</i>																														
<i>Trochamminoides spp.</i>																														
<i>Uvigerinammina jankoi</i>																														
<i>Verneulinoides polystrophus</i>																														
number of species	2	6	3	13	19	16	14	17	10	13	12	11	13	15	9	9	24	20	15	25	26	15	6	4	4	9	6	7		

ZONATION

problematicum

jankoi

jankoi/s

AGE

TURONIAN

CONIACIAN

SANTONIAN

Table 3.3.

HOLE 398D	CORE	48	48	48	47	47	47	47	47	47	47	47	46	46	46	46	46	46	45	45	45	45	45							
	SECTION	2	2	1	1	5	5	4	4	3	3	2	2	1	1	4	4	3	3	2	2	1	1	6	6	5	5	4	4	
	INTERVAL (top)	110	25	102	24	90	23	99	15	88	13	87	13	91	10	94	49	112	20	104	23	104	13	94	13	60	11	90	13	
		r											r																	
Ammodiscus cretaceus													2																	
Ammodiscus planus																														
Ammosph. pseudopauiculolata																														
Arenobulimina dorbignyi		2	3			1	2					2	6	1	1	1	2	6			2	9	3		5	1?	1	12	4	
Aschemonella carpathica																														
Clavulinoides eggeri		1	1																											
Clavulinoides subparisiensis		8	1	3	2	16	22		16	5	1	13	1	7		4	8	14	10	9	32	4	7	11	6	10	37	70	8	
Dorothia crassa		3	5	4	9	2	3		1				1				2	5	14	2	7	5	5	5	5	4	4	10	6	
Dorothia oxycona											1																		1?	
Dorothia sp. 398			7	1	2	3	1							3	2	1	5													
Dorothia sp. 41																														
Gaudryina pyramidata		1	8	17	33	19	5		15	7	11	8	2	16	15	10	4	2				1					1	18	11	
Gaudryina sp.398																														
Glomospira charoides		5	2	4	11	1			1	1	9			2			2		1		2			6		4	1	6	3	
Glomospira gordialis			1		1																		1							
Glomospira irregularis																														
Glomospira serpens																														
Glomospirella gaultina																														
Goesella rugosa			1		9				11	1		3	2	8			6	1	2	1	2			9	1	2	2			
Bulbobaculites problematicus																														
Haplophragmoides aff. bulloides																														
Haplophragmoides cf. concavus																														
Haplophragm. fraudulentus																														
Haplophragmoides herbichi																														
Haplophragm. perexplicatus s.l.																													1	
Haplophragmoides sp.1																														
Hormosina crassa												3																		
Hormosina excelsa																														
Hormosina gigantea		9	5	16	3	1																						3		
Hormosina ovuloides																														
Hormosina ovulum		6	7	5			1		1	3			1			3											1			
Hyperammina subdiscreta																														
Hyperammina-fragments		1														1	1													
Kalamopsis grzybowskii																														
Karriella conversa																														
Karriella horrida																														
Labrospira pacifica																														
Matanzia varians																2		2					1							
Paratrochamminoides sp.1																														
Paratrochamminoides sp.2																														
Paratrochamminoides spp.																														
Plectrocurvoides / Recurvoides												3											1					3		
Pr.(?) cf. globigerinaeformis																														
Praecyst. globigerinaeformis																														
Pseudobulimina munda																														
Reophax aff. dentaliniformis																														
Reophax pilulifer																														
Rhabdammina sp. (quadratisch)																														
Rhabdammina spp.																														
Rhizammina indivisa				2	5				3	10			1			26											14	41	25	
Rzehakina epigona																														
Rzehakina inclusa																														
Saccammina placenta																														
Saccammina placenta cf.																														
Saccammina sphaerica																														
Spiroplectammina dentata		8	14	7	46	38	9		12	11	5	2		10	6	9	14	9	14	15	4	4	9	21	11	3	1	4	2	
Spiroplectammina cf. israelkyi																														
Spiroplectammina laevis																1		4	9		11		8	9	1	1	4		1	
Spiroplectammina sp. (smooth)			3		1	5			2	1	1		1	2		2		4	3				8		3	1	5	5		
Subreophax guttifer																														
Subreophax scalaris																								1						
Trochammina altiformis																														
Trochammina bulloidiformis																														
Trochammina deformis																														
Trochammina gyroidinaeformis																														
Trochammina spp.																														
Trochamminoides cf. dubius																														
Trochamminoides cf. proteus																														
Trochamminoides spp.																														
Uvigerinammina jankoi																														
Verneulinoides polystrophus																														
number of species		10	12	10	10	10	7	0	9	6	10	7	5	9	5	6	12	9	6	10	7	7	7	4	11	5	7	11	10	10

ZONATION

gigantea acme

gigantea

AGE

CAMPANIAN

Table 3.4.

HOLE 398D																								CORE SECTION INTERVAL (top)				
45	45	45	45	45	44	44	44	44	44	44	43	43	43	43	43	42	42	42	42	41	41	41	41	number of species				
3	3	2	2	1	1	6	5	4	3	2	1	5	5	4	3	2	1	1	7	6	6	5	5					
91	10	91	12	93	10	85	86	93	29	99	94	107	32	94	91	89	90	4	15	126	26	6	97	12	130	20	48	
1																								Ammodiscus cretaceus				
2																								Ammodiscus planus				
5	8	2	9	2	1	10	13		5	8	17		4	4	3	1		1		1			2		1	1	Ammosph. pseudopauclouclata	
1 1 3																								Arenobulimina dorbignyi				
3 2 27 14 14 8 6 76 63 3 1 1																								Aschemonella carpathica				
4	3		5	9	9	8	6	6	5	10	2	3	1		5	4	6	3	1	1		3		3	4	4	Clavulinoides eggeri	
2																								Clavulinoides subparisiensis				
5 20 5																								Dorothia crassa				
12 6																								Dorothia oxycona				
3																								Dorothia sp. 398				
1																								Dorothia sp. 41				
10	2	7	11	9	3		2	14	40	43	35	36	17	9	11	15	43	15	5	10	22	6	2	10	5	11	Gaudryina pyramidata	
3 2 1 1 3																								Gaudryina sp.398				
1 5 11 8 1 2 2 3 1 1 1 1																								Glomospira charoides				
1																								Glomospira gordialis				
1																								Glomospira irregularis				
1 2 1																								Glomospira serpens				
1																								Glomospirella gaultiana				
2		3	1	1	2	8	3	11	2	8	5	5	3	5		1	8	8	6	2	3	1	3	1	4	6	Goesella rugosa	
9 20 30																								Bulbocaulites problematicus				
5																								Haplophragmoides aff. bulloides				
4 1 1 5 2 11 10 5 2 3 1 2 2 6 5 2 1 1																								Haplophragmoides cf. concavus				
1																												Haplophragm. fraudulentus
1																								Haplophragmoides herbichii				
1																								Haplophragm. perexplicatus s.l.				
1																								Haplophragmoides sp.1				
1																								Hormosina crassa				
1																								Hormosina excelsa				
1																								Hormosina gigantea				
1																								Hormosina ovuloides				
1																								Hormosina ovulum				
1																								Hyperammina subdiscreta				
1																								Hyperammina-fragments				
1																								Kalamopsis grzybowskii				
1																								Karrieriella conversa				
1																								Karrieriella horrida				
1																								Labrospira pacifica				
2 4 2 3 8 3 6 1 1																								Matanzia varians				
1																								Paratrochamminoides sp.1				
1																								Paratrochamminoides sp.2				
1																								Paratrochamminoides spp.				
1																								Plectrocurvoides / Recurvoides				
1																								Pr.(?) cf. globigerinaeformis				
1																								Praecyst. globigerinaeformis				
1																								Pseudobolivina munda				
1																								Reophax aff. dentaliniformis				
1																								Reophax pilulifer				
3																								Rhabdammina sp. (quadratisch)				
44	7	3	35	60	13	21		3	9	5	29	29	9	6	5	15	12	4	2					3	3	28	Rhabdammina spp.	
1																								Rhizammina indivisa				
1																								Rzehakina epigona				
1																								Rzehakina inclusa				
1																								Saccammina placenta				
1																								Saccammina placenta cf.				
10	5	12	8	8	12	17	20	7	2	33	48	27	30	24	6	23	36	33	12	6	8	24	11	5	8	9	8	Saccammina sphaerica
1																								Spiroplectammina dentata				
1																								Spiroplectammina cf. israelskyi				
2	2	8	4	1	4	4		7	6	5				1		5												Spiroplectammina laevis
3	8	4	6	7	8	8	10	10	1		7	3	2	1	1		7	6	6		14						16	Spiroplectammina sp. (smooth)
1																								Subreophax guttifer				
1																								Subreophax scalaris				
1																								Trochammina altiformis				
1																								Trochammina bulloidiformis				
1																								Trochammina deformis				
1																								Trochammina gyroidinaeformis				
1																								Trochammina spp.				
1																								Trochamminoides cf. dubius				
1																								Trochamminoides cf. proteus				
1																								Trochamminoides spp.				
1																								Uvigerinammina jankoi				
1																								Verneulinoides polystrophus				
8	9	9	10	11	10	10	10	9	12	9	15	14	14	10	12	9	10	14	14	11	8	8	4	7	8	10	16	ZONATION
varians												acme												AGE				
MAASTRICHTIAN																												

lation models suggest formation of warm saline Cretaceous deep water masses in the broad shelf seas of the Tethys ocean or from cooler sources in the North Pacific depending on climatic conditions (Kruijs & Barron, 1990). The resulting fundamental differences in warm saline oxygen-depleted and cooler well-oxygenated deep water masses must have had significant influence on the composition and diversity of the deep sea benthic biota.

Benthic foraminifera are arguably the most important group recording environmental changes in the deep sea due to their high fossilization potential. Additionally, they are the only amoeboid protozoans classified solely on the basis of the morphology of their hard parts. They are primary consumers and form the bulk of the benthic biomass in the deep ocean today (Shirayama, 1984; Altenbach, 1988; Gooday *et al.*, 1992; Gooday, 1994). One group of benthic foraminifera is of special interest for micropalaeontological studies in Cretaceous abyssal environments. This is the suborder Textulariina whose members build their tests from agglutinated foreign particles held in an organic or mineralized ground mass and were thus able to thrive in a carbonate-free deep-sea environment below the calcite compensation depth (CCD). A recent biogeographical survey of agglutinated foraminifera in Upper Cretaceous and Palaeocene deep sea sediments of the North Atlantic revealed more than 200 species (Kuhnt & Kaminski, 1990). Most of these species are cosmopolitan and have been also observed in abyssal environments of the Tethys and Pacific oceans (Neagu, 1970; Krashennikov, 1973, 1974; Geroch & Nowak, 1984; Wightman & Kuhnt, 1992). The Upper Cretaceous sediments at all these deep sea localities contain an unusually complete and well-preserved record of agglutinated foraminifera so that observed changes in fossil assemblage composition probably reflect the original biodiversity patterns and may be used as a tracer of changes in global deep water circulation.

In this study we consider abundance and simple species diversity counts of late Cretaceous (92–64Ma) deep-sea agglutinated foraminifera from DSDP and ODP sites in the Atlantic and Pacific oceans and from outcrop sections in the western Mediterranean (Moullade *et al.*, 1988; Kuhnt &

Kaminski, 1990; Wightman & Kuhnt, 1992). Variations in abundance and species diversity in the different basins are correlated using magnetostratigraphy and biostratigraphic zonations. We compare the resulting time-calibrated diversity curves to sedimentary expressions of palaeoceanographic events such as organic-rich, biosiliceous intervals, and changing redox conditions within pelagic sediments.

Material and Methods

For the DSDP/ODP-material, samples of standard 20cc size were dried, weighed, and wet-sieved through a 63 μ m screen. Very consolidated samples were first boiled in water with a small amount of Calgon to help break them up before sieving. In all cases the complete residue was picked for benthic foraminifera. Data are recorded in numbers of individuals per sample.

Even in the absence of planktonic bio-markers, the biochronological resolution based on benthic foraminifera was sufficiently precise to allow us to compare diversity curves. We used the agglutinated foraminiferal zonation of Geroch & Nowak (1984), which has been adapted to DSDP/ODP material by Moullade *et al.* (1988) & Kuhnt (1992).

For the diversity plots we took into account exclusively agglutinated foraminifera, to avoid bias by the fluctuating CCD in the late Cretaceous ocean. We used a simple measure of diversity because the volume of sample analysed, as well as sedimentation rates in the abyssal red clays are fairly constant. The observed faunal density and diversity patterns are intercorrelated in most cases since the Ocean Drilling Project does not allow to increase the sample size in cases of poor faunal recovery. However, the species composition in low diversity samples is in virtually all cases restricted to a taxonomically consistent group of ammodiscids and astrorhizids, and even if we combine a large number of low-diversity samples we do not significantly increase the number of species.

Results

Census counts of deep water agglutinated foraminifera are presented for DSDP Site 385, 386, and 398D

NORTH ATLANTIC

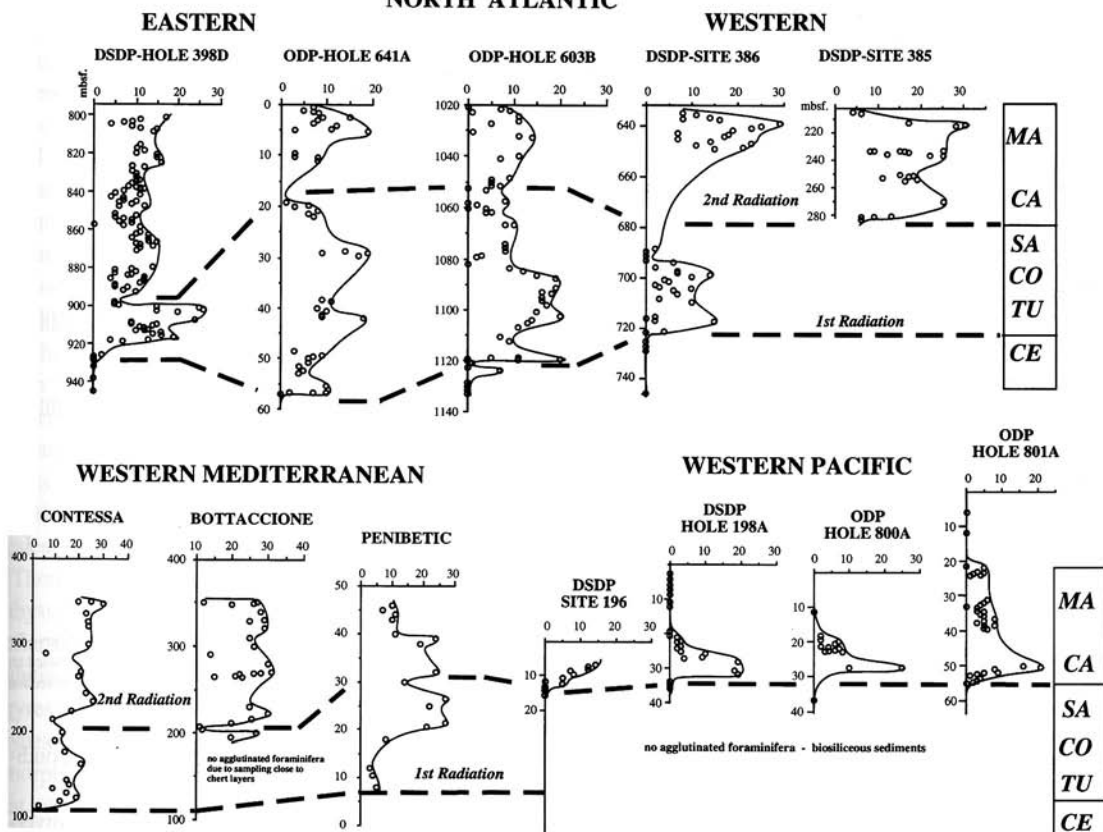


Fig. 1. Diversity of Late Cretaceous abyssal agglutinated foraminifers. Horizontal scale: number of species per sample; vertical scale: meters below surface / sediment thickness in meters; CE=Cenomanian, TU=Turonian, CO=Coniacian, SA=Santonian, CA=Campanian, MA=Maastrichtian. Dashed lines indicate the onset of foraminiferal radiations after the Cenomanian/Turonian and Santonian/Campanian paleoceanographic events.

(Tables 1-3). These data are complemented by published distribution charts compiled from Kuhn (1990) for the western Mediterranean Scaglia facies, from Moullade *et al.* (1988) for DSDP Hole 603B and ODP Hole 641A and from Wightman & Kuhnt (1992) for the Western Pacific. From the resulting diversity curves of deep water agglutinated foraminifera (Fig. 1), we deduce the following general trends:

Cenomanian assemblages of deep-water agglutinated foraminifera generally show low diversity (about 15 species) including many long-ranging, ubiquitous forms such as many species of the genera *Ammodiscus*, *Glomospira*, *Glomospirella*, *Saccamina*, *Recurvoides*, *Hyperammina*, *Rhizammina* and *Hippocrepina*. The latest Cenomanian deep-sea

environments of the North Atlantic were characterized by strongly oxygen-depleted, or even anoxic, bottom water conditions, resulting in a distinct layer of black, laminated, biosiliceous, organic-rich claystones (De Graciansky *et al.*, 1982; Herbin *et al.*, 1986; Schlanger *et al.*, 1987). This anoxic interval is generally devoid of benthic fossils and coincides with extinctions in the marine microbiota (Hart & Leary, 1991) including several species of deep water agglutinated foraminifera such as *Hippocrepina depressa*, *Pseudobolivina variabilis*, *Plectrocurvoides irregularis*, *Haplophragmoides falcatosuturalis*, *Recurvoides nonioninoides*, *R. imperfectus*.

Above this barren interval, sample diversity increased throughout the Turonian to reach a first

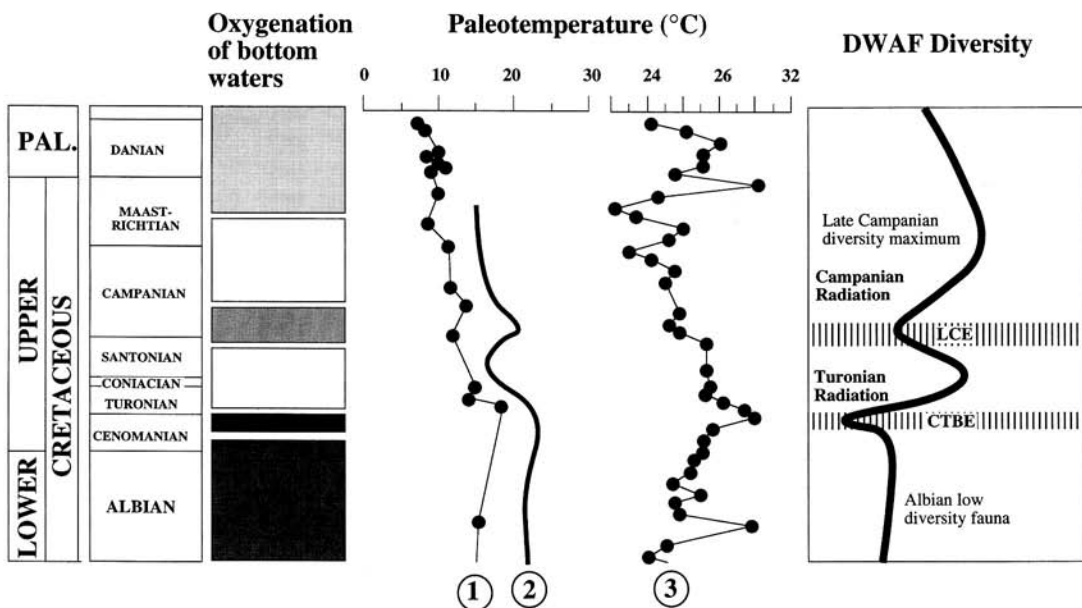


Fig. 2. Cretaceous palaeoceanography and diversity of deep water agglutinated foraminifera (DWF). 1= isotopic bottom water temperature curve for the equatorial Pacific based on benthic foraminifers (Spicer & Corfield, 1992), 2= isotopic temperate surface water temperature trend-curve based on oxygen isotopic compositions of inoceramids and belemnites (Arthur *et al.*, 1985), 3= isotopic surface water temperature curve for the Gubbio section (Italy) based on bulk planktonic calcareous microfossils (Spicer & Corfield, 1992).

maximum in the Coniacian/Santonian. Many of the taxa characterizing Turonian to Santonian assemblages (i.e. *Uvigerinammina jankoi* and several species of the genera *Haplophragmoides*, *Karrerulina*, and *Paratrochamminoides*) are not known from Lower Cretaceous or Cenomanian deep sea sediments. They must have evolved in a rapid radiation after Oceanic Anoxic Event (OAE) 2 or migrated into the deep-sea basin from shallow-water areas or marginal troughs (Kuhnt, 1992). The typical abyssal fauna of smooth-walled small *Haplophragmoides*, *Praecystamina*, and *Glomospira* first described by Krashenninikov (1974) from the Indian Ocean may have evolved *in situ* after the OAE 2.

Diversity again decreased near the Santonian/Campanian boundary at many sites, coeval with a change in the depositional environment from well oxygenated brownish-reddish deep-sea claystones to greenish, radiolarian-rich sediments (Empson-Morin, 1984; Moullade *et al.*, 1988; Kuhnt *et al.*, 1989). This event has been termed OAE 3 (Jenkyns, 1980; Arthur *et al.*, 1985), al-

though there is no evidence of truly anoxic conditions in the deep sea.

After the earliest Campanian period of low-diversity assemblages, a second agglutinated foraminiferal radiation occurred in the early-middle Campanian, leading to diversity maxima in the late Campanian and early Maastrichtian. New species occur within the genera *Hormosina*, *Paratrochamminoides*, *Haplophragmoides*, *Rzehakina*, and *Bolivinopsis*. At this time, many of the future "Palaeogene Flysch-Type" taxa first appear in the deep sea record.

The late Maastrichtian is characterized by a progressive decline of abyssal agglutinated foraminiferal assemblages in both the North Atlantic and Western Pacific oceans, whereas abundance and diversity remained stable in the Western Mediterranean.

DISCUSSION

Published oxygen isotope data from Upper Cretaceous pelagic sediments (Fig.2) show a general

cooling trend, beginning in the early Turonian and ending in the earliest Palaeocene (Spicer & Corfield, 1992). Since the early Turonian the predominating sedimentation of deep sea red claystones indicates oligotrophic conditions and well-oxygenated deep-water masses in the world ocean. A fundamental change in the mode of deep water formation from warm, saline tropical sources to cool polar sources after the Cenomanian/Turonian boundary (Herbert & Sarmiento, 1991), coincides with these climatic and sedimentary events.

The change in deep water circulation coincides with the variation of abundance and diversity we observed in deep water agglutinated foraminifera. Changes in the mode of intermediate and deep water mass formation have already been suggested as the driving force for faunal turnovers in Palaeogene calcareous deep water benthic foraminifera (Thomas, 1990) and Ostracoda (Benson, 1990). The abyssal agglutinated foraminiferal fauna observed after the Turonian radiation resembles modern agglutinated faunas of oligotrophic central oceanic gyres (Gooday, 1994) in its composition of morphotypes and related habitat preferences. In particular, morphotypes which characterize the infaunal habitat of the Recent ocean (Gooday, 1990) such as *Karrerulina*, *Haplophragmoides*, *Cystamina* and *Buzasina* occur for the first time in large abundance in abyssal assemblages. Interestingly these forms occur in greater abundance in highly diversified assemblages, whereas the abundance of epifaunal morphotypes such as ammodiscids and tubular astrophorididae shows no correlation to the diversity of the total assemblage (Fig. 3). This difference may be linked to different adaptive strategy to changing selection pressure. Within the oxygen depleted environment during and immediately after the palaeoceanographic events the infaunal niche is either not occupied or colonized by opportunists, which can cope with low oxygen levels in the pore waters. During the Turonian, when oxygenation levels increase and the redox line within the sediment is lowered, the infaunal niche becomes available for specialized K-selected forms. This general trend towards the predominance of K-selected species in the late Cretaceous was only interrupted by a short interval in the earliest Campanian, when there was

a temporary return to low-diversity r-selected assemblages (Kuhnt *et al.*, 1989).

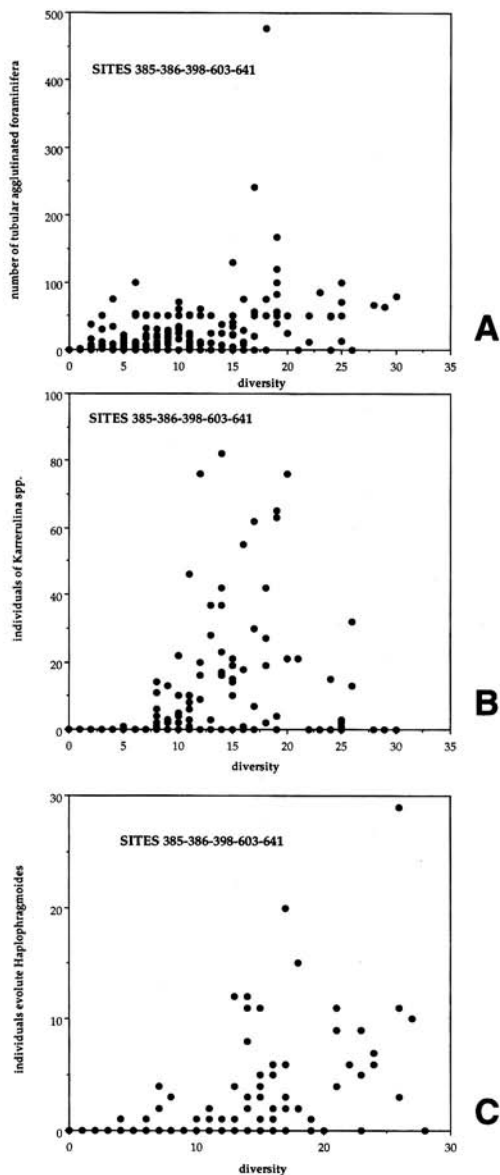


Fig. 3. Abundance of epifaunal ubiquitous species such as tubular forms (A) and infaunal specialists such as *Karrerulina* (B) and *Haplophragmoides* (C) compared to total species diversity.

CONCLUSION

The observed abundance and diversity changes of abyssal agglutinated foraminifera in the late Cretaceous may have been caused by the following succession of events:

(1) widespread oxygen depletion in the deep ocean led to a dramatic reduction of abyssal foraminiferal populations;

(2) when the circulation system changed back to "normal", oxygen-rich deep-water masses, recolonization of the abyssal ocean occurred from marginal seas and the small and isolated surviving relict populations of deep-sea foraminifera may have enabled *in situ* speciation to occur;

(3) with the establishment of stable oligotrophic environmental conditions, the intensity of speciation decreased with the advent of geographically widespread populations and as the advantage of K-selected forms increased.

Overall species diversity is inversely related to the general trend of deep water paleotemperatures and reflects a general trend towards formation of cooler oxic deep water masses beginning in the early Turonian. Deep water agglutinated foraminifera therefore responded to and reflect first-order patterns of global deep water circulation, especially during periods of the ocean history, when the CCD was high and calcareous benthic biota are missing in abyssal sediments.

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