GEOLOGICA ULTRAIECTINA

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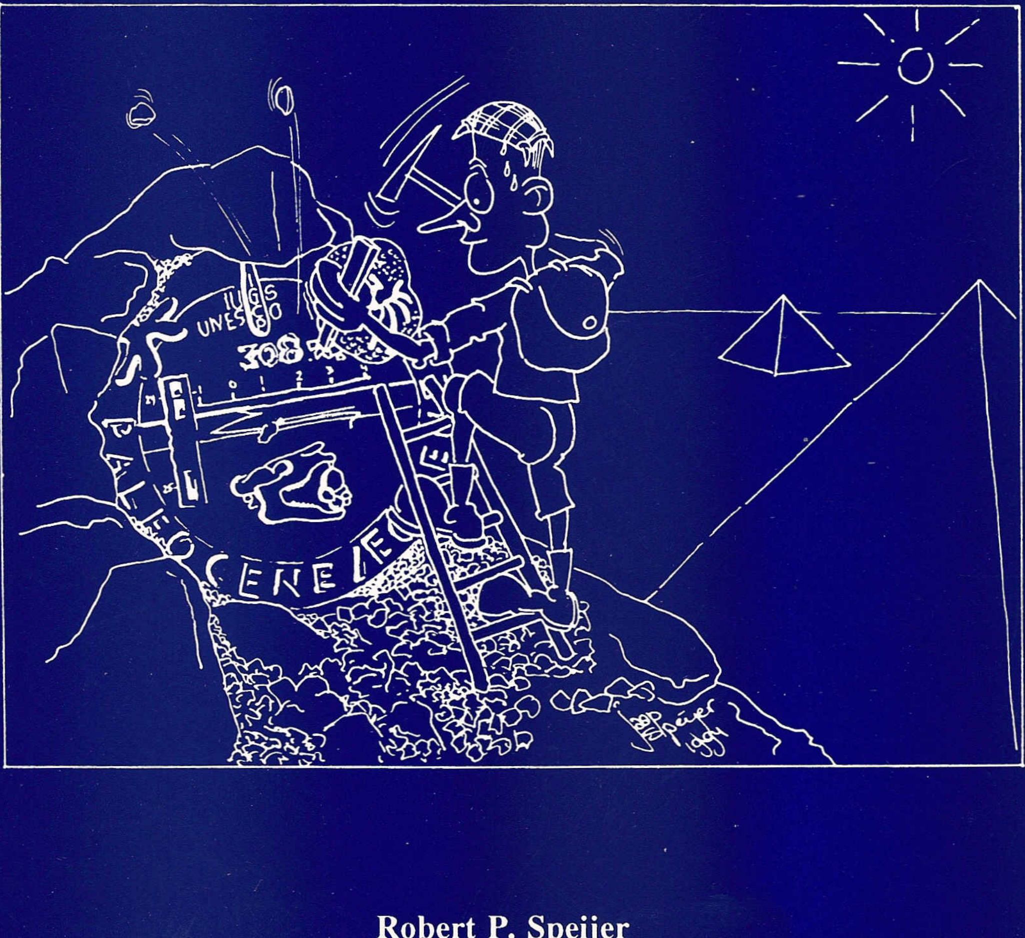
Extinction and recovery patterns in benthic foraminiferal paleocommunities across the Cretaceous/Paleogene and Paleocene/Eocene boundaries



Robert P. Speijer

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Extinction and recovery patterns in benthic foraminiferal paleocommunities across the Cretaceous/Paleogene and Paleocene/Eocene boundaries

Extinctie en herstel patronen in fossiele gemeenschappen van benthonische foraminiferen over de Krijt/Paleogeen en Paleoceen/Eoceen grenzen

(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad van doctor aan
de Universtiteit Utrecht, op gezag van de
Rector Magnificus, Prof. Dr. J.A. van Ginkel,
ingevolge het besluit van het College van Dekanen
in het openbaar te verdedigen op woensdag
23 november 1994 des voormiddags te 10.30 uur

door
Robert Pieter Speijer
geboren op 13 september 1963 te Veldhoven

PROMOTORES: PROF. DR. J.E. MEULENKAMP
PROF. DR. G.J. VAN DER ZWAAN

to the late H.G. Foppe

Contents

Most chapters will appear in (or be submitted to):
Marine Micropaleontlogy (Ch. II, V, VI)
Micropaleontology (Ch. III)
Bulletin de la Societé Belge de Geologie (Special Issue:
Paleocene/Eocene boundary events; Ch. IV)

Summary

In this thesis Late Cretaceous to Early Paleogene (66-54 Ma) benthic foraminiferal distribution patterns in the southern Tethys (northern margin of Africa) are discussed. We focus in particular on extinction and recovery patterns in middle neritic (50-100 m) to upper bathyal (200-600 m) benthic foraminiferal paleocommunities across the Cretaceous/Paleogene (K/P; 65 Ma) and Paleocene/Eocene (P/E; 55 Ma) boundaries. The studied material is largely derived from the more or less well-known profiles of El Kef (Tunisia), Gebel Duwi, Gebel Oweina, Wadi Nukhl (all Egypt), and Nahal Avdat (Israel).

As in the recent situation, also Late Cretaceous to Early Paleogene communities were distinctly arranged along a depth gradient. Related gradients in nutrient supply (decreasing with depth), sea-floor oxygenation, and environmental stability (both generally increasing with depth) determined the major differences between the various neritic and bathyal habitats. Shallow water communities were often oligotypic and strongly dominated by only a few species, whereas upper bathyal communities consisted of a highly diverse mixture of deep and shallow water species.

This study documents two major reorganizations of foraminiferal distribution patterns and paleocommunity composition, associated with important paleoceanographic and paleoclimatic events that coincided with the K/P and P/E transitions. During both "mass" extinctions all studied bathymetric compartments were affected, although to a variable extent: at the K/P boundary mainly the shallower domain was affected, whereas the deeper water assemblage was changing most across the P/E boundary. During both events the intermediate (upper bathyal) domain of the southern Tethys was severely perturbed; consequently, Late Cretaceous and early Eocene upper bathyal assemblages are very dissimilar, having few species in common.

The K/P transition was marked by sudden widespread oxygen and nutrient deficiency in intermediate Tethyan waters. For some 100 kyr, a suite of shallow water species (better able to resist the adverse conditions) replaced the Late Cretaceous upper bathyal community. Eventually, a relatively impoverished Paleocene upper bathyal community returned, indicating ameliorated bottom conditions. Meanwhile, many species with higher nutrient demands, in particular those with elongate ("endobenthic") test shapes, had suffered extinction, whereas most oligotrophic deep-sea species were hardly affected. This extinction selectivity is explained by the enormous decrease in nutrient supply to the sea-floor, following the collapse of pelagic primary production, that characterizes the K/P boundary event.

The P/E transition was marked by sudden widespread (perhaps global) oxygen deficiency in deep and intermediate watermasses, which caused the extinction of many cosmopolitan deep-sea species, in particular the ones with bi-convex ("epibenthic") test shapes. Although generally considered as a deep-sea phenomenon, the P/E boundary dysoxic event affected southern Tethyan shallow water communities as well. However, due to more effective oxygen deficiency survival strategies, most shallow water species were able to survive the period of enhanced oxygen stress. Within this period, a few opportunistic species were able to settle in the deeper parts of the basin, temporarily replacing the bathyal community. After some 50 kyr, a relatively impoverished Eocene upper bathyal community gradually returned, indicating re-establishement of more normal

conditions.

We propose a comprehensive paleoceanographic-paleoclimatic model for the Late Cretaceous to Early Paleogene, which may explain the main patterns of benthic foraminiferal distribution and the boundary turnovers. Both events were associated with widespread bottom oxygen deficiency. We infer that during these events ventilation was severely reduced, due to sudden inhibition of deep and/or intermediate water formation. At the K/P boundary the formation of low latitude saline intermediate water was blocked, due to sudden cooling and decreasing wind-stress in the (sub)tropics, possibly related to the impact of a large asteroid. During the earliest Paleocene a cooler (high latitude) deep watermass penetrated into intermediate depths of the Tethys and eventually replaced the saline Tethyan water. This situation persisted until the end of the Paleocene, when polar warming, possibly induced by excessive volcanic CO_2 output, blocked the formation of these high latitude cool deep and intermediate waters. At the same time, deep and intermediate water formation in the Tethys was (re-)installed, resulting again in an oceanic circulation reversal. During both transitions from one circulation mode to the other, ventilation of intermediate Tethys waters became temporarily reduced.

The sum of the effects of both events is a stepwise extinction of many successful lineages that originated in the Cretaceous; however at the same time new habitats were created leading to the development of more advanced Cenozoic lineages, many of which persist to the present day.

Samenvatting

In dit proefschrift worden de Laat Krijt tot Vroeg Paleogene (66-54 Ma) distributie patronen van benthonische foraminiferen in de zuidelijke Tethys (de huidige noordelijke rand van Afrika) besproken. In het bijzonder wordt aandacht besteed aan extinctie en herstel patronen in midden neritische (50-100 m) tot boven bathyale (200-600 m) fossiele gemeenschappen van benthonische foraminiferen op de Krijt/Paleogeen (K/P; 65 Ma) en Paleoceen/Eoceen (P/E; 55 Ma) overgangen. Het bestudeerde materiaal is voornamelijk afkomstig van de (deels zeer bekende) secties van El Kef (Tunesië), Gebel Duwi, Gebel Oweina, Wadi Nukhl (allen Egypte) en Nahal Avdat (Israël).

Evenals in de huidige situatie waren gemeenschappen tijdens het Laat Krijt tot Vroeg Paleogeen gerangschikt volgens een diepte gradiënt. De hieraan gekoppelde gradiënten in nutriënten toevoer (afnemend met diepte), zuurstof concentratie en stabiliteit van milieu factoren (beide normaliter toenemend met diepte) bepaalden de belangrijkste verschillen tussen de diverse neritische en bathyale biotopen. Ondiep water associaties waren veelal oligotypisch en werden sterk gedomineerd door slechts enkele soorten, terwijl boven bathyale associaties een zeer divers mengsel bevatten van diep en ondiep water soorten.

Deze studie documenteert twee grote reorganisaties in distributie patronen van foraminiferen en in de samenstelling van fossiele gemeenschappen; deze reorganisaties zijn geassocieerd met de twee belangrijke paleoceanografische en paleoklimatologische gebeurtenissen, die samen vielen met de K/P en P/E overgangen. Tijdens deze "massa" extincties werden alle bathymetrische compartimenten beïnvloed, zij het in zeer verschillende mate: op de K/P overgang werd vooral het ondiepere domein getroffen, terwijl op de P/E overgang juist de diepwater associaties de grootste veranderingen ondergingen. Tijdens beide gebeurtenissen werd het intermediaire (boven bathyale) domein van de zuidelijke Tethys sterk verstoord; dientengevolge vertonen associaties van het Laat Krijt en vroeg Eoceen in dit domein weinig overeenkomst en hebben zij weinig soorten gemeenschappelijk.

De K/P overgang werd gemarkeerd door een plotseling wijd verbreid tekort aan zuurstof en nutriënten in intermediair Tethys water. Gedurende zo'n 100.000 jaar verving een groep ondiep water soorten (die beter bestand waren tegen de ongunstige omstandigheden) de boven bathyale gemeenschap van het Laat Krijt. Naderhand keerde een Paleocene, enigszins verarmde, boven bathyale gemeenschap terug, duidend op verbeterde zeebodem omstandigheden. Tegelijkertijd stierven veel soorten met hogere nutriënten vereisten uit, in het bijzonder soorten met een langwerpige ("endobenthische") schaalvorm, terwijl de meeste oligotrofe diepzee soorten juist nauwelijks aangetast werden. Deze extinctie selectiviteit wordt verklaard door de enorme reductie van nutriënten toevoer naar de zeebodem, volgend op de ineenstorting van primaire produktie in het oppervlakte water, die de K/P gebeurtenis kenmerkte.

De P/E overgang werd gemarkeerd door een plotseling wijd verbreid (mogelijk mondiaal) tekort aan zuurstof in de diepe en intermediaire watermassa's, hetgeen de extinctie van vele kosmopolitische diepzee soorten veroorzaakte, in het bijzonder van de soorten met een biconvexe ("epibenthische") schaalvorm. Hoewel de crisis op de P/E grens algemeen als een diepzee verschijnsel wordt beschouwd, tastte het zuurstof gebrek ook ondiep water gemeenschappen aan. Echter, door gebruik van effectieve

overlevingsstrategiën (o.a. tegen zuurstof tekorten), waren veel ondiep water soorten in staat om de periode van verhoogde zuurstof stress te overleven. Gedurende deze periode waren enkele opportunistische soorten tevens in staat om zich te vestigen in diepere delen van het bekken; zij vervingen tijdelijk de boven bathyale gemeenschap. Tijdens het vroegste Eoceen keerde, na zo'n 50.000 jaar, een enigszins verarmde, boven bathyale gemeenschap terug, duidend op het herstel van meer normale bodemomstandigheden.

In dit proefschrift wordt een veelomvattend en complex paleoceanografisch-paleoklimatologisch model voor het Laat Krijt tot Vroeg Paleogeen voorgesteld, dat de belangrijkste distributie patronen van benthonische foraminiferen, evenals de faunistische omslagen op de grensnivo's, kan verklaren. Beide gebeurtenissen waren geassocieerd met wijd verbreide zuurstof tekorten op de zeebodem. In het model wordt dit verklaard door sterk gereduceerde ventilatie van de zeebodem door een plotselinge onderdrukking van diep en/of intermediair watervorming. Op de K/P grens werd de vorming van salien tropisch-subtropisch intermediair water geblokkeerd door een plotselinge afkoeling en afnemende windkracht in de (sub)tropen, mogelijk gerelateerd aan de inslag van een grote asteroïde. Tijdens het vroegste Paleoceen drong een koelere (van hoge breedte afkomstige) diepere watermassa door tot in intermediaire diepten van de Tethys en verving uiteindelijk het saliene Tethys water. Deze situatie hield stand tot aan het eind van het Paleoceen, toen opwarming van de polen, mogelijk veroorzaakt door de uitstoot van grote hoeveelheden vulkanisch CO_2, de vorming van koel diep en intermediair water blokkeerde. Tegelijkertijd werd de vorming van diep en intermediair water in de Tethys (opnieuw) in gang gezet, hetgeen wederom resulteerde in een omkering in oceanische circulatie. Tijdens beide overgangen van de ene naar de andere circulatie wijze, werd de ventilatie van het intermediaire Tethys water tijdelijk sterk gereduceerd.

De optelsom van de effecten van beide gebeurtenissen is een stapsgewijs uitsterven van vele succesvolle geslachten, die waren ontstaan tijdens het Krijt; tegelijkertijd werden er echter nieuwe biotopen gecreëerd hetgeen leidde tot de ontwikkeling van meer geavanceerde Cenozoïsche geslachten, waarvan vele vandaag de dag nog bestaan.

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In the first place I have to thank Johan Meulenkamp and Bert van der Zwaan for setting up the project and its financial support. Furthermore, discussions with the latter greatly improved the quality of the thesis; his input, moral support and comments on earlier drafts of the chapters were invaluable. Of course, fruitful and stimulating discussions with other colleagues at the department, as Jan van Dam, Frits Hilgen, Frans Jorissen, Lucas Lourens, Albert van der Meulen, Eelco Rohling, Henko de Stigter and Jan-Willem Zachariasse, were indispensable as well.

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I thank Gerrit van 't Veld and Geert Ittmann for all samples they processed and for accepting me in their laboratory to do a few samples myself in the evening, when I was "occasionally" too impatient to wait for the next day to see the first results. Tom van Hinte made the *Autocad* drawings and was always prepared to do even a sixth or seventh revision when needed. Wil den Hartog prepared all photographs and plates with his usual high quality standard. Ank Pouw was often very helpful in providing me with all things one may need for the preperation of papers, sheets, etc., and was always highly interested in the human aspect of life at the faculty. I thank all our librarians for their devotion to provide me with even the most obscure references.

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Above all, I thank my parents for enabling me to get involved into such an unfamiliar study as geology and for their never-ending attention for my scientific interests and personal well-being. Finally, I am greatly indebted to Astrid Teunen, who gave me all her love and the moral support required, while receiving merely increasing piles of papers and jumble all over the place in return; hopefully this will get into the right balance again soon.

- CHAPTER I -

Introduction

Background and purpose of investigation

The fossil record enables geologists to divide the geological record into distinct, regionally and "world-wide" recognizable, stratigraphic units. Many of the boundaries between these units are marked by a pronounced turnover in the fossil record; some of these are so extreme that they are viewed upon as mass extinctions. This is the case if extinction pertained to a great number of taxa belonging to a wide variety of taxonomic groups, and if the process took a relatively short period (up to a few million years!) in geological time.

The turnover at the Cretaceous/Paleogene (K/P) boundary is generally considered as one of the most severe mass extinctions that ever occurred in geological history (Sepkoski, 1982, 1993) and, consequently, received considerable attention. Highly controversial aspects of this (and in fact any other) mass extinction are the cause and mode of the transition, since these are critical to argue for a sudden, catastrophic (e.g. impact) or a more gradual event. The seemingly instantaneous extinction of virtually all planktonic foraminifera at the K/P boundary is considered as one of the key elements to argue for a sudden and global event (Smit, 1990). This however, has been refuted by other workers who argue for stepwise extinctions, starting below the boundary and progressing above it (MacLeod and Keller, 1994). The benthic foraminiferal record shows a much less conspicuous turnover, that is particularly indistinct in deep-sea assemblages (e.g. Beckmann, 1960; Thomas, 1990a). Nevertheless, also in the group of bottom dwelling foraminifera many genera became extinct at the end of the Cretaceous (Loeblich and Tappan, 1988).

The next following event at the Paleocene/Eocene (P/E) boundary, is not considered as an example of mass extinction (Sepkoski, 1982, 1993). Yet, the largest extinction in deep-sea foraminifera during the last 90 Ma occurred at that boundary (Tjalsma and Lohmann, 1983; Thomas, 1992). In contrast, shallow water assemblages are thought to have remained largely unaffected (Berggren and Schnitker, 1983).

During the last decade various papers discussed benthic foraminiferal turnovers across the K/P and P/E boundaries in detail. The majority of this research has been performed on material recovered by deep-sea drilling in middle-high latitude sites (e.g. Dailey, 1983; Thomas, 1990b; Nomura, 1991; Katz and Miller, 1991; Widmark and Malmgren, 1992a). Consequently, the understanding of extinction and recovery patterns, as well as paleoenvironmental interpretations, are biased towards prevailing conditions in those regions. In order to get a more balanced picture of the boundary events and their impact on evolutionary patterns of benthic foraminifera, we performed studies on shallow marine (upper bathyal to neritic) assemblages from the southern Tethys. During the time span considered, this part of the former Tethys Ocean covered extensive areas of North Africa. This region is of particular interest, since during the Late Cretaceous to Early Paleogene it may have encompassed source areas for warm and saline deep water formation (Brass et al., 1982), as well as areas of wind-induced upwelling (Parrish and Curtis, 1982).

We studied various K/P and P/E boundary sequences in Tunisia, Egypt and Israel in detail and established a paleobathymetric framework, which enabled us to reveal differential responses along environmental gradients during the faunal turnovers. The prime goals of this research are:

- the achievement of a better understanding of the response of benthic foraminiferal paleocommunities to global environmental perturbations, and in particular of differential extinction and recovery effects between various ecological compartments.
- to gain insight in local environmental conditions at the sea-floor during the perturbations and to place these local conditions within a regional and global paleoceanographic and paleoclimatic framework.
- to verify and/or constrain proposed scenario's describing the causes for these major extinctions.

These topics are treated in five chapters, that will be published as separate papers.
In Chapter II we give an elaborate quantitative account of the faunal turnover across the K/P boundary of EL Kef, Tunisia. Additional sequences from Egypt and Israel provide the paleobathymetric and biogeographic framework. We focus on the relationships between changing food supply, redox conditions, benthic foraminiferal response, and extinction selectivity. Subsequently, our results are related to major perturbations in paleoclimate and paleocirculation.

In Chapter III we switch to the P/E boundary and slightly deviate from the main theme, as we focus on the phylogeny of the planktonic foraminifer *Globanomalina luxorensis*, because of its biostratigraphic value for recognition of the P/E boundary in Tethyan sequences.

In Chapters IV, V, and VI extinction and recovery patterns within different bathymetric compartments across the P/E boundary are discussed. The implications of our results are placed in the context of paleoceanographic and paleoclimatic change, and in particular the consequences for existing P/E boundary scenario's are reviewed.

In Chapter IV we focus on two upper bathyal sequences in northern Egypt and Israel. This chapter was written and accepted for publication in 1992, but since then additional research revealed that some terminology and conclusions need revision. For the sake of convenience we summarize here the most substantial discrepancies between this chapter and Chapters III, V, and VI:

- the P/E bounary event is considered as a late Paleocene event in Chapter IV. However, in the near future the P/E boundary will most likely officially be re-defined at the level of the benthic foraminiferal extinction (see Chapter III). In the expectation that this will happen soon, we already adopt and use the P/E boundary in this sense in the other chapters.
- biozonal terminology in Chapter IV is according to the biozonal scheme of Berggren (1969). In the other chapters on the P/E boundary, we adopt the latest biozonal scheme of Berggren et al. (1994). This scheme differs from the previous one in the definition of the P-notation: the former Zones P5-P6a are now combined into the new Zone P5, since *Morozovella subbotinae* has been dismissed as a zonal marker; the former Zone P6b is now Zone P6a. Due to these revisions, sedimentation rate estimates for these sections are probably highly overestimated (see also Chapter VI).
- some taxonomic revisions at generic and/or species level were required after additional taxonomic studies. The following names have been modified: *Gavelinella hyphalus* (now *Cibicidoides hyphalus*), *Anomalinoides* sp. 1 (now *Gyroidinoides* sp. 1), *Anomalinoides* cf. *praeacuta* (now combined with *A. praeacutus*), *Cibicidoides* sp. 1 (now *C. pharaonis*), *Gaudryina pyramidata* (now split into *G. nekhlensis* for the Paleocene and *G.* cf. *ellisorae* for the Eocene), *Bulimina rugifera* (now *B. callahani*), *Gyroidinoides depressus* (now *Valvalabamina*

depressa), *Gyroidinoides planulatus* (now *Valvalabamina planulata*), *Cibicidoides commatus* (now *C. pseudoacutus*), *Gavelinella danica* (now *Anomalinoides rubiginosus*), *Spiroplectammina knebeli* (now *Spiroplectinella esnaensis*), *Siphogenerinoides eleganta* (now *Siphogenerinoides* cf. *eleganta*), and *Gavelinella ekblomi* (now *Anomalinoides zitteli*). Between brackets are the names as they are adopted in Chapters V and VI.

- the suggestion that various species may have permanently extended their depth range from shallower into deeper waters during the early Eocene has not been confirmed during subsequent research: some species appeared to be already present in deeper waters during the Paleocene (be it very rare, e.g *Bulimina farafraensis*); other species did not enter from local shallower depths, but apparently entered the region from outside the study area (*"Siphogenerinoides eleganta"* and *"Gavelinella ekblomi"*).

- most importantly, the conclusion that the Abu Rudeis (or Wadi Nukhl) area was continuously well ventilated appeared erroneous: detailed re-sampling of the boundary sequence revealed the presence of a thin sapropelitic bed precisely at the P/E boundary (see Chapter VI).

In Chapter V we discuss the impact of the P/E event on paleocommunities from a shallow water (middle neritic) Egyptian site, located at the present day Red Sea coast. In Chapter VI we integrate all our data from Egypt on the P/E boundary, in order to reveal differential biotic responses in deep to shallow water (upper bathyal to middle neritic) paleocommunities.

Finally, in Chapter VII we compare our results of the two boundary events and synthesize these into general concepts of biotic extinction and recovery, and place them into a Late Cretaceous to Early Paleogene paleoceanographic and paleoclimatic framework.

- CHAPTER II -

Extinction and survivorship patterns in southern Tethyan benthic foraminiferal assemblages across the Cretaceous/Paleogene boundary

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ABSTRACT

We performed a detailed quantitative analysis on upper bathyal benthic foraminiferal assemblages derived from the Cretaceous/Paleogene (K/P) boundary sequence of El Kef, Tunisia. We compared the faunal patterns with additional records from K/P profiles in Egypt and Israel, in order to evaluate distributional patterns in different bathymetric zones. The record of El Kef shows a succession of three distinctive paleocommunities. The Late Maastrichtian paleocommunity is highly diversified, stable, and does not show any signs of gradual change towards the boundary. The boundary and the earliest to early Paleocene are marked by an abrupt extinction and gradual recovery sequence: a sudden drop in diversity and proliferation of opportunistic low oxygen tolerant shallow water taxa at the K/P boundary is followed by gradual diversification due remigration of Lazarus taxa and subsequent immigration of new taxa during the early Paleocene. The faunal changes reflect major perturbations in redox and trophic conditions at the sea-floor. These changes invoked distinct (partly temporal) contractions and expansions of benthic foraminiferal bathymetric distributions.

At least locally, and perhaps regionally, the extinctions are due to sudden oxygen deficiency, that was most severe just above the boundary. On a global scale dysoxic conditions can not account for the observed extinctions: in the constantly well ventilated deep-sea the same (but there much less common) species became extinct as well. Since particularly species adapted to high and heterogeneous nutrient resources suffered extinction, it appears that the prolonged suface fertility crisis invoked the world-wide extinctions.

The combination of our data with evidence from elsewhere suggests that in El Kef the latest Maastrichtian was a time of high fertility conditions due to moderate upwelling of nutrient rich water. Concomitant thorough ventilation of the sea-floor prevented the development of a distinct OMZ. At the start of the Paleocene near-cessation of intermediate water refreshment led to a stronlgy developed OMZ, despite the depressed surface fertility. The early Paleocene shows ameliorating surface and seafloor conditions, due to intensified circulation and ventilation.

We suggest that a cooling event at the K/P boundary superimposed on a long-term cooling trend blocked the formation of Tethyan intermediate warm and saline water. This cooling event could have been triggered by the impact of an extra-terrestrial object, and amplified by various positive feedback mechanisms. The deep watermass that originated at high latitudes, possibly penetrated into shallower parts of the Tethys during the early Paleocene.

Introduction

Since the bolide impact hypothesis has been put forward to explain the mass-extinction at the end of the Cretaceous (Alvarez et al., 1980), the Cretaceous-/Paleogene (K/P) boundary has become one of the most controversial themes in

Earth Sciences. Huge amounts of data and ideas were reported in support of an extraterrestrial event, a more (gradual) earthy cause, or a combination of both (see overviews in Sharpton and Ward, 1990; Sutherland, 1994). In recent years, focus has slightly shifted to gain a better understanding of extinction and survivorship selectivity, and of ecosystem recovery in the aftermath of the mass-extinction event (e.g. Gerstel et al., 1987; Archibald and Bryant, 1990; Gallagher, 1991; Rhodes and Thayer, 1991; Sheehan and Fastovsky, 1992; Jäger, 1993; Hansen et al., 1993; Raup and Jablonski, 1993).

Especially, the well-documented planktonic foraminiferal extinction at the K/P boundary has already for a long time been the subject of intense research (e.g. Luterbacher and Premoli-Silva, 1964; Smit, 1982; Brinkhuis and Zachariasse, 1988; D'Hondt and Keller, 1991; Huber, 1991b; Keller, 1993). In combination with a major turnover in calcareous nannofossils (e.g. Bramlette and Martini, 1964; Romein, 1979b; Perch-Nielsen, 1981; Alcala-Herrera et al., 1992; Pospichal, 1994), a negative excursion in the $\delta^{13}C$ record (e.g. Stott and Kennett, 1989; Zachos et al., 1989; Magaritz et al., 1992; Keller et al., 1993) and a drop in $CaCO_3$ accumulation (e.g. Arthur et al., 1987; Keller and Lindinger, 1989), this extinction clearly marks a major collapse of the pelagic ecosystem (Perch-Nielsen et al., 1982; Hsü and McKenzie, 1985; Arthur et al., 1987; Zachos et al., 1989). It seems likely that this breakdown had a profound effect on benthic ecosystems, since these largely depend on the vertical food supply from the overlying surface waters (see Van der Zwaan et al., 1992 and references therein).

Various quantitative studies have been performed on benthic foraminiferal assemblages across the K/P boundary (Dailey, 1983; Keller, 1988b; Thomas, 1990b; Nomura, 1991; Kaiho, 1992; Keller, 1992; Schmitz et al., 1992; Widmark and Malmgren, 1992a; Kuhnt and Kaminski, 1993). The general idea resulting from these studies is that deep-sea assemblages were much less severely affected than continental margin assemblages. However, both shallow and deep water assemblages yield species of highly successful Cretaceous lineages that became extinct (e.g. *Praebulimina*, *Sitella*, *Eouvigerina*, *Orthokarstenia*, and *Stensioeina*) or were reduced (e.g. *Bolivinoides*, *Gavelinella*, and *Neoflabellina*) during the earliest Paleocene (see Loeblich and Tappan, 1988). These species are usually much less abundant in deep-sea assemblages than in shallower ones, making the extinction in the deep-sea much less conspicuous. Clearly, shallow as well as deep water extinctions must somehow be a response to the environmental change across the K/P boundary. Thomas (1990a) suggested that the differential effects on the deep and shallower benthic ecosystems might be related to the pelagic productivity breakdown: the already oligotrophic deep-sea ecosystems would hardly be affected by such an event, in contrast to shallower systems composed by species with higher nutrient demands.

In this paper we present a quantitative benthic foraminiferal analysis on samples from the El Kef section in Tunisia. This section provides an expanded and probably continuous record across the K/P boundary, enabling a detailed analysis of extinction and survivorship patterns. A similar study was previously performed on largely the same set of samples by Keller (1988b). In that paper, a major drop in sea-level and oxygen content during the earliest Paleocene was postulated to explain the benthic foraminiferal sequence. Our taxonomy differs from the one used by Keller (1988b) and also our interpretation of the data is substantially different. Surprisingly, we encountered some discrepancies between Keller's and our census data, which could have bearing on paleobathymetric interpretations. We analysed a longer stratigraphic sequence; we primarily expanded our research further down into the Maastrichtian sequence to discern background variability in frequency patterns and possible long-term trends. In addition, we also provide a higher resolution coverage of the Paleocene, in particular of the lowermost Paleocene. The main difference in interpretation is that we consider the faunal patterns primarily as a reponse to changes in trophic and redox conditions, caused by changes in intermediate water formation, rather than being a reflection of major sea-level variations.

Finally, we compare our data from the El Kef sequence with additional data from Egyptian and Israelian K/P sequences, in order to evaluate changes in southern Tethyan paleocommunities in a broader context.

Material and methods

The investigated samples were obtained from the Maastrichtian-Paleocene El Haria Formation as exposed in a section near the town of El Kef, Tunisia (Fig. 1). This paper only discusses results from the uppermost thirty metres of the Maastrichtian marls and the lowermost ten metres of the Paleocene shales and marls (Fig. 2). We primarily used the widely distributed AFN-coded samples, collected in 1982 by T. Romein and J. Smit as members of the Cretaceous/Paleocene Working Group of the International Committee on Stratigraphy.

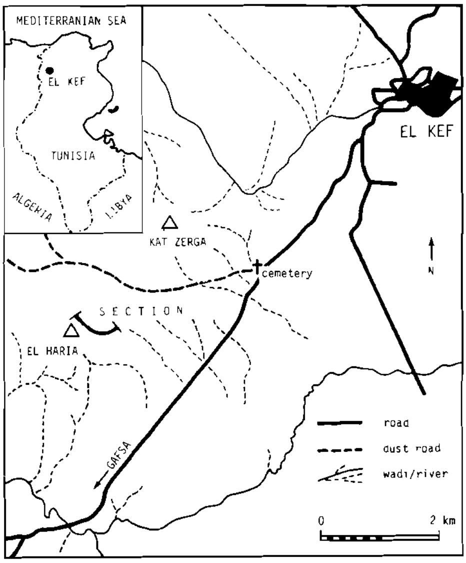

Fig. 1. Location map of the El Kef section (from Brinkhuis and Zachariasse, 1988).

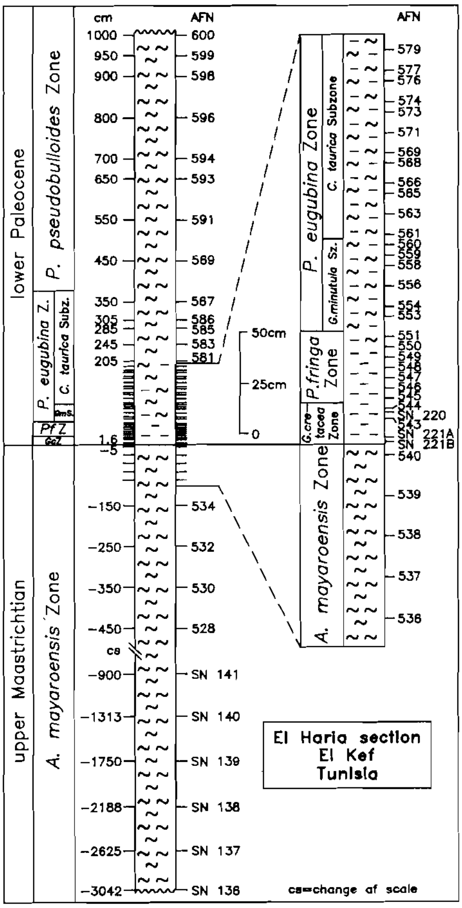

Fig. 2. Lithological sequence and biostratigraphic results (adopted from Brinkhuis and Zachariasse, 1988) of the El Kef section. Note the change in scale in the lower part of the section; figures on the left side of the column indicate distance (cm) relative to the K/P boundary.

A. Nederbragt and J. Smit (Free University of Amsterdam) provided additional SN-coded samples collected in 1992.

The samples were washed, sieved and separated into four size fractions; a split (obtained by use of an Otto microsplitter) of the 125-595 µm fraction, containing 200-300 specimens, was used for foraminiferal counts. All specimens were picked and stored in Chapman-slides. Benthic foraminifera were, whenever possible, identified at species level. Only the Nodosariacea and most badly preserved agglutinants were lumped at a higher taxonomic level. After finishing our census counts we condensed the initial dataset (132 taxa), lumping all highly infrequent taxa into higher order groupings. Fisher-α diversity (cf. Murray, 1991), however, is based on the initial census data. Foraminiferal numbers (specimens/gr dry sediment) were derived from seperately dried and weighed samples, which were washed over a 63 µm mesh sieve. We used the entire > 63 µm fraction so we could also establish planktonic foraminiferal numbers for the earliest Paleocene, since up to three metres above the K/P boundary planktonic foraminifera are smaller than 125 µm in diameter (Brinkhuis and Zachariasse, 1988).

Additional samples from other marly sequences covering the K/P boundary interval were obtained from one section in Israel (Nahal Avdat) and three in Egypt (Gebel Duwi, Gebel Qreiya and Wadi Nukhl; see Fig. 3). Romein (1979a,b) studied the nannoflora of the upper part of the Ghareb Formation and the Taqiye Formation of the Nahal Avdat section; we used the same IR-coded samples. Samples from Wadi Nukhl (western Sinai) were first collected in 1984 and again in 1993, with closer sample spacing. The K/P boundary is situated in the basal part of the (lower) Esna Shale Formation, one metre above a hardground of Late Maastrichtian age (compare the nearby Matulla section of Shahin, 1992). Samples from Gebel Duwi (or Bir Inglisi III, near Quseir at the Red Sea coast; see for detailed map: Speijer and Van der Zwaan, 1994a) were collected from an outcrop in the Dakhla Formation, in 1993. Foraminiferal associations of the Gebel Qreiya section (NE of Qena; Luger, 1988) were examined during a visit of the first author to Dr Luger (Bremen) in 1993. Faunal abundances of the additional samples are treated semi-quantitatively.

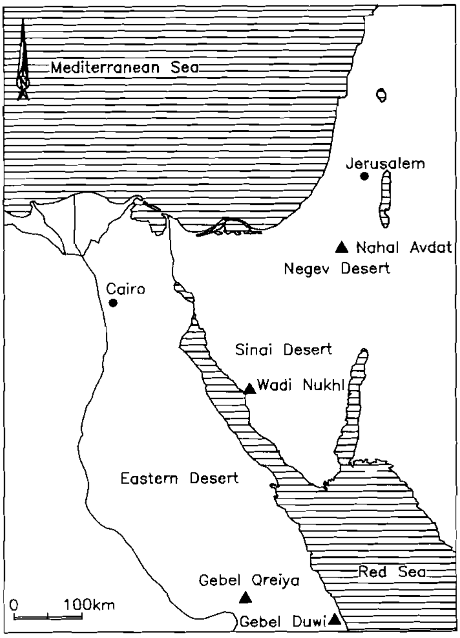

Fig. 3. Location of additional K/P profiles in Egypt and Israel.

Biostratigraphy

Since the K/P boundary interval in the El Kef section is expanded and probably complete, the section was chosen to serve as a Global Stratotype Section and Point (GSSP) for the K/P boundary (Salaj, 1994). Many researchers discussed the biostratigraphy of this or a nearby parallel section (Verbeek, 1977; Salaj, 1978 and 1980; Wonders, 1980; Perch-Nielsen, 1981; Brinkhuis and Zachariasse, 1988; Keller, 1988a;

Pospichal, 1994). We adopted the planktonic foraminiferal biozonation of Brinkhuis and Zachariasse (1988; Fig. 2), who largely processed the same (AFN) samples. In disagreement with their definition, we shifted the position of the K/P boundary to the base of the boundary clay, in accordance with the position of the GSSP.

For an elaborate account of definitions of the biozonation and taxonomic discussions we refer to Brinkhuis and Zachariasse (1988). We confine ourselves to some brief remarks. The lower part of the section belongs to the uppermost Maastrichtian *Abathomphalus mayaroensis* Zone. Because the zonal marker is extremely rare, proposed alternatives are the *Pseudotextularia deformis* Zone (Keller, 1988a) and the *Racemiguembelina fructicosa* (total range) Zone; *Racemiguembelina fructicosa* appears slightly earlier than *A. mayaroensis* in this and other localities (Nederbragt, written communication, 1992). The lower SN-coded samples belong to the upper half of the *R. fructicosa* zone. The presence of *Micula prinsii* confirms the presence of the youngest part of the Maastrichtian at the top of the section (Pospichal, 1994). The base of the *Guembelitria cretacea* Zone corresponds to the K/P boundary and the base of the boundary clay. The other Paleocene zones and the uppermost subzone are marked by the entry of their respective nominate zonal markers; the lowermost subzone is defined by the entry of *Parvularugoglobigerina eugubina*. The lowermost three biozones are in the following discussions generally taken together and referred to as "earliest (or lowermost) Paleocene". Although the validity of *Parasubbotina pseudobulloides* as a reliable synchronous marker has been questioned (Macleod and Keller, 1991a), we maintain this species as a zonal marker, because of its widespread use in accordance with the biozonal schemes of Berggren et al. (1985). The *P. pseudobulloides* Zone is generally referred to as "early (or lower) Paleocene" in further discussions.

The sections from which we derived the additional data suffer various flaws to render a detailed quantitative account useful: we encountered either biostratigraphic incompleteness or extreme condensation compared with El Kef and significant reworking of Cretaceous material into the lowermost Paleocene (cf. Keller et al., 1990). In all sections the uppermost Maastrichtian is present, judging from the presence of *Plummerita reicheli* (= *P. hantkeninoides*), a species that is considered to indicate a latest Maastrichtian age (Luger, 1988; Rosenfeld et al., 1989; Masters, 1993). In Gebel Qreiya this age assignment is confirmed by the presence of *M. prinsii* (Luger, 1988). The other sections yield Late Maastrichtian markers such as *Micula murus*, *Lithraphidites quadratus*, or *Nephrolithus frequens*, (Romein, 1979a,b; Faris, 1982; A. Henriksson, written communication, 1993); the absence of the delicate species *M. prinsii* might be due to the rather poor preservation of the nannofossils. In none of the sections the *G. cretacea* and *Parvularugoglobigerina fringa* Zones were recognized. In Nahal Avdat the *P. eugubina* Zone is also missing, although this may be due to a relatively wide sample spacing (Romein, 1979a,b). In the other sections this zone is very thin (< 10 cm). Finally, in all sections the *P. pseudobulloides* Zone was recovered and yielded samples with little, if any, reworking. Next to the Maastrichtian samples, it is those samples that we used for our comparison with El Kef.

Results

The Maastrichtian marls of all sections are homogeneous throughout, indicating good ventilation of the sea-floor leading to thorough bioturbation. The same applies to the early Paleocene marls in all localities. In

El Kef the lowermost three metres of the Paleocene show preservation of sedimentary lamination, pointing at an absence of burrowing organisms probably due to oxygen deficiency at the sediment-water interface. Increasing oxygen levels during the early Paleocene are suggested by homogeneous sediments and the concomitant appearance of abundant pyritized (*Chondritis*?) burrow fills (diameter < 0.6 mm). Apparently, some small organisms were able to settle as oxygen levels increased and occasionaly penetrated the sediment below the redox front. The timing of appearance and subsequent disappearance of sedimentary laminations and pyritized burrows corresponds accurately with major changes in the faunal and geochemical records, suggesting a close relationship between both.

As mentioned earlier, biological production failure seems to mark the K/P boundary; $CaCO_3$ and $\delta^{13}C$ records of these samples of El Kef have previously been published by Keller and Lindinger (1989). We present additional data from El Kef (Fig. 4) on the collapse in marine productivity, by means of planktonic and benthic foraminiferal numbers (PFN and BFN; > 63 μm) and P/B ratios (expressed as %P=P/P+B). PFN and BFN values generally increase with increasing productivity, but obviously a decrease in sedimentation rate would give the same result. Since there is still much controversion with respect to completeness and the exact amount of time involved with-

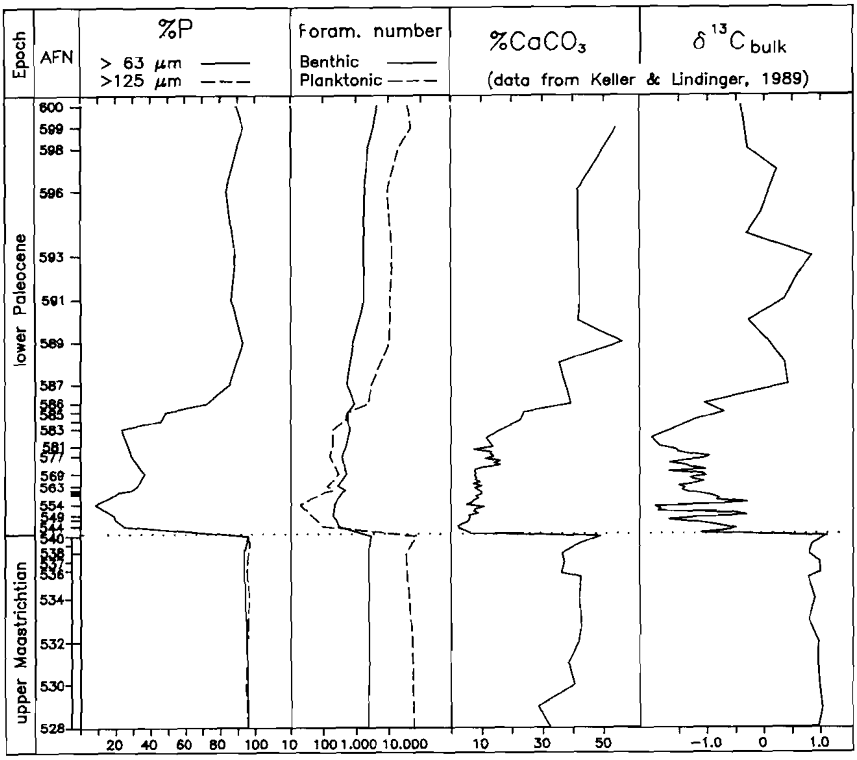

Fig. 4. The proportion of planktonic foraminifera (%P) and paleoproductivity proxies for the K/P boundary sequence of El Kef. Maastrichtian sample ticks on the left side of the vertical line mark the samples for which %P > 125 μm has been calculated; (fewer) sample ticks on the right side of this line mark the samples for which the other calculations have been performed.

in the boundary clay (Macleod and Keller, 1991b; Olsson and Liu, 1993; Berggren et al., 1994), we refrain from correcting for possible variations in sedimentation rate. We assume, however, that average sedimentation rate was highest during the Late Maastrichtian and early Paleocene and that it was somewhat depressed (possibly by a factor two, due to a decrease in $CaCO_3$ accumulation) during the earliest Paleocene.

As expected PFN and BFN values show a marked fall (three orders, and one order of magnitude, respectively) at the K/P boundary, coinciding with the negative excursions in the $CaCO_3$ and $\delta^{13}C$ records and thus strongly suggesting a crisis in primary production. This sharp fall was followed by a very gradual increase during the earliest Paleocene. At three metres above the K/P boundary, PFN values increase sharply; at this level the first sporadic specimens in the > 125 µm size fraction were encountered (Brinkhuis and Zachariasse, 1988) and $CaCO_3$ values are restored to Maastrichtian values. Only in the top of the section BFN and PFN values returned to Maastrichtian values. The $\delta^{13}C$ record did not recover to the former Maastrichtian situation. This could suggest that the early Paleocene was not as fertile as the Late Maastrichtian.

To get a first impression of the overall benthic foraminiferal changes we calculated Fisher-α diversity for the El Kef assemblages on the basis of the initial non-condensed data set that contained 132 taxa (Fig. 5). Similar to the previously discussed paleoproductivity proxies, this record shows a major fall at the K/P boundary and gradual recovery in the lower Paleocene.

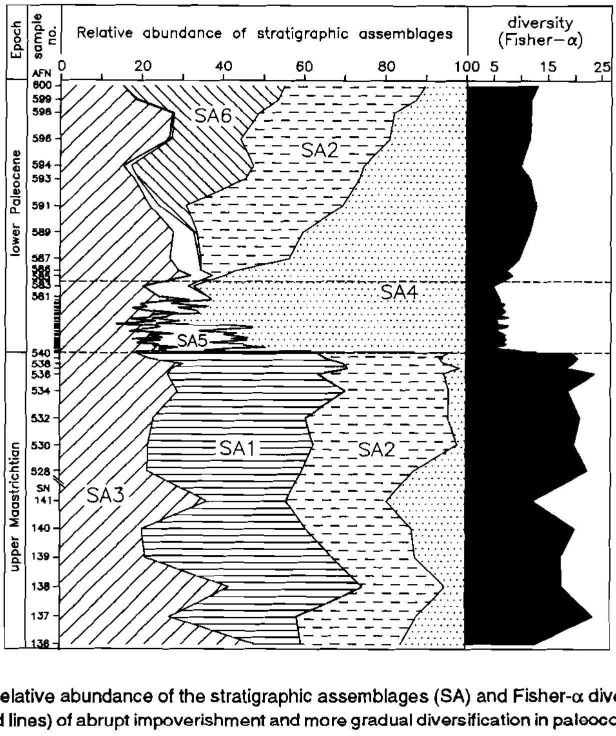

Fig. 5. Cumulative relative abundance of the stratigraphic assemblages (SA) and Fisher-α diversity visualise the two major steps (dashed lines) of abrupt impoverishment and more gradual diversification in paleocommunity development at El Kef. Note the change of scale as in figure 2.

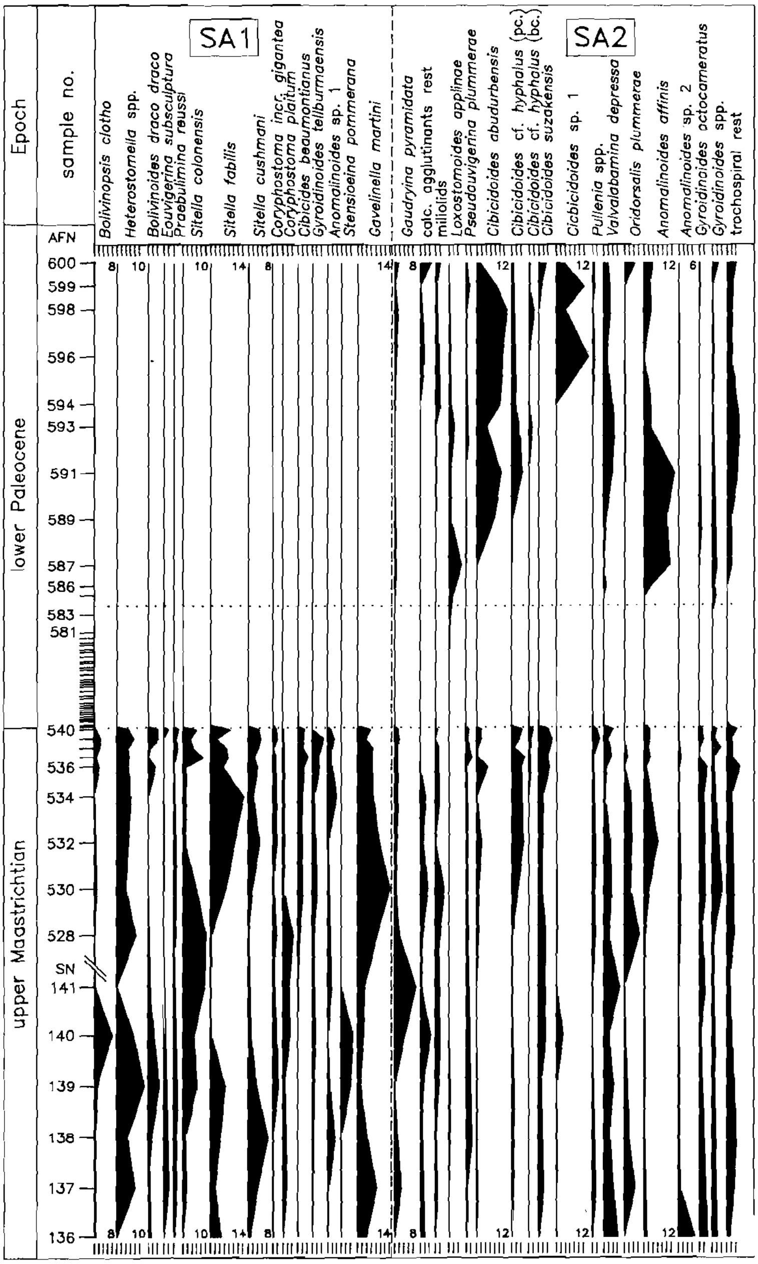

Fig. 6. Frequency range chart of the sixty most common taxa in the El Kef K/P boundary profile. SA 1-6 indicate groupings of taxa with corresponding distributional patterns. Note the change of scale as in figure 2.

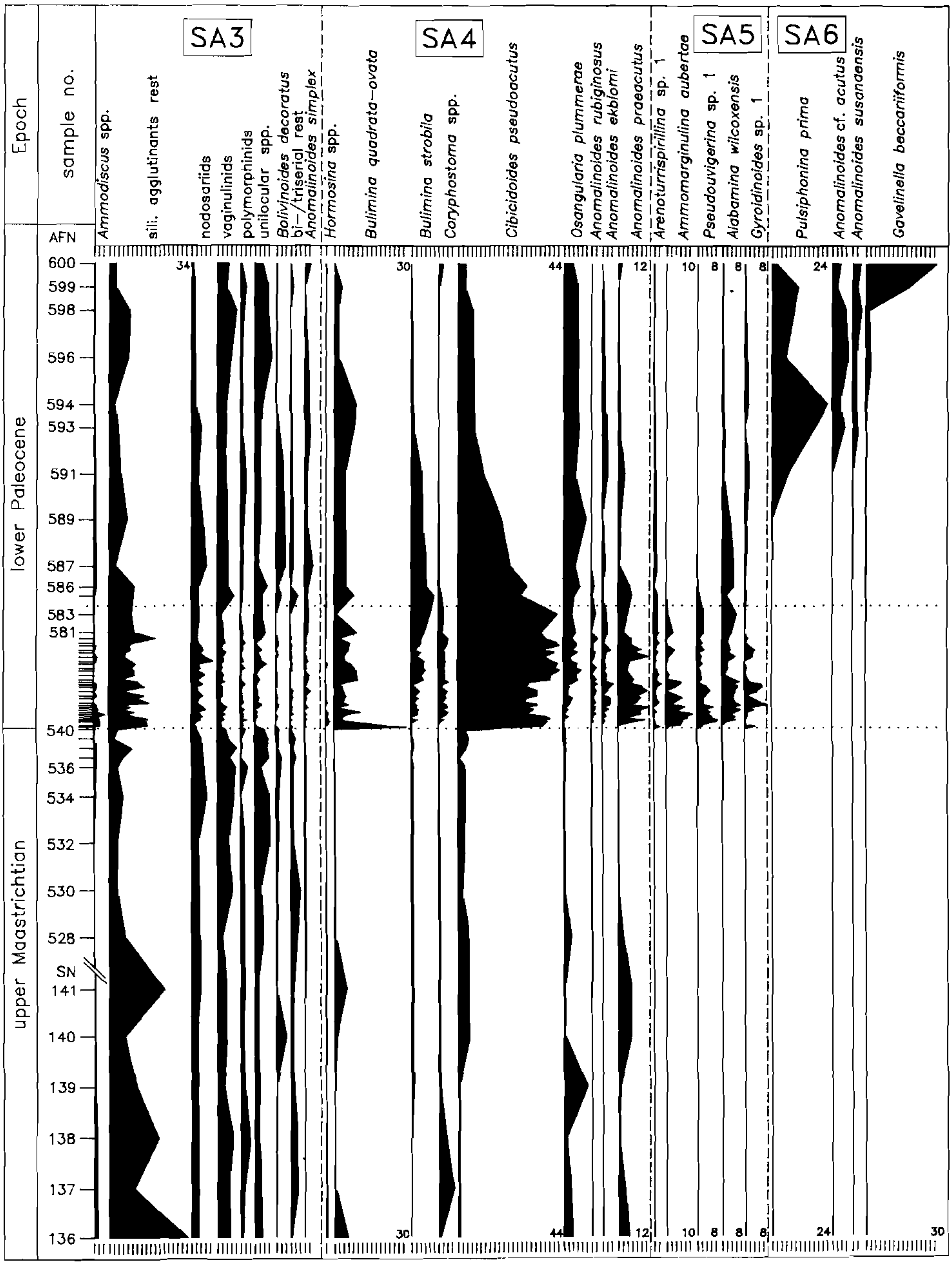

Fig. 6. (Continued)

Table 1. Frequency data of the sixty most common taxa in the El Kef K/P boundary profile.

Sample AFN (or SN)	136	137	138	139	140	141	528	530	532	534	536	537	538	539	540	221b	221a	543	220	544	545	546	547	548	549	550	551	553	554
cm rel. to K/P boundary	-3042	-2625	-2188	-1750	-1313	-900	-450	-350	-250	-150	-85	-65	-45	-25	-5	1.2	3.6	12.5	15.6	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	62.5	67.5
Bolivinopsis clotho	0.4	0.8	0.4	1.2	8	0.5	0	1.3	0	0	2.2	0.9	2.2	3	0.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterostomella spp.	0	7.9	4.5	11.9	7.3	0	8.2	3.9	4.9	6.1	4.8	5.2	4.5	7.4	5.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bolivinoides draco draco	1.3	0	1.5	4.8	2.5	0.5	0	0	0	0	3.1	0	0.7	4.4	4.2	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Eouvigerina subsculptura	0	2.4	1.9	0	1.1	0	0	0	0.4	0	0	0.4	0	0	1.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praebulimina reussi	0.4	1.2	1.1	2	1.1	0	0.8	0.9	0.9	1.5	0	0.9	1.5	1	1.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sitella colonensis	0	1.6	1.1	6.3	5.1	9.7	10.2	6.1	0.9	1.5	1.3	8.7	4.5	3.4	6	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0
Sitella fabilis	4.6	2	4.2	6.3	0.4	0	0.4	6.5	10.6	14.6	5.3	7.4	6.7	2.5	8.3	2.5	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Sitella cushmani	0.8	4	8.7	3.6	1.1	0	0	1.7	4.9	2	4	2.6	4.1	5.4	4.6	0.7	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Coryphostoma incrassata gigantea	0	0.4	0	2.4	1.5	0	1.6	0	1.8	1	1.3	1.3	0	2	1.4	0.7	0	0.3	0	0	0	0	0	0	0	0	0	0	0
Coryphostoma plaitum	0	1.6	1.5	0.8	3.3	2.9	4.7	0.4	0.9	0.5	0.9	1.3	1.1	1	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cibicides beaumontianus	0	0	0	0	0	0	0.8	2.2	1.3	2	2.6	4.3	1.9	2.5	2.8	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Gyroidinoides tellburmaensis	0	0.4	0.4	0.8	1.5	1	0.8	2.2	0.9	1	3.1	2.6	3.7	4.9	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides sp. 1	0	0.4	3.4	0.8	0	1.9	2	1.3	0.4	4	2.2	1.3	1.9	3	1.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stensioeina pommerana	0	0.4	0	4	5.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gavelinella martini	3.8	8.3	4.2	1.2	2.5	2.9	8.6	14.3	9.7	7.1	6.2	6.5	6.7	3.4	5.6	0.4	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Gaudryina pyramidata	0	2.8	1.1	0	4.4	9.2	2	0.4	0.9	1.5	0.9	1.3	1.1	2	1.4	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0
calc. agglutinants rest	1.7	0.8	0.4	1.2	4.7	0.5	1.2	3.5	1.3	2.5	0	0.4	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0
miliolids	0	1.2	0	1.6	2.2	0.5	2	3.9	0	2	1.8	1.3	1.5	0	0.9	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Loxostomoides applinae	0	0	0.4	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudouvigerina plummerae	0.4	0.4	2.7	1.6	0.4	0.5	1.2	0.9	0.9	1	0.4	2.6	1.5	1	1.4	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0
Cibicidoides abudurbensis	0	0.8	0	0.4	0	0	0.8	0.9	2.2	0	4.8	0.4	0.4	2	1.9	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Cibicidoides cf. hyphalus (pc)	0	0.8	0.8	1.2	0.4	0.5	0.4	3	5.3	4	4.4	5.6	1.1	3.4	4.6	0	0.6	0	0	0	0	0	0	0	0	0	0	0	0
Cibicidoides cf. hyphalus (bc)	0	0	0	0	0	0	0	0.4	0	0	0.9	0.4	0.7	1	1.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cibicidoides suzakensis	0.4	2.4	1.5	1.2	3.3	2.4	3.5	1.3	1.8	2	4.8	3.9	4.9	5.9	4.2	1.1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cicbicidoides sp. 1	0	0	0.8	0	2.9	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pullenia spp.	0	1.6	0.8	0.8	0	0	1.2	0.9	1.8	1	0.4	0.4	1.5	3	1.9	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0
Valvalabamina depressa	6.3	4.3	2.3	4.4	2.2	7.2	2.3	3.9	3.1	0.5	1.3	3.5	3	2	4.2	0.4	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Oridorsalis plummerae	0	4.7	1.9	1.2	0.7	0	6.6	2.6	3.1	3	0	1.3	0.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides affinis	1.3	0.8	0	0.4	0.7	0	0.4	2.2	6.2	3	0.9	2.6	1.5	2.5	2.3	1.1	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides sp. 2	7.1	0.8	0.4	0.8	0.4	0	0.8	0.9	0.9	0	0.4	0.9	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyroidinoides octocameratus	3.8	2.8	1.9	0.8	0.7	2.9	1.2	3	1.8	2	3.5	0	0.4	2	1.4	0.4	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Gyroidinoides spp.	2.1	2	1.1	0.8	1.5	0	0.8	4.3	2.7	1	0.9	0.9	3.4	1	1.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
trochospiral rest	1.3	3.2	4.2	3.2	1.5	1	3.1	3	3.1	2	5.7	2.2	2.6	2	4.2	1.1	0.9	0	0	0	0	0	0	0	0	0	0	0	0
Ammodiscus spp.	1.7	0.4	0.8	0	0.4	0	0.4	0	0	0.5	0.9	0.9	1.1	0	0.5	0.4	2.6	2.4	2.2	2.2	1.7	4.7	0.9	1.9	1.4	1.2	0	0	1.3
sili. agglutinants rest	34.2	10.7	21.6	11.9	6.9	24.2	7	3.5	3.5	6.1	3.5	5.6	9.7	2	3.7	12.3	17	16.5	14.4	17.2	11.4	7.9	11	5.4	9.2	5	17.5	11.5	15.4
nodosariids	2.9	2.8	3	1.6	2.2	3.9	3.5	2.6	3.1	6.6	5.3	5.2	4.5	4.4	2.3	2.1	0.9	2.4	4	3.3	4.7	3.7	3	6.2	5.1	3.3	2.6	3.4	4.9
vaginulinids	5.4	4.7	6.8	2.8	4	3.9	2	6.5	4.9	7.1	7.9	5.2	8.2	4.9	3.7	1.1	1.8	1.4	2.9	2.8	1.7	3.3	1.8	3.5	4.1	2.5	1.4	1.5	2.3
polymorphinids	0.8	1.6	4.2	1.6	0.7	1.9	0.8	1.3	2.2	0	3.1	0	0.4	0.5	2.3	0	1.2	0.7	2.9	0.6	1.3	1.4	0.6	1.9	0	0.4	1.4	0.8	0.8
unilocular spp.	2.9	3.6	1.5	2	1.1	1	3.9	2.6	6.6	6.6	2.6	6.1	5.2	5.9	4.2	0.7	0.6	0.3	0.7	0.3	1.3	0.9	1.2	0	1.8	3.3	1.4	1.9	1.5
Bolivinoides decoratus	0	0	0.8	0	4.4	0	0.4	0.4	0.9	1	1.8	2.2	0.4	1	1.4	0.4	0	0	0.4	0.3	0.8	0	0	0.4	0.9	1.2	0.3	0.8	0.5
bi-/triserial rest	0.4	3.2	3	1.2	0.4	1.4	2.7	4.3	1.3	0.5	0.9	2.2	0.7	2.5	0.5	1.1	0.3	0.3	0.7	0.3	0	1.4	0.3	0.8	0.9	0.4	0.3	1.1	0.8
Anomalinoides simplex	0	0	0	0	0	0	0.8	0.4	0.4	0.5	0.4	0	0	0.5	0	0.7	0.3	0.3	0.7	0.8	0	0.9	0	0	1.4	0.4	0.3	0.8	0.5
Hormosina spp.	0.4	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0.3	1.7	0.7	1.4	0.4	0.9	0.9	0	0	0	0.6	0.4	0.5
Bulimina quadrata-ovata	5.8	0.4	0	0	1.1	5.3	0.4	0	0	0	0.4	0.4	0	0	0	31.7	21.7	4.5	3.6	3.3	3.8	6	11.3	4.6	0.9	6.2	3.7	4.6	5.1
Bulimina strobila	0	0	0	0.8	0.7	1.9	1.6	0	0.9	0.5	0.9	0	0.7	1	0.5	0.4	0.6	1	2.9	0.8	0	2.8	3	3.1	2.3	2.5	1.1	3.1	1.5
Coryphostoma spp.	0.8	6.7	3.4	0.4	0.7	1	0.4	0	0	0	0	0	0	0	0	0	0.3	1	2.5	0.3	1.7	3.7	4.2	1.5	4.1	3.7	1.7	3.4	2.8
Cibicidoides pseudoacutus	0.8	0	0.8	0.4	5.1	4.8	5.1	1.7	3.1	3	3.1	0.4	3.4	4.9	3.2	29.2	37.8	39.5	26.6	40.8	38.6	28.8	31.6	33.5	29	35.1	29.6	30.3	34.9
Osangularia plummerae	3.8	2.8	1.1	10.3	0.4	0.5	3.1	0.4	0	0.5	0	0.4	0.7	1	0.9	0	0.3	0.3	0.7	0	2.1	0	0.9	1.9	0.9	2.1	2.9	3.8	1.8
Anomalinoides rubiginosus	0	0	0	0	0	0	0.4	0	0	0	0.4	0	0	0	0	0	0	1	0	0.6	0.8	1.9	0.9	1.5	1.8	0.8	2	0.8	1.3
Anomalinoides ekblomi	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	1	0.7	0.3	1.7	0.9	0.9	2.7	0.9	3.3	3.7	3.4	0.3
Anomalinoides praeacutus	4.6	2.8	0	0.8	5.8	5.8	2	0	0.4	0	0.4	0.4	0.4	0	0	0	0.6	7.2	11.9	3.6	5.5	9.8	9.6	10	13.8	4.1	8.3	10	8.5
Arenoturrispirillina sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5	0.9	0.3	0	0	0.4	0	1.2	0	0	1.2	2.3	1.1	1
Ammomarginulina aubertae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.4	6.2	7.2	6.8	9.2	9.3	11.6	4.2	5.8	8.3	2.5	3.4	6.9	5.1
Pseudouvigerina sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.1	1.8	8.2	9	6.7	6.4	4.7	5.7	3.5	6.9	2.9	2.6	2.7	3.8
Alabamina wilcoxensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.1	5.8	4.7	5.5	3.7	5.7	8.1	4.1	7.9	5.5	4.6	4.9
Gyroidinoides sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.6	0.6	0	0	0.6	0.8	0.9	1.2	3.8	1.8	9.9	6.9	3.1	0.5
Pulsiphonina prima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides cf. acutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides susanaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gavelinella beccariiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No. specimens	240	253	264	252	275	207	256	231	226	198	227	231	267	203	216	284	341	291	278	360	236	215	335	260	217	242	348	261	390
No. species	38	58	49	48	54	35	57	51	52	46	56	48	53	49	49	33	36	23	22	22	23	25	27	23	25	26	27	26	28

Table 1. (Continued)

Sample AFN (or SN)	556	558	559	560	561	563	565	566	568	569	571	573	574	576	577	579	581	583	585	586	587	589	591	593	594	596	598	599	600
cm rel. to K/P boundary	77.5	87.5	92.5	97.5	102.5	113	123	128	138	143	153	163	168	178	183	193	205	245	285	305	350	450	550	650	700	800	900	950	1000
Bolivinopsis clotho	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterostomella spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bolivinoides draco draco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eouvigerina subsculptura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praebulimina reussi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sitella colonensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sitella fabilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sitella cushmani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coryphostoma incrassata gigantea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coryphostoma plaitum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cibicides beaumontianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyroidinoides tellburmaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stensioeina pommerana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gavelinella martini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaudryina pyramidata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	1	0.4	0	0	0	0.6	1.3	0	1.5
calc. agglutinants rest	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.9	0.9	0	4.5
miliolids	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	1.9	1.3	0.9	0.5	1.9
Loxostomoides applinae	0	0	0	0	0	0	0	0.3	0	0	0	0.4	0.3	0	0	0	0	0.7	1.4	3	5.6	0.8	0.5	2.4	0.8	0.6	0.4	0	0
Pseudouvigerina plummerae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	1.4	0.4	0	0.4	1.5	0.4
Cibicidoides abudurbensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.6	10.5	4.3	10.1	11.3	13.4	8.5	1.5
Cibicidoides cf. hyphalus (pc)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	4.6	3.3	1.6	1.6	1.7	1	0.8
Cibicidoides cf. hyphalus (bc)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	1.4	0	0	2.2	0	0.4
Cibicidoides suzakensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
Cicbicidoides sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13.8	3.9	12	3.4
Pullenia spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9	0	1	0.8
Valvalabamina depressa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.3	0	1.1	3.7	4.8	3.9	1.3	3	3	1.9
Oridorsalis plummerae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0.4	0	0	0	4.2
Anomalinoides affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	11.2	9.8	13.2	2.9	3.5	0	3	2.5	3.8
Anomalinoides sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	0	0	0
Gyroidinoides octocameratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.1	0	0	0	0	0	0.5	0
Gyroidinoides spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.4	0.8	2	2.3	0.9	1.4	0	0.9	0	0	2.3
trochospiral rest	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0.7	0	0	2	1.9	4.6	5.7	4.7	1.9	2.2	2.5	4.2
Ammodiscus spp.	0.4	1.2	1.3	0	0	0	0	0.3	0	0.9	1.4	0	0.3	0.8	0.4	0.5	0.4	0	0.5	1.3	1	0	0.9	0	0	0.3	0.4	0.5	0.4
sili. agglutinants rest	5.5	15.4	13.4	12.6	5	11.1	10.8	9.7	11.6	9.9	6.6	7.2	9.2	8.7	10.2	20.3	11.1	9.8	10.6	11	2.6	8	5	3.8	2.3	8.5	9.1	3	2.7
nodosariids	2.9	2.3	5	3.3	2.7	5.9	2.5	3.8	3	9.4	5.7	3.8	5.2	4.2	3.1	2.6	2.7	3.6	3.2	3.4	6.6	4.9	2.7	4.3	1.9	1.9	2.2	1	0.8
vaginulinids	2.2	2.3	1	3.3	1.9	2.8	1.3	2.1	1.7	2.7	2.4	3.8	2	1.9	3.5	2.8	2.7	1.8	7.3	4.6	5.1	5.7	3.2	3.8	3.9	6	8.2	4	4.9
polymorphinids	0.7	0.8	2	1.1	0.4	0.4	0.4	1.9	0	1.3	0.5	0.4	0.9	0.8	2	0.5	1.3	0	0.9	0.8	1	1.5	2.7	0.5	0.8	0.6	1.3	2.5	0.4
unilocular spp.	1.5	0.8	1	1.6	2.3	0.8	1.7	2.4	5.2	3.1	2.4	1.3	2.9	1.1	0.4	3.3	4.9	3.3	3.2	5.5	1.5	2.7	2.3	2.4	3.5	7.5	5.6	6	3.4
Bolivinoides decoratus	0	0	0.3	0.5	0	0.4	0	0.5	0	0	0.5	0.9	0	1.1	1.2	0.7	0	0	2.3	0.8	4.1	3.4	3.7	1	0	0.6	0.4	0.5	0.4
bi-/triserial rest	1.1	0	0	0	0	0	0.8	0.5	0.9	0.4	0.9	0.4	0.3	0.8	0	0.5	0	0	3.2	0	1.5	0.8	0.5	0	0.8	0	0	1	0
Anomalinoides simplex	2.6	0	0.7	1.1	1.5	2	0	0.8	0.4	1.3	0.9	0	0.6	0.4	0.8	0.5	1.3	1.8	0.9	1.7	3.6	0.8	0.9	2.4	2.3	1.3	0.4	0	2.3
Hormosina spp.	0	0.4	0.3	0	0	0	0	0.3	0.9	0	0	0	0.3	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0
Bulimina quadrata-ovata	4	3.5	2	5.5	10.3	9.9	9.6	8.8	7.3	4.9	4.2	5.1	6.1	6.5	6.6	2.1	9.8	0.7	8.7	5.1	5.6	5.3	4.6	8.6	9.7	1.9	1.7	3	0
Bulimina strobila	3.7	1.5	0.7	3.3	5.4	4.3	6.3	5.4	5.2	5.8	2.8	4.3	1.7	3.8	4.3	4.5	5.8	8.3	10.1	6.8	7.1	4.9	4.6	1	1.6	1.3	1.3	0	0
Coryphostoma spp.	4	1.2	2	4.4	2.7	2.8	2.9	2.7	3	3.1	2.8	3	2.3	3.8	3.9	4.3	1.8	2.5	1.4	0.8	0.5	0	0	0.5	0	0.3	0	0.5	1.9
Cibicidoides pseudoacutus	35.2	29.3	31.2	31.3	40.6	41.1	44.6	42.6	43.8	41.3	37.7	42.6	35.4	44.5	43.4	38.5	36.4	43.8	27.5	30.4	23	19.3	11.4	7.1	7	7.2	6.5	3	3.4
Osangularia plummerae	1.8	2.3	2	4.4	6.1	5.1	7.9	5.6	6	3.6	2.8	6	3.5	5.7	5.5	3.5	5.3	3.6	4.6	7.2	5.1	9.8	5	6.7	5.8	6.6	7.4	6	3.8
Anomalinoides rubiginosus	2.2	0.8	2.7	1.1	2.3	0.4	1.3	2.4	0.4	0.4	1.4	1.7	0.6	0.8	0.8	2.8	0	1.8	0.5	1.3	0	0	0	0	0	0	0	0	0
Anomalinoides ekblomi	2.2	3.5	5	1.6	1.9	2	0.8	1.6	1.3	0.9	1.4	1.7	3.7	1.5	0.8	1.2	2.2	1.8	0.5	0.4	1.5	0	2.3	2.4	1.2	1.9	0.9	0	0
Anomalinoides praeacutus	12.8	10.4	6.4	6	6.9	5.1	3.8	4.3	4.7	5.4	13.2	6.4	10.1	6.1	5.5	5.7	2.2	4.3	6	5.1	0.5	1.1	2.7	0.5	0	0	0	0	1.5
Arenoturrispirillina sp. 1	0.7	1.5	3.4	1.6	1.1	2	1.3	0.3	0.4	0.9	0.5	1.7	0.6	1.1	2.3	0.7	2.2	1.4	1.8	0	1.5	0.4	0	0	0	0	0	0	0
Ammomarginulina aubertae	0	4.2	6	6.6	0.4	1.2	0	0	0	0.4	0.9	2.6	3.5	0.4	0	0.2	3.1	0.7	0	0	0	0	0	0	0	0	0	0	0
Pseudouvigerina sp. 1	5.5	3.9	1.7	0.5	1.9	1.6	1.3	0.5	2.1	1.3	1.9	0.9	2.9	1.5	2.3	0.9	2.7	2.9	0.9	0.4	0	0.4	0	0	0	0	0	0	0
Alabamina wilcoxensis	5.5	6.9	4.7	7.7	5	0.8	2.1	2.4	2.1	2.7	5.7	2.6	3.5	3	2.3	2.6	4	6.2	1.8	5.1	5.1	3.4	0.5	1	0.4	0	0.4	0.5	0
Gyroidinoides sp. 1	5.5	7.7	7	2.2	1.5	0.4	0.4	0.8	0	0	3.3	3.4	4.3	1.5	0.4	1.2	0	0	0.9	0	0.5	0.8	1.8	0	1.6	0.6	0	0	0
Pulsiphonina prima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.8	18.6	24.5	6	9.5	11.5	1.9
Anomalinoides cf. acutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5.2	3.5	6.9	6.1	2	3.4
Anomalinoides susanaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	2.4	1.6	1.6	3.9	2	3.4
Gavelinella beccariiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0	0	0.5	0.4	0	0	0.4	2.5	1.3	19	31.1
No. specimens	273	259	298	182	261	253	240	373	233	223	212	235	347	263	256	423	225	276	218	237	196	264	219	210	257	319	231	200	264
No. species	22	22	27	25	21	22	21	30	21	24	25	24	26	26	23	27	22	20	28	26	30	37	37	34	33	39	36	34	40

In figure 6 frequency data of the sixty most common taxa of the condensed data set (Table 1) are arranged according their sequential distribution. In this way, six stratigraphic assemblages (SA 1-6) are discriminated, each with a specific range. SA 1 consists of taxa that are restricted to the Maastrichtian; all these taxa became (at least locally) extinct at the K/P boundary. SA 2 contains all Lazarus taxa, i.e. Maastrichtian taxa with an absence interval in the lowermost Paleocene. SA 3 contains all taxa that are present in the entire sequence; most of these taxa (mainly lump categories, especially all Nodosariacea) show a fairly constant frequency pattern. Taxa of SA 4 have the same stratigraphic distribution as SA 3, but show a marked relative abundance increase in the lowermost Paleocene. SA 5 consists of taxa that first appear at the base of the boundary clay; most taxa decline in relative numbers or disappear in the lower Paleocene. SA 6 contains taxa that first appear in the lower Paleocene.

For each stratigraphic assemblage the cumulative frequencies are displayed in figure 5; this graph clearly shows three stages in the benthic foraminiferal development: Maastrichtian, earliest Paleocene, and early Paleocene. The Maastrichtian assemblage (SN 136 to AFN 540) is highly diversified (average $\alpha = 19.2$); two negative diversity excursions (SN 136 and SN 141) mainly result from a squeeze effect by the large proportion of lumped silicious agglutinants. The assemblage is dominated by SA 1 taxa (together up to 46%): *Heterostomella* spp., *Sitella colonensis*, *S. fabilis* and *Gavelinella martini* reach peak abundances of 10-15%. Although individual frequencies strongly vary, the assemblage as a whole is fairly stable up to the K/P boundary: only two common species, *Stensioeina pommerana* and *Oridorsalis plummerae*, disappear (well) below the K/P boundary; not a single (common) species appears just below the boundary.

The K/P boundary is marked by the (partly temporal) exit of 75% of the taxa (SA 1, 2; excluding lumped taxa above generic level) that are present in the uppermost metre of the Maastrichtian. Scattered occurrences (together up to 5%) of these taxa in the three basal Paleocene samples are thought to be reworked contaminants, as are the co-occurring large planktonic foraminifera. Almost 50% of the disappearing taxa are Lazarus taxa, that reappear higher in the section.

The earliest Paleocene assemblage (SN 221b to AFN 583) is poorly diversified (average $\alpha = 6.6$); the relatively high diversity in the two basal Paleocene samples is considered to be an artifact caused by the presumed reworking from the Upper Cretaceous. All samples are dominated by SA 4 taxa (up to 77%), and for all but the lowermost sample the dominant taxon is *Cibicidoides pseudoacutus* (29-45%). Other important constituents as *Bulimina quadrata-ovata*, *Anomalinoides praeacutus* and *Ammomarginulina aubertae*, reach peak abundances of 10-32%. Most common taxa in this assemblage were either absent or subordinate during the Maastrichtian. Faunal composition is fairly constant within this timeslice. There is however a marked increase in relative abundance of *C. pseudoacutus*, coinciding with a decrease of SA 5 taxa (Figs. 4, 5).

The transition from the earliest Paleocene to the early Paleocene assemblage is much more gradual than the K/P transition; therefore, the boundary is arbitrarily drawn at the first distinct decrease of *C. pseudoacutus* and the concomitant increase in diversity (between AFN 583 and AFN 585; Fig. 5). The early Paleocene assemblage is moderately diversified (average $\alpha = 10.9$). Initially, SA 3 species are still dominant (in particular *C. pseudoacutus*), but the proportion of reappearing Lazarus taxa (SA 2) steadily increases up to a level where new taxa of SA 6 appear at the expense of taxa of SA 3 and 5. *Cibicidoides abudurbensis*, *Cibicidoides sp. 1*, *Anomalinoides affinis*, *Bulimina strobila*, *C. pseudoacutus*, *Pulsiphonina prima*, and *Gavelinella beccarii-*

formis reach peak abundances of 10-31%. This assemblage clearly evolves with time and it does not appear to have stabilized at the top of the studied interval, in view of for instance the sudden increase of *Gavelinella beccariiformis.* Overlying samples (AFN 600-610) have been studied, but foraminiferal preservation deteriorated so dramatically that these samples were not quantified because of the possibility of introducing preservational artifacts.

39% of the latest Maastrichtian taxa in El Kef (present in the upper metre, excluding lumped taxa above generic level) disappeared at the K/P boundary and did not return. Some of these (*Coryphostoma incrassata gigantea* and *Cibicides beaumontianus*) persisted in the lower part of the *P. pseudobulloides* Zone in Wadi Nukhl (Table 2), but eventually became extinct in this area also. In addition, we have observed *Bolivinopsis clotho* and *Praebulimina reussi* in younger Paleocene assemblages from Egypt and Israel (unpubl. data), so these taxa merely show a K/P exodus from El Kef. Specimens of most other taxa have been observed in relatively low numbers in beds immediately overlying the K/P boundary in Egypt and Israel. As explained earlier, their rare occurrence combined with common *Globotruncana* and/or *Rugoglobigerina* strongly suggests that these specimens are reworked, apparently a common phenomena in these areas (cf. Luger, 1988; Keller et al., 1990).

Stages in southern Tethyan paleocommunity and paleoenvironmental development

Semi-quantitative data of the additional K/P profiles of Gebel Duwi, Gebel Qreiya, Wadi Nukhl, and Nahal Avdat are listed in Table 2. The table lists all common taxa of El Kef, and in addition those taxa that are common in any of the other localities. As explained earlier, we can not compare the earliest Paleocene faunal sequence with the one from El Kef, but we can at least address Late Maastrichtian and early Paleocene biogeographic and paleobathymetric patterns and discuss the overall faunal change across the K/P boundary.

Late Maastrichtian

Late Maastrichtian assemblages from Wadi Nukhl and Nahal Avdat bear great resemblance with the one from El Kef. Very similar assemblages were also documented by Benjamini et al., (1992) and Keller (1992); also the ones described by LeRoy (1953) and Said and Kenawy (1956) are probably comparable. Very little is known on Maastrichtian benthic foraminiferal paleobathymetric distribution in North Africa, but comparison with Campanian-Maastrichtian paleoslope models of North America (Sliter and Baker, 1972; Olsson, 1977; Nyong and Olsson, 1984; Olsson and Nyong, 1984) suggests greatest similarity with upper bathyal assemblages. Therefore, the highly diverse Maastrichtian assemblage of El Kef, northern Egypt, and Israel seems indicative for a similar upper bathyal (300-500 m) setting. High P/B ratio's (> 95% P; Fig. 4) confirm such an assignment. Also Keller (1988b, 1992) inferred an upper bathyal-outer neritic position for this assemblage.

The Late Maastrichtian assemblage from Gebel Qreiya differs significantly from these upper bathyal assemblages; diversity is much lower and especially the taxa of SA 1-2 are absent. Instead we find *Orthokarstenia oveyi*, *Pyramidina aegyptiaca*, *Elhasaella allanwoodi*, *Neobulimina canadensis*, and *Anomalinoides umboniferus*; not a single specimen of these species was encountered in the upper bathyal assemblage. The Late Maastrichtian assemblage of Gebel Duwi is even more dissimilar; it has very few taxa in common with the bathyal assemblage (mainly in the lump

Time-slice	upper Maastrichtian				lower Paleocene			
Locality	Nukh	Avdat	Qreiya	Duwi	Nukh	Avdat	Qreiya	Duwi
Bolivinopsis clotho	*	*						
Heterostomella spp.	*	*						
Bolivinoides draco draco	*	C						
Eouvigerina subsculptura	*	C						
Praebulimina reussi	C	*						
Sitella colonensis								
Sitella fabilis	*							
Sitella cushmani	*	C	*					
Coryphostoma incrassata gigantea	C	*			C			
Coryphostoma plaitum	*	*						
Cibicides beaumontianus	*	*			*			
Gyroidinoides teliburmaensis	*	*						
Anomalinoides sp. 1	*	*						
Stensioeina pommerana								
Gavelinella martini	*	*						
Gaudryina pyramidata	*	*			C	*		
calc. agglutinants rest	*	*	*		C	*	*	*
miliolids								
Loxostomoides applinae	*	*			*	*	*	*
Pseudouvigerina plummerae	*	*			*			
Cibicidoides abudurbensis	C	C	*		C	*	*	
Cibicidoides cf. hyphalus (pc)	*				*	*		
Cibicidoides cf. hyphalus (bc)	*	*			*	*		
Cibicidoides suzakensis	*	*			*	*		
Cicbicidoides sp. 1								
Pullenia spp.	*	*			*	*		
Valvalabamina depressa	*	*	*		*	C	*	*
Oridorsalis plummerae	*	*	*		*	*		*
Anomalinoides affinis	*	*			*	*	*	
Anomalinoides sp. 2								
Gyroidinoides octocameratus	*	*	*		*			
Gyroidinoides spp.	*	*	*		*	*	*	
trochospiral rest	*	*	*	*	*	*	*	*
Ammodiscus spp.								*
sili. agglutinants rest	*	*	*	*	*		*	*
nodosariids	*	*	*	*	*	*	*	*
vaginulinids	*	*	*	*	C	*	*	*
polymorphinids	*	*	*		*	*	*	*
unilocular spp.	*	*			*	*		
Bolivinoides decoratus	*	*			*	*		
bi-/triserial rest	*	*	*	*	*	*	*	*
Anomalinoides simplex		*			*	*		
Hormosina spp.								
Bulimina quadrata-ovata	*	*	*		*	*	*	
Bulimina strobila	*		C		*	*	*	
Coryphostoma spp.	*				*		*	
Cibicidoides pseudoacutus	C	*	C		C	C	C	*
Osangularia plummerae	C	*	*		C	C	*	*
Anomalinoides rubiginosus					*	*		
Anomalinoides ekblomi								
Anomalinoides praeacutus	*				*	*	*	*
Arenoturrispirillina sp. 1								
Ammomarginulina aubertae								
Pseudouvigerina sp. 1								
Alabamina wilcoxensis	*		*		*		*	
Gyroidinoides sp. 1								
Pulsiphonina prima							*	
Anomalinoides cf. acutus					*	*		
Anomalinoides susanaensis					*		*	
Gavelinella beccariiformis					C	C		
Gyroidinoides cf. cibaoensis	*	*						
Gyroidinoides girardanus						*	C	*
Orthokarstenia oveyi			*	C				
Pyramidina aegyptiaca			*	C				
Elhasaella allanwoodi			*	C				
Anomalinoides umboniferus			C	C			*	C
Neobulimina canadensis			*	C				*
Cibicidoides sp. 2				*				C
Alabamina midwayensis								*
Pseudoeponides cf. elevatus								*
Siphogenerinoides sp. 1							*	*

categories), whereas the previously mentioned taxa of Gebel Qreiya are very abundant. In both foraminiferal associations planktonic foraminifera are abundant (80% in Gebel Qreiya; 50% in Gebel Duwi), but much less so than in the bathyal association (> 90%). Luger (1985) described a Maastrichtian assemblage from central Egypt (Naqb Asyut section) that appears very similar to the one from Gebel Qreiya, and he inferred a middle neritic (50-100 m paleodepth) biofacies. In Gebel Qreiya the P/B ratio is higher than in Naqb Asyut, suggestive for slightly deeper conditions (middle-outer neritic, 75-150 m) there. Judging from the increasing dissimilarity with the upper bathyal assemblage, we regard the Gebel Duwi assemblage as an even shallower fauna (middle neritic, 50-100 m). Paleogeographic considerations substantiate the view of an epicontinental basin that deepened from the shore along the Arabian shield in northwestern direction (Luger, 1988; Said, 1990c,d), a situation that persisted at least to early Eocene times (Speijer and Van der Zwaan, 1994b).

In sharp contrast with the Paleocene (Aubert and Berggren, 1976; Saint-Marc and Berggren, 1988; Saint-Marc, 1993) very little is known on Late Maastrichtian benthic foraminiferal distribution in Tunisia. Apart from El Kef we were only able to retrieve documentation from an area southeast of El Kef (Said, 1978); the briefly described fauna shows considerable similarity with the one from El Kef. Therefore, we can not assess with certainty whether biofacial distribution similar to the one in Egypt existed in Tunisia, but since many of the shallow water taxa are also known from West Africa (Petters, 1982), it seems plausible that similar shallow assemblages indeed existed in Tunisia. In any case, the El Kef assemblage seems to represent a relatively deep offshore fauna very similar to the deepest biofacies as seen in Egypt and Israel and is thus widely distributed along the southern Tethyan rim.

Planktonic foraminiferal assemblages from El Kef dominated by few heterohelicids and relative scarceness of globotruncanids, the $\delta^{13}C$ record, as well as global climate models, suggest high fertility in surface waters induced by (possibly intermittent) coastal upwelling (Parrish and Curtis, 1982; Reiss, 1988; Keller and Lindinger, 1989; Kroon and Nederbragt, 1990; Nederbragt, 1992). The resulting high organic flux apparently favoured most common taxa as *Heterostomella* spp., *Sitella* spp. and *G. martini*. Such a preference for high nutrient conditions would explain why these taxa are usually infrequent or even absent in deep-sea assemblages. At the same time the presence of rich food resources may explain why many common bathyal (and therefore most likely oligotrophic) taxa such as *Gavelinella beccariiformis*, *Cibicidoides hyphalus*, *Nuttalides truempyi*, *Gyroidinoides globosus* and *Bulimina trinitatensis* were absent in this region during the Late Maastrichtian. Despite the high organic flux, a clear OMZ did not develop at this depth, judging from the high diversity of the benthic assemblage; oxygen advection was apparently sufficient. Results from ostracode studies concur very well with this view on the Maastrichtian paleoenvironmental setting (Donze et al., 1982; Peypouquet et al., 1986).

Earliest Paleocene

The rather peculiar earliest Paleocene assemblage of El Kef has to our knowledge

Table 2. Semi-quantitative data of additional K/P profiles. Data of the lowermost Paleocene are not considered because of considerable reworking and/or hiatuses. Species in lower block were very rare or absent in El Kef.
* marks average abundance < 5%; C marks average abundance > 5%.

not been described from other areas. An exception might be one of the assemblages studied by Said (1978); in this mainly biostratigraphic work on a section 50 km SE of El Kef the presence of abundant *B. quadrata-ovata* and *Cibicidoides alleni* (= *C. pseudoacutus*?) next to several Nodosariacea are mentioned for the earliest-early Paleocene. This might well be a very similar assemblage, but more helpful information is unfortunately not available. Aubert and Berggren (1976) analysed various Paleocene sequences from Tunisia, but none of them yielded an assemblage similar to the one from El Kef, although there are many species in common. The following common species in El Kef were not mentioned by these authors: *Anomalinoides ekblomi*, *Ammomarginulina aubertae*, *Pseudouvigerina* sp. 1, *Alabamina wilcoxensis*, and *Gyroidinoides* sp. 1; of these species *A. aubertae* and *A. ekblomi* have been recorded in boreal areas (Brotzen, 1948; Gradstein and Kaminski, 1989; Kuhn, 1992). We observed *Pseudouvigerina* sp. 1 in a K/P boundary profile of the Maastrichtian type-area (unpubl. data). Clearly, these species were not common constituents of Tunisian Paleocene assemblages.

The Maastrichtian and the early Paleocene assemblages of Gebel Qreiya show the greatest similarity with the earliest Paleocene fauna of El Kef; especially the agreement in presence and proportion of *Cibicidoides pseudoacutus* and *Bulimina strobila* next to *B. quadrata-ovata*, *Osangularia plummerae*, *A. wilcoxensis* (SA 4, 5) is striking, although also *Valvalabamina depressa*, *Gyroidinoides octocameratus*, and *Oridorsalis plummerae* (Lazarus taxa, SA 2 in El Kef) are present, and most taxa of SA 5 are absent in Gebel Qreiya. Since these middle-outer neritic Egyptian assemblages show the best correspondance, it could be argued that the earliest Paleocene assemblage of El Kef also represents middle-outer neritic deposition (cf. Keller, 1988b, 1992).

Low diversity, high dominance (*C. pseudoacutus*) and preservation of lamination indicate considerable oxygen deficiency at the seafloor during the earliest Paleocene. The two basal Paleocene samples (K/P + 1.2 and 3.6 cm) show a unique spike in abundance of *B. quadrata-ovata*, a taxon that seems to be a morphological analogue of the modern endobentic *Globobulimina*. The latter is able to live deep in the sediment where it feeds on degraded organic matter and/or associated bacteria under nearly anoxic conditions (Corliss, 1985; Buzas et al., 1993; Jorissen et al., 1994). *Bulimina quadrata-ovata* could have adopted a similar strategy; peak values at the K/P boundary suggest that for some time this taxon was the most successful one in coping with oxygen deficient conditions. A corresponding peak in total organic carbon (TOC) content (3-5%; Keller and Lindinger, 1989) at a time of low primary production (Fig. 4) suggests that oxygen deficiency was most severe at that stage. The subsequent decrease in *B. quadrata-ovata* and TOC signals slightly better ventilation, enabling more taxa to (re-)occupy their niche (e.g. *B. strobila*, *Anomalinoides rubiginosus*, *A. ekblomi*, and *Alabamina wilcoxensis*). Slightly ameliorating conditions were apparently especially suitable for the proliferation of the epibenthic *C. pseudoacutus* and lasted up to the early Paleocene.

A minor faunal change (decrease in SA 5) one metre above the K/P boundary coincides with a rise in planktonic foraminiferal numbers, and with a compositional turnover in the pelagic ecosystem (Brinkhuis and Zachariasse, 1988), interpreted to reflect elevated nutrient levels. This suggests that SA 5 taxa were particularly well adapted to minimal food supply under oxygen deficient conditions. Conclusions drawn from the ostracode record across the K/P boundary seem to support our interpretation (Donze et al., 1982; Peypouquet et al., 1986).

It is unlikely that the described dysoxic conditions are the result of increased primary production, since all fertility proxies indicate a sharp decrease at the K/P boundary (Fig. 4). A decrease in ventilation seems an acceptable altemative explanation. A similar situation is inferred from benthic foraminiferal pattems at the K/P boundary of Caravaca in souhtem Spain (Coccioni et al., 1993). In various other continental margin deposits anoxic or dysoxic conditions can be inferred from (a combination of) lamination, pyrite, or organic or trace element enrichments (e.g. Austria: Lahodynsky, 1988; Denmark: Ekdale and Bromley, 1984; Schmitz, 1985; Kunzendorf et al., 1990; Israel: Magaritz et al., 1985; Japan: Kaijwara and Kaiho, 1992; Kazachstan: Sarkar et al., 1992; New Zealand: Gilmour and Anders, 1989; Seymour Island: Huber, 1988; Spain: Wiedmann, 1988; Kuhnt and Kaminski, 1993). Apparently, oxygen deficiency seems to have been a widespread phenomenon during the earliest Tertiary, especially in Tethyan regions, although its duration may have varied from place to place.

Early Paleocene

As during the Late Maastrichtian, the early Paleocene fauna's of Wadi Nukhl and Nahal Avdat bear great resemblance with the one from El Kef; most taxa of SA 2-4, and 6 are present, some of the more common ones also in similar relative frequencies (e.g. *C. abudurbensis, C. pseudoacutus, Osangularia plummerae*, and *G. beccariiformis*). Early Paleocene assemblages from other areas in Israel and Tunisia also show this similarity (Aubert and Berggren, 1976; Benjamini et al., 1992; Keller, 1992). Many species belong to the cosmopolitan shallow marine Midway Fauna (see Berggren and Aubert, 1975). In contrast, *G. beccariiformis* is often abundant in Late Cretaceous-Paleocene deep-sea deposits (Tjalsma and Lohmann, 1983; Van Morkhoven et al., 1986), particularly at high southem latitudes (Katz and Miller, 1991; Widmark, in prep.); but it is also found in locally subsiding basins of Tunisia (Aubert and Berggren, 1976; Saint-Marc and Berggren, 1988). The mixture of shallow and deep marine components indicates an intermediate bathymetric position, probably upper bathyal (200-400 m), in accordance with Tunisian and Egyptian paleobathymetric models for the Paleocene (Saint-Marc and Berggren, 1988; Saint-Marc, 1993; Speijer, 1994b). Low frequencies of *Angulogavelinella avnimelechi* and *Nuttallides* sp. 1 (lumped in "trochospiral rest") substantiate this paleodepth assignment (Van Morkhoven et al., 1986).

The early Paleocene assemblages of Gebel Qreiya and Gebel Duwi are different from the upper bathyal assemblages, although less different than during the Late Maastrichtian; this applies in particular to the much more diverse Gebel Duwi fauna. As argued earlier, these assemblages indicate middle-outer neritic deposition (Luger, 1985). Similar shallow water assemblages were present in Tunisia during the early Paleocene (Aubert and Berggren, 1976).

The sequential (re-)appearance of many taxa and the resulting diversification in El Kef clearly reflects progressive amelioration of the bottom environment, as was already suggested by the disappearance of lamination. The retum of only the less common Maastrichtian taxa and the appearance of the probably oligotrophic deep-sea marker *Gavelinella beccariiformis* indicate a reduced food supply compared with the Late Maastrichtian; the $\delta^{13}C$ record as well as PFN and BFN values confirm this view. In their study on the ostracods of El Kef, Peypouquet et al. (1986) suggested increasing but still slightly depressed oxygen and nutrient levels during the lower part of the *P. pseudobulloides* Zone, in comparison with the Late Maastrichtian. Planktonic foraminifera as well as dinoflagellates suggest a retum to more stable conditions and optimum niche differentiation (Brinkhuis and Zachariasse, 1988).

Discussion

Quasi-paleobathymetric changes

Superficially, the faunal sequence of El Kef seems to reflect sea-level variations; an abrupt major shallowing from about 300-500 m to 75-150 m at the K/P boundary, followed by a more gradual deepening from about 75-150 m to 200-400 m during the early Paleocene. However, the tight coincidence between faunal change and proxy records for oxygenation and productivity suggest a more complex situation. We consider food and oxygen supply to be fundamental parameters in determining overall patterns in foraminiferal composition and abundance (e.g. Harman, 1964; Van der Zwaan, 1982; Lutze and Coulbourne, 1984; Jorissen, 1987; Corliss and Chen, 1988; Sjoerdsma and Van der Zwaan, 1992; Sen Gupta and Machain-Castillo, 1993). Paleoecological model simulations predict, that a significant change in either one of these parameters could result in considerable community alteration e.g. reflecting a quasi-bathymetric change (Sjoerdsma and Van der Zwaan, 1992). We consider the Gulf of Mexico "delta effect" (Pflum and Frerichs, 1976) to be the expression of such a change. These authors showed that in the Mississippi delta front the bathymetric distribution of many species differs from the distribution in other parts of the Gulf of Mexico: enhanced food supply and local changes in other environmental parameters generated these modifications. Extreme examples of deep water community turnover and temporal replacement by a shallow water community, have been documented for the P/E boundary deep-sea extinction event (Maud Rise: Thomas, 1990b; Egypt: Speijer and Van der Zwaan, 1994b); in both localities a shallow water species (*Tappanina selmensis* and *Anomalinoides aegyptiacus*, respectively) suddenly dominated a low diversity assemblage, replacing a highly diverse deep-sea assemblage. In both instances these turnovers are thought to have resulted from oxygen deficiency, in combination with a drop in primary production. Major sea-level variations can be excluded with certainty for this event (Speijer and Van der Zwaan, 1994a,b).

Although we realise that proposing a similar scenario for El Kef is speculative, lacking detailed information from shallower parts of the basin, we have strong arguments against sea-level changes in the order of magnitude as pointed out above. A major sea-level fall in a marginal basin would invoke erosion and re-distribution of nearby shallow water deposits, and lead to re-deposition in deeper parts of the basin. In El Kef the lithological sequence merely shows a drop in carbonate content, resulting from carbonate production failure (see discussion above); reworked shallow water organisms as well as other coarse grained sediment particles are entirely absent. Extremely stable Late Maastrichtian P/B ratios (Fig. 4) also argue against a gradual shallowing trend just below the K/P boundary (Brinkhuis and Zachariasse, 1988). In addition, the postulated Late Maastrichtian sharp eustatic sea-level drop (Haq et al., 1987) can not be called upon to confirm a hypothetical sea-level pattern of El Kef (cf. Keller, 1988b), merely because the sea-level drop does not coincide with the K/P boundary. In contrast, the eustatic curve suggests just the opposite: a gradual but very minor sea-level rise across the K/P boundary.

We interpret the apparent deepening during the early Paleocene primarily as reflecting gradual ecosystem restoration, as soon as redox and trophic conditions ameliorated, starting with the remigration of many Lazarus taxa in an otherwise rather empty ecological space. Subsequent immigration of other taxa eventually led to a normal Paleocene upper bathyal community. Conversely, Keller (1988b) suggested further shallowing to middle-outer neritic conditions in the early Paleocene based on suddenly abundant *T. selmensis* and *Fursenkoina* sp. Surprisingly, we did not encounter any of these taxa in the > 125 µm fraction of the mentioned samples (AFN 591 and 594; Table 1 of Keller, 1988b, based on the > 150 µm fraction). We noticed, however, that these small and slender species are indeed common in the smaller size fraction of all Paleocene samples (*T. selmensis* is particularly abundant in the lowermost Paleocene, decreasing upwards; Speijer, 1992). Perhaps more importantly, peak values of *T. selmensis* are not particularly indicative for neritic conditions, although that is generally their preferred habitat (Van Morkhoven et al., 1986); Thomas (1990b) indicated that this species adopted a rather opportunistic strategy in dysoxic and/or nutrient rich environments independent of bathymetry, similar to modern bolivinids (see Sen Gupta and Machain-Castillo, 1993 and references therein). Interestingly, MacLeod and Keller (1991b) argued, partially based on the apparent sudden proliferation of *T. selmensis* and *Fursenkoina* sp., that there might be a hiatus just between AFN 589 and AFN 590. In contrast, the absence of a distinct faunal break at this level within a period of gradual diversification in our record (we merely note the entry of *P. prima*), as well as in the records of Brinkhuis and Zachariasse (1988) argues against a significant hiatus.

We feel strengthened in our interpretation by the nicely corresponding trends in ostracode community succession (Donze et al., 1982; Peypouquet et al., 1986); in particular, their paleoxygenation curve fits extremely well with our interpretation (note that the "*Mayaroensis* Zone s. z. non nommee" in these papers corresponds to our *G. cretacea* Zone and possibly also our *P. fringa* Zone). Although minor sea-level variations can not be excluded on the basis of our data, we believe that such variations probably were not crucial to the prominent paleoenvironmental changes during the earliest Paleocene. Thus, rather than bathymetry controled faunal changes, we suggest that a major disturbance in oxygen and food supply was the fundamental cause to most of the faunal changes observed.

Temporal and permanent paleobathymetric rearrangements

We believe to have good indications of changes in benthic foraminiferal depth distribution during the earliest-early Paleocene; we relate this to distinct perturbations in trophic and redox conditions at the seafloor. We demonstrated in a previous section, that the earliest Paleocene assemblage of El Kef shows great similarity with the Late Maastrichtian middle-outer neritic assemblage of Gebel Qreiya (most notably due to abundant *C. pseudoacutus* and common *B. strobila* and *B. quadrata-ovata*). As pointed out, it is very unlikely that appearance and disappearance of this assemblage is due to major sea-level fluctuations. Assuming that neritic assemblages in Tunisia were indeed similar to the ones in Egypt (see earlier discussion), we infer a downward expansion of this assemblage into deeper parts of the basin during the earliest Paleocene. Inescapably, this would imply that many of these typical outer neritic taxa were better adapted to sustain under oxygen deficient, low productive conditions. Some evidence that these neritic taxa were indeed adapted to oxygen deficiency, comes from the Naqb Asyut section (Luger, 1985), where preservation of lamination suggests general oxygen deficiency at the seafloor. As mentioned earlier, the Maastrichtian assemblages from this section resemble the ones from Gebel Qreiya and the earliest Paleocene of El Kef. Apparently, some shallow parts of the southern Tethyan margin were poorly ventilated during the

Maastrichtian, in contrast to upper bathyal environments that were much better aerated. A very similar situation also existed in Egypt during the late Paleocene to early Eocene (Speijer and Van der Zwaan, 1994b). Moreover, at the P/E boundary, sudden oxygen deficiency in the upper bathyal site of Wadi Nukhl led to the temporal immigration of highly opportunistic, low oxygen tolerant, shallow water taxa. The striking similarity of the P/E sequence of Wadi Nukhl and the K/P sequence of El Kef, suggests to us that our interpretation of El Kef is a realistic one.

The appearance of *G. beccariiformis* in the early Paleocene upper bathyal assemblage illustrates the opposite pattem of upward migration from deeper into shallower parts of the Tethys. At all upper bathyal localities studied we did not encounter a single specimen of *G. beccariiformis* in the Maastrichtian samples; in the early Paleocene it becomes one of the most common species in this bathymetric zone of the southem Tethys (see also Aubert and Berggren, 1976; Saint-Marc and Berggren, 1988). During the Maastrichtian this species was a ubiquitous cosmopolitan deep-sea taxon, especially at high southern latitudes (e.g. Thomas, 1990b; Nomura, 1991; Widmark, in prep.), but it has only been recorded in the deeper bathyal deposits of the northern Tethys (Spain: Keller, 1992; Austria and Romania: unpubl. data). These distribution pattems indicate that the upper depth limit for this taxon became shallower at the start of the Paleocene. Similar upward bathymetric expansion may also be applicable to other immigrant taxa (in particular to the rather infrequent *Angulogavelinella avnimelechi*), but there is too little information on the Maastrichtian bathymetric distribution of these taxa to sustain this speculation. We believe that the upward expansion of *Gavelinella beccariiformis* resulted from the penetration of a different watermass into the basin in combination with the slightly more oligotrophic conditions of the early Paleocene (see later discussion).

Extinction and survivorship selectivity

The faunal patterns in figure 4 and table 2 show a differential extinction among the main morphotypes: elongate bi-/triserial taxa were much more severly affected than trochospiral taxa. This pattem is very consistent in bathyal as well as neritic assemblages; despite the higher number of trochospiral taxa in our data set, we record only four extinctions in this morphogroup, versus ten in the other. In modem environments abundance of the bi-/triserial morphogroup (in particular, *Bulimina*, *Bolivina*, and *Stainforthia*) is often related to depressed oxygen levels, enhanced food levels, or to a combination of both (e.g. Van der Zwaan, 1982; Lutze and Coulbourn, 1984; Corliss and Chen, 1988; Sen Gupta and Machain-Castillo, 1993).

We consider the Maastrichtian upper bathyal environment of El Kef to be rich in food and well ventilated; the much shallower environment of Gebel Duwi could have been equally productive and well ventilated, judging from the reddish-pink colour of the sediments and the enormous abundance of foraminifera. Therefore, we argue that particularly the high amount of food determined the high numbers of the bi-/triserial morphogroup in these deposits during Maastrichtian times. The scarceness or even absence of taxa that became extinct at the K/P boundary in usually oligotrophic deep-sea environments, concurs with this view: if one considers the K/P event primarily as a productivity crisis, the differential extinction between the main morphogroups can easily be understood. Futhermore, it provides an explanation why there is a differential extinction effect between the different compartments of the ocean, i.e. between the deep-sea and marginal basins. The collapse of the pelagic ecosystem not only caused a decrease in the amount of food supply to the sea-floor, but also to a reduction in nutrient heterogeneity, as evidenced by oligotaxic algal (e.g. *Thoracosphaera*, *Braarudosphaera*) blooms that characterize the earliest Paleocene (Romein, 1979a,b; Perch-Nielsen et al., 1982; Pospichal, 1994). Since some recent foraminifera were noted to be selective feeders (e.g. Lee, 1974; Murray, 1991), it seems not unlikely that at least some of the extinctions may be due to this reduction of nutrient heterogeneity.

One could argue that oxygen deficiency could also have been instrumental in the extinctions. In El Kef the drop in productivity is clearly accompanied by oxygen deficiency, resulting in a very sharp extinction level. A similar situation might have existed in the other upper bathyal sites, but since the lowermost Paleocene has not been preserved very well in these areas we can only speculate. Nevertheless, the record of Wadi Nukhl clearly reveals that not all extinctions were synchronous; the extinctions of *C. incrassata gigantea* and *C. beaumontianus* are clearly delayed (reworking is excluded), but eventually these species also became extinct during the early Paleocene. Such extinction lags have also been observed in deep-sea records (Dailey, 1983; Thomas, 1990b; Nomura, 1991; Widmark and Malmgren, 1992a), although in some cases it was suspected that this could be a taphonomic artifact (Dailey, 1983). These lags and the general absence of oxygen deficiency at the K/P boundary in the deep-sea demonstrate that on a global scale a sudden dys-/anoxic event can be excluded as the main cause for the extinctions.

With the present data we can only speculate on where the Lazarus taxa (SA 2) of El Kef survived, but most likely at least some of them survived in deep-sea environments and remigrated together with *G. beccariiformis*. Taxa such as *Gaudryina pyramidata*, *Pseudouvigerina plummerae*, *V. depressa*, and *Pullenia spp.* are widely documented from Upper Cretaceous deep-sea deposits (e.g. Sliter, 1977a,b; Dailey, 1983; Thomas, 1990b; Nomura, 1991; Widmark and Malmgren, 1992b). They apparently depended less on amount and heterogeneity of the food supply than the species that became extinct, but could not withstand the dysoxic conditions in El Kef.

Paleoceanographic and paleoclimatic developments

Basically, our results can be reduced into signals of two main paleoenvironmental events: at the K/P boundary a sudden drop in (surface and bottom) fertility and oxygenation, followed by recovery during the early Paleocene. The surface productivity failure appears to have be an ocean-wide phenomenon (Perch-Nielsen et al., 1982; Hsü and Mckenzie, 1985; Arthur et al., 1987; Stott and Kennett, 1989; Zachos et al., 1989), although at certain places this may not be true (New Zealand: Hollis, 1993). Restoration of ocean productivity up to pre-boundary levels is thought to have taken place over a time-span of 0.3 to 1.5 Ma (Arthur et al., 1987; Stott and Kennett, 1989; Zachos et al., 1989). This time-span probably stretches beyond our record of El Kef; although we can not provide a reliable age estimate of the top of the section, the $\delta^{13}C$ record of El Kef (Fig. 4; Keller and Lindinger, 1989) indeed does not recover to pre-boundary values. Temporal oxygen deficiency also seems to have been widespread, in particular in (sub)tropical marginal basins (e.g. Austria: Lahodynsky, 1988; Israel: Magaritz et al., 1985; Japan: Kaijwara and Kaiho, 1992; Kazachstan, Sarkar et al., 1992; Spain: Wiedmann, 1988; Coccioni et al., 1993; Kuhnt and Kaminski, 1993).

Oxygenation at the sea-floor depends on the balance between oxygen supply and consumption (e.g. Demaison and Moore, 1980). Below the mixed layer oxygen is supplied through turbulent mixing and advection, whereas it is consumed by degradation of organic matter and respiration (e.g. Southam et al., 1982). Furthermore, oxygenation solubility decreases with increasing temperature and aging of the water, i.e. longer exposure to organic breakdown, results in decreasing oxygen contents. There is compelling evidence that supply of organic matter was greatly reduced during the earliest Paleocene. In spite of this, oxygenation at the bottom was depressed; therefore we can only conclude that oxygen supply to intermediate waters also strongly diminished. The general pattern in the deep-sea suggest that oxygenation of deep water remained virtually unaffected. This decoupling suggests that during the Maastrichtian the deep and (sub)tropical intermediate watermasses could well have originated in different source areas. There is considerable oxygen isotopic evidence that deep and intermediate waters originated both at high and low latitudes (Brass et al., 1982; Saltzman and Barron, 1982; Barrera et al., 1987; Barrera and Huber, 1990; Kennett and Barker, 1990). Benthic foraminiferal $\delta^{18}O$ values from El Kef are considerably lower than in many deep-sea records, suggesting higher bottom water temperatures, although unfortunately diagenetic depletion of ^{18}O can not be entirely excluded (Keller and Lindinger, 1989). This warm intermediate water may have been formed by high evaporation within the Tethys.

Global circulation model (GCM) studies have shown that the warm Late Cretaceous (and early Eocene) may have been characterized by strong atmospheric contrasts between the tropics and subtropics (Barron and Washington, 1985; Barron, 1986; Crowley and North, 1991). This would result in strong trade winds blowing across the southern Tethys shelves. Not only would this enhance evaporation and form potentially dense, saline deep and/or intermediate water, but at the same time it would invoke coastal upwelling and high primary production (Parrish and Curtis, 1982; Barron, 1985). For the latter there is ample evidence in the sedimentary record of North Africa: phosphatic and/or organic rich (potential source rock) deposits are widely distributed (Wiedmann et al., 1978; Busson and Cornee, 1986; Bock, 1987; Notholt et al., 1989; Negra and M'rabet, 1991; Almogi-Labin et al., 1993; Mostafa, 1993), and also the faunal/floral record suggests high surface fertility (Peypouquet, 1986; Reiss, 1988; Nederbragt, 1992; Almogi-Labin et al., 1993; Eshet et al., 1994).

Before the end of the Cretaceous this general situation gradually changed; widespread depostion of organic rich and/or phosphatic sediments stopped or diminished within the Maastrichtian (Bock, 1987; Negra and M'rabet, 1991; Almogi-Labin et al., 1993; Mostafa, 1993). Nevertheless, faunal/floral records suggest a fairly high productive belt in the southern Tethys until the end of the Cretaceous (Peypouquet et al., 1986; Nederbragt, 1992; Almogi-Labin et al., 1993). The Maastrichtian and in particular the latest Maastrichtian was a time of gradual but persistent surface cooling at high latitudes (Barrera et al., 1987; Barrera and Huber, 1990; Kennett and Barker, 1990; Frakes et al., 1992), but also, and perhaps more importantly, within the (sub)tropics (Douglas and Woodruff, 1981; Gerstel et al., 1986; Méon, 1991; Lécuyer et al., 1993). The coincidence between Maastrichtian cooling and decrease in upwelling intensity in the (sub)tropics, strongly suggest a causal relationship. Such a relationship is indeed expected from GCM studies: lower temperatures would invoke weaker atmospheric contrasts between the tropics and the subtropics, this in turn would lead to less intense upwelling and reduced evaporation (Barron and Washington, 1985; Barron, 1986; Crowley and North, 1991).

Latest Maastrichtian gradual changes in El Kef have been recorded in land-derived pollen records (Méon, 1991), dinoflagellates (Brinkhuis and Zachariasse, 1988), and planktonic foraminifera (Keller, 1988a; Kerr, 1994), although the latter has been refuted (Smit, 1990; Kerr, 1994). Nevertheless, apart from the pre-boundary disappearance of two common species, our benthic foraminiferal record does not show a gradual turnover within the latest Maastrichtian. If it took place, a gradual change did not seriously affect environmental conditions at the sea-floor. In contrast, at the K/P boundary bottom conditions deteriorated abruptly. As discussed earlier, we suggest that this resulted from cessation of intermediate water ventilation (cf. Rohling et al., 1991). In our view cessation of intermediate water formation in the Tethys was caused by a sudden cooling event superimposed on the long-term trend. Although information on earliest Paleocene climate is far from straightforward, there is considerable evidence that the (sub)tropics indeed cooled significantly. The pollen record of Tunisia shows a further increase in "northern european" components (Méon, 1991). Similarly, boreal species of dinoflagellates appear in El Kef (H. Brinkhuis, pers. communication, 1994). The low latitude planktonic foraminiferal community appears more heavily perturbed at the K/P boundary than boreal communities, although the latter are eventually also replaced during the early Paleocene (Keller, 1993; Keller et al., 1993; Schmitz et al., 1992; MacLeod and Keller, 1994). The warm-temperate gastropod bioprovince expanded and replaced the tropical gastropod bioprovince in the earliest Tertiary (Kollmann, 1979). Furthermore, changes in paleosol composition in Texas also suggest cooler and more humid conditions across the K/P boundary (Lehman, 1990).

Some oxygen isotope records substantiate a surface cooling event at the K/P boundary (Perch-Nielsen, et al., 1982; Hsü et al., 1985; Barrera et al., 1987; Zachos et al., 1989; Kennett and Barker, 1990; Stott and Kennett, 1990b; Lécuyer et al., 1993), whereas other records show no change or even suggest a warming event (Perch-Nielsen et al., 1982; Shackleton, 1986; Barrera and Keller, 1990; Smit, 1990; Schmitz et al., 1993). This points either to differential temperature changes in the earliest Paleocene (Perch-Nielsen et al., 1982) or some records are just not accurate or reliable, due to diagenetic overprint (e.g. Magaritz et al., 1992).

In our view abrupt cooling at the K/P boundary led to cessation of intermediate water formation within the Tethys, in turn leading to temporal oxygen deficiency in this stagnant watermass due to excess oxygen consumption by organic breakdown. We adopt a modified version of the model proposed by Brinkhuis and Zachariasse (1988) and Rohling et al. (1991) with respect to the collapse of the pelagic ecosystem. These authors argued that a regressive pulse at the K/P boundary reduced the evaporative surface of the Tethyan shelves and thus the amount of produced dense saline deep water. In turn, this would result in a temporal decrease in nutrient advection from the deep waters to the surface mixed layer. Subsequent oligotrophy would have played an important role in the collapse of the (sub)tropical pelagic ecosystem. We propose a very similar scenario; the main difference is that we regard the cooling event to be the operative mechanism and we suggest that this only affected intermediate waters and not the entire deeper water column.

The collapse of carbonate production may have acted as a positive cooling feedback. Carbonate production supplies CO_2 to the mixed layer and the atmosphere (Broecker and Peng, 1982). Assuming constant CO_2 consumption rates by weathering on this time-scale, a decrease in carbonate production would lead to lower atmospheric CO_2 contents and several degrees cooling (Caldeira et al., 1990).

A critical point in this discussion is the timing and duration of sea-floor oxygen deficiency. In most records, the initiation of oxygen deficiency is recorded at the base of the boundary clay that marks the K/P boundary. Duration of such conditions seem to vary from place to place, although estimates of these relatively short-lived paleoenvironmental changes are still difficult to assess. Keller (1988a,b) estimated a duration of about 300 kyr for the oxygen deficient period, based on numeric ages of 66.4 Ma for the K/P boundary and 66.1 Ma for the FAD of *P. pseudobulloides* (Berggren et al., 1985). Brinkhuis and Zachariasse (1988) arrived at a duration of about 100 kyr; a similar duration can be derived from revised age-calibrated bioevents (Groot et al., 1989; Berggren et al., 1994; see also Fig. 1 in Berggren, 1994). Kajiwara and Kaiho (1992) suggested a period of 70 kyr (based on Berggren et al., 1985) of anoxic conditions in an upper bathyal section on Hokkaido (Japan). Adoption of the new time scale of Berggren et al. (1994) reduces this period to only 25 kyr. In the middle-upper bathyal sequence of Caravaca (southern Spain) the dysoxic event lasted less than a few thousand years following the K/P boundary (Coccioni et al., 1993). But, re-establishment of a normal deep-sea assemblage took 50-100 kyr. Similar results were obtained from the middle bathyal Sopelana section (northern Spain; Kuhnt and Kaminski, 1993). Assuming that the estimated durations are at least in a relative sense correct, then El Kef has recorded an anomalously long oxygen deficient period. We can think of several reasons for this retardation in re-establishing more vigourous ventilation:

- if refreshment progressed from deeper to shallower areas then a relatively shallow locality as El Kef should indeed show some delay.
- the rate of refreshment and oxygen supply may have been compensated by gradually increasing supply of marine (and terrestrial?) organic matter.
- basin configuration (Tunisian Trough; Burollet, 1956) was such that it prevented rapid restoration

With only few datapoints we are not able to be more decisive on this matter.

The early Paleocene remained a relatively cool period (Oberhänsli and Hsü, 1986; Frakes, 1992). Ice-rafted deposits on Spitsbergen even suggest seasonal ice formation at high latitudes (Dalland, 1977; Frakes et al., 1992). Only during the late Paleocene temperatures rose again, to finally reach the early Eocene thermal maximum (Kennett and Stott, 1991; Zachos et al., 1994).

Maastrichtian and Paleocene biogeographic patterns of *G. beccariiformis* suggest that this species favoured a watermass that originated at high latitudes (Katz and Miller, 1991; Widmark, in prep.). The regional bathymetrical expansion of *G. beccariiformis* from the deep-sea into the souhtern Tethyan upper bathyal domain during the early Paleocene, may indicate the upward penetration of the deeper (cooler) watermass to shallower depths. During the middle Paleocene other high latitude (Austral) species (*Pullenia coryelli* and *Alabamina creta*, Widmark, 1993, and in prep.) joined *G. beccariiformis* (unpubl. data from Wadi Nukhl and Nahal Avdat). *Gavelinella beccariiformis* as well as the other taxa persisted in upper bathyal environments of the southern Tethys to the end of the Paleocene, when they became extinct (Speijer, 1994a; Speijer and Van der Zwaan, 1994b). This pattern suggests that intermediate water formation in the Tethys remained very reduced during the Paleocene.

Remains the question what caused the gradual and abrupt climatic changes. The Late Cretaceous gradual cooling may have been caused by decreasing atmospheric CO_2 contents (Berner, 1994), or enhanced explosive volcanism (Axelrod, 1981 and references therein). Taking the amount of evidence presented in favour of an extraterrestrial event at the K/P boundary in consideration and its tight coincidence with the perturbation in the marine realm, it seems likely that this event was the prime cause. The operative mechanism however remains elusive, despite the great number of speculations on lethal consequences of an asteroid or cometary impact (e.g. prolonged global darkening, acid rain, marine poisoning, nuclear winter, global wildfires, etc, see e.g. Silver and Schultz, 1982; Sharpton and Ward, 1990). If sudden and relatively short-term cooling after the impact could have provoked a rapid breakdown of the carbonate producing pelagic system, then the lack of CO_2 production in surface waters may have acted as a strong positive cooling feedback, operating on longer time scales (Caldeira et al., 1990). In turn, the subsequent late Paleocene gradual warming may also have been controled by increasing atmospheric CO_2: after full recovery of the carbonate producing pelagic system later in the early Paleocene (Arthur et al., 1987), metamorphic degassing resulting from the India-Asia collision may have raised temperatures to Late Cretaceous levels (Kerrick and Caldeira, 1994).

Conclusions

During the Late Cretaceous intermediate Tethys water was formed by high evaporation due to high (sub)tropical temperatures and high wind-stress, resulting from strong atmospheric contrasts between the Tethys and the African continent. A cooling event at the K/P boundary, superimposed on a long-term cooling trend, blocked the formation of this warm and saline intermediate water, resulting in poor refreshment and oxygen deficiency at the sea-floor. Gradual restoration of bottom conditions, possibly resulted from upward expansion of the deeper watermass, originating in a high latitude source area.

Changes in trophic and redox conditions on the sea-floor invoked the temporal replacement of a stable upper bathyal paleocommunity by one consisting of opportunistic shallow water taxa.

In contrast to deep-sea paleocommunities, the shallower ones were severely affected by the K/P event. In particular taxa that presumably depended on high and heterogeneous nutrient resources (mostly with a test shape that suggests an endobenthic living position) suffered extinction during the earliest Paleocene. We primarily relate the differential effects in the bathymetric compartments and the ecological groups to the prolonged period of reduced surface fertility.

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Appendix - Taxonomic notes

We largely adopted species concepts used by Cushman (1946), Aubert and Berggren (1976), and Salaj et al. (1976), but in some instances we deviated from these and used additional documentation. As far as possible, we refer to descriptions by previous workers on North African material and deep-sea K/P boundary sequences. For classification at (supra-)generic level we largely followed Loeblich and Tappan (1988).

Ammodiscacea
Ammodiscidae
***Arenoturrispirillina* sp. 1**
(Pl. IX, Fig. 3)

1976 *Ammodiscoides* sp. ? *Arenoturrispirillina* sp. ?. Aubert and Berggren: p. 407, pl. 1, fig. 2
1988 *Ammodiscus lajollaensis* Sliter. Keller: pl. 4, fig. 5
Remarks: a coiled tubular species with a distinct conical test shape.

Lituolacea
Lituolidae
Ammomarginulina aubertae
Gradstein and Kaminski
(Pl. IX, Fig. 5)

1989 *Ammomarginulina aubertae* Gradstein and Kaminski: p. 74, pl. 3, figs.1-8; pl. 4, figs. 1-3; text fig. 2
Remarks: this laterally strongly compressed planispiral species has a transparent test made up of non-calcareous grains. It has about 13-15 narrow chambers in the last (often uncoiling) whorl.

Spiroplectamminacea
Spiroplectamminidae
Bolivinopsis clotho (Grzybowski)
(Pl. I, Fig. 1)

1946 *Bolivinopsis? clotho* (Grzybowski). Cushman: p. 103, pl. 44, figs. 10-13
Remarks: this species has a smoothly finished slender test with almost parallel sides. The initial planispiral part is broader than the early biserial part. Slightly oblique sutures tend to curl back towards the aperture. Mostly, only broken specimens are encountered.

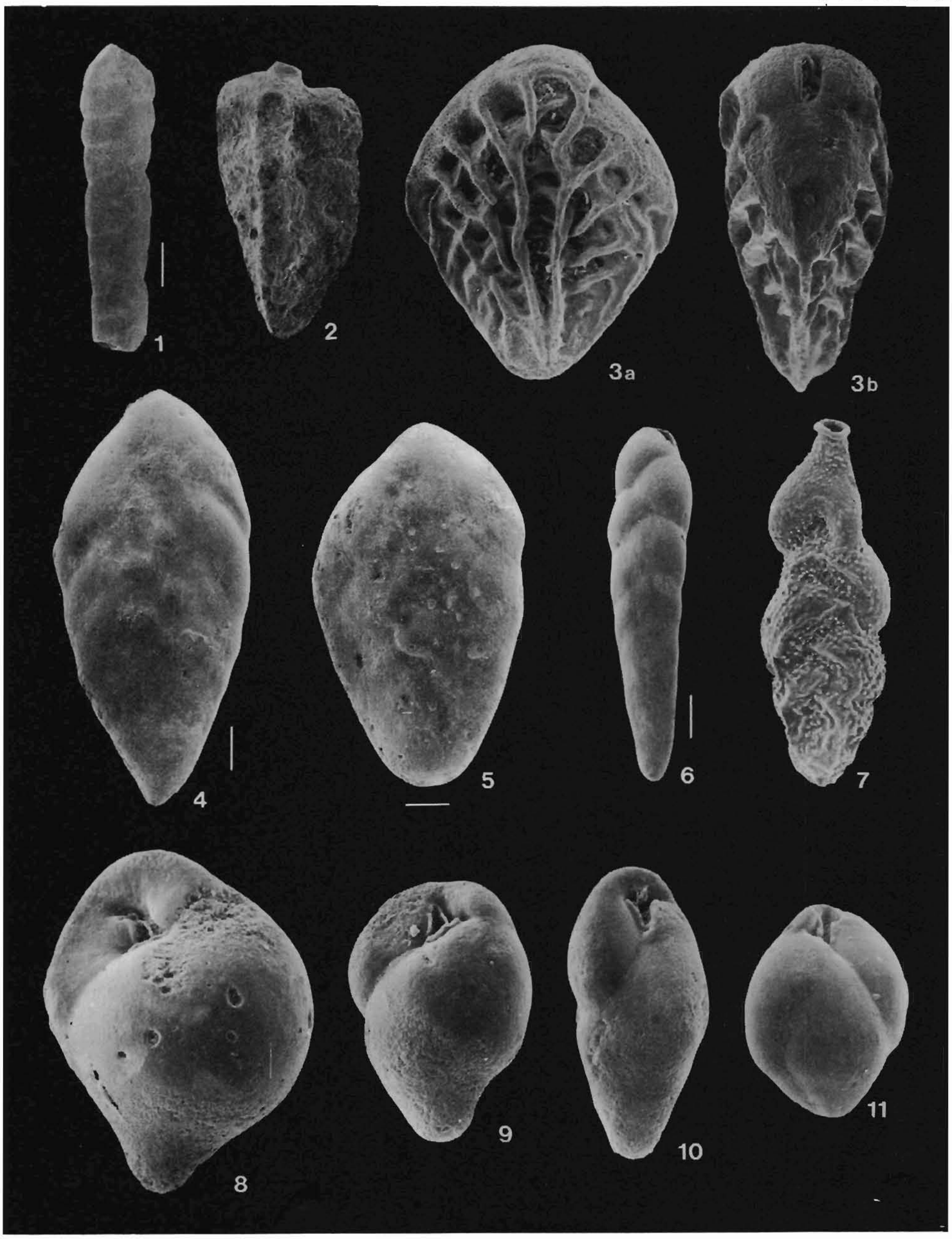
Verneuilinacea
Verneuilinidae
Gaudryina pyramidata Cushman
(Pl. IV, Fig. 1)

1926 *Gaudryina laevigata* Franke var. *pyramidata* Cushman: p. 587, pl. 16, fig.8
1946 *Gaudryina pyramidata* Cushman. Cushman: p. 36, pl. 8, fig. 14
1953 *Gaudryina pyramidata* Cushman. LeRoy: p. 31, pl. 1, figs. 17-18
1956 *Gaudryina pyramidata* Cushman. Said and Kenawy: p. 124, pl. 1, fig. 26

Plate I. Maastrichtian taxa (SA 1)

Fig. 1 *Bolivinopsis clotho* (Grzybowski), sample AFN 536 (X60)
Fig. 2 *Heterostomella austinana* Cushman, sample AFN 528
Fig. 3 *Bolivinoides draco draco* (Marsson), sample AFN 540
Fig. 4 *Coryphostoma incrassata gigantea* (Wicher), sample AFN 528 (X60)
Fig. 5 *Coryphostoma incrassata gigantea* (Wicher), sample AFN 528 (X60)
Fig. 6 *Coryphostoma plaitum* (Carsey), sample AFN 528 (X60)
Fig. 7 *Eouvigerina subsculptura* McNeil and Caldwell, sample AFN 540
Fig. 8 *Sitella colonensis* (Cushman and Hedberg), sample AFN 528
Fig. 9 *Sitella cushmani* (Sandidge), sample AFN 528
Fig. 10 *Sitella fabilis* (Cushman and Parker), sample AFN 540
Fig. 11 *Praebulimina reussi* Morrow, sample AFN 540
All magnifications X120 unless indicated otherwise (bar = 100 μm).

PLATE I



1976 *Gaudryina pyramidata* Cushman. Salaj et al.: p. 149, pl. 3, figs. 6-7

1983 *Gaudryina pyramidata* Cushman. Dailey: p. 766, pl. 1, fig. 6

1988 *Gaudryina pyramidata* Cushman. Keller: pl. 4, figs. 13-16

1991 *Gaudryina pyramidata* Cushman. Nomura: p. 22, pl. 5, fig. 11

1992a *Gaudryina pyramidata* Cushman. Widmark and Malmgren: p. 111, pl. 10, fig. 3

Remarks: a large well known species with a robust triangular shape and a low apertural face.

Heterostomella austinana Cushman
(Pl. I, Fig. 2)

1946 *Heterostomella austinana* Cushman. Cushman: p. 41, pl. 11, figs. 2-7

1956 *Heterostomella austinana* Cushman. Said and Kenawy: p. 126, pl.1, fig. 45

1988 *Trifarina esnaensis* LeRoy. Keller: pl. 3, figs. 15, 16

Remarks: this species has an early triserial part, but is largely biserially arranged, retaining a truncated triangular shape. The sides are somewhat concave and the test is often slightly bent.

Bolivinacea

Bolivinidae

Loxostomoides applinae (Plummer)
(Pl. IV, Fig. 3)

1926 *Bolivina applini* Plummer: p. 69, pl. 4, fig. 1

1951 *Loxostomum applinae* (Plummer). Cushman: p. 43, pl. 12, fig. 18

1953 *Loxostomum applinae* (Plummer). LeRoy: p. 37, pl. 8, fig. 1

1956 *Loxostomum clavatum* (Cushman). Said and Kenawy: p. 144, pl. 4, fig. 21

1976 *Loxostomoides applinae* (Plummer). Aubert and Berggren: p. 420, pl. 4, fig. 11

1976 *Loxostomoides applinae* (Plummer). Salaj et al.: p. 155, pl. 7, fig. 6

1985 *Loxostomoides applinae* (Plummer). Luger: p. 106, pl. 7, fig. 1

1992 *Loxostomoides applinae* (Plummer). Kuhn: p. 63, pl. 14, figs. 6-7

Remarks: this species is characterized by the crenulated base of the biserially arranged chambers and the longitudinal striae, fusing into low costae on the earlier part of the test.

Tappanina selmensis (Cushman)
(Pl. VII, Fig. 2)

1933 *Bolivinita selmensis* Cushman: p. 58, pl. 7, figs. 3-4

1946 *Bolivinita selmensis* Cushman. Cushman: p. 114, pl. 49, figs. 1-2

1946 *Bolivinita costifera* Cushman. Cushman: p. 115, pl. 49, fig. 3

1948 *Bolivinita selmensis* Cushman. Brotzen (emend.): p.56, fig. 16, pl. 9, fig. 7

1951 *Eouvigerina excavata* Cushman. Cushman: p. 38, pl. 11, fig. 12

1976 *Tappanina selmensis* (Cushman). Aubert and Berggren: p. 420, pl. 4, fig. 12

1988 *Tappanina selmensis* (Cushman). Keller: pl. 2, fig. 8

1990b *Tappanina selmensis* (Cushman). Thomas: p. 591, pl. 1, fig. 9

1992 *Tappanina selmensis* (Cushman). Kuhn: p. 62, pl. 13, figs. 18-20

Remarks: the concave chambers and the sutural costae give this species a very distinct appearance, which can not be confused with any other species.

Bolivinoididae

Bolivinoides decoratus (Jones)
(Pl. IX, Fig. 2)

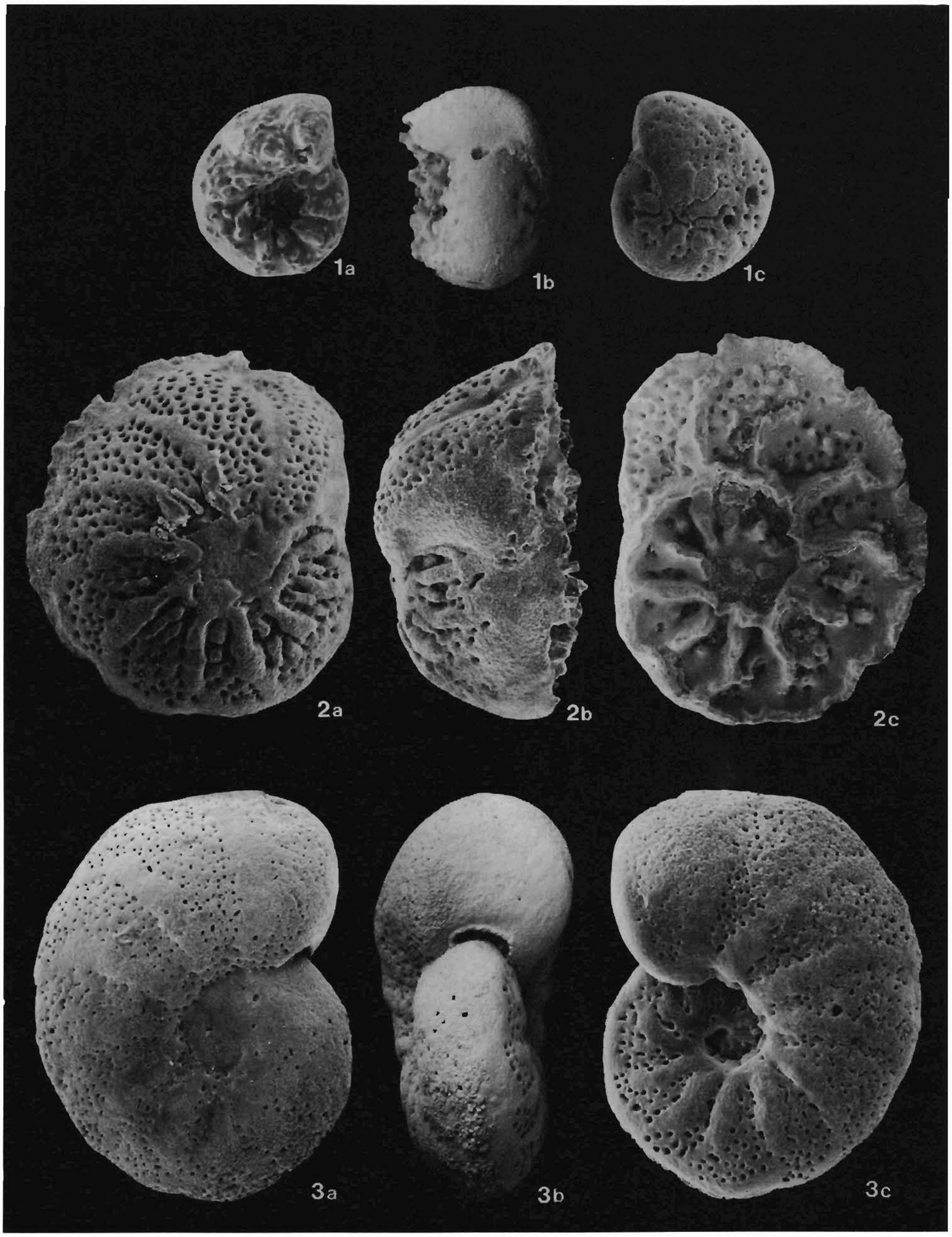
1886 *Bolivina decorata* Jones: p. 330, pl. 27, figs. 7, 8

1977 *Bolivinoides decoratus* decoratus (Jones).

Plate II. Maastrichtian taxa (SA 1)

Fig. 1 *Gavelinella martini* (Sliter), sample AFN 528
Fig. 2 *Stensioeina pommerana* Brotzen, sample SN 140
Fig. 3 *Anomalinoides* sp. 1, sample AFN 528
All magnifications X120.

PLATE II



Koch: p. 51, pl. 12, figs. 5-6
Remarks: a fairly small not very distinctive biserial species with 4-5 protrusions from the chamber's base, forming irregular knobs on the earlier part of the test.

Bolivinoides draco draco (Marsson)
(Pl. I, Fig. 3)

1878 *Bolivina draco* Marsson: p. 157, pl. 3, fig. 25
1956 *Bolivinoides draco* draco (Marsson). Said and Kenawy: p. 140, pl. 3, fig. 41
1983 *Bolivinoides draco* draco (Marsson). Dailey: p. 766, pl. 2, fig. 8
1988 *Bolivinoides draco* draco (Marsson). Keller: pl. 1, figs. 10, 11
1991 *Bolivinoides draco* (Marsson). Nomura: p. 21, pl. 1, fig. 5
Remarks: a very distinctive species with chamber protrusions fusing into strongly elevated ridges.

Eouvigerinacea
Eouvigerinidae
Eouvigerina subsculptura McNeil and Caldwell
(Pl. I, Fig. 7)

? 1950 *Eouvigerina aegyptiaca* Nakkady: p. 686, pl. 89, fig. 18
1956 *Eouvigerina aegyptiaca* Nakkady. Said and Kenawy: p. 141, pl. 4, fig. 2
1981 *Eouvigerina subsculptura* McNeil and Caldwell: p. 231, pl. 18, figs. 20, 21
1983 *Eouvigerina americana* Cushman. Dailey: p. 766, pl. 2, fig. 11
1988 *Uvigerina maqfiensis* LeRoy. Keller: pl. 3, figs. 11, 12
1992a *Eouvigerina subsculptura* McNeil and Caldwell. Widmark and Malmgren: p. 111, pl. 1, fig. 8
Remarks: a distinct slender biserial species tending to become uniserial in the later part. The chambers are decorated by pustules, fusing into ridges at the chamber margins. Possibly *E. aegyptiaca* should be regarded as senior synonym, unfortunately the type description of this species is not very clear.

Turrilinacea
Turrilinidae
Praebulimina reussi Morrow
(Pl. I, Fig. 11)

1845 *Bulimina ovulum* Reuss: p. 37, pl. 8, fig. 57; pl. 13, fig. 73
1934 *Bulimina reussi* Morrow: p. 195, pl. 29, fig. 12
1946 *Bulimina reussi* Morrow. Cushman: p. 120, pl. 51, figs. 1-5
1956 *Bulimina reussi* Morrow. Said and Kenawy: p. 143, pl. 4, fig. 15
1983 *Praebulimina reussi* (Morrow). Dailey: p. 768, pl. 2, fig. 7
1988 *Buliminella cushmani* Sandidge. Keller: pl. 1, fig. 3 (Not fig. 4)
Remarks: a slightly lobate triserial species with strongly overlapping whorls. The aperture opens at the tip of the apertural face.

Pseudouvigerina plummerae Cushman
(Pl. IV, Fig. 2)

1927 *Pseudouvigerina plummerae* Cushman: p. 115, pl. 23, fig. 8
1946 *Pseudouvigerina plummerae* Cushman. Cushman: p. 116, pl. 49, figs. 14-16
1948 *Angulogerina cuneata* Brotzen: p. 64, pl. 6, fig. 10
1976 *Angulogerina cuneata* Brotzen. Aubert and Berggren: p. 424, pl. 6, fig. 2
1983 *Pseudouvigerina plummerae* Cushman. Dailey: p. 768, pl. 3, fig. 1
1992 *Pseudouvigerina cuneata* (Brotzen). Kuhn: p. 67, pl. 15, figs. 15-17
Remarks: a triserial species with a terminal aperture on a short neck. The chamber margin is decorated by a perforate double keel, that is

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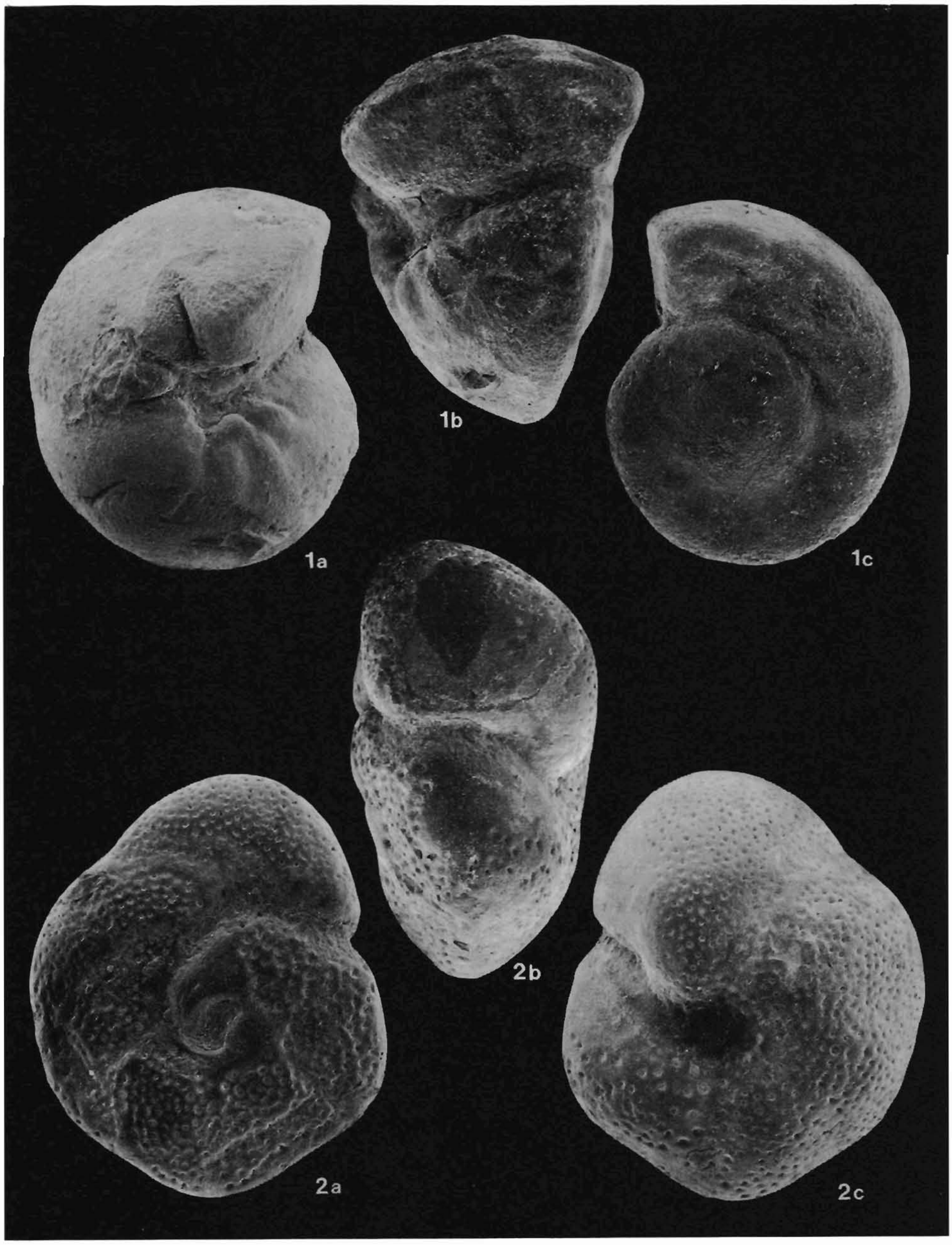
Plate III. Maastrichtian taxa (SA 1)

Fig. 1 *Gyroidinoides tellburmaensis* Futyan, sample AFN 528
Fig. 2 *Cibicides beaumontianus* (d'Orbigny), sample AFN 528
All magnifications X120.

PLATE III



only slightly interrupted at the base of the chamber. *Pseudouvigerina cuneata* is probably a junior synonym.

Pseudouvigerina sp. 1
(Pl. IX, Fig. 4)

Remarks: this species differs from *P. plummerae* in its angular sides and rough surface with poremounds, especially at the margins of the chambers. These poremounds sometimes fuse to form a single interrupted keel.

Sitella colonensis (Cushman and Hedberg)
(Pl. I, Fig. 8)

1930 *Buliminella colonensis* Cushman and Hedberg: p. 65, pl. 9, figs. 6, 7
1946 *Buliminella colonensis* Cushman and Hedberg. Cushman: p. 120, pl. 50, figs. 23-24
1956 *Buliminella carseyae* Plummer. Said and Kenawy: p. 142, pl. 4, fig. 8
1988 *Buliminella cushmani* Sandidge. Keller: pl. 1, fig. 4 (Not fig. 3)
Remarks: a thick very tightly coiled top shaped species with about 6 chambers to a whorl.

Sitella cushmani (Sandidge)
(Pl. I, Fig. 9)

1932 *Buliminella cushmani* Sandidge: p. 280, pl. 42, figs. 18, 19
1946 *Buliminella cushmani* Sandidge. Cushman: p. 119, pl. 50, fig. 15
1953 *Buliminella cushmani* Sandidge. LeRoy: p. 22, pl. 8, fig. 12
1956 *Buliminella laevis* (Beissel). Said and Kenawy: p. 142, pl. 4, fig. 6
1983 Praebulimina carseyae (Plummer). Dailey: p. 768, pl. 2, fig. 4
1991 *Buliminella sp. 1*. Nomura: pl. 1, fig. 17
Remarks: this species resembles *S. colonensis*, but is more slender, less tightly coiled, and has only 4-5 chambers to a whorl.

Sitella fabilis (Cushman and Parker)
(Pl. I, Fig. 10)

1936 *Buliminella fabilis* Cushman and Parker: p. 7, pl. 2, fig. 5
1946 *Buliminella fabilis* Cushman and Parker. Cushman: p. 119, pl. 50, fig. 13
1988 *Buliminella carseyae* Plummer. Keller: pl. 1, figs. 5, 6
Remarks: a much more slender species than other *Sitella* in the material.

Buliminacea
Buliminidae
Bulimina strobila Marie
(Pl. VII, Fig. 3)

1941 *Bulimina strobila* Marie: p. 265, pl. 32, fig. 302
1976 *Bulimina asperoaculeata* Brotzen. Aubert and Berggren: p. 421, pl. 5, fig. 4
1976 *Bulimina velascoensis* Cushman. Salaj et al.: p. 156, pl. 7, fig. 14
1988 *Bulimina farafraensis* LeRoy. Keller: pl. 3, figs. 13, 14
1992 *Bulimina asperoaculeata* Brotzen. Kuhn: p. 65, pl. 15, figs. 3-4
Remarks: a distinct triangular species with concave sides and irregular ridges at the margins. The chambers are crescent shaped.

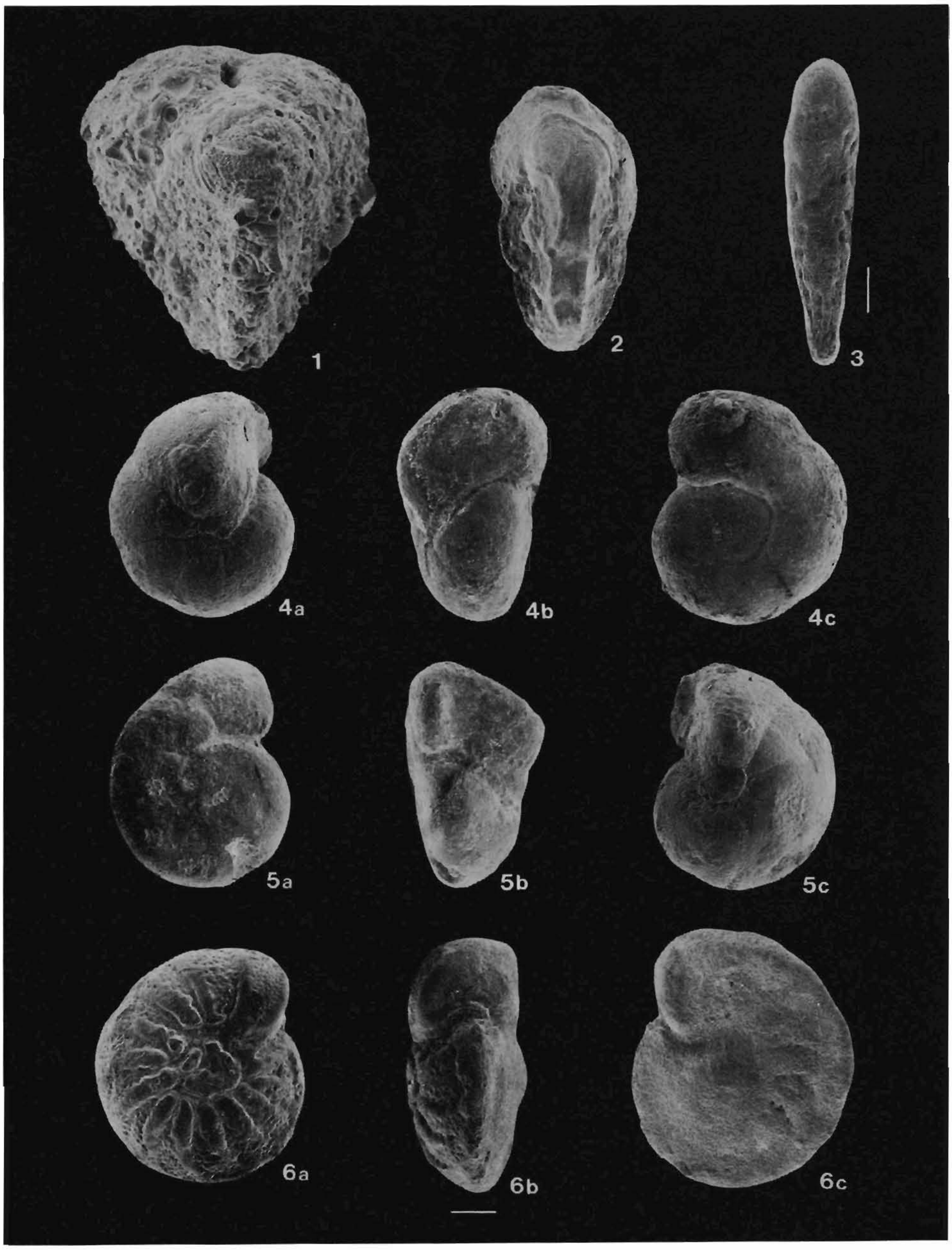
Bulimina quadrata-ovata **plexus**
(Pl. VII, Fig. 4)

1926 *Bulimina quadrata* Plummer: p. 72, pl. 4, figs. 4, 5

Plate IV. Lazarus taxa, absent in the earliest Paleocene (SA 2)

Fig. 1 *Gaudryina pyramidata* Cushman, sample AFN 540
Fig. 2 *Pseudouvigerina plummerae* Cushman, sample AFN 528
Fig. 3 *Loxostomoides applinae* (Plummer), sample AFN 599(X60)
Fig. 4 *Gyroidinoides octocameratus* (Cushman and Hanna), sample AFN 599
Fig. 5 *Valvalabamina depressa* (Alth), sample AFN 599
Fig. 6 *Cibicidoides abudurbensis* (Nakkady), sample AFN 528 (X60)
All magnifications X120 unless indicated otherwise (bar = 100 μm).

PLATE IV



1953 *Bulimina pupoides* d'Orbigny. LeRoy: p. 22, pl. 8, fig. 21
1956 *Bulimina kickapooensis* Cole. Said and Kenawy: p. 142, pl. 4, fig. 12
1976 *Bulimina quadrata* Plummer. Aubert and Berggren: p. 422, pl. 5, fig. 9
1976 *Bulimina quadrata* Plummer. Salaj et al.: p. 156, pl. 7, figs. 3-4
1985 *Bulimina quadrata* Plummer. Luger: p. 107, pl. 7, fig. 6
1985 *Bulimina reussi* Morrow. Luger: p. 107, pl. 7, fig. 7
Remarks: this plexus comprises all smooth finely perforate "globular" *Bulimina* species. Due to compression and often poor preservation it appeared impossible to determine the majority of the specimens at species level. Therefore, all specimens were assigned to this plexus.

Fursenkoinacea
Fursenkoinidae

Coryphostoma incrassata gigantea (Wicher)
(Pl. I, Figs. 4, 5)

1946 *Bolivina incrassata* Reuss. Cushman: p. 127, pl. 53, figs. 10, 11
1953 *Bolivina incrassata* Reuss. LeRoy: p. 20, pl. 10, figs. 4-5
1956 *Bolivina incrassata* Reuss. Said and Kenawy: p. 144, pl. 4, fig. 19
1956 *Bolivina incrassata* Reuss var. *gigantea* Wicher: p. 120, pl. 12, figs. 2-3
1988 *Bolivina incrassata gigantea* Wicher. Keller: pl. 3, figs. 1, 2
1991 *Coryphostoma incrassata* (Reuss). Nomura: p. 22, pl. 1, fig. 3
Remarks: an extremely large variety of *C. incrassata* (up to 1 mm in length), showing fine striae and small slightly elevated knobs on the central part of the test.

Coryphostoma plaitum (Carsey)
(Pl. I, Fig. 6)
1926 *Bolivina plaitum* Carsey: p. 26, pl. 4, fig. 2
1931 *Loxostoma plaitum* (Carsey). Plummer: p. 182, pl. 10, figs. 5-7
1953 *Loxostomum plaitum* (Carsey). LeRoy: p. 37, pl. 4, fig. 12
1988 *Coryphostoma plaitum* (Carsey). Keller: pl. 3, figs. 5, 6
Remarks: a very slender species, smooth with fine striae, often slightly twisted in the later part.

Coryphostoma sp. 1
(Pl. VII, Fig. 1)

Remarks: this species resembles *C. incrassata incrassata*, but is narrower and has more obliquely arranged chambers. The aperture is sometimes almost terminal.

Siphoninacea
Siphoninidae

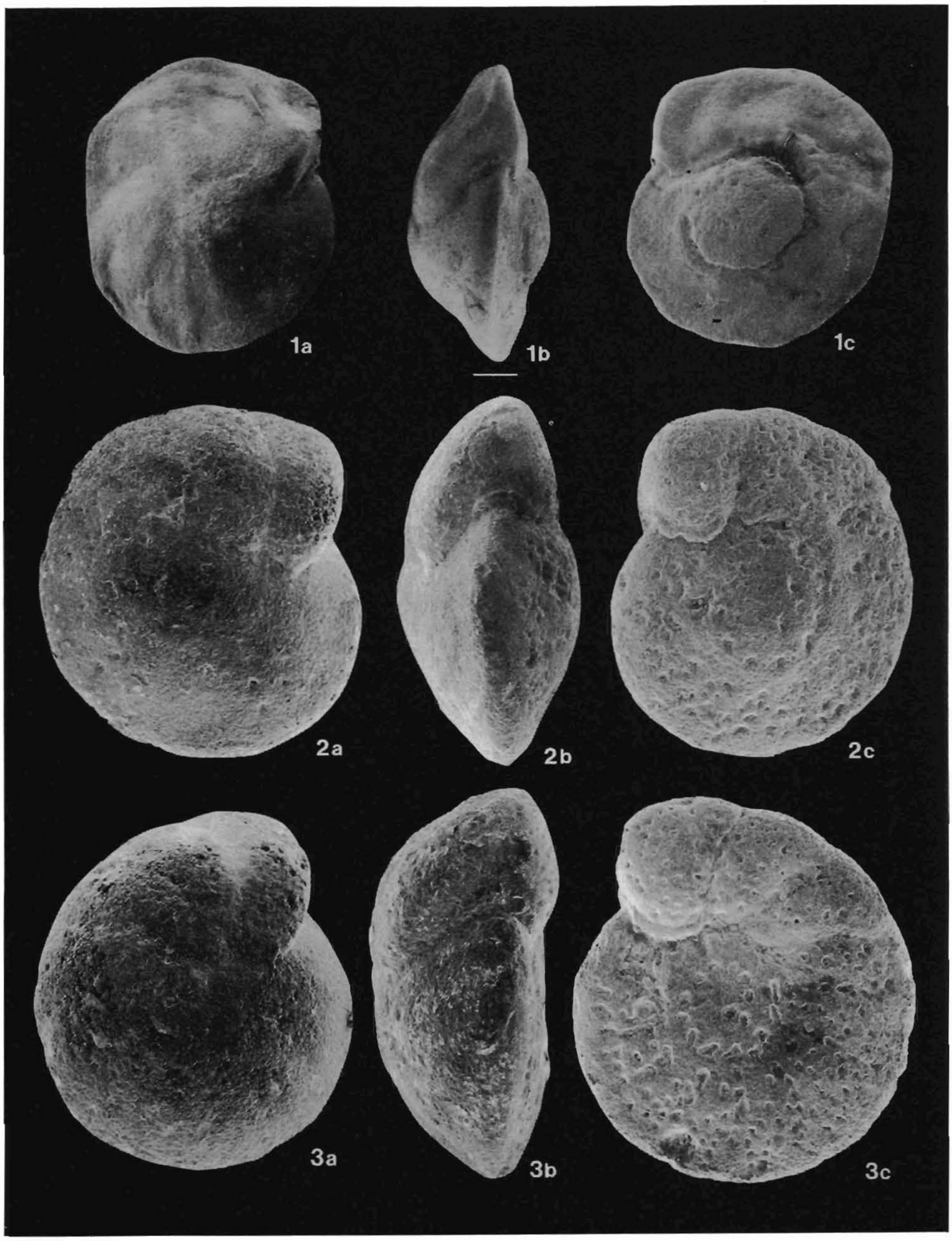
Pulsiphonina prima (Plummer)
(Pl. X, Fig. 1)

1926 *Siphonina prima* Plummer: p. 148, pl. 12, fig. 4
1946 *Siphonina prima* Plummer. Cushman: p. 142, pl. 59, figs. 3-5
1951 *Siphonina prima* Plummer. Cushman: p. 55, pl. 15, figs. 7-9
1975 *Pulsiphonina prima* (Plummer). Berggren and Aubert: p. 156, pl. 3, fig. 5
1992 *Pulsiphonina prima* (Plummer). Kuhn: p. 97, pl. 28, figs. 8, 9
Remarks: a distinct small species with about five chambers to a whorl. The chamber's margins are decorated by calcite lamellae (not visible with SEM). This species lacks the slightly protruding tip as in other species (e.g. *P. wilcoxensis*).

Plate V. Lazarus taxa, absent in the earliest Paleocene (SA 2)

Fig. 1 *Cibicidoides suzakensis* (Bykova), sample AFN 539 (X60)
Fig. 2 *Cibicoides* cf. *hyphalus* (Fisher), sample AFN 599 (bi-convex morphology)
Fig. 3 *Cibicoides* cf. *hyphalus* (Fisher), sample AFN 599 (plano-convex morphology)
All magnifications X120 unless indicated otherwise (bar = 100 μm).

PLATE V



Discorbinellacea

Parrelloididae

Cibicidoides abudurbensis (Nakkady)

(Pl. IV, Fig. 6)

1950 *Cibicides abudurbensis* Nakkady: p. 691, pl. 90, figs. 35-38
1976 *Cibicidoides azzouzi* Salaj et al.: p. 159, pl. 12, figs. 4, 5
Remarks: a very robust species. The more flattened umblical side is apparently poreless and frequently recristallized; the convex spiral side has large pores and strongly raised sutures, with a relatively small central spiral knob. It differs from *C. pseudoacutus* in its flattened umbilical side and the more distinctly raised sutures. *Cibicidoides azzouzi* is probably a junior synonym.

Cibicidoides* cf. *hyphalus (Fisher)

(plano-convex morphology; Pl. V, Fig. 3)

cf. 1969 *Anomalinoides hyphalus* Fisher: p. 197, pl. 3
1986 *Cibicidoides hyphalus* (Fisher). Van Morkhoven et al.: p. 359, pl. 116
Remarks: this species is similar to the figured specimens in Van Morkhoven et al. (1986), but different from the holotype (see discussion in Speijer and van der Zwaan, 1994b). It differs from the biconvex morphology in its flat spiral side.

Cibicidoides* cf. *hyphalus (Fisher)

(biconvex morphology; Pl. V, Fig. 2)

cf. 1969 *Anomalinoides hyphalus* Fisher: p. 197, pl. 3
1986 *Cibicidoides hyphalus* (Fisher). Van Morkhoven et al.: p. 359, pl. 116
Remarks: this species is more convex on the spiral side than *C. hyphalus* (plano-convex morphology); it differs from *C. pseudoacutus* in its less pronounced and larger spiral knob.

Cibicidoides pseudoacutus (Nakkady)

(Pl. VII, Fig. 6)

1950 *Anomalina pseudoacuta* Nakkady: p. 691, pl. 90, figs. 29-32
1976 *Cibicides commatus* Morozova. Salaj et al.: p. 158, pl. 11, figs. 1, 2
1988 *Anomalinoides acuta* (Plummer). Keller: pl. 2, figs. 9, 10, 12, 13
Remarks: a large species with a very characteristic semi-involute spiral side, of which the center is extremely pronounced by secondary calcite. This spiral plug is surrounded by a deep spiral slit and flaplike extensions from the last whorl. Although these features suggest a closer affinity to Anomalinoides, we get the impression that this species is merely a more tightly coiled representative of *Cibicidoides.*

Cibicidoides suzakensis (Bykova)

(Pl. V, Fig. 1)

1976 *Cibicides suzakensis* Bykova. Salaj et al.: p. 158, pl. 16, figs. 7, 8
Remarks: a very large almost plano-convex bell shaped species with a slightly protruding spiral knob. Relatively small pores are present on both sides.

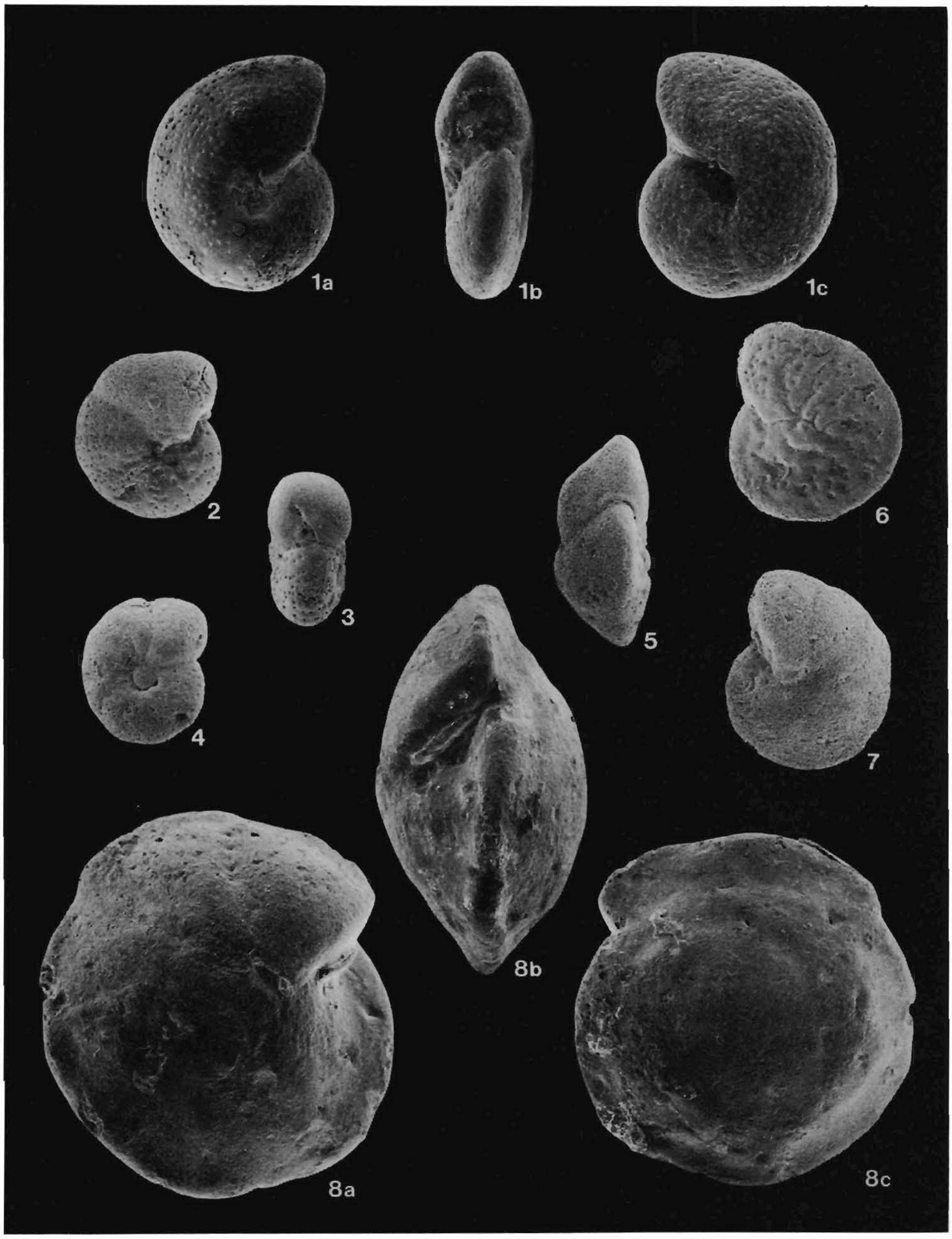
***Cibicidoides* sp. 1**

Remarks: a small nearly plano-convex species with about 11-13 chambers to a whorl. The umbilical side is smooth, the spiral side is coarsely pitted. The sutures are thickened and slightly raised.

Plate VI. Lazarus taxa, absent in the earliest Paleocene (SA 2)

Fig. 1 *Anomalinoides affinis* (Hantken), sample AFN 599
Figs. 2-4 *Anomalinoides* sp. 2, sample SN 136
Figs. 5-7 *Cibicidoides* sp. 1, sample AFN 599
Fig. 8 *Oridorsalis plummerae* (Cushman), sample AFN 599
All magnifications X120.

PLATE VI



Planorbulinacea

Cibicididae

Cibicides beaumontianus (d'Orbigny)

(Pl. III, Fig. 2)

1840 *Truncatulina beaumontiana* d'Orbigny: p. 35, pl. 3, figs. 17-19
1946 *Cibicides beaumontianus* (d'Orbigny) Brotzen. Cushman: p. 160, pl. 65, fig. 12
1988 *Pullenia quinqueloba* (Reuss). Keller: pl. 1, fig. 17 (Not fig. 16)
Remarks: a conspicuous very large glossy-white planoconvex species with large pores on both sides and 5-7 chambers to a whorl.

Chilostomellacea

Alabaminidae

Alabamina wilcoxensis Toulmin

(Pl. IX, Fig. 7)

1941 *Alabamina wilcoxensis* Toulmin: p. 603, pl. 81, figs. 10-14
1956 *Alabamina wilcoxensis* Toulmin. Said and Kenawy: p. 152, pl. 6, fig. 18
1988 *Alabamina midwayensis* Brotzen. Keller: pl. 2, figs. 5-7
Remarks: this species differs from *A. midwayensis* in the almost flat spiral side and the higher umbilical side.

Valvalabamina depressa (Alth)

(Pl. IV, Fig. 5)

1850 *Rotalina depressa* Alth: p. 266, pl. 13, fig. 21
1946 *Gyroidina depressa* (Alth). Cushman: p. 139, pl. 58, figs. 1-4
1953 *Gyroidina orbicularis* d'Orbigny. LeRoy: p. 35, pl. 7, figs. 12-14
1976 *Valvulineria* cf. *cetera* (Bykova). Salaj et al.: p. 157, pl. 10, figs. 3, 4
1983 *Gyroidinoides depressus* (Alth). Dailey: p. 767, pl. 6, figs. 10-12
1991 *Gyroidinoides planulatus* (Cushman and Renz). Nomura: p. 22, pl. 3, fig. 10
Remarks: this species is characterized by its entirely evolute spiral side with slightly raised oblique, curved sutures. The umbilical sutures are almost straight and sometimes slightly incised around the umbilicus, which is covered by an umbilical flap in well preserved specimens. The apertural face is inflexed.

Osangulariidae

Osangularia plummerae Brotzen

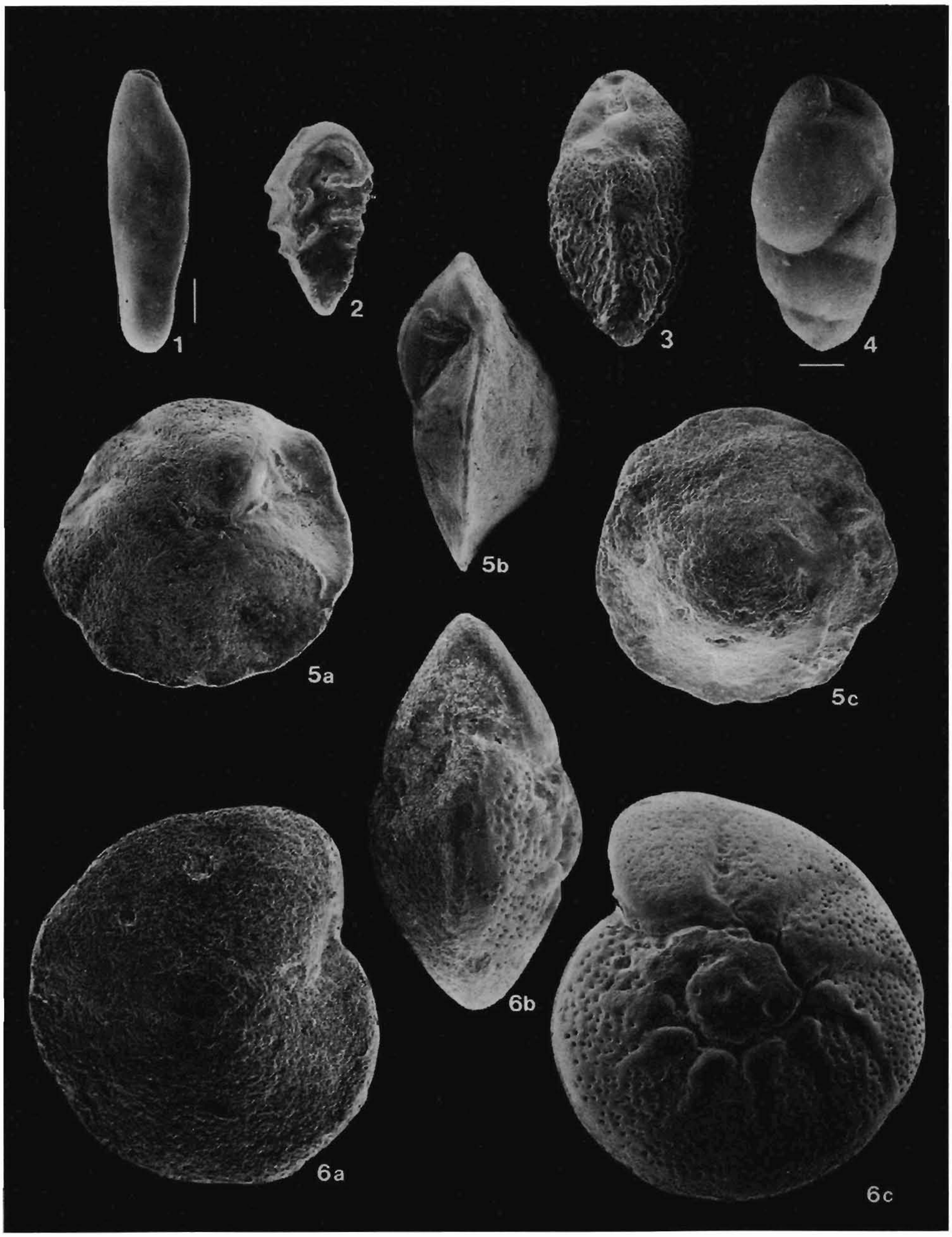
(Pl. VII, Fig. 5)

1926 *Truncatulina culter* (Parker and Jones). Plummer: p. 147, pl. 10, fig. 1; pl. 15, fig. 2
1940 *Osangularia plummerae* Brotzen: p. 30, text-fig. 8
1976 *Osangularia plummerae* Brotzen. Aubert and Berggren: p. 429, pl. 8, fig. 5
1976 *Osangularia plummerae* Brotzen. Salaj et al.: p. 161, pl. 8, fig. 4
1985 *Osangularia plummerae* Brotzen. Luger: p. 110, pl. 8, fig. 6
1988 *Osangularia cordieriana* (d'Orbigny). Keller: pl. 1, figs. 12, 13
1992 *Osangularia plummerae* Brotzen. Kuhn: p. 85, pl. 23, figs. 1-3
Remarks: a usually equally convex species, with sometimes slightly raised oblique sutures on the spiral side. The flush sutures on the umbilical side are straight to gently curved.

Plate VII. Ubiquitous taxa, most abundant in earliest Paleocene (SA 4)

Fig. 1 *Coryphostoma* sp. 1, sample AFN 548 (X60)
Fig. 2 *Tappanina selmensis* (Cushman), sample AFN 543
Fig. 3 *Bulimina strobila* Marie, sample AFN 599
Fig. 4 *Bulimina quadrata* Plummer, sample AFN 548 (X60)
Fig. 5 *Osangularia plummerae* Brotzen, sample AFN 548
Fig. 6 *Cibicidoides pseudoacutus* (Nakkady), sample AFN 548
All magnifications X120 unless indicated otherwise (bar = 100 μm).

PLATE VII



Oridorsalidae

Oridorsalis plummerae **(Cushman)**
(Pl. VI, Fig. 8)

1926 *Truncatulina tenera* H. B. Brady. Plummer: 146, pl. 9, fig. 5
1948 *Eponides plummerae* Cushman: p. 44, pl. 8, fig. 9
1951 *Eponides plummerae* Cushman. Cushman: p. 52, pl. 14, figs. 20, 23
1953 *Eponides lunatus* (Brotzen). LeRoy: p. 30, pl. 9, figs. 24-26
1956 Eponides lunatus (Brotzen). Said and Kenawy: p. 148, pl. 5, fig. 3
1956 *Eponides mariei* Said and Kenawy: p. 148, pl. 5, fig. 2
1956 *Eponides sigali* Said and Kenawy: p. 148, pl. 5, fig. 6
1976 *Eponides plummerae* Cushman. Aubert and Berggren: p. 426, pl. 7, fig. 4
1976 *Eponides lotus* (Schwager). Salaj et al.: p. 157, pl. 10, fig. 2
1976 *Eponides plummerae* Cushman. Salaj et al.: p. 157, pl. 10, fig. 1
1983 *Oridorsalis biconvexus* (Marie). Dailey: p. 767, pl. 5, figs. 8, 11, 12
1983 *Oridorsalis umbonatus* (Reuss). Dailey: p. 767, pl. 6, figs. 1-3
1988 *Oridorsalis umbonatus* (Reuss). Keller: pl. 1, figs. 14, 15
1992 *Eponides plummerae* Cushman. Kuhn: p. 75, pl. 19, figs. 16-18
1992 *Oridorsalis?-complex* Widmark and Malmgren: p. 112, pl. 7, fig. 4

Remarks: similar to the modern representative *O. umbonatus*, this species is considered to have a high degree of morphological variability with respect to convexity of both sides, angularity and the shape of the sutures.

Heterolepidae

Anomalinoides* cf. *acutus **(Plummer)**
(Pl. X, Fig.2)

cf. 1926 *Anomalina ammonoides* (Reuss) var. *acuta* Plummer: p. 149, pl. 10, fig. 2
cf. 1951 *Anomalina acuta* Plummer. Cushman: p. 62, pl. 18, figs. 3-6

Remarks: this species is similar to *A. acutus*, but differs in its less compressed an more tightly coiled test.

Anomalinoides affinis **(Hantken)**
(Pl. VI, Fig. 1)

1875 *Pulvinulina affinis* Hantken: p. 78, pl. 10, fig. 6
1926 *Truncatulina welleri* Plummer: p. 143, pl. 9, fig. 6
1953 *Anomalina desertorum* LeRoy: p. 17, pl. 7, figs. 18-20
1976 *Anomalinoides welleri* (Plummer). Aubert and Berggren: p.430, pl. 9, fig. 5
1976 *Anomalinoides affinis* (Hantken). Salaj et al.: p. 162, pl. 9, figs. 1, 2
1983 *Anomalinoides welleri* (Plummer). Dailey: p. 766, pl. 8, figs. 6-8

Remarks: a distinct flattened, bi-umbilicate, biconvex species. The spiral side is semi-involute, the umbilical side is completely involute. The open umbilicus is surrounded by usually indistinct umbilical flaps. Near the periphery the large pores are aligned into elongate pore depressions. The limbate sutures are flush with the test surface. We follow Salaj et al. (1976) in regarding *A. welleri* as a junior synonym.

Anomalinoides ekblomi **(Brotzen)**
(Pl. VIII, Fig. 2)

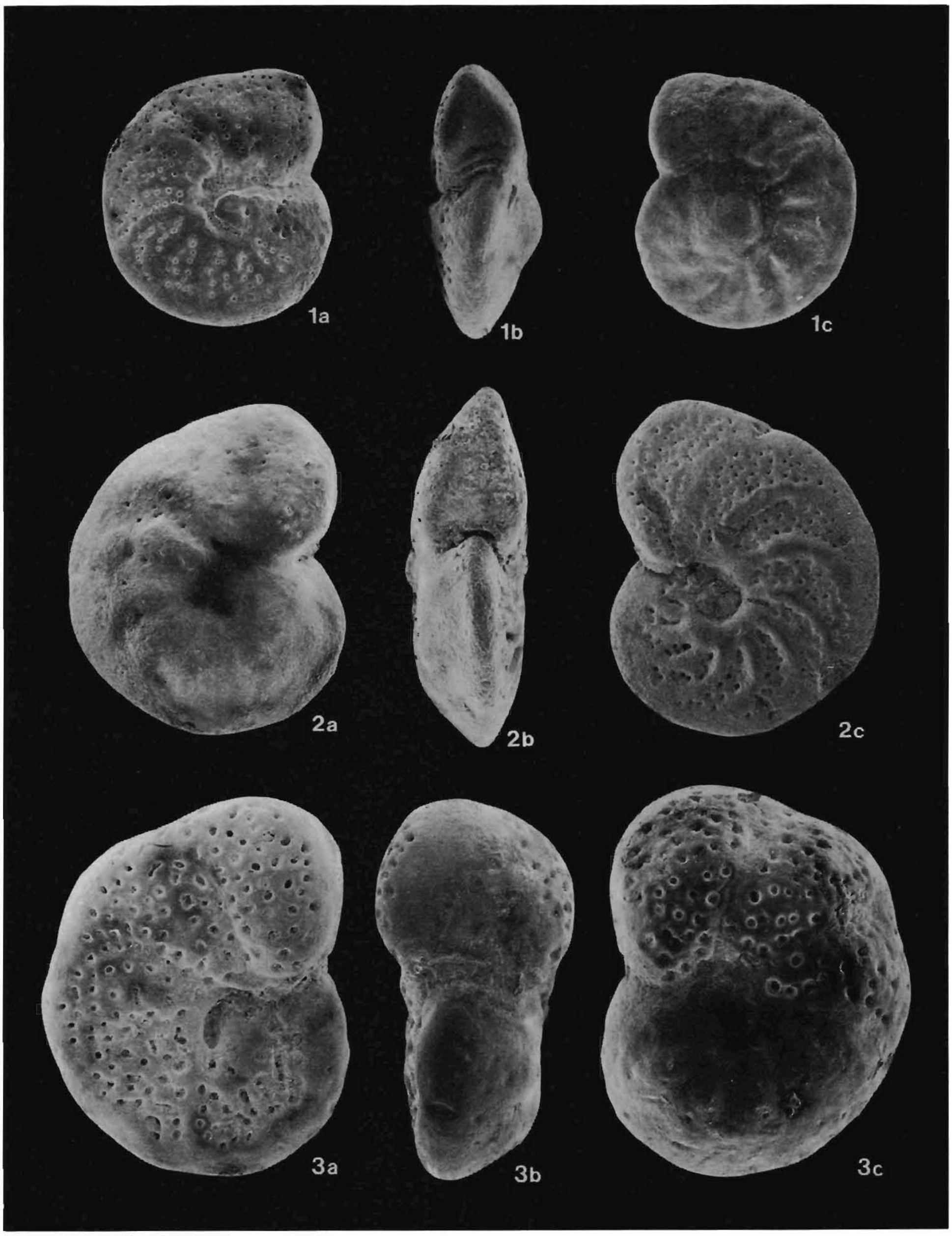
1948 *Cibicides ekblomi* Brotzen: p. 82, pl. 13, fig. 2
1992 *Anomalinoides ekblomi* (Brotzen). Kuhn: p. 92, pl. 26, figs. 4-6

Remarks: this laterally compressed species shows distinct elevated, limbate, and curved sutures on the umbilical side, as well as large pores. The spiral side is very smooth with only a few large pores and almost entirely involute.

Plate VIII. Ubiquitous taxa, most abundant in earliest Paleocene (SA 4)

Fig. 1 *Anomalinoides praeacutus* (Vasilenko), sample AFN 548
Fig. 2 *Anomalinoides ekblomi* (Brotzen), sample AFN 548
Fig. 3 *Anomalinoides rubiginosus* Brotzen, sample AFN 548
All magnifications X120.

PLATE VIII



Anomalinoides praeacutus (Vasilenko) (Pl. VIII, Fig. 1)

1950 *Anomalina praeacuta* Vasilenko: p. 208, pl. 5, figs. 2, 3
1976 *Anomalinoides praeacuta* (Vasilenko). Aubert and Berggren: p. 430, pl. 9, fig. 2; pl. 12, fig. 5
1976 *Anomalinoides acuta* (Plummer). Salaj et al.: p. 161, pl. 9, figs. 3, 6
1992 *Anomalinoides acutus* (Plummer). Kuhn: p. 91, pl. 26, figs. 10-13

Remarks: a very distinct species with considerable morphological variability. The spiral side is always semi-involute and may develop a transparent plug which covers the earlier whorls. The sutures on this side are flush to strongly raised and large pores are confined to the the later half of the last whorl. The umbilical side has a distinct irregular plug surrounded by umbilical flaps. The sutures on this side are flush to slightly raised and large pores are evenly distributed over the entire surface. The aperture is extra-umbilical to peripheral and is covered by a distinct lip.

Anomalinoides rubiginosus (Cushman) (Pl. VIII, Fig. 3)

1926 *Anomalina rubiginosa* Cushman: p. 607, pl. 21, fig. 6
1946 *Anomalina rubiginosa* Cushman. Cushman: p. 156, pl. 64, figs. 4-6
1948 *Anomalinoides danica* Brotzen: p. 87, pl. 14, fig. 1
1953 *Anomalina granosa* (Hantken). LeRoy: p. 17, pl. 6, figs. 1-3
1956 *Anomalina granosa* (Hantken). Said and Kenawy: p. 153, pl. 6, fig. 20
1976 *Gavelinella danica* (Brotzen). Aubert and Berggren: p. 433, pl. 11, fig. 5; pl. 12, fig. 1
1976 *Gavelinella rubiginosa* (Cushman). Aubert and Berggren: p. 433, pl. 12, fig. 3
1976 *Anomalina danica* (Brotzen). Salaj et al.: p. 162, pl. 9, figs. 4, 5
1983 *Gavelinella danica* (Brotzen). Dailey: p. 766, pl. 9, figs. 6-8
1985 *Gavelinella rubiginosa* (Cushman). Luger: p. 112, pl. 9, fig. 6
1991 *Anomalinoides danicus* (Brotzen). Nomura: p. 21, pl. 2, fig. 4
1992 *Anomalinoides rubiginosus* (Cushman). Kuhn: p. 96, pl. 27, figs. 18-23

Remarks: a very distinct large, coarsely perforate, glossy-white species with 6 to 9 chambers in the last whorl. This species shows a large degree of variation in the amount of inflation of the chambers and the decoration with secondary calcite. The spiral side is only slightly evolute. We follow van Morkhoven et al. (1986) in regarding *A. danicus* as a junior synonym.

Anomalinoides simplex (Brotzen) (Pl. IX, Fig. 1)

1948 *Cibicides simplex* Brotzen: p. 83, pl. 13, figs. 4, 5

Remarks: a small but robust species with 6-8 chambers to a whorl. It is coarsely perforate on the umbilical side, smooth and frequently recristallized on the spiral side.

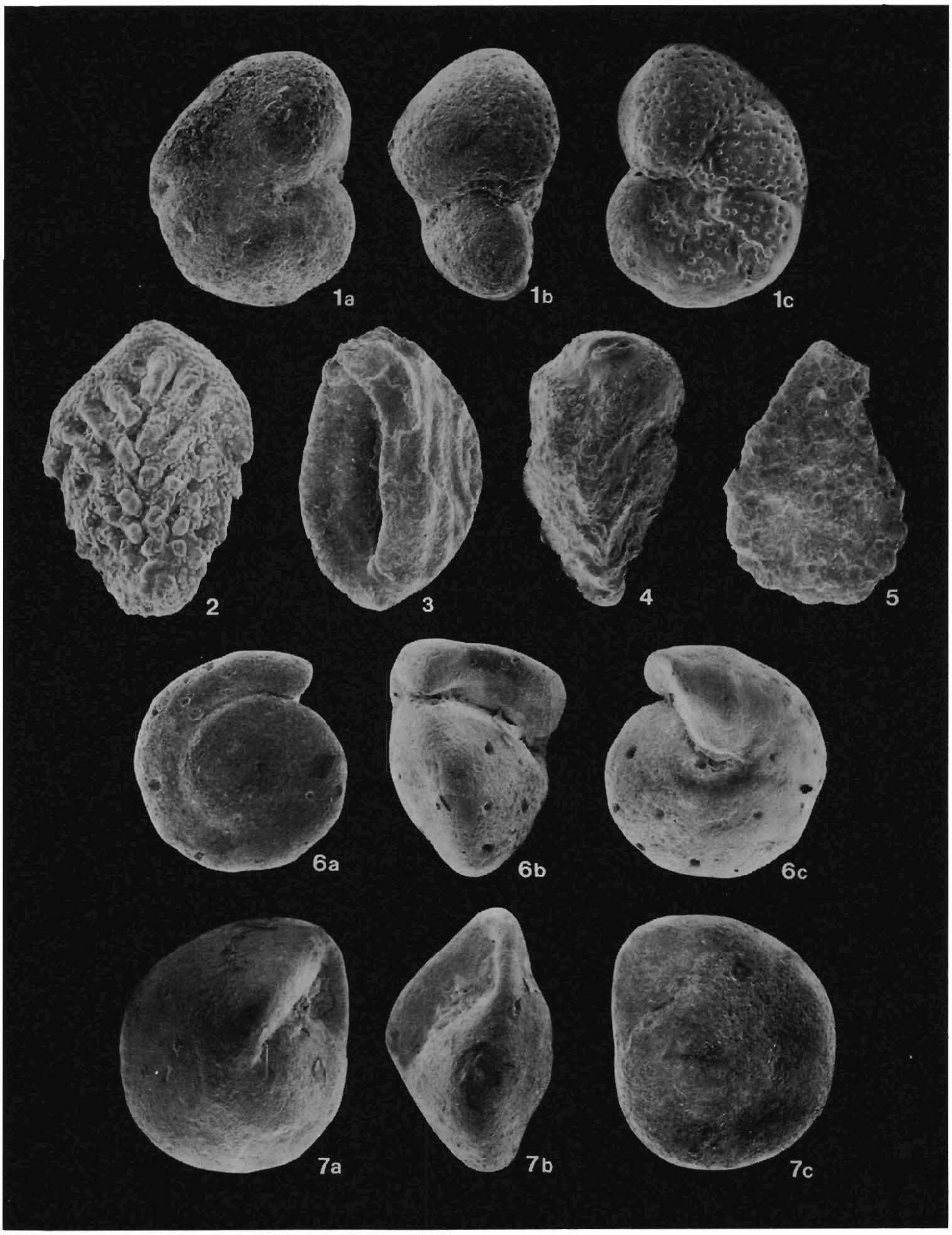
Plate IX. Ubiquitous taxa (SA 3)

Fig. 1 *Anomalinoides simplex* (Brotzen), sample AFN 599
Fig. 2 *Bolivinoides decoratus* (Jones), sample AFN 540

Earliest Paleocene taxa (SA 5)

Fig. 3 *Arenoturrispirillina* sp. 1, sample AFN 548
Fig. 4 *Pseudouvigerina* sp. 1, sample AFN 548
Fig. 5 *Ammomarginulina aubertae* Gradstein and Kaminski, sample AFN 548
Fig. 6 *Gyroidinoides* sp. 1, sample AFN 548
Fig. 7 *Alabamina wilcoxensis* Toulmin, sample AFN 548
All magnifications X120.

PLATE IX



Anomalinoides susanaensis (Browning)
(Pl. X, Fig. 3)

1959 *Cibicides susanaensis* Browning (in Mallory, 1959): p. 271, pl. 32, figs. 11, 12
1976 *Cibicidoides susanaensis* (Browning). Aubert and Berggren: p. 432, pl. 11, fig. 2
1976 *Cibicidoides susanaensis* (Browning). Salaj et al.: p. 160, pl. 12, figs. 1, 2
1985 *Gavelinella* cf. *lellingensis* (Brotzen). Luger: p. 112, pl. 9, figs. 7, 8
Remarks: a large robust species with strongly raised, limbate and strongly curved sutures on both sides. The umbilical side shows large pores and a small umbilical knob; the spiral side shows no distinct pores.

Anomalinoides sp. 1
(Pl. II, Fig. 3)

1953 *Anomalina* sp. K LeRoy: p. 19, pl. 3, figs. 26-28
Remarks: a large bi-umbilicate species with rounded periphery and distinctly limbate, almost straight, sutures on both sides

Anomalinoides sp. 2
(Pl. VI, Figs. 2-4)

Remarks: a very small bi-umbilicate species with about ten chambers to a whorl. Small apertural flaps enable distinction between the two sides

Gavelinellidae
Gyroidinoides octocameratus
(Cushman and Hanna)
(Pl. IV, Fig. 4)

1927 *Gyroidina soldanii* d'Orbigny *octocamerata* Cushman and Hanna: p. 223, pl. 14, figs. 16-18
1992 *Gyroidina octocamerata* Cushman and Hanna. Kuhn: p. 82, pl. 24, figs. 1-3
Remarks: umbilical features are very similar to those of *V. depressa*, but the spiral side shows a depressed central area, the sutures are straight and oblique, and the periphery is more lobate.

Gyroidinoides tellburmaensis Futyan
(Pl. III, Fig. 1)

1976 *Gyroidinoides tellburmaensis* Futyan: p. 532, pl. 81, figs. 10-12
Remarks: a distinct species, that strongly resembles *G. girardanus*, but can be distinguished by the very oblique, slightly depressed, sutures on the spiral side and the very high and angular apertural face.

Gyroidinoides sp. 1
(Pl. IX, Fig. 6)

Remarks: this species consists of 2-3 narrow whorls, each with 8-10 chambers. The spiral side is slightly convex, whereas the umbilical side is conical. All sutures are entirely flush with the surface.

Stensioeina pommerana Brotzen
(Pl. II, Fig. 2)

1936 *Stensioeina pommerana* Brotzen: p. 165
1950 *Stensioeina esnehensis* Nakkady: p. 689, pl. 90, figs. 8-10
1977 *Stensioeina pommerana* Brotzen. Koch: p. 51, pl. 11, figs. 1-4
Remarks: a very conspicuous species, due to the ridges on the spiral sutures and the large pores and umbilical flaps on the umbilical side

Gavelinella beccariiformis (White)
(Pl. X, Fig. 4)

1928 *Rotalia beccariiformis* White: p. 287, pl. 39, figs. 2-4

Plate X. Early Paleocene taxa (SA 6)

Fig. 1 *Pulsiphonina prima* (Plummer), sample AFN 599
Fig. 2 *Anomalinoides* cf. *acutus* (Plummer), sample AFN 599
Fig. 3 *Anomalinoides susanaensis* (Browning), sample AFN 599 (X60)
Fig. 4 *Gavelinella beccariiformis* (White), sample AFN 599
All magnifications X120 unless indicated otherwise (bar = 100 μm).

PLATE X

1976 *Gavelinella beccariiformis* (White). Aubert and Berggren: p. 433, pl. 11, fig. 4
1976 *Stensioeina beccariiformis* (White). Salaj et al.: p. 163, pl. 13, figs. 6, 7
1983 *Gavelinella beccariiformis* (White). Dailey: p. 766, pl. 9, figs. 4, 9
1990 *Gavelinella beccariiformis* (White). Thomas: p. 590, pl. 3, fig. 5
1991 *Stensioina beccariiformis* (White). Nomura: p. 21, pl. 1, figs. 8, 9
1992 *Valvulineria beccariiformis* (White). Kuhn: p. 91, pl. 26, figs. 1-3
1992 *Gavelinella beccariiformis* (White). Widmark and Malmgren: p. 111, pl. 5, fig. 3
Remarks: a very distinct species with large umbilical flaps covering the umbilicus. Both sides are usually coarsely perforate, but the spiral side is sometimes nearly poreless. Secondary calcite forms ridges on the umbilical side. Umbilical features suggest a relationship with Stensioina, but the spiral side lacks the pattern of elevated ridges that is so characteristic for this genus.

Gavelinella martini (Sliter)
(Pl. II, Fig. 1)

1968 *Gyroidinoides quadratus martini* Sliter: p. 121, pl. 22, fig. 9
1990 *Scaraficatina*? sp. Widmark: p. 87, pl. 19, fig. 5
Remarks: a small but very distinct species by the presence of spines on the concave spiral side and the large flaps covering the umbilicus.

Globanomalina luxorensis, a pelagic marker for the Paleocene/Eocene boundary

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ABSTRACT

Recently, it has been proposed to re-define the Paleocene/Eocene (P/E) boundary and place it at the level that coincides with the deep-sea benthic foraminiferal extinction and the concomitant negative shift in the $\delta^{13}C$ record. This paper discusses the phylogeny and distribution of the planktonic foraminifer, *Globanomalina luxorensis*, which lowest common occurrence marks this newly proposed boundary in many localities of the circum-Mediterranean region. Below the P/E boundary this taxon is very rare and always subordinate relative to its precursor *Globanomalina chapmani*. In the earliest Eocene this taxon evolved into *Pseudohastigerina wilcoxensis*. Also in Pakistan and New Zealand *G. luxorensis* appears to be a common species just above the P/E boundary. We propose to adopt the lowest common occurrence of *G. luxorensis* as a marker for the P/E boundary, at least in the circum-Mediterranean region.

Introduction

The late Paleocene to early Eocene was a time of increased benthic and planktonic foraminiferal turnover. The extinction of many cosmopolitan deep-sea benthic taxa is well documented for all oceanic basins (e.g. Tjalsma, 1977; Schnitker, 1979; Tjalsma and Lohmann, 1983; Boersma, 1984; Thomas, 1990b, 1992; Katz and Miller, 1991; Nomura, 1991; Pak and Miller, 1992) and for many continental margin deposits (e.g. Hillebrandt, 1962; Braga et al., 1975; Kaiho, 1988; Kaiho et al., 1993; Molina et al., 1994; Speijer, 1994a; Speijer and Van der Zwaan, 1994b). It appears to have been a rather short event (<10ky; Kennett and Stott, 1991), occurring within Zones P5 and NP9 (Tjalsma and Lohmann, 1983; Thomas, 1990b; Katz and Miller, 1991; Nomura, 1991; Pak and Miller, 1992; Aubry et al., 1994; Speijer, 1994a; Speijer and Van der Zwaan, 1994b). The taxonomic turnover in planktonic foraminifera is less apparent and much more gradual; however, many morozovellids and acarininids (dis)appear within Zone P5 (Toumarkine and Luterbacher, 1985; Berggren et al., 1994).

Evolutionary changes from *Globanomalina chapmani* to *Pseudohastigerina wilcoxensis* are of particular interest for biostratigraphic correlations, since the entry of *P. wilcoxensis* is often used to approximate the Paleocene/Eocene (P/E) boundary (Berggren, 1960; Berggren et al., 1967). The "*Pseudohastigerina* datum" was proposed to indicate the P/E boundary in open marine sequences (Berggren et al., 1967). In low latitude areas this datum has proven to be very useful. Unfortunately, there is increasing evidence pointing to the diachronicity of this taxon in middle to high latitudes (Berggren et al., 1994). An additional problem is the precise taxonomic position of this species. The trochospirally coiled *Globanomalina* gradually evolved into the planispirally coiled *Pseudohastigerina* by the development of an involute spiral side, the concomitant inflation of the chambers and a shift of the aperture from an umbilical-extraumbilical position to an equatorial position (Berggren et al., 1967; Blow, 1979). Since the evolution from *Globanomalina* to *Pseudohastigerina* appears unpunctuated (Banner, 1989), it is difficult to pinpoint the P/E boundary consistently on the basis of the first appearance of *Pseudohastigerina*.

Presently, the IGCP Project 308 "Paleocene/Eocene Boundary Events in Time and Space" Working Group is committed to establish a Global Stratotype Section and Point (GSSP) for the P/E boundary. As is the case for the Cretaceous/Paleogene (K/P) boundary, the aim is to re-define the P/E boundary at a level of distinct global paleoenvironmental change. The best level within the concerned time-slice seems to be the one corresponding with the global extinction of the benthic foraminifer *Gavelinella beccariiformis* and associated species. This level coincides with a distinct negative spike in the marine $\delta^{13}C$ record (Kennett and Stott, 1991). A possibly coinciding carbon isotope excursion has also been measured in paleosol carbonates and enamel apatite of terrestrial mammals at the boundary between the Clarkforkian and Wasatchian mammal zones (Koch et al., 1992). Assuming that the level of this event will eventually be chosen as the official P/E boundary, we will further refer to it as such.

In the Southern Ocean the entry of the planktonic foraminifer, *Globanomalina australiformis* coincides with the P/E boundary (Kennett and Stott, 1991). To date, there is no unequivocal documentation of any pelagic marker (dis)appearing at the P/E boundary in the (sub)tropical realm. However, the entry of *P. wilcoxensis* in bathyal deposits from the Sinai and the Negev, was noted immediately above the exit of *Gavelinella beccariiformis* and associated species (Speijer, 1994a). After a re-study of these specimens from the Negev and Sinai sections, we now regard them as representatives of *Globanomalina luxorensis* (Nakkady, 1950), which is the precursor of *P. wilcoxensis* (Banner, 1989). During subsequent study of the benthic foraminiferal extinction event in Egyptian deposits (Speijer and Van der Zwaan, 1994a,b) the common presence of *G. luxorensis* in the upper part of the upper Paleocene to lower Eocene Esna shales was noted. The present study investigates the taxonomy and biostratigraphic value of *G. luxorensis* in the circum-Mediterranean region and also discusses these topics for very closely related species described from other parts of the world. Since transitional forms between *Globanomalina* and *Pseudohastigerina* are so abundant in Egypt, continuous sections across the P/E boundary could very well reveal a detailed documentation of the evolution from *G. chapmani* through *G. luxorensis* to *P. wilcoxensis*.

Material and methods

The late Paleocene to early Eocene *Globanomalina-Pseudohastigerina* lineage is studied on the basis of samples from many localities in Egypt, Israel, Tunisia and Spain (Fig. 1). Samples were collected during field trips conducted by various teams from the Institute of Earth Sciences, Utrecht University, between 1974 and 1993. Additional samples were kindly supplied by Drs Henk Brinkhuis (Bou Dabbous), Peter Luger (Darb Gaga and Pyramidal Hill; see also Luger, 1985) and Birger Schmitz (Gebel Oweina and Gebel Gurnah).

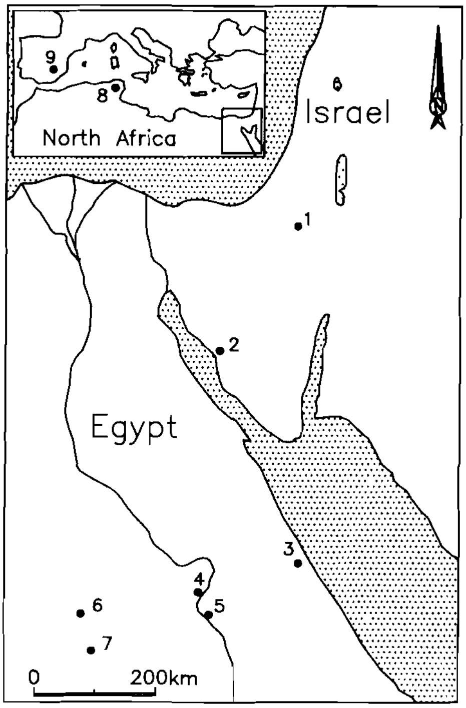

Fig. 1. Provenance of the investigated samples: 1-Nahal Avdat (Israel), 2-Wadi Nukhl, 3-Bir Inglisi, 4-Gebel Gumah, 5-Gebel Oweina, 6-Pyramidal Hill, 7-Darb Gaga (all in Egypt), 8-Bou Dabbous (Tunisia), 9-Caravaca (Spain).

In order to avoid confusion in terminology, the P-notation used for planktonic foraminiferal biozones in this paper is according the latest biozonal schemes (Berggren et al., 1994; see also Fig. 1 in Berggren, 1994), unless indicated otherwise. The P-notation in this new biozonal scheme is significantly different from previous widely used ones, especially for the part of the time scale under discussion.

Earlier proposed phylogenetic relationships of the *Globanomalina-Pseudohastigerina* lineage.

Recently, Pearson (1993) summarized most of the earlier proposed phylogenetic relationships in the *Globanomalina-Pseudohastigerina* lineage. Homibrook (1958b) was the first to suggest that the low trochoid asymmetric *G. pseudoiota* was ancestral to the planispiral *G. iota* (= *P. micra*). In their discussion on the origin and development of *Pseudohastigerina*, Berggren et al. (1967) considered the trochospiral *G. chapmani* to be the direct precursor of *P. wilcoxensis*. Most transitional forms described under various names were regarded as junior synonyms for *G. chapmani* by these authors. Only *G. pseudoiota* was considered a junior synonym for *P. wilcoxensis*. McGowran (1968) did not really elaborate on this lineage, but he briefly mentioned the possiblities that *G. chapmani* or *G. imitata* could be ancestral to *G. pseudoiota* and *G. ovalis*. These taxa in turn would be ancestral to *P. iota* (= *P. micra*). Cordey et al. (1970) reconsidered the evolution of *Pseudohastigerina*: based on a biometric analysis, they considered at least the younger members of *G.* (*Pseudohastigerina*) *pseudoiota* as transitional types between *P. wilcoxensis* and *P. sharkriverensis*. Blow (1979) essentially followed Berggren et al. (1967) regarding the phylogeny of this lineage. Only the rather subjective distinction between *G. chapmani* and *P. wilcoxensis* was defined in such a way, that several primitive *P. wilcoxensis* of Berggren et al. (1967) were regarded as *G. chapmani*. Finally, Banner (1989) proposed a lineage of *Globanomalina* starting with *G. archaeocompressa* through *G. compressa*, *G. chapmani*, *G. ovalis* and *G. luxorensis* to *P. wilcoxensis*. Only truly planispiral specimens were to belong to *P. wilcoxensis*, all specimens with a clear low trochospiral tendency and an asymmetric aperture were regarded either as *G. ovalis* or *G. luxorensis*. According this author *G. pseudoiota* is a junior synonym of *G. ovalis*.

In summary, there appears to be considerable concensus on the phylogenetic linkage of *G. chapmani* to *P. wilcoxensis*. The discussion has mainly focused on the assignment of transitional types to either *G. chapmani*, or *P. wilcoxensis*, or to one or more intermediate species.

Taxonomy

Globanomalina Haque, 1956, emended Banner, 1989

The genus *Globanomalina* is applied to the smooth walled, finely perforate, non-spinose and low-trochoid lineage in Paleocene to early Eocene planktonic foraminifera (Banner, 1989). In most *Globanomalina* species the aperture is confined to the umbilical side (see e.g. *G. chapmani*); only in *G. luxorensis* it transgresses the periphery and opens somewhat at the spiral side. Earlier species in this lineage are not considered in this paper.

Globanomalina chapmani (Parr)
(Pl. I, Figs. 1-3)

1938 *Globorotalia chapmani* Parr: p. 87, pl. 3, figs. 8, 9 (Western Australia).
1953 *Globorotalia membranacea* (Ehrenberg). LeRoy: p. 32, pl. 3, figs. 13, 14
1957 *Globorotalia elongata* Glaessner. Bolli: p. 77, pl. 20, figs. 11-13
1957 *Globorotalia elongata* Glaessner. Loeblich and Tappan (partim): p. 189, (?pl. 45, fig. 5); pl. 46, fig. 5; (?pl. 48, fig. 5); pl. 49, fig. 7; pl. 54, figs. 1-5; pl. 59, fig. 4; pl. 60, fig. 9; (?pl. 63, fig. 2)
1957 *Globorotalia troelseni* Loeblich and Tappan: p. 196, pl. 60, fig. 4; pl. 63, fig. 5
1966 *Globorotalia emilei* El-Naggar: p. 208, pl. 17, fig. 9
1966 *Globorotalia troelseni* Loeblich and Tappan. El-Naggar: p. 238, pl. 17, fig. 10
1967 *Globorotalia chapmani* Parr. Berggren et al. (partim): p. 277, text-fig. 1; text-fig. 3, no. 1; text-fig. 4, no. 1; pl. 1, figs. 3-6; NOT pl. 1, figs. 1-3
1975 *Globorotalia chapmani* Parr. Stainforth et al.: p. 176, fig. 42, Nos. 1-6.
1979 *Globorotalia (Turborotalia) chapmani* Parr, sensu Berggren et al., 1967. Blow (partim): p. 1059, pl. 116, figs. 1, (?2; ?pl. 106, fig. 1); NOT: pl. 116, figs. 3-5
1979 *Globorotalia troelseni* Loeblich and Tappan. Blow: p. 899, pl. 89, figs. 6-10; pl. 90, figs. 1, 2; pl. 234, figs. 1-6
1985 *Planorotalites chapmani* (Parr). Luger: p. 102, pl. 20, figs. 8, 9
1985 *Planorotalites chapmani* (Parr). Toumarkine and Luterbacher: p. 108, fig. 12, nos. 5-8
1993 *Globorotalia chapmani* Parr. Haig et al.: p. 276, pls. 1, 2

Morphological characteristics:

The test consists of 11-15 chambers, that increase rapidly in size, with 4.5-7 chambers to the final whorl. The sutures are depressed and almost radial on the umbilical side and more curved on the spiral side. The lobate periphery shows an imperforate band, which may develop into an indistinct keel on the earlier chambers of the last whorl (*"troelseni"* morphology). Lateral compression of the test varies considerably; the earliest specimens are

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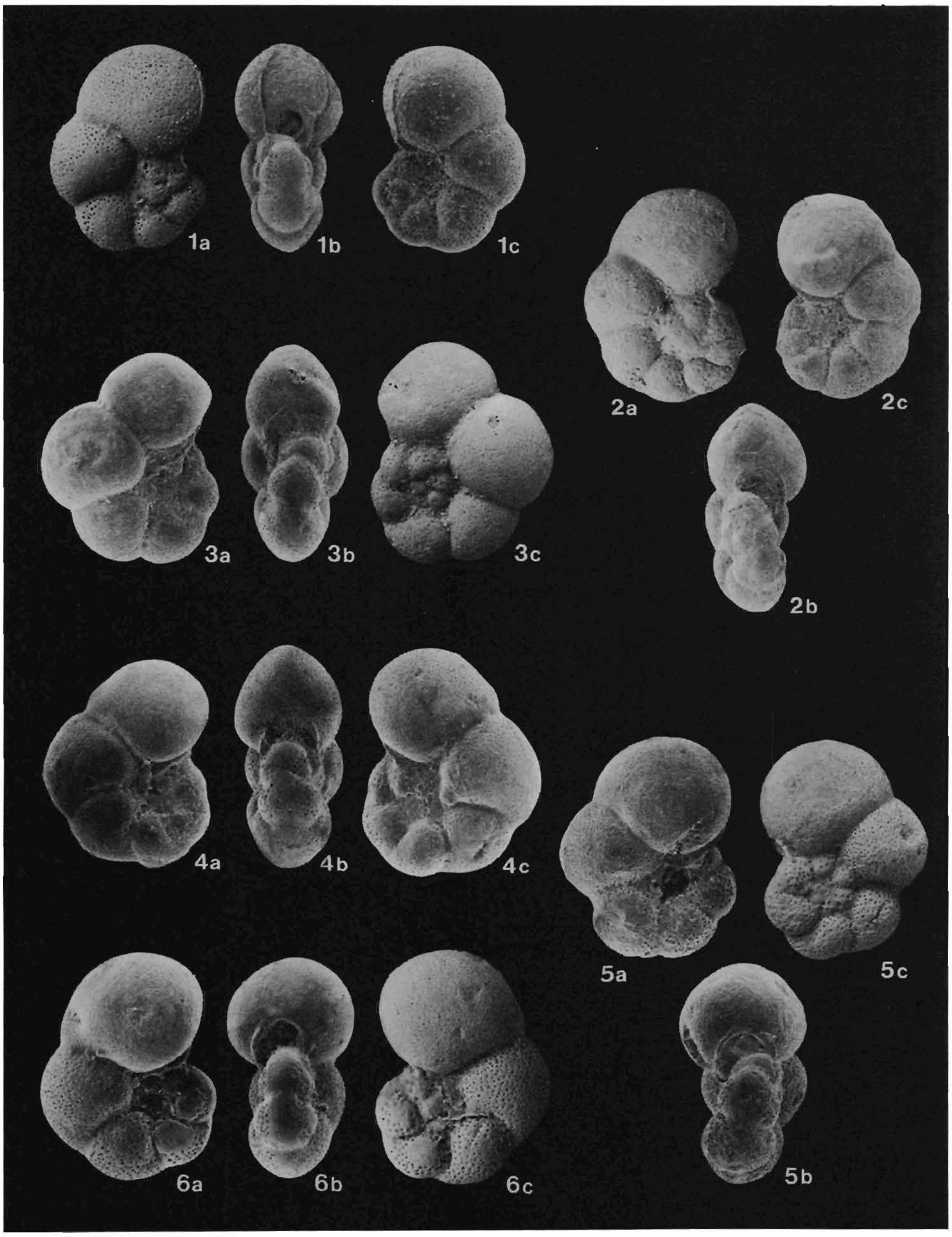
Plate I (all magnifications X 120)

Figs. 1-3: ***Globanomalina chapmani***
Fig. 1: *"troelseni"*-morphology with a poor keel development on the earlier chambers (sample 21283/1; upper Paleocene, Darb Gaga)
Fig. 2: specimen with nearly 7.5 chambers to the last whorl (sample S 1371; upper Paleocene, Wadi Nukhl)
Fig. 3: specimen with a relatively small last chamber (sample P/E - 1 m; upper Paleocene, Gebel Oweina)

Figs. 4-6: ***Globanomalina luxorensis***
Fig. 4: laterally compressed specimen with a nearly equatorially symmetric aperture (sample P/E + 10 m; lower Eocene, Gebel Oweina)
Fig. 5: inflated specimen (sample S 1031; lower Eocene, Bir Inglisi)
Fig. 6: inflated specimen with a distinct imperforate peripheral band as in the *G. chapmani "troelseni"* morphology; the aperture only slightly transgresses the periphery (sample P/E + 10 m; lower Eocene, Gebel Oweina)

PLATE I



usually more compressed and generally have fewer chambers than the later ones. The aperture is moderately to highly arched and bordered by a distinct lip extending from the umbilicus to the peripheral margin. The aperture never transgresses the peripheral margin onto the spiral side.

Remarks:

Haig et al. (1993) show some of the variation in *G. chapmani* by (E)SEM images of the holotype and topotypes from the upper Paleocene (Zone P4) of Perth, Australia. The more inflated morphotype with more numerous chambers is apparently not present in assemblages from the type-area. All specimens show the imperforate peripheral band (McGowran, 1964).

Synonymy:

The species listed above have previously been put in synonymy with *G. chapmani* (see e.g. Berggren et al., 1967; Stainforth et al., 1975; Blow, 1979; Toumarkine and Luterbacher, 1985). *Globorotalia elongata* Glaessner is certainly not conspecific with *G. chapmani* (Berggren et al., 1967; Stainforth et al., 1975; Blow, 1979; Toumarkine and Luterbacher, 1985).

Differential diagnosis from *G. luxorensis*:

In *G. chapmani* the aperture does not extend to the spiral side as in *G. luxorensis.*

Biostratigraphic distribution in Egypt:

Zones P3-P6

Globanomalina luxorensis (Nakkady)
(Pl. I, Figs. 4-6; Pl. II, Figs. 1-4)

1950 *Anomalina luxorensis* Nakkady: p. 691, pl. 90, figs. 39-41 (Western Sinai, Egypt)
1953 *Anomalina luxorensis* Nakkady. LeRoy: p. 18, pl. 18, figs. 5-7
1956 *Globanomalina ovalis* Haque: p. 148, pl. 14, fig. 3
1958a *Globigerina pseudoiota* Hornibrook: p. 34, pl. 1, figs. 16-18
1958b *Globigerina pseudoiota* Hornibrook. Hornibrook: p. 665, figs. 23, 26-28
1959 *Anomalina luxorensis* Nakkady. Nakkady: pl. 5, fig. 1
1967 *Globorotalia chapmani* Parr. Berggren et al. (partim): Pl. 1, figs. 1-3; NOT: p. 277, text-fig. 1; text-fig. 3, no. 1; text-fig. 4, no. 1; pl. 1, figs. 3-6
1967 *Pseudohastigerina wilcoxensis* (Cushman and Ponton). Berggren et al. (partim): p. 278, text-fig 2, d-f, m-r. NOT text-fig. 2, (?a-c, ?g-l), s-v; text-fig. 3, 2-5; text-fig. 4, 2-5; (?text-fig. 5, 1-9); text-fig. 6, 1-6
1973 *Pseudohastigerina pseudoiota* (Hornibrook). Samanta: p. 475, pl. 7, figs. 3, 4
1975 *Pseudohastigerina wilcoxensis* (Cushman and Ponton). Stainforth et al.: p. 243, fig. 99, no. 6 ("transitional to *G. chapmani*")
1979 *Globorotalia (Turborotalia) chapmani* Parr, sensu Berggren et al., 1967. Blow (partim): p. 1059, pl. 116, figs. 3-5; pl. 111, fig. 5 (recorded as "ex interc. *G. (T.) chapmani* and *P. wilcoxensis*"). NOT pl. 106, fig. 1; pl 116, figs. 1, 2
1989 *Globanomalina ovalis* Haque. Banner (partim): p. 175, pl. 1, figs. 1, 4 (?fig. 3); pl. 2, fig. 1, (?fig. 2); NOT pl. 3, figs. 1, 2
1990a *Pseudohastigerina wilcoxensis* (Cushman and Ponton). Stott and Kennett: p. 560, pl. 5, figs. 5, 6

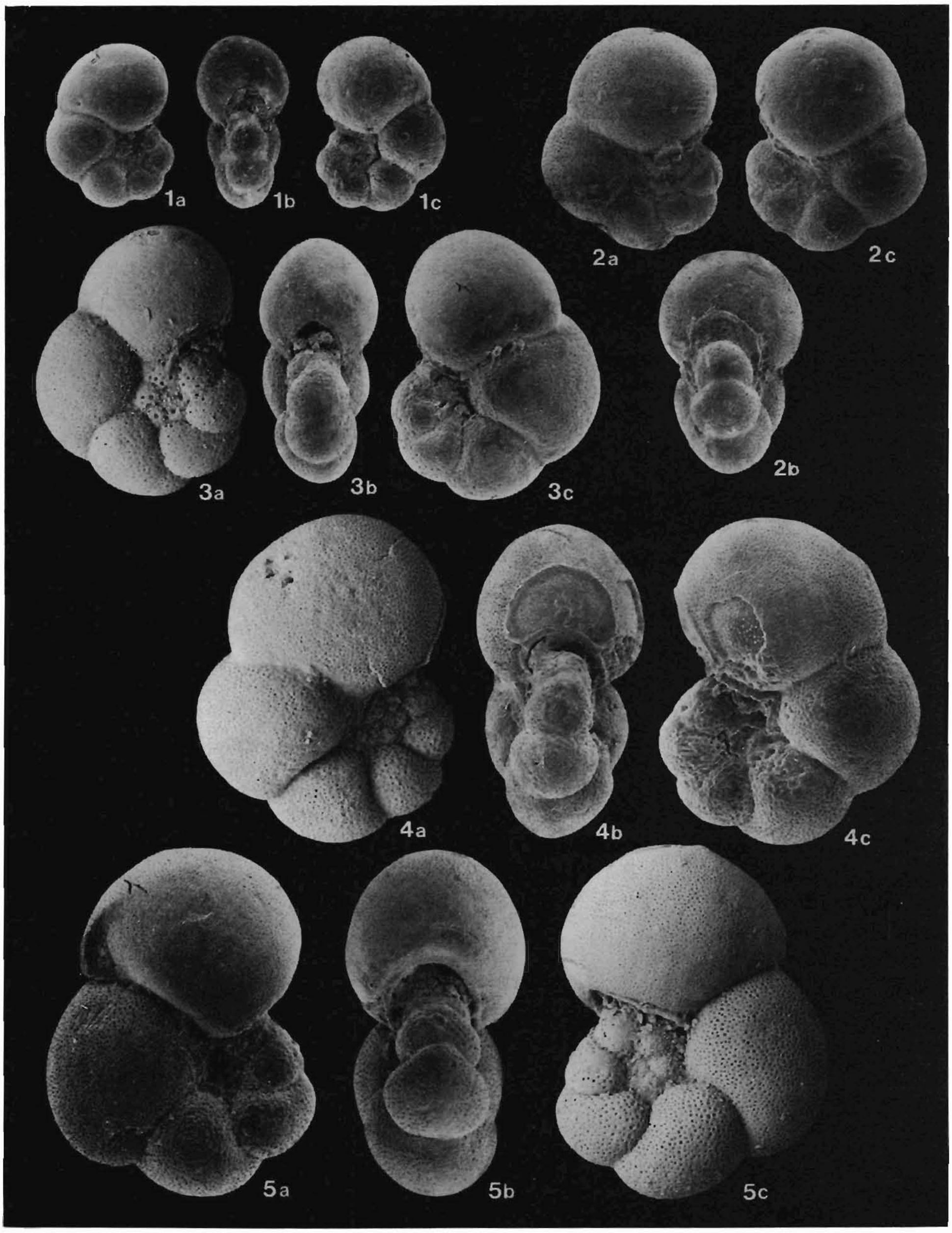
Morphological characteristics:

The test consists of about 13-15

Plate II (all magnifications X 120)

Figs. 1-4: ***Globanomalina luxorensis***
Fig. 1: juvenile specimen (sample 3382/27; lower Eocene, Pyramidal Hill)
Fig. 2: tightly coiled specimen with only five chambers to the last whorl (sample 20283/5; lower Eocene, Darb Gaga)
Fig. 3: specimen with distinct pore-pits on spiral side of earlier chambers (sample P/E + 10 m; lower Eocene, Gebel Oweina)
Fig. 4: large specimen with equatorially asymmetric aperture (sample P/E + 23 m; lower Eocene, Gebel Oweina)
Fig. 5: ***Pseudohastigerina wilcoxensis***, early large specimen with diagnostic apertural features but distinct trochospiral coiling mode (sample P/E + 10 m; lower Eocene, Gebel Oweina)

PLATE II



chambers, increasing rapidly in size as added, with 5 to 7 (generally 6) chambers to the last whorl. Most specimens are inflated and have a circular last chamber in apertural view. However, lateral compression strongly varies, resulting in more flattened specimens with an oval last chamber in apertural view. The sutures are strongly depressed, almost radial on the umbilical side and more curved on the spiral side. Sometimes the spiral side is almost entirely evolute, but mostly it is semi-involute. Sporadic specimens are semi-involute on both sides. The shape of the aperture ranges from high-arched and strongly asymmetric equatorially, to low-arched and almost symmetric equatorially. The aperture is bordered by a distinct lip, forming a small umbilical flap, partly covering the umbilicus. The aperture transgresses the peripheral margin, but it does not open in the trace of the spiral suture. The test is finely perforate, although pore-pits may suggest larger pores on the earlier chambers. Most specimens show an imperforate marginal band, or at least less dense pore distribution at the periphery in the earlier chambers of the last whorl.

Remarks:

This species has often been treated as a junior synonym of *G. chapmani* (Berggren et al., 1967, Blow, 1979). However, it appears very useful for biostratigraphic purposes to separate this species from *G. chapmani* (see below). Blow (1979) proposed to include many specimens of *P. wilcoxensis* as figured by Berggren et al. (1967) into the concept of *G. chapmani*. Both these specimens as well as several specimens figured in Blow (1979) are considered as *G. luxorensis* in this paper.

Synonymy:

The holotypes of both *G. ovalis* and *G. pseudoiota* show an asymmetric equatorial aperture, which does not open into the trace of the spiral suture. These apertural and other characteristics (e.g. number and shape of chambers) fall well within the range of variation of *G. luxorensis* as observed in Egyptian populations. Thus, *G. ovalis* and *G. pseudoiota* can be regarded as junior synonyms of *G. luxorensis*.

Differential diagnosis from *P. wilcoxensis*:

In *G. luxorensis* the aperture extends to the dorsal side, but it does not open in the trace of the spiral suture as in *P. wilcoxensis*.

Biostratigraphic distribution in Egypt: Zones P4-P7 (possibly higher).

Pseudohastigerina Banner and Blow, 1959, emended Blow, 1979

The genus *Pseudohastigerina* is applied to the smooth walled, finely perforate, non-spinose, (almost) planispiral lineage in Eocene planktonic foraminifera. All species have an (almost) symmetric equatorial aperture opening in the trace of the spiral suture (cf. Blow, 1979).

Pseudohastigerina wilcoxensis (Cushman and Ponton)
(Pl. II, Fig. 5)

1932 *Nonion wilcoxensis* Cushman and Ponton: p. 64, pl. 8, fig. 11 (Alabama, USA)
1960 *Hastigerina eocenica* Berggren: p. 85, pl. 5, figs. 1, 2; pl. 10, fig. 2; text-figs. 13-16
1967 *Pseudohastigerina wilcoxensis* (Cushman and Ponton). Berggren et al. (partim): p. 278, text-fig. 2, (?a-c, ?g-l), s-v; text-fig. 3, 2-5; text-fig. 4, 2-5; (?text-fig. 5, 1-9); text-fig. 6, 1-6. NOT: text-fig. 2, d-f, m-r
1975 *Pseudohastigerina wilcoxensis* (Cushman and Ponton). Stainforth et al.: p. 243, fig. 99, nos. 1-5
1979 *Pseudohastigerina wilcoxensis* (Cushman and Ponton). Blow: p. 1193, pl. 159, figs. 8, 9; pl. 161, figs. 10, 11
1985 *Pseudohastigerina wilcoxensis* (Cushman and Ponton). Luger: pl. 20, figs. 10-12
1985 *Pseudohastigerina wilcoxensis* (Cushman and Ponton). Toumarkine and Luterbacher (partim): p. 108, fig. 12, 9-11, (?12)

Morphological characteristics:

The almost planispiral test consists of about 13-15 strongly inflated chambers with 5-7 chambers to the last whorl. Lateral compression varies somewhat. The depressed sutures are slightly curved on both sides. On both sides the earlier whorl can be slightly visible. Pore distribution is less dense on the peripheral margin, but an imperforate peripheral band is never present. The symmetric equatorial aperture is bordered by a distinct lip and opens in the trace of the spiral suture.

Remarks:

This description of *P. wilcoxensis* largely follows the concept of Blow (1979). It differs from Berggren et al. (1967) in the exclusion of clearly trochospiral specimens with an asymmetric equatorial aperture (= *G. luxorensis*). At the entry of *P. wilcoxensis* in the early Eocene, only in large specimens the aperture opens in the trace of the spiral suture. Smaller specimens always have the apertural characteristics of *G. luxorensis*. Thus, the specific difference between *G. luxorensis* and *P. wilcoxensis* is initially only well visible in the later stages of ontogenetic development. Later in the Eocene, *P. wilcoxensis* shows heterochronic predisplacement (McNamara, 1990), when also smaller specimens show these apertural features.

Synonymy:

Pseudohastigerina eocenica is generally regarded as a junior synonym of *P. wilcoxensis* (Berggren et al., 1967; Stainforth et al., 1975; Blow, 1979).

Biostratigraphic distribution in Egypt:

Zones P5-P7 (probably higher).

Proposed phylogeny

Our analysis of late Paleocene-early Eocene foraminiferal assemblages strongly suggests the following phylogenetic lineage: *G. chapmani---->G. luxorensis---->P. wilcoxensis*. Within Zone P4 populations of *G. chapmani* contain forms with more inflated chambers, generally 6 to the last whorl. Most specimens show an aperture in umbilical-extraumbilical position, but extremely rare specimens show a more involute spiral side and a strongly asymmetric equatorial aperture. The apertural lip only slightly transgresses the imperforate peripheral band. These specimens are regarded as the first true *G. luxorensis*. This species remains very rare up to the P/E boundary. Only just above this boundary *G. luxorensis* becomes the dominant species in the lineage. The first specimens of *P. wilcoxensis* appear in small numbers somewhat higher above the P/E boundary (upper part of Zones P5, NP9). These early specimens are always large compared to the numerous specimens of *G. luxorensis*. At that level juvenile specimens with a *P. wilcoxensis* morphology are not encountered, suggesting that initially only under specific circumstances the *P. wilcoxensis* morphology developed at a late stage of ontogenetic development of *G. luxorensis*. This feature clearly shows the arbitrary division of these two species/genera in this time-slice and is probably the root of taxonomic confusion.

Essentially, the phylogeny proposed here does not differ from earlier proposed phylogenies (Berggren et al., 1967; Blow, 1979). The main difference is the nomination of a separate species for transitional specimens. The sudden increase in frequency of *G. luxorensis* relative to *G. chapmani* at the P/E boundary indicates an acceleration in the gradual evolution from *G. chapmani* to *P. wilcoxensis*. The exact cause for this remains elusive, but is clearly related to the global paleoceanographic change at the P/E boundary.

Temporal and spatial distribution of *Globanomalina luxorensis*

In Egypt this species has previously been recorded in many localities under its proper name (Nakkady, 1950, 1959; LeRoy, 1953; Ansary and Fahmy, 1969) but also as *P. wilcoxensis* (Luger, 1985; Faris et al., 1985; Speijer, 1994a) and *G. troelseni* (El-Naggar, 1966). It is usually found in the Esna shales (Zones P5-6), but it was also recorded by Nakkady (1959) in the Tarawan chalk (Zone P4). These observations are confirmed in the present study. In Zone P4 and in the lower part of Zone P5 (Tarawan chalk and basal part of the Esna shales) this taxon is extremely rare; in the upper part of Zone P5, just above the P/E boundary and in Zone P6 *G. luxorensis* is very common in Egyptian deposits. Samples from Israel, Tunisia and Spain confirm this pattern. The sudden lowest common occurrence of this taxon appears to be a very useful tool for biostratigraphic correlations and for delineation of the P/E boundary, at least in the circum-Mediterranean region.

In Pakistan the entry of *G. luxorensis* falls within Zone P5 (Haque, 1956; Samanta, 1973; Gibson, 1994), and in terms of calcareous nannofossil biozonation, within (the upper part of) NP9 (Haq, 1972; Bybell, 1994). In New Zealand the entry of *G. luxorensis* is in the Waipaian Stage (Hornibrook, 1958a). This is in the upper part of Zone NP9, (just?) above the extinction level of *Gavelinella beccariiformis, Neoflabellina* and other species (Hornibrook, 1958a; Hornibrook and Edwards, 1971; Kaiho et al., 1993). Therefore, the entry of *G. luxorensis* (nearly?) coincides with the P/E boundary in New Zealand.

In summary, *G. luxorensis* occurs already within Zone P4, but it is only (just) above the P/E boundary (P5, NP9) that this species becomes the most common representative of the lineage in continental margin deposits from widely separated regions in low and middle latitudes.

In deep neritic to bathyal deposits of the circum-Mediterranean region the lowest common occurrