

Palaeocene–Eocene deep water agglutinated foraminifera from the Numidian Flysch (Rif, Northern Morocco): their significance for the palaeoceanography of the Gibraltar gateway

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ABSTRACT - A lower bathyal to abyssal agglutinated foraminiferal fauna (over 78 taxa belonging to 31 genera) is documented from Palaeocene–Eocene deep-water sediments of the Numidian Flysch (Talaá Lakrah Unit) in Northern Morocco. The sample locality is adjacent to the Strait of Gibraltar, which comprised an oceanic 'gateway' between the Tethys Ocean and the North Atlantic during the Palaeogene. The chronostratigraphy of the section is based upon long-distance comparisons with the stratigraphic ranges of identified species in the North Atlantic region and the Polish Carpathians. Although no major evolutionary turnover among deep-water agglutinated foraminifera (DWF) is observed across the Palaeocene/Eocene boundary, a change from Palaeocene *Aschemocella*- and *Trochamminoides*-dominated assemblages to an early Eocene *Glomospira* assemblage is recognized. This *Glomospira* biofacies occurs throughout the North Atlantic and western Tethys and may indicate lowered productivity and widespread oxygenated deep-water conditions during the early Eocene greenhouse conditions. A change to an overlying *Reticulophragmium amplexens* biofacies in green claystones reflects renewed higher productivity. Taxonomic affinities and the succession of benthic foraminiferal assemblages from the Gibraltar gateway display greater affinities to Tethyan assemblages than North Atlantic assemblages. This is interpreted as faunal evidence for a late Palaeocene to early Eocene equivalent of 'Mediterranean outflow water', flowing from the western Tethys into the Atlantic. *J. Micropalaeontol.* 15(1): 1–19, April 1996.

INTRODUCTION

The Palaeocene/Eocene boundary witnessed the greatest turnover in the taxonomic composition of deep-water benthic foraminiferal faunas of any time during the last 80 million years. At this time, the last of the typically Cretaceous benthic foraminifera became extinct, and the new deep-sea faunas of the Eocene migrated down into the ocean basins from the continental margins (Berggren & Olsson, 1986). Unfortunately, few continuous oceanic Palaeocene–Eocene records with deep-water agglutinated foraminifera (DWF) are available from the North Atlantic area. In the northeastern North Atlantic, lithofacies changes associated with the Thulean volcanism and the onset of biosiliceous sedimentation render the sediments unfavourable for foraminiferal preservation, and many of the exposed sediments in passive margin settings in the Atlantic area are complicated by sequence boundaries.

One of the few land sections containing well-preserved assemblages of DWF across the Palaeocene/Eocene boundary is in the Numidian Talaá Lakrah Flysch of northern Morocco. This series comprises a succession of distal deep-sea turbiditic sediments with thick hemipelagic layers that was deposited within the oceanic gateway between the North Atlantic and the western Tethys. This section enables us to examine faunal changes in a continuous deep-sea setting below the CCD. The main objective of this study is to investigate the nature of the Palaeogene turnover in DWF in the Talaá Lakrah Flysch and assess their biostratigraphic and palaeoecological

significance in light of palaeoceanographic changes that took place in the early Palaeogene.

GEOLOGIC SETTING

The Moroccan Rif mountain chain is an area of complex geology, characterized by numerous sub-basins and troughs that were folded and overthrust during the Miocene collision of the African and Iberian plates and an intermediate Alboran microplate. Deep ocean sediments are mainly preserved in the 'flysch nappes' of the External Rif Zone, which was originally situated between the Alboran Block and the North African continental margin. Five different facial-tectonic units are distinguished (Durand-Delga, 1972; Suter, 1980; Wildi, 1983): (1) the Predorsalian Unit formed by the continental margin sediments of the Alboran microcontinent; (2) the Mauretania Flysch Unit, deposited in a deep trench adjacent to the Alboran Block; (3) the Massylian Flysch Unit, which represents the basinal sedimentation of the ocean gateway between North Africa and Alboran/Iberia. The Massylian Flysch is generally restricted to the Cretaceous; (4) the Numidian Flysch Unit, situated in a similar palaeogeographic position relative to the Massylian Flysch, but which may overlap with the Mauretania and Tellian sequences. The Numidian Flysch is comprised of uppermost Cretaceous, Palaeogene and Miocene deep water turbiditic sequences; (5) the Tellian deep water sediments deposited adjacent to the North African continental margin.

We sampled a continuous section within the lower part of the Numidian Flysch sequence in a Numidian subunit known as the Talaa Lakrah Flysch. The Talaa Lakrah Flysch Unit was first defined by Didon *et al.* (1973), based on the Miocene turbiditic sandstone unit exposed in the Strait of Gibraltar on the northern coast of Morocco approximately 18 km ENE of Tangier, near the village of Talaa Lakrah (Fig. 1). The unit consists of Campanian to Miocene deep-water sediments, and has been included in the Numidian Flysch, which is a geographically widespread unit extending from Sicily along the coast of North Africa to the Strait of Gibraltar. The Numidian Flysch represents the compressional phase of tectonics between the North African and European continents. The flysch unit is overthrust onto Cretaceous deep-water sequences that were probably based on oceanic substratum. The sediments comprising the Numidian Flysch are generally believed to be derived from the North African continent. However, a part of the detrital input to the Talaa Lakrah Unit may have been derived from the Alboran microplate.

The outcrop of the Palaeogene portion of the Talaa Lakrah Unit sampled in this study is situated above a retaining wall behind a Moroccan military outpost, immediately west of the mouth of the Lediane valley. The section is overturned, and consists of steeply dipping

turbidite sandstones and interbedded claystones. The base of the sampled section is identified by a c. 1 m thick sandstone ledge, overlain by dark bluish-grey, tectonically disturbed claystones. The sandstones in the sequence thin upwards, and the sand/shale ratio decreases. The colour of the hemipelagic claystones changes from bluish-grey at the base to reddish-brown, and then to greenish-grey at the top. The colour changes may reflect changing oxygenation of the bottom waters and sediment surface rather than sediment input, and invites comparisons to the coeval oceanic sequences of the North Atlantic.

MATERIAL AND METHODS

Fifteen large samples (Table 1) were collected from the Talaa Lakrah outcrop (Fig. 2). Samples were dried, weighed, and disaggregated by repeated boiling and drying using sodium carbonate solution. Samples were washed over a 63 μm screen. All foraminifera from the >125 μm fraction were picked and mounted onto cardboard microscope slides. In this material, the 63–125 μm fraction did not yield identifiable foraminifera.

Smear slides were made of each sample, but all samples were barren of nannofossils. The green samples were tested for palynomorphs and found to be barren.

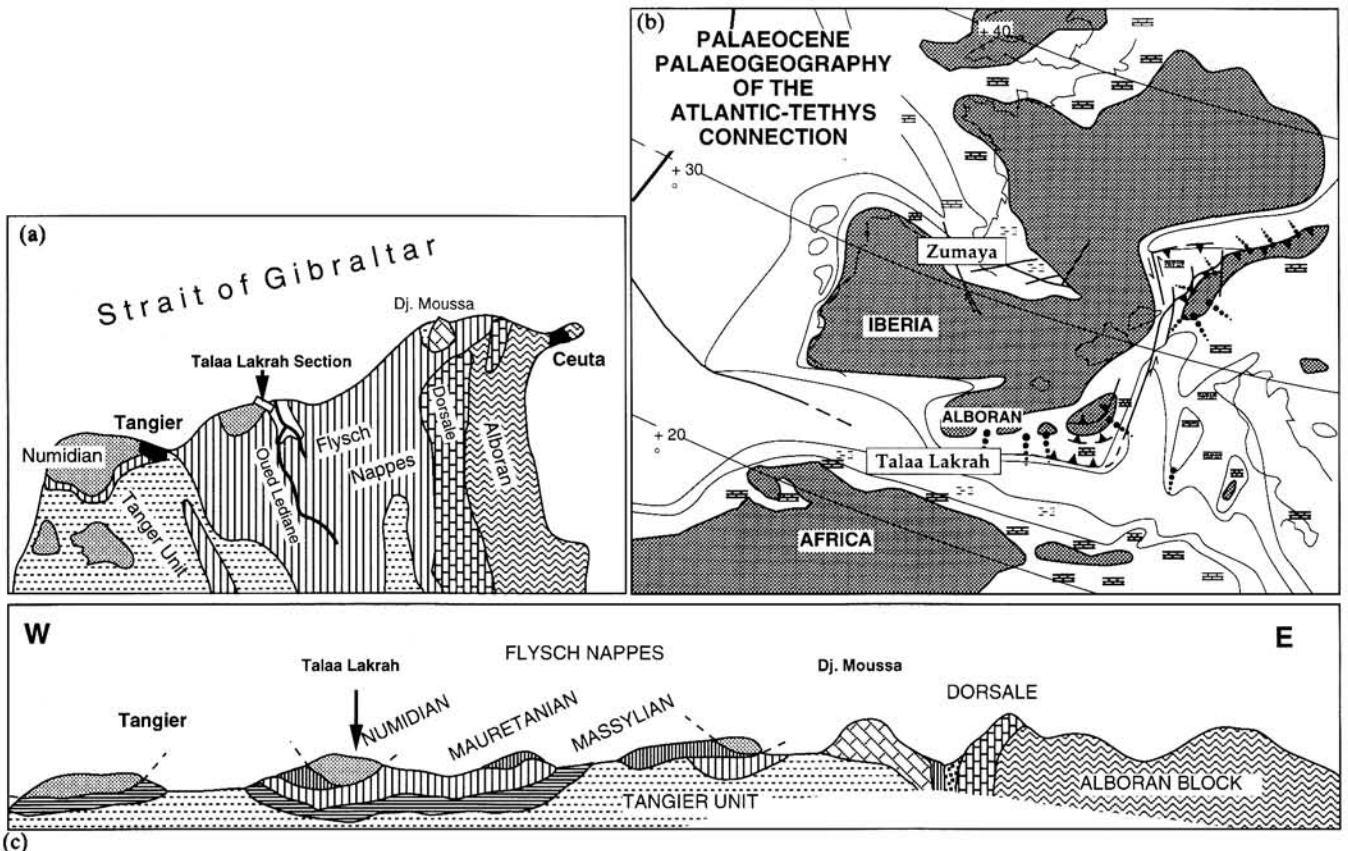


Fig. 1. (a) Simplified geological map of the Northern Rif (after Didon *et al.*, 1973 and Suter, 1980). (b) Palaeogene palaeogeography of the western Mediterranean (modified after Dercourt *et al.*, 1985) with the position of the sampled locality. (c) Simplified geological cross-section along the Moroccan side of the Strait of Gibraltar (after Didon *et al.*, 1973).

sample	colour	sediment	foraminiferal abundances (individuals/g)
JDR1	dark grey	fissile claystone	0.96
JDR2	mottled brown-grey-purple	brittle fissile claystone	0.17
JDR3	chocolate brown	fissile claystone	0.54
JDR4	chocolate brown	fissile claystone	0.8
JDR5	chocolate brown	fissile claystone	0.4
JDR6	chocolate brown	fissile claystone	0.48
JDR7	chocolate brown	hard fissile claystone	0.31
JDR8	ginger brown	fissile claystone	0.38
JDR9	ginger brown	fissile claystone	0.05
JDR10	brown-purple	highly fissile claystone	0.14
JDR11	ginger brown with green reduction spots	fissile claystone	0.07
JDR12	green	massive sandyclaystone	0.09
JDR13	green	fissile claystone	0.8
JDR14	ginger brown	friabletofissileclaystone	0.15
JDR15	green	friable green mudstone	0.3

Table 1. Lithologic description, weights, abundance of foraminifera.

BIOSTRATIGRAPHY

Because the Palaeogene autochthonous claystones were all barren of calcareous nannofossils, and palynomorphs were probably oxidized, the DWAF provide the only stratigraphic control to constrain the age of the sediments. The chronostratigraphy is necessarily based upon long-distance comparisons will the stratigraphic ranges of identified species in the North Atlantic region and the Polish Carpathians (Fig. 3).

The Palaeocene to Eocene benthic foraminiferal biostratigraphy of the North Sea region has been calibrated to the standard chronostratigraphy by the use of dinoflagellate zones (Charnock & Jones, 1990). In the Zumaya section of northern Spain, the stratigraphic ranges of DWAF are

calibrated to planktonic foraminiferal zones in the Palaeocene to lower Eocene (Fig. 3). The DWAF biostratigraphy at Site 647 in the southern Labrador Sea is calibrated by the use of standard nannofossil zones (Kaminski *et al.*, 1989), but this record only extends upward from lower Eocene Zone NP11. Although nearby DSDP Site 112 penetrated into the Palaeocene, the hole was spot-cored, and did not recover the Palaeocene/Eocene boundary (Miller *et al.*, 1982). The biostratigraphy of DWAF in Trinidad was calibrated to the standard, low-latitude planktic foraminiferal zonation by Kaminski *et al.* (1988). This biostratigraphic scheme was based upon isolated samples from Zones P1c to P8. However, the Palaeocene/Eocene boundary in Trinidad is represented by

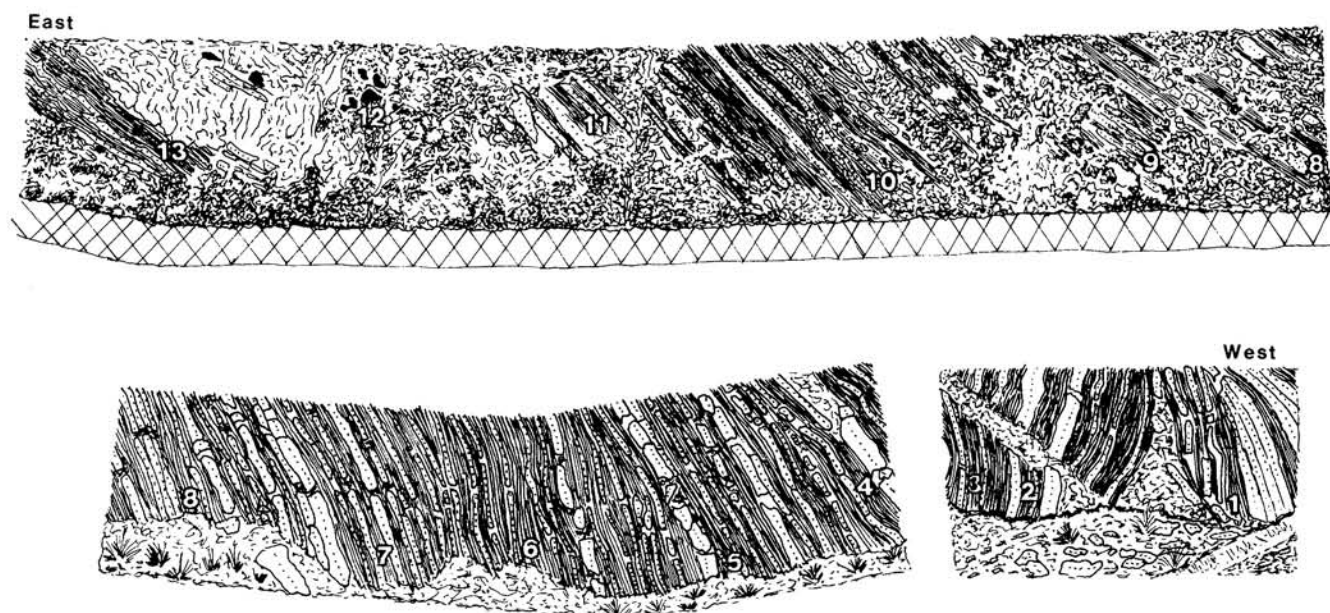


Fig. 2. View of the sampled outcrop at the beach west of the Lediane valley, redrawn from photos. Numbers 1–13 refer to collected samples.

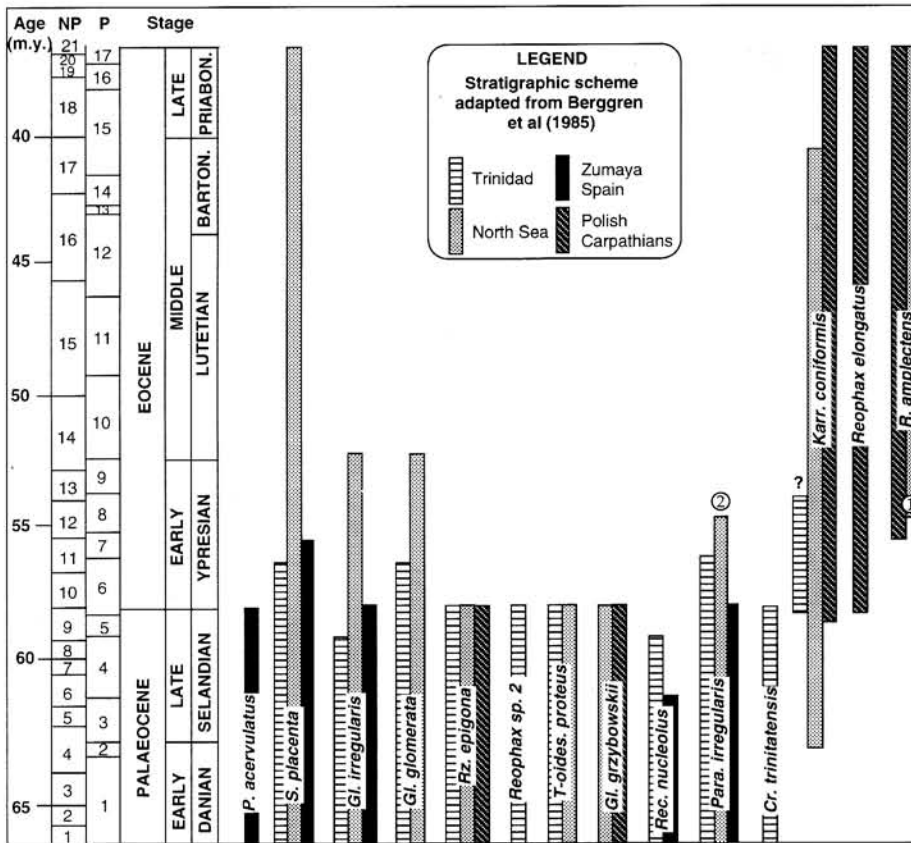


Fig. 3. Ranges of selected Palaeogene DWF species from the Polish Carpathians (Geroch & Nowak, 1984), the Basque Basin of northern Spain (Kaminski, 1988), Trinidad (Kaminski *et al.*, 1988), and the North Sea (Charnock & Jones, 1990). Calibration to planktonic zones applies only to Trinidad and Zumaya. Notes: (1) FO of *R. amplexiens* is in Zone P8 in the North Sea (M.A. Charnock, pers. comm., 1994); (2) reported as *Conglophragmium coronatum* by Charnock & Jones, 1990.

an unconformity (Bolli, 1957). In the abyssal North Atlantic, Palaeocene claystones are extremely poor in agglutinated foraminifera. Assemblages consist generally of few long-ranging forms which do not allow any biostratigraphic zonation. Near the Palaeocene/Eocene boundary there is a major change in lithology with lower Eocene sediments becoming increasingly biosiliceous. Normal deep-sea claystones with diverse agglutinated foraminiferal assemblages have been described only from the Labrador and Norwegian Seas (Kaminski *et al.*, 1990).

The Palaeogene DWF biostratigraphy for the western Tethys is based on the zonation of Geroch & Nowak (1984). This zonation is based upon composite sections from the Silesian flysch basin in Poland. Because these sediments are largely noncalcareous, direct calibration to the standard plankton zones is not possible, and benthic foraminiferal assemblages were determined based largely on their superposition. The Geroch & Nowak zonation, while providing an excellent framework for correlation in flysch sediments, is a scheme that still requires direct calibration to the geomagnetic polarity time scale.

The Palaeogene foraminiferal micropalaeontology of the Gibraltar seaway has not been formally described. The only previous micropalaeontological study from the north coast of Morocco is a preliminary note by Morgiel & Olszewska (1982). In the Talaa Lakrah section, the interval from approximately the middle Palaeocene to middle Eocene is exposed in a continuous stratigraphic succession. In contrast to the Zumaya section which is a shallowing-upward sequence across the Palaeocene/Eocene boundary, the Talaa Lakrah Flysch remains a distal turbidite depositional environment throughout the Palaeogene with a more or less continuous record of hemipelagic deposition (Fig. 4). All the hemipelagic claystones we sampled yielded well-preserved DWF.

The DWF assemblages recovered from the Talaa Lakrah samples are generally diverse and show no signs of size sorting. Rare abraded specimens of calcareous benthic foraminifera in Samples 2, 5, 14, and 15 are considered to be redeposited from a shallow bathymetric setting. We recognized a total of 78 species and taxonomic groups in our samples (Table 2), but because a number of our counting

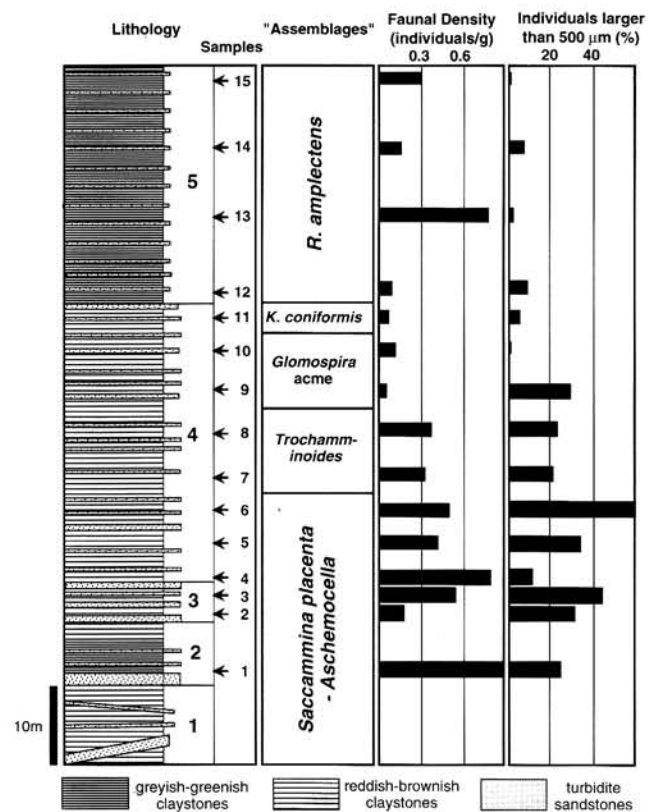


Fig. 4. Simplified lithologic section of the Palaeocene–Eocene of the Talaa Lakrah section with the stratigraphic extent of the observed benthic foraminiferal biofacies, and important assemblage parameters.

groups include more than one species, our estimates of the faunal diversity must be regarded as a lower limit. Changes in relative percentages of selected species and morphogroups are compiled in Fig. 5.

We discriminate five assemblages within the sampled interval based on the total ranges and relative abundances (Fig. 5) of characteristic species and taxonomic groups:

1. *Aschemocella*–*Saccamina placenta* assemblage

Samples at the base of the studied section (samples 1–6) are characterized by common occurrence of *Aschemocella* spp. and *Saccamina placenta*. The abundance of the former taxon reaches 30% in sample 6. Other common forms include species of *Rhabdammina* and *Paratrochamminoides*. In the modern deep ocean, tubular taxa are common in turbulent settings affected by deep currents (Kaminski, 1985). The species *A. carpathica* was first described from the upper surfaces of turbidite mudstones in the Romanian Flysch Carpathians (Neagu, 1964). Late Cretaceous *Aschemocella*-dominated assemblages occur mainly in areas with large amounts of fine-grained detrital supply provided by mud-turbidites. High abundances of *Aschemocella* may reflect high amounts of organic detritus from terrigenous sources, which provide nutrients for these large taxa.

2. *Trochamminoides*/*Paratrochamminoides*–*Recurvoides* assemblage

Samples 7–8 are dominated by the *Paratrochamminoides* and *Recurvoides* groups. Ammodiscids are also significant, but less dominant than in samples 9–14 (see below). The assemblage consists of numerous individuals and species, many of which are yet undescribed. The abundance of diverse *Paratrochamminoides* in the lower half of the studied section invites comparison to the Upper Cretaceous red clay environments of abyssal turbidite basins (= Flysch-type, high diversity, *Paratrochamminoides*-faunas of Kuhnt & Kaminski, 1989). These Late Cretaceous *Paratrochamminoides* assemblages probably characterized more oligotrophic environments. The Maastrichtian part of the Talaa Lakrah section also contains numerous *Paratrochamminoides* (Kuhnt & Kaminski, 1989). Although much of the Palaeocene to lower Eocene part of the Talaa Lakrah section does consist of reddish-brown sediments, there is a significant influence of detrital material.

The taxonomic composition and stratigraphic position of this assemblage is reminiscent of the 'Trochamminoideschichten' of Majzon (1943) from the Carpathian flysch. Morgiel & Olszewska (1981) recognized an acme of *Trochamminoides* spp. (inc. *Paratrochamminoides* s.s.) in the Palaeocene of the Polish Carpathians. However, Morgiel & Szymakowska (1978) correlated this acme to the lowermost Eocene. Reddish claystones containing common flattened *Paratrochamminoides* are also known from the lower Eocene *Subbotina patagonica* Zone (= Zones P7–P8) of the North Sea.

3. *Glomospira*–*Ammodiscus* assemblage

Samples 9 and 10 contain more than 60% ammodiscids (*Glomospira*, *Ammodiscus*, and *Glomospirella*). This assemblage correlates with *Glomospira*-dominated assemblages observed in other parts of the Atlantic (Kaminski *et al.*, 1989) and western Tethys (Winkler, 1984). The interval is characterized by numerous small specimens of *Glomospira* spp. and *Ammodiscus tenuissimus*. A distinctive taxon in this interval is an undescribed species of *Glomospira* that has very irregular coiling. Our species *Glomospira* sp. 5 is a form that is probably new, and appears to be related to the Palaeogene species *Ammodiscus pennyi*.

The faunal abundance and the average size of specimens in this interval diminishes upsection, attaining minimum values in samples 10 and 11 (Fig. 4). This agrees with trends in calcareous benthic assemblages in the lower Eocene of the North Atlantic, which are reported to be depauperate (Berggren & Olsson, 1986).

4. *Karrerulina conformis* assemblage

The first occurrence of *K. conformis* is observed in sample 11, which also contains the maximum abundance of the genus (Fig. 5). In Trinidad the first occurrence (FO) of this species was observed in the lower Eocene (Zone P6b), at Site 647 its FO was observed within Zone NP11, below the *Glomospira* horizon. The stratigraphic distribution of *Karrerulina* species may be controlled by palaeoceanog-

sample	JDR1	JDR2	JDR3	JDR4	JDR5	JDR6	JDR7	JDR8	JDR9	JDR10	JDR11	JDR12	JDR13	JDR14	JDR15
Bathysiphon sp.		2													
Rhabdammina cylindrica	11		1		3						1	1	1		27
Rhabdammina annulata													2		
Rhabdammina sp.	35	1	11	5	1	3	10	5		1		2	1	4	7
Rhizammina cf. indivisa	14		14	57	16	6	8	16	2	2	2		35	2	21
Rhabdammina robusta			13				9								
Rhizammina sp.	6		1			5									
Psammosphaera irregularis				4				1							
Psammosphaera sp.			1	17	1	1	1	1	1		1				2
Saccamina grzybowskii	4	2	10	14	13	3	5	3	4				12		
Saccamina placenta	5	8	4	7	3	2					2				
Saccamina sp.															
Lagenammina sp.	1														
Hyperammina rugosa											1		4	7	
Tolypammina (?) sp.		1													
Ammodiscus cretaceus	1	4	2		13	8	2	6	22		8	2	18	26	
Ammodiscus tenuissimus	14	17	17	28	28	10	18	24	14	5	4	6	37	1	13
Ammodiscus peruvianus	3	2		9	3	3	4	3	3		1	6	12	15	
Ammodiscus cf. pennyi	1					1		1					6	1	
Glomospira glomerata	1	2	9	4	5	3			1					2	
Glomospira charoides	7	9	17	6	26	5	7	13	30	56	3	6	5	15	5
Glomospira gordialis	2	1	2	17	1		2								
Glomospira serpens		3	3			6			2	1				4	
Glomospira irregularis	1				1	1	1	2					1		
Glomospira sp. 4		1		2			7								
Glomospira sp.		3	11		5		1	10							
Glomospirella biedai						2									
Glomospirella grzybowskii	1	1		2		4	3	2	1						
Glomospirella sp.	2	5			3			2			2				
Rzehakina epigona			1												
Aschemocella carpathica						29									
Aschemocella grandis	14		42	5	20	11									
Aschemocella sp.	13	1			10	27									
Kalamopsis grzybowskii				1			3								
Reophax sp.				8			1							1	
Reophax elongatus														9	
Subreophax pseudoscalaris								3							8
Subreophax scalaris	12	4	24	18	7	16	3	38				2	2	2	
Subreophax sp.	7	1		6	3	5		6	4	5	1	1	2		2
Hormosinella distans													1		
Cribrostomoides trinitatis	1														
Cribrostomoides sp.														1	
Haplophragmoides horridus				1											1
Haplophragmoides porrectus	1	1													
Haplophragmoides walteri	5	2	2		2		4	7	6		1		39		
Haplophragmoides sp.		1											3		
Lituotuba sp.		1	1		1	2						1			
Lituotuba lituliformis								1							
Paratrochamminoides acervulatus	2	3		1	4	3	3		5				1		
Paratrochamminoides draco	1				1										
Paratrochamminoides folius						1									
Paratrochamminoides gorayskii						3		5							
Paratrochamminoides cf. gorayskii	1	8		5	2			1	1						
Paratrochamminoides heteromorphus	1	1				1		1					1		
Paratrochamminoides irregularis	5	4	11	1	5		1		1						
Paratrochamminoides mitratus	9	2	5	4	1	11	8	15	3					2	
Paratrochamminoides olszewskii	1	2	4	2	3		1		2		1		1	1	
Paratrochamminoides uviformis					1	1		1							
Paratrochamminoides sp. 4			1			7	1	2	3	4					
Paratrochamminoides sp.	18	7	15	42	20	15	16	22	11	4	8	3	13	11	5
Trochamminoides dubius	16	2	1							1					
Trochamminoides proteus		1	2			1	1								
Trochamminoides septatus											1				
Trochamminoides subcoronatus		6			7	5	3	3	2	2		1	4	4	
Trochamminoides variolarius			3	5	5										
Trochamminoides sp.		1				6	7	1						3	
Ammosphaeroidina sp.	4	1	2		2	2						1	20		
Recurvoides nucleolus	2		2								2		1	1	1
Recurvoides ex gr. gerochi			15	8	4	3	1	20	5	1		2			
Recurvoides cf. imperfectus													6		
Recurvoides sp. 2					1										
Recurvoides sp.	21	3			47	13	20	22		8	1	1	17	6	18
Reticulophragmium amplexens												22	1	59	144
Paratrochammina spp.	5	2		3	6	5	1	2							
Gerochammina conversa					5			2	2						
Karrerulina coniformis											4		4	1	
Karrerulina horrida								1							1
Karrerulina (?) spp.			1	1	3	2	2	2		3		1			4

Table 2. Distribution of autochthonous agglutinated foraminifera in the examined samples.

raphic factors such as organic matter flux, since modern representatives of this group live infaunally.

5. *Reticulophragmoides amplexens* assemblage

Samples 12 to 15 are characterized by the common occurrence of *R. amplexens*, which is a typical form of middle to upper Eocene sediments in the Atlantic and

western Tethys. Other characteristic forms in the uppermost part of the section are *Reophax elongatus* and *Karrerulina coniformis*. Geroch & Nowak (1984) reported the range of *Reophax elongatus* as middle to upper Eocene in the Polish Carpathians. The ranges of all of these taxa extend to the Eocene/Oligocene boundary in the North Atlantic (Kaminski *et al.*, 1989).

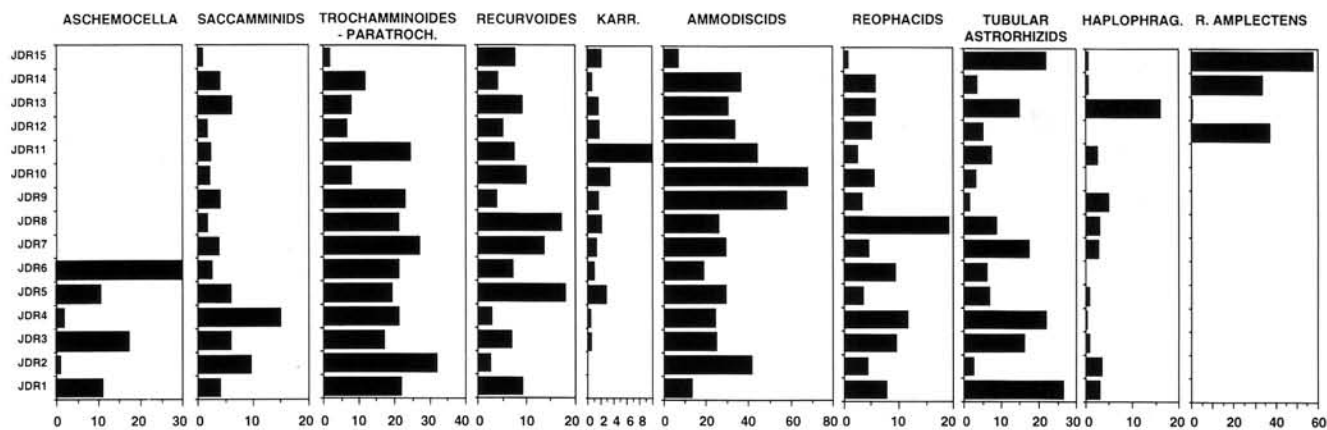


Fig. 5. Relative abundances of selected species and taxonomic groups in the Talaa Lakrah Flysch.

Reticulophragmium amplectens is believed to have evolved from an early Eocene ancestor by the acquisition of additional chambers and advancing the development of alveoles with ontogeny. Jurkiewicz (1967) had already reported that alveolar structure usually begins closer to the proloculus in specimens from younger stratigraphic horizons. Alveoles first appear between the 10th and 17th chamber in the microspheric generation of primitive individuals, and between the 5th and 13th chambers in more advanced individuals. Myatlyuk (1970) considered the smaller early Eocene morphotype of *R. amplectens* with 10 chambers in the last whorl and few alveoles to be a separate species, and named it *Cyclammina intermedia*. Although lower Eocene assemblages from the North Sea and the Carpathians undoubtedly contain the '*Cyclammina intermedia*' morphotype, this form is absent from our samples of the Numidian Flysch. In this regard, they are more similar to early Eocene specimens from Labrador, which consist of 'advanced' forms of *R. amplectens* with well-developed alveoles.

FAUNAL TURNOVER AT THE PALAEOCENE/EOCENE BOUNDARY

A major turnover of deep-water calcareous benthic foraminiferal taxa at the Palaeocene/Eocene boundary has been observed in all the world's oceans (Tjalsma, 1977; Schnitker, 1979; Tjalsma & Lohmann, 1983; Thomas & Shackleton, 1991; Pak & Miller, 1992). Utilizing benthic foraminiferal oxygen isotope records, Shackleton (1986) suggested that deep oceanic waters had a temperature of approximately 10°C in the earliest Palaeocene, increasing to 12°C in the early Eocene and then decreasing again. Miller *et al.* (1987a) suggested that the world ocean was ice-free throughout most of the Palaeocene and Eocene. Their oxygen isotope studies on calcareous benthic foraminifera also indicate rapid warming of sea water from mid-Palaeocene to early Eocene times, followed by a step-wise deterioration culminating in the late Eocene glaciations. Superimposed on this first-order trend are fluctuations that correspond to rapid climatic change. Kennett & Stott (1991) documented a rapid *c.* 8°C warming of Antarctic surface

waters that coincided with a 4‰ drop in foraminiferal $\delta^{13}\text{C}$ and the extinction of about half of the calcareous benthic taxa. These authors suggested that deep water circulation was reduced resulting in lowered oxygenation of the deep sea. These isotopic changes have been confirmed in all the ocean basins (Stott, 1992), and show that the deep sea warmed to about 10°C. These unusually warm temperatures persisted for about 100 000 years. More importantly, the surface-to-deep foraminiferal $\delta^{13}\text{C}$ gradient decreased from about 1.7‰ in the Palaeocene to near zero at Site 690 (Stott, 1992), which suggests that marine organic productivity was severely diminished. This observation corroborates the findings of Miller *et al.* (1987b) who noted decreased sediment grain size in the Pacific, which implies weaker trade winds and consequently reduced upwelling. The Palaeocene/Eocene warming has been attributed to increased supply of CO₂, as a consequence of global tectonic activity (e.g. opening of the Norwegian–Greenland Sea) and volcanism in the North Atlantic region (Owen & Rea, 1985).

The impact of climatic changes at the Palaeocene/Eocene (P/E) boundary on DWAF is still poorly documented. While all DWAF localities studied so far display a reduction in both abundance and taxonomic diversity from the upper Palaeocene to the lower Eocene, this turnover cannot be attributed to a single environmental cause (Kaminski, 1991). The bathyal foraminiferal assemblages of Zumaya Spain and the West Greenland, Labrador, and Norwegian continental shelves occur in shallowing-upward sequences. In these areas, Palaeocene agglutinated faunas are replaced by calcareous assemblages, or barren intervals. In the North Sea and Norwegian Sea regions, the boundary is contained within volcanoclastic sediments. In the central North Atlantic the P/E boundary occurs within a lithologic change from claystones to radiolarites that are barren of foraminifera. Biostratigraphic data from the upper Maastrichtian to middle Eocene Gurnigel-Schlieren flysch of Switzerland (Winkler, 1984) reveal the last occurrences of six species of DWAF at or just below the P/E boundary. No taxa with first occurrences near the boundary were recorded. In the Polish External Carpathians (Geroch & Nowak, 1984), five species have last occurrences approximately at

the P/E boundary and two species have first occurrences just above the boundary. In the Guayaguayare and Lizard Springs Formations of Trinidad 15 species display LOs at or just below the boundary and only one incoming species occurs just above the boundary (Kaminski *et al.*, 1988). The most dramatic faunal turnover of DWAF near the P/E boundary has been observed in the North Sea. As many as 20 species display LOs immediately below the P/E boundary and 35 species have FOs just above the boundary (Charnock & Jones, 1990). However, the effects of local palaeoenvironmental change in the North Sea area have probably amplified the magnitude of the faunal change.

At Talaa Lakrah, the following taxa have last occurrences between samples 5 and 9 (broadly coincident with the P/E boundary):

Saccamina placenta
Glomospira gordialis
Glomospira grzybowskii
Glomospira sp. 4
Aschemocella carpathica
Aschemocella grandis
Kalamopsis grzybowskii
Paratrochamminoides draco
Paratrochamminoides gorayskii
Paratrochamminoides irregularis
Paratrochamminoides uviformis
Trochamminoides proteus
Trochamminoides variolarius

The only first occurrences observed in the sample 5–9 interval are *Karrerulina horrida* and *Subreophax pseudoscalaris*.

Aschemocella assemblages appear to comprise a statistically independent end-member of Late Cretaceous DWAF assemblages that are typically developed in fine-grained turbidite environments, such as the Maastrichtian flysch of the Carpathians and the lower bathyal turbidite units in the Campo de Gibraltar. In the Talaa Lakrah section, the occurrence of *Aschemocella* is restricted to samples from the Palaeocene that are associated with thick-bedded sandstones. Their disappearance across the P/E boundary may result from reduced amounts of organic detritus from terrigenous sources as well as marine organic productivity.

The majority of first and last occurrences across the P/E boundary in this section are among species that are known from the Palaeocene and Eocene at other localities. At Talaa Lakrah, these constitute local biostratigraphic events. In general, it appears that calcareous-cemented agglutinated taxa were especially prone to extinction at the Palaeocene/Eocene boundary. Therefore, the magnitude of the faunal turnover of agglutinated taxa is more pronounced at the marginal North Atlantic sites and is less important in the Tethyan sites below the CCD.

EARLY–MIDDLE EOCENE GLOMOSPIRA EVENT

Assemblages with common *Ammodiscus* and *Glomospira* have been found in the lower Eocene of the Alpine–Carpathian region (Jurkiewicz, 1967; Morgiel & Szymakowska, 1978; Morgiel & Olszewska, 1981, 1982) and the Moroccan flysch (Morgiel & Olszewska, 1982). Winkler

(1984) discovered a level with common *Glomospira* in the lower part of Zone NP10–NP12 (undifferentiated) in the Schlieren flysch of the Alpine Flysch Zone of Switzerland. In the southern Labrador Sea, *Glomospira* spp. range throughout the Eocene and basal Oligocene at Site 647, but display a distinct acme in Zones NP13–NP15 (Kaminski *et al.*, 1989). Characteristic species of this assemblage consist of *Glomospira irregularis*, *Glomospira charoides*, *Ammodiscus cretaceus*, *Karrerulina coniformis*, *Trochamminoides* spp. and *Haplophragmoides walteri*. At Site 643 in the Norwegian Sea the total range of *Glomospira* spp. is confined to the lower Eocene (Kaminski *et al.*, 1990). The so-called ‘*Glomospira* Event’ is consequently of biostratigraphic use in the North Atlantic and western Tethys, bearing in mind the observation that it may be diachronous from east to west. In the Tellien Units in northern Morocco, we also observed a lower Eocene biosiliceous lithofacies which may correlate with the *Glomospira* Event in the Numidian Flysch. Immediately above these biosiliceous sediments are claystones with *Reticulophragmoides amplexens*.

Kuhnt & Kaminski (1989) noted increased abundances of ammodiscids, especially the genus *Glomospirella*, in lower Campanian green claystones reflecting poorly oxygenated benthic conditions in the North Atlantic. This distinct assemblage, termed ‘Biofacies B’, was subsequently found at different Cretaceous horizons at other deep sea localities such as in the Barremian at ODP Site 765 on the Argo Abyssal Plain (Kaminski *et al.*, 1991). In the lower-middle Eocene at ODP Site 647, an interval with abundant *Glomospira* is characterized by an increase in deposition of biogenic silica (Bohrmann & Stein, 1989) and organic carbon (Kaminski *et al.*, 1989), which is consistent with a scenario of increased biogenic productivity. Some modern species of *Glomospira* appear to be environmentally tolerant, and thrive in environments where oxygen and salinity levels are low. They have the ability to survive on organic-rich substrates, such as in an area of active petroleum seepage in the Gulf of Mexico. Alve (1990) recognized an *Ammodiscus*? [= *Glomospirella*] *gullmarenensis* assemblage in temperate water masses in Drammensfjord, southeast Norway, characterized by reduced salinity and very low dissolved oxygen content. Kaminski *et al.* (1989) speculated that *Glomospira* feed epifaunally on organic detritus, and was consequently well-adapted to areas of high productivity.

However, other aspects of the DWAF assemblages in the Talaa Lakrah section question the validity of this model for the lower Eocene reddish claystones. Both the abundance and relative size of DWAF decline steadily from the Palaeocene, reaching minimum values in the *Glomospira* acme (Fig. 4). The environmental significance of size and abundance trends in deep-sea benthic foraminifera has been examined by Pederson *et al.* (1988) and Herguera & Berger (1991) in their studies of modern and Pleistocene productivity in the Pacific. These studies demonstrated that both the average size of certain benthic foraminifera as well as benthic foraminiferal accumulation rates are positively correlated with the flux of organic matter to the sea floor, and can serve as good proxies for palaeoproductivity. At the

same time, the relative proportion of tubular forms reaches a minimum (Fig. 5). Because modern tubular taxa such as *Rhabdammina* and *Saccorhiza* have been found to be suspension feeders (Altenbach *et al.*, 1988; Linke & Lutze, 1993), the decline in tubes over this interval may be related to the reduction in food particles carried in suspension by bottom currents. It may simply be the case that *Glomospira* is an opportunist, inhabiting environments that have undergone rapid change, or occupying niches that have been left vacant by other species.

RETICULOPHRAGMOIDES AMPECTENS ACME

Deep-water clastic sediments containing large proportions of *Reticulophragmium ampectens* are typically referred to the middle Eocene in the Polish Carpathians. In Poland, its first occurrence was reported in the lower Eocene (Zone NP12) by Olszewska & Smagowicz (1977). Its total range in the Polish Carpathians was given as lower to upper Eocene by Morgiel & Olszewska (1981), and its partial range and optimum occurrence characterizes the middle Eocene *Cyclammina ampectens* Zone of Geroch & Nowak (1984). In the Austrian Alps, *R. ampectens* was reported from the lower to lower middle Eocene Buntmergelserie (Rögl *et al.*, 1986). In the Central North Sea the *R. ampectens* acme is observed immediately above the lower/middle Eocene boundary as determined by palynological and micropalaeontological evidence, occurring in a unit of high gamma ray values (M.A. Charnock, pers. comm., 1994). At Site 647 in the southern Labrador Sea its FO occurs in the upper part of Zone NP11 (below the *Glomospira* event), and its greatest abundance occurs in the middle Eocene. However, at Talaa Lakrah its first occurrence is above the *Glomospira* event, which is consistent with its occurrence in the Carpathians.

The palaeoecology of *R. ampectens* is not well understood, however, its symmetrical shape and circular outline recalls that of the modern deep-sea species *Melonis barleeaanum*, a mobile infaunal detritivore (Corliss, 1985). Moreover, *R. ampectens* is one of the dominant taxa in the Eocene of the Labrador margin (beneath the oxygen minimum zone) but only comprises 5–10% of the assemblage at abyssal Site 647. This agrees with findings of Corliss & Chen (1988) and Corliss & Fois (1991), who observed a shift from dominant infaunal taxa in the upper-middle bathyal zone to dominant epifaunal taxa in the lower bathyal to abyssal zone. This changeover is related to the amount of food available to the infauna. If *R. ampectens* was indeed infaunal, then its dominance in the greenish claystones above the *Glomospira* event indicates a return to the more productive and/or less well oxygenated oceanographic conditions that favour significant proportions of infauna.

PALAEOENVIRONMENT AND PALAEOCEANOGRAPHY OF THE PALAEOGENE NUMIDIAN FLYSCH BASIN

The Palaeogene of the Talaa Lakrah Flysch is characterized by diverse flysch-type agglutinated foraminifera and a lack of autochthonous calcareous forms. They are interpreted as

autochthonous assemblages and can be viewed as remnants of former benthic communities that flourished beneath the CCD.

It is surprising that two otherwise common early Palaeogene species are absent entirely (*Spiroplectammina spectabilis*) or extremely rare (a single specimen of *Rzehakina epigona* in sample 3) in our material from the Talaa Lakrah Flysch. *Spiroplectammina spectabilis* and *R. epigona* are among the most common and characteristic species of DWAF in Palaeocene deep-water sediments deposited along the North African continental margin, in Trinidad, and in the Central North Sea. Both species preferably occur in dark greenish shales with enhanced content of organic carbon and may characterize environments with high organic flux rates. Consequently, the absence of these species at Talaa Lakrah might reflect low abundances of organic matter or other nutrients.

Although the assemblages consist mainly of cosmopolitan species, the relative succession of benthic foraminiferal assemblages from the Gibraltar gateway displays a greater affinity to Tethyan assemblages than to assemblages from the North Atlantic. In particular the presence of an assemblage consisting of diverse species of *Paratrochamminoides* and *Trochamminoides* overlain by a *Glomospira*-dominated assemblage provides evidence of strong links with the Carpathian Palaeocene–Eocene deposits. This gives us some insight into the nature of the deep water masses. For example, studies of carbon isotopes (Katz & Miller, 1991) have revealed that the Southern ocean was a source of deep water during the late Palaeocene and again during the early Eocene, but that the supply of deep water decreased near the Palaeocene/Eocene boundary. This interpretation is supported by the observation of a late Palaeocene erosional hiatus on the Bermuda Rise, indicating strong bottom currents flowing into the North Atlantic from the south (Mountain & Miller, 1992). Sediment deposition resumed on the Bermuda Rise during the latest Palaeocene, a result of the reduction in deep-water circulation. General ocean circulation models have suggested that the eastern Tethys was a likely zone of high evaporation and therefore a prime site for the formation of warm, saline deep water (WSDW) (Barron & Peterson, 1990). It is possible that the change in the oxidation state of the sediments at Talaa Lakrah and the loss of large specimens is a reflection of differing bottom water sources. We suggest that the appearance of lower Eocene reddish shales reflects a proximal WSDW source which was well oxygenated and nutrient depleted.

The abrupt appearance of an *R. ampectens* dominated assemblage above the *Glomospira* event horizon may have palaeoceanographic significance. At DSDP Site 401 in the Bay of Biscay, Pak & Miller (1992) noted a change from an earliest Eocene *Nuttalides truempyi* assemblage to an assemblage dominated by *Buliminella grata*, *Stilostomella gracillima* and *Bulimina semicostata* in Zone P6c. In Zones P8–P9 *Stilostomella* (an infaunal form) was dominant. This shift from epifaunal-dominated assemblages to ones dominated by infauna in the middle part of the early Eocene also points to similar changes in oxygenation and/or

palaeoproductivity. Because the Bay of Biscay is distal to any proto-Mediterranean outflow water flowing northward around Portugal as an eastern boundary current, perhaps the assemblage changes in the Gibraltar and Biscay regions are linked. Indeed, based on their comparison of stable isotopic data, Pak & Miller believed that Site 401 monitored deep water of a western Tethyan origin.

CONCLUSIONS

The diverse (>78 taxa) DWAF assemblages of the Talaa Lakrah Flysch compare well with the diverse cosmopolitan flysch-type agglutinated assemblages in the sense of Gradstein & Berggren (1981). The depositional environment of the Palaeogene Talaa Lakrah turbidites was lower bathyal or abyssal, and below the calcium carbonate compensation depth.

The taxonomic affinities and relative succession of benthic foraminiferal assemblages from the Gibraltar gateway are more Tethyan than Atlantic. In particular, diverse *Paratrochamminoides* and *Trochamminoides* and the presence of an interval of reddish claystones with *Glomospira* provide strong links with the Palaeocene–Eocene assemblages of the Carpathians. We interpret this as faunal evidence for a late Palaeocene to early Eocene equivalent of ‘Mediterranean outflow water’, with bottom water flowing from the western Tethys into the Atlantic as it does today.

Despite the now well-documented Palaeocene/Eocene boundary extinction event among calcareous benthic foraminifera, there is surprisingly little taxonomic turnover among DWAF in the Talaa Lakrah section (in terms of species extinctions and originations). However, changes in the size, abundance, and relative proportions of agglutinated foraminifera across the Palaeocene/Eocene boundary interval undoubtedly reflect environmental changes that took place in the western Tethys. Reductions in the abundance and size of DWAF from the Palaeocene to the lower Eocene indicate decreasing nutrients and/or palaeoproductivity. An early Eocene *Glomospira*-dominated biofacies can be attributed to a period of well-oxygenated, oligotrophic conditions, probably caused by reduced particulate organic matter flux. The sparse assemblages from oxygenated sediments may be linked to lowered surface water productivity during the early Eocene climatic optimum and/or warm, well-oxygenated deep water masses of possible Tethyan origin. The return to greenish-grey, biosiliceous claystones with successive *Karrerulina*-dominated and *R. amplexans*-dominated assemblages signalled the return to a more eutrophic environment.

TAXONOMIC NOTES

Because of the current need for revision of the suprageneric classification of the agglutinated foraminifera, the taxa

below are simply listed alphabetically by genus. For the sake of brevity, only primary references and revisions of primary types are cited.

Ammodiscus cretaceus (Reuss, 1845)

(Pl. 1, figs 1–2)

1845 *Operculina cretacea* Reuss: 35, pl. 13, figs 64, 65

Ammodiscus cf. *pennyi* Cushman & Jarvis, 1928

1928 *Ammodiscus pennyi* Cushman & Jarvis: 87, pl. 12, figs 4–5

Ammodiscus peruvianus Berry, 1928

(Pl. 1, fig. 3)

1928 *Ammodiscus peruvianus* Berry: 342, pl. 27

Ammodiscus tenuissimus Grzybowski, 1898

(Pl. 1, fig. 4)

1898 *Ammodiscus tenuissimus* Grzybowski: 282, pl. 10, fig. 35

Ammosphaeroidina sp.

(Pl. 2, fig. 15)

Aschemocella carpathica (Neagu, 1964)

(Pl. 2, fig. 3)

1964 *Aschemonella carpathica* Neagu: 582, text-fig. 1/5–8, 2/2–4, 3/1–3, 4/166, pl. 27, figs 1–3

Aschemocella grandis (Grzybowski, 1898)

(Pl. 2, fig. 4)

1898 *Reophax grandis* Grzybowski: 277, pl. 10, figs 13–15

1993 *Aschemocella grandis* (Grzybowski); Kaminski & Geroch: 249, pl. 2, figs 8–10

Bathysiphon sp.

Fragments of elongate cylindrical tubes, thin walled and finely agglutinated.

Cribrostomoides trinitatis Cushman & Jarvis, 1928

(Pl. 2, fig. 14)

1928 *Cribrostomoides trinitatis* Cushman & Jarvis: 21, pl. 12, figs 12a–b

Glomospira charoides (Jones & Parker, 1860)

(Pl. 1, fig. 12)

1860 *Trochammina squamata* Jones & Parker var. *charoides* Jones & Parker: 304

1990 *Glomospira charoides* (Jones & Parker); Berggren & Kaminski: 60, pl. 1, fig. 2

Glomospira glomerata (Grzybowski, 1898)

(Pl. 1, fig. 13)

1898 *Ammodiscus glomeratus* Grzybowski: 285, pl. 11, fig. 4

Glomospira gordialis (Jones & Parker, 1860)

(Pl. 1, fig. 14)

1860 *Trochammina squamata* Jones & Parker var. *gordialis* Jones & Parker, p. 304

1990 *Glomospira gordialis* (Jones & Parker); Berggren & Kaminski: pl. 1, fig. 1

Glomospira irregularis (Grzybowski, 1898)

(Pl. 1, fig. 9)

1898 *Ammodiscus irregularis* Grzybowski: 285, pl. 11, figs 2, 3

1993 *Glomospira irregularis* (Grzybowski); Kaminski & Geroch: 256, pl. 6, figs 6–8b

Explanation of Plate 1

Figs. 1–2, *Ammodiscus cretaceus* (Reuss), Sample 5. **Fig. 1:** ×69, **Fig. 2:** ×37. **Fig. 3**, *Ammodiscus peruvianus* Berry, Sample 9, ×55. **Fig. 4**, *Ammodiscus tenuissimus* Grzybowski, Sample 6, ×66. **Figs. 5–8**, *Glomospira* sp. 5, **Fig. 5:** Sample 6 ×22, **Fig. 6:** Sample 3 ×18, **Fig. 7:** Sample 1 ×13, **Fig. 8:** Sample 7 ×35. **Fig. 9**, *Glomospira irregularis* Grzybowski, Sample 2, ×125. **Figs. 10–11**, *Glomospirella biedai* Samuel, **Fig. 10:** Sample 7, ×35, **Fig. 11:** Sample 6, ×37. **Fig. 12**, *Glomospira charoides* (Jones & Parker), Sample 10, ×69. **Fig. 13**, *Glomospira glomerata* (Grzybowski), Sample 6, ×16. **Fig. 14**, *Glomospira gordialis* (Jones & Parker), Sample 9, ×69. **Fig. 15**, *Glomospira serpens* (Grzybowski), Sample 3, ×55. **Fig. 16**, *Rzehakina epigona* (Rzehak), Sample 3, ×69.

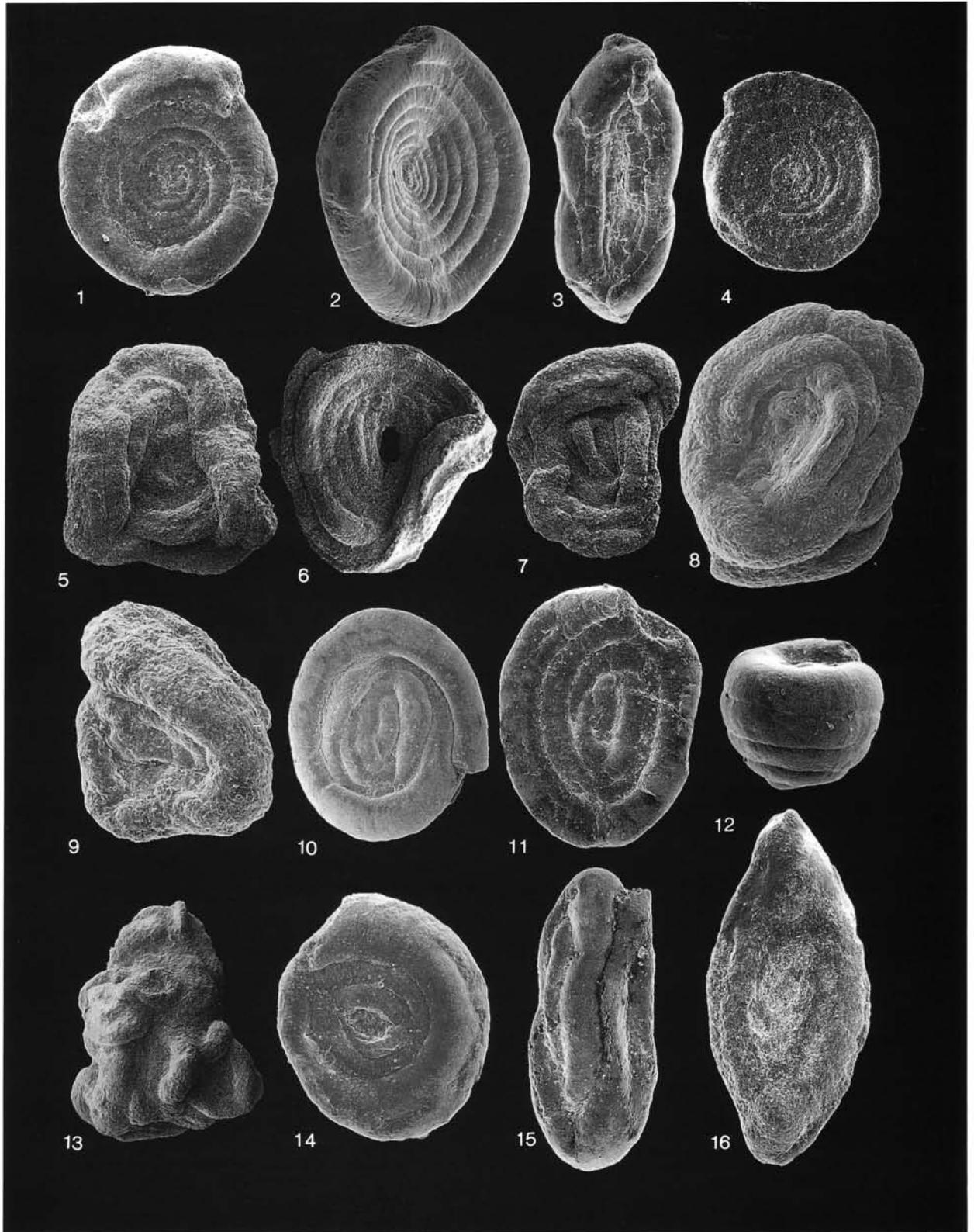


Plate 1

Glomospira serpens (Grzybowski, 1898)

(Pl. 1, fig. 15)

1898 *Ammodiscus serpens* Grzybowski: 285, pl. 10, figs 31–331993 *Glomospira serpens* (Grzybowski); Kaminski & Geroch: 256, pl. 6, figs. 2–5*Glomospira* sp. 5

(Pl. 1, figs 5–8)

Medium to large-sized test, arranged in planispiral to irregularly glomospiral coils. Test wall thick, and relatively coarsely agglutinated. Although the test may be large, the chamber increases in diameter slowly and does not become more irregular with ontogeny, as in some other species of *Glomospira*. Differs from *Ammodiscus pennyi* in its irregularly glomospiral coiling. *Glomospira irregularis* differs in its more enrolled streptospiral coiling.

Glomospirella biedai Samuel, 1977

(Pl. 1, fig. 11)

1977 *Glomospirella biedai* Samuel: 29, pl. 3, fig. 16; pl. 21, fig. 3*Glomospirella grzybowskii* (Jurkiewicz, 1960)

(Pl. 1, fig. 10)

1960 *Glomospira grzybowskii* Jurkiewicz: 342, pl. 38, figs 7, 10, 11*Haplophragmoides horridus* (Grzybowski, 1901)1901 *Haplophragmium horridum* Grzybowski: 270–271, pl. 7, fig. 121993 *Haplophragmoides horridus* (Grzybowski); Kaminski & Geroch: 275, pl. 15, figs 6–8*Haplophragmoides porrectus* Maslakova, 1955

(Pl. 2, fig. 11)

1955 *Haplophragmoides porrectus* Maslakova: 47, pl. 3, figs 5–6*Haplophragmoides walteri* (Grzybowski, 1898)

(Pl. 2, fig. 10)

1898 *Trochammina walteri* Grzybowski: 290, pl. 11, fig. 31.1993 *Haplophragmoides walteri* (Grzybowski); Kaminski & Geroch: 263, pl. 10, figs 3a–7c*Hormosinella distans* (Brady, 1881)

(Pl. 2, fig. 6)

1881 *Reophax distans* Brady: 50*Hyperammina rugosa* Verdenius & Van Hinte 1983

(Pl. 1, fig. 7)

1983 *Hyperammina rugosa* Verdenius & Van Hinte: 187, pl. 1, figs 12–14*Kalamopsis grzybowskii* (Dyląganka, 1923)

(Pl. 2, fig. 11)

1923 *Hyperammina grzybowskii* Dyląganka: 65–661993 *Kalamopsis grzybowskii* (Dyląganka); Kaminski & Geroch, 281, pl. 17, figs 5a–8*Karrerulina coniformis* (Grzybowski, 1898)1898 *Gaudryina coniformis* Grzybowski: 295, pl. 12, fig. 71993 *Karrerulina coniformis* (Grzybowski); Kaminski & Geroch: 269, pl. 13, figs 1–4*Gerochammina conversa* (Grzybowski, 1901)

(Pl. 2, figs 16)

1901 *Gaudryina conversa* Grzybowski: 285, pl. 7, figs 15, 161993 *Gerochammina conversa* (Grzybowski); Kaminski & Geroch: 279, pl. 13, figs 5a–11*Karrerulina horrida* Myatlyuk, 1970

(Pl. 2, fig. 17)

1970 *Karrieriella horrida* Myatlyuk: 114–115, pl. 5, fig. 9; pl. 33, figs 15–16c*Lagenammina* sp.*Lituotuba lituiformis* (Brady, 1879)1879 *Trochammina lituiformis* Brady: 59, pl. 5, fig. 16*Paratrochammina* spp.

We place in the genus *Paratrochamminoides* all forms with irregular streptospiral, glomospiral, trochospiral, or triloculine coiling (which may uncoil in the later stage) and irregular rounded to elongate chambers. *Trochamminoides* is distinguished by its irregular planispiral coiling. The family Lituotubidae is in need of revision. Specimens classified here as *Paratrochammina* spp. are mostly badly preserved and/or fragmentary.

Paratrochamminoides acervulatus (Grzybowski, 1896)1896 *Trochammina acervulata* Grzybowski: 284, pl. 9, fig. 4 a–c1981 *Trochammina acervulata* Grzybowski; Liszka & Liszkowa: p. 176, pl. 3, fig. 1a–c

Explanation of Plate 2

Figs. 1–2, *Saccammina placenta* (Grzybowski), **Fig. 1:** Sample 9, ×59. **Fig. 2:** Sample 5, ×33. **Fig. 3, *Aschemocella carpathica*** (Neagu), Sample 3 ×9. **Fig. 4, *Aschemocella grandis*** (Grzybowski), Sample 3 ×8. **Fig. 5, *Kalamopsis grzybowskii*** (Dyląganka), Sample 4, ×35. **Fig. 6, *Hormosinella distans*** (Brady), Sample 13, ×69. **Figs. 7–8, *Reophax elongatus*** Grzybowski, Sample 13, ×35. **Fig. 9, *Subreophax scalaris*** (Grzybowski), Sample 3, ×55. **Fig. 10, *Haplophragmoides walteri*** (Grzybowski), Sample 9, ×90. **Fig. 11, *Haplophragmoides porrectus*** Maslakova, Sample 1, ×95. **Fig. 12, *Reticulophragmium amplexens*** (Grzybowski), Sample 12, ×42. **Fig. 13, *Recurvoides nucleolus*** (Grzybowski), Sample 1, ×45. **Fig. 14, *Cribrostomoides trinitatensis*** Cushman & Jarvis, Sample 1, ×25. **Fig. 15, *Ammosphaeroidina* sp.**, Sample 13, ×103. **Fig. 16, *Gerochammina conversa*** (Grzybowski), Sample 5, ×68. **Fig. 17, *Karrerulina horrida*** Myatlyuk, Sample 8, ×68.

Explanation of Plate 3

Fig. 1, *Trochamminoides dubius* (Grzybowski), Sample 1, ×50. **Fig. 2, *Trochamminoides dubius*** (Grzybowski), Sample 8, ×48. **Fig. 3, *Trochamminoides dubius*** (Grzybowski), Sample 1, ×38. **Fig. 4, *Trochamminoides dubius*** (Grzybowski), Sample 3, ×38. **Fig. 5, *Trochamminoides variolarius*** (Grzybowski), Sample 3, ×38. **Fig. 6, *Paratrochamminoides uiformis*** (Grzybowski), Sample 7, ×38. **Fig. 7, *Trochamminoides subcoronatus*** (Grzybowski), ×27. **Fig. 8, *Paratrochamminoides draco*** (Grzybowski), ×26. **Fig. 9, *Trochamminoides septatus*** (Grzybowski), Sample 11, ×74. **Fig. 10, *Paratrochamminoides* sp. 4**, Sample 4, ×20. **Fig. 11, *Paratrochamminoides* sp. 4**, Sample 5, ×18. **Fig. 12, *Trochamminoides proteus*** (Karrer), Sample 5, ×26.

Explanation of Plate 4

Figs. 1a–2, *Paratrochamminoides* sp. 5, Sample 8, **Fig. 1:** ×52, **Fig. 2:** ×36. **Figs. 3–5, *Paratrochamminoides heteromorphus*** (Grzybowski), **Fig. 3:** Sample 1, ×40; **Fig. 4:** Sample 2, ×27, **Fig. 5,** Sample 3, ×13. **Figs. 6–7, *Paratrochamminoides gorayskii*** (Grzybowski), **Fig. 6:** Sample 6, ×27, **Fig. 7:** Sample 4, ×72. **Fig. 8, *Paratrochamminoides irregularis*** (White), Sample 5, ×20. **Fig. 9, *Paratrochamminoides mitratus*** (Grzybowski), Sample 8, ×20. **Fig. 10, *Paratrochamminoides olszewskii*** (Grzybowski), Sample 7, ×38.

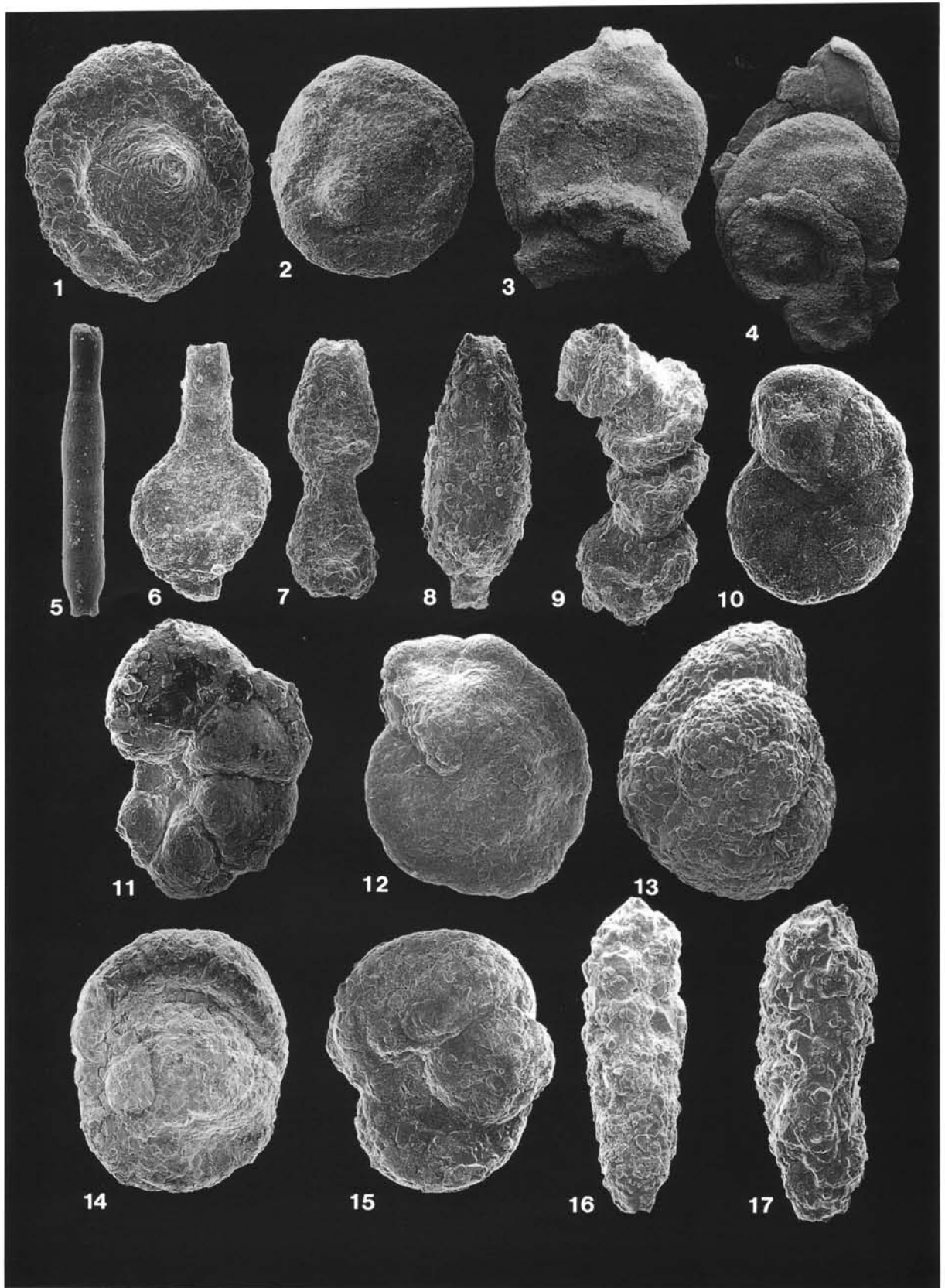


Plate 2

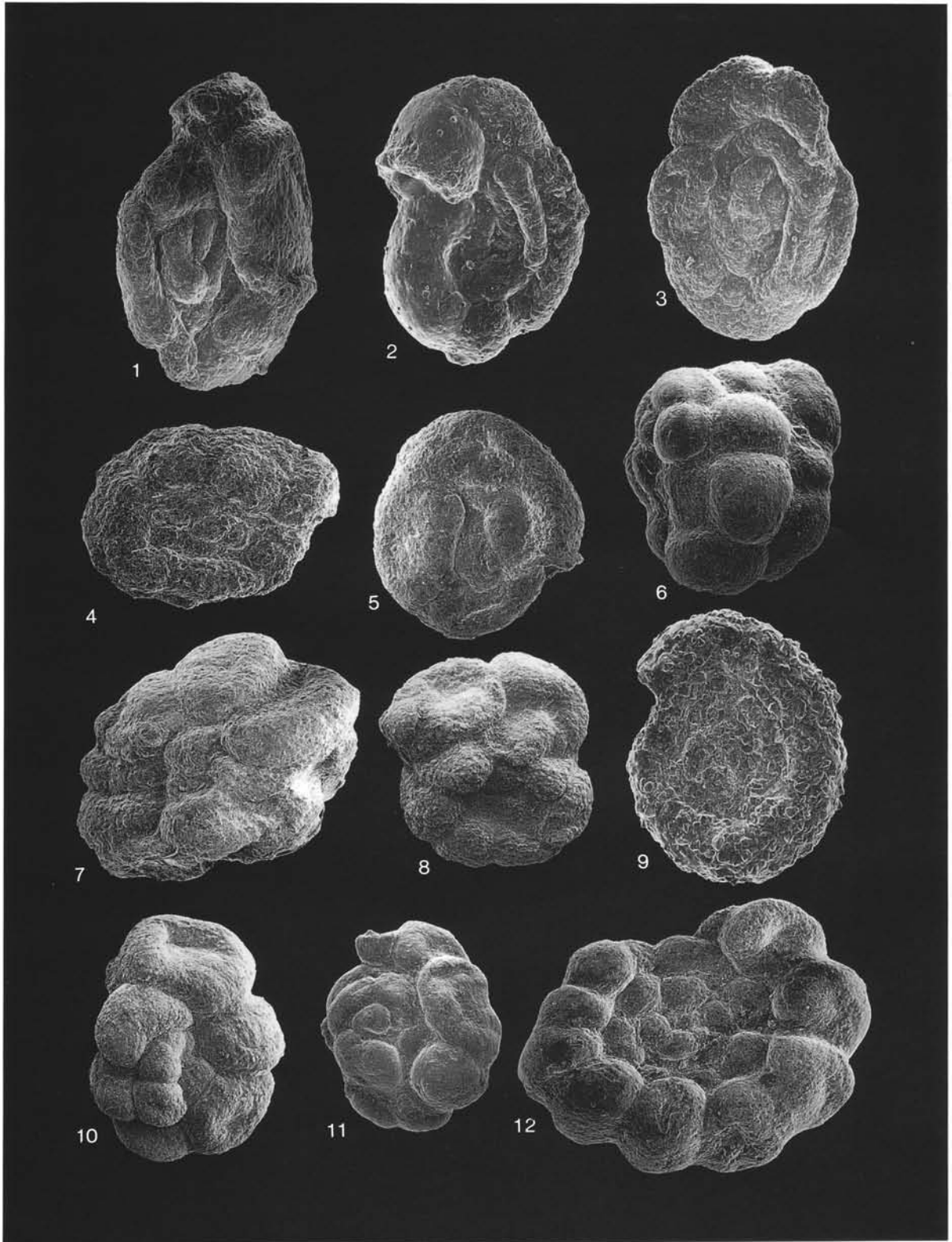


Plate 3

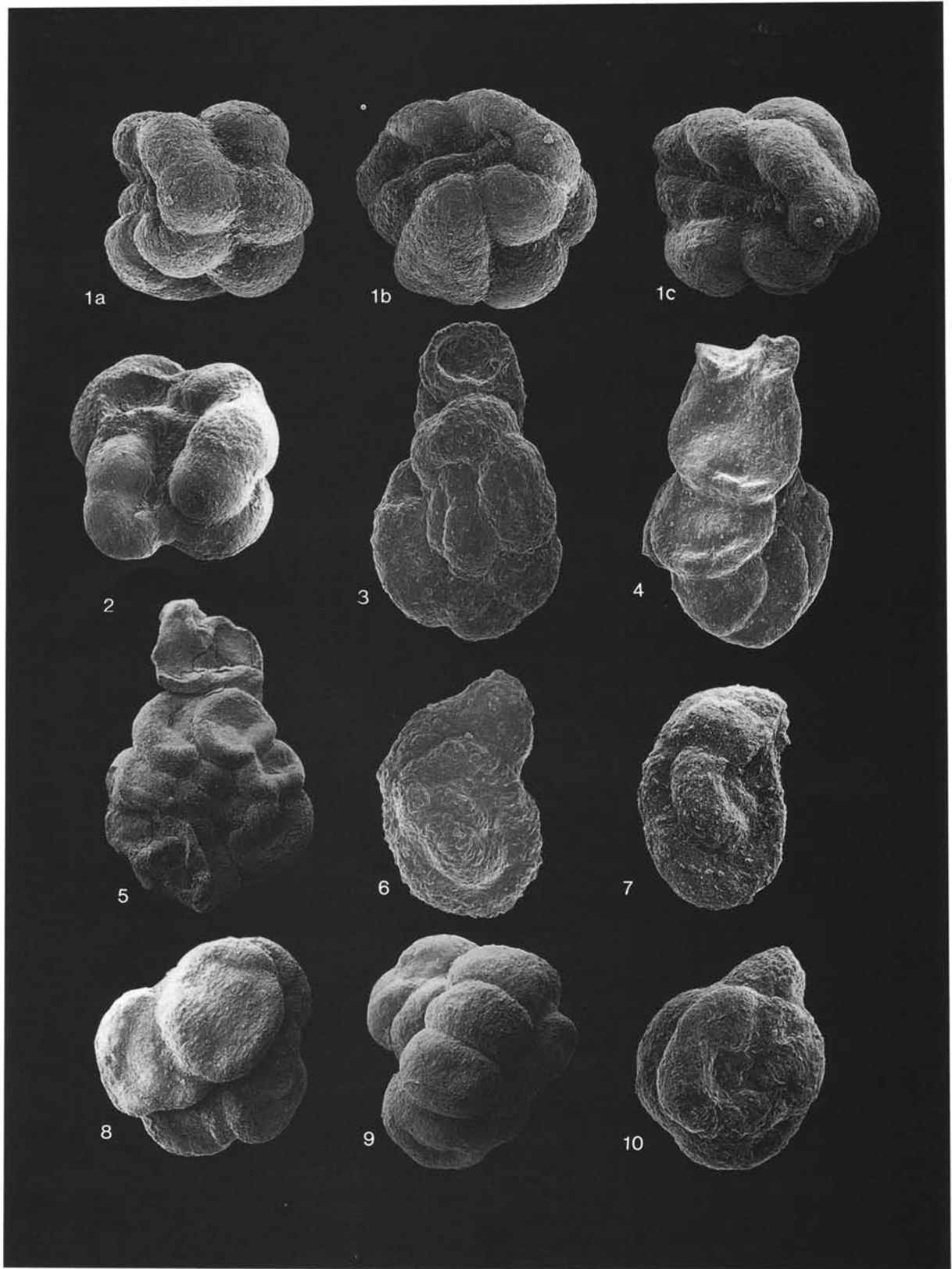


Plate 4

Paratrochamminoides draco (Grzybowski, 1901)

(Pl. 3, fig. 8)

- 1901 *Trochammina draco* Grzybowski, p. 280, pl. 8, fig. 10
 1993 *Paratrochamminoides draco* (Grzybowski); Kaminski & Geroch: 277, pl. 16, fig. 5a–c

Paratrochamminoides gorayskii (Grzybowski, 1898)

(Pl. 4, figs 6–7)

- 1898 *Ammodiscus gorayskii* Grzybowski, p. 283, pl. 11, fig. 5
 1993 *Paratrochamminoides gorayskii* (Grzybowski); Kaminski & Geroch, 255, pl. 5, fig. 8a–d

Paratrochamminoides heteromorphus (Grzybowski, 1898)

(Pl. 4, figs 3–5)

- 1898 *Trochammina heteromorpha* Grzybowski: 286, pl. 11, fig. 16
 1993 *Paratrochamminoides heteromorphus* (Grzybowski); Kaminski & Geroch, 258, pl. 7, figs 3a–5b

Paratrochamminoides irregularis (White, 1928)

(Pl. 4, fig. 8)

- 1928 *Trochamminoides irregularis* White: 307, pl. 42, fig. 1
 1990 *Paratrochamminoides irregularis* (White); Kuhnt: 320, pl. 5, fig. 10

Paratrochamminoides mitratus (Grzybowski, 1901)

(Pl. 4, fig. 9)

- 1901 *Trochammina mitrata* Grzybowski, p. 280, pl. 8, fig. 3
 1993 *Paratrochamminoides mitratus* (Grzybowski); Kaminski & Geroch: 278, pl. 16, figs 4a,b; 6a,b

Paratrochamminoides olszewskii (Grzybowski, 1898)

(Pl. 4, fig. 10)

- 1898 *Trochammina olszewskii* Grzybowski: 298, pl. 11, fig. 6
 1993 *Paratrochamminoides olszewskii* (Grzybowski); Kaminski & Geroch: 257, pl. 7, figs 1a–2b

Paratrochamminoides uviformis (Grzybowski, 1901)

(Pl. 3, fig. 6)

- 1901 *Trochammina uviformis* Grzybowski: 281, pl. 8, figs 1–2
 1993 *Paratrochamminoides uviformis* (Grzybowski); Kaminski & Geroch: 278, pl. 16, figs 4a,b; 6a,b

Paratrochamminoides sp. 4

(Pl. 3, figs 10–11)

Test medium to large, coiling irregularly glomospiral, rounded inflated chambers with depressed sutures increasing rapidly in size after first whorl. The glomospiral coiling and rapidly enlarging chambers distinguish this species from *P. acervulatus* (Grzybowski, 1896).

Paratrochamminoides sp. 5.

(Pl. 4, figs 1a–2)

Specimens small, compact, quadrate in outline, possessing rounded chambers. Coiling changes abruptly and at 180° angles, and is arranged around two orthogonal axes as in the genus *Thalmanammina*. Wall smooth, finely finished. Only a few specimens were found in our samples, but its distinctive mode of coiling sets this apart from all previously described species of *Paratrochamminoides*.

Psammospaera irregularis (Grzybowski, 1896)

- 1896 *Keramospaera irregularis* Grzybowski: 273, pl. 8, figs 12–13
 1964 *Psammospaera irregularis* (Grzybowski); Grün *et al.*: 248, pl. 3, fig. 7

Recurvoides cf. *imperfectus* Hanzliková, 1965

- 1965 *Recurvoides imperfectus* Hanzliková: 38, text fig. 7

Recurvoides nucleolus (Grzybowski, 1898)

(Pl. 2, fig. 13)

- 1960 *Recurvoides deflexiformis* (Noth); Geroch: 52, pl. 5, fig. 6
 1993 *Recurvoides nucleolus* (Grzybowski); Kaminski & Geroch: 265, pl. 11, fig. 4a–d.

Recurvoides ex gr. *gerochi* Pflaumann, 1964

- 1960 *Recurvoides* sp. 1., Geroch: 52, pl. 3, fig. 13
 1964 *Recurvoides gerochi* Pflaumann: 102–104, pl. 14, fig. 1 a–d

Recurvoides sp. 2

Large streptospiral test, relatively coarse grained, chambers increase rapidly in size.

Reophax elongatus Grzybowski, 1898

(Pl. 2, figs 7–8)

- 1898 *Reophax elongatus* Grzybowski: 279, pl. 10, figs 19–20

Reticulophragmium amplexens (Grzybowski, 1898)

(Pl. 2, fig. 12)

- 1898 *Cyclammina amplexens* Grzybowski: 292, pl. 12, figs 1–3
 1993 *Reticulophragmium amplexens* (Grzybowski); Kaminski & Geroch: 266, pl. 11, figs 5–7c

Rhabdammina annulata Grzybowski, 1896

- 1896 *Rhabdammina annulata* Grzybowski: 276, pl. 8, figs 8–9

1981 *Reophax* cf. *subnodulosa* Grzybowski; Liszka & Liszkowa: p. 166, pl. 1, fig. 4a

Rhabdammina cylindrica (Glaessner, 1937)

- 1937 *Rhabdammina cylindrica* Glaessner: 354, pl. 1, fig. 1

Rhabdammina robusta (Grzybowski, 1898)

(Pl. 1, figs 2, 18)

- 1898 *Dendrophrya robusta* Grzybowski: 273, pl. 10, fig. 7
 1993 *Rhabdammina robusta* (Grzybowski); Kaminski & Geroch: 247, pl. 1, figs 7–9b, 16a,b

Rhizammina cf. *indivisa* Brady, 1884

- 1884 *Rhizammina indivisa* Brady: 277, pl. 29, figs 5–7

Rzehakina epigona (Rzehak, 1895)

(Pl. 1, fig. 16)

- 1895 *Silicina epigona* Rzehak: 214, pl. 6, fig. 1

Saccammina grzybowskii (Schubert, 1902)

- 1902 *Reophax grzybowskii* Schubert: 20, pl. 1, fig. 13

1993 *Saccammina grzybowskii* (Schubert); Kaminski & Geroch: 248, pl. 2, figs 1a–4b

Saccammina placenta (Grzybowski, 1898)

(Pl. 2, figs 1–2)

- 1898 *Reophax placenta* Grzybowski: 276–277, pl. 10, figs 9–10
 1993 *Saccammina placenta* (Grzybowski); Kaminski & Geroch: 249, pl. 2, figs 5–7

Subreophax pseudoscalaris (Samuel, 1977)

- 1977 *Reophax pseudoscalaria* Samuel: 36, pl. 3, fig. 4a–b

1988 *Subreophax pseudoscalaris* (Samuel); Kaminski *et al.*: 187, pl. 3, figs 5–6

Subreophax scalaris (Grzybowski, 1896)

(Pl. 2, fig. 7)

- 1896 *Reophax guttifera* Brady var. *scalaria* Grzybowski: 277, pl. 8, fig. 26

1988 *Subreophax scalaris* (Grzybowski); Kaminski *et al.*: 187, pl. 2, figs 16–17

Trochamminoides dubius (Grzybowski, 1898)

(Pl. 3, figs 1–2)

- 1901 *Ammodiscus dubius* Grzybowski: 274, pl. 8, figs 12, 14
 1970 *Trochamminoides dubius* (Grzybowski); Neagu: 38, pl. 2, fig. 20

Trochamminoides folius (Grzybowski, 1898)

- 1898 *Trochammina folium* Grzybowski, p. 288, pl. 11, figs 7–9
 1993 *Trochamminoides folius* (Grzybowski); Kaminski & Geroch: 261, pl. 9, figs 1a–4b

Trochamminoides proteus (Karrer, 1866)

(Pl. 3, fig. 12)

- 1866 *Trochammina proteus* Karrer, pl. 1, fig. 8

1928 *Trochamminoides proteus* (Karrer); White: 308, pl. 42, fig. 2

Trochamminoides septatus (Grzybowski, 1898)

(Pl. 3, fig. 9)

- 1898 *Ammodiscus septatus* Grzybowski: 283, pl. 11, fig. 1
 1993 *Trochamminoides septatus* (Grzybowski); Kaminski & Geroch: 255, pl. 5, fig. 9a–c

Trochamminoides subcoronatus (Grzybowski, 1896)

(Pl. 3, fig. 6)

1896 *Trochammina subcoronata* Grzybowski: 283–284, pl. 9, fig. 3a–c

1988 *Trochamminoides subcoronatus* (Grzybowski); Kaminski *et al.*:

192, pl. 4, fig. 19

Trochamminoides variolarius (Grzybowski, 1898)

(Pl. 3, fig. 5)

1898 *Trochammina variolaria* Grzybowski: 288, pl. 11, fig. 15

1993 *Trochamminoides variolarius* (Grzybowski); Kaminski & Geroch: 261, pl. 9, figs 5a–6c

ACKNOWLEDGEMENTS

Field work was assisted by the German Research Council (DFG), project number WI-127/2, as part of the ALKAPECA project at the University of Tübingen. We are grateful to the Geological Survey of Morocco (Drs Bensaïd & Dahmani) for permission to work in the area. Drs Klaus Reicherter and Thomas Pletsch (University of Tübingen) helped collect samples. Jim Davy, Toby Stiles, George Dumitrescu, and Vaila Holbourn assisted with photography and drafting. Drs. W.A. Berggren (WHOI) and M.A. Charnock (SPT) kindly reviewed the manuscript. JDR acknowledges the support of an Advanced Course Studentship from the Natural Environment Research Council. This is contribution number 36 of the Deep-Water Agglutinated Foraminiferal Project.

Manuscript received December 1993.

Manuscript accepted June 1995.

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The British Micropalaeontological Society Foundation was instigated during late 1995 and is a fund specifically aimed at supporting the *Journal of Micropalaeontology*. Members (and non-Members) may make voluntary contributions to the Foundation. The following persons have contributed at least £25 during 1996.

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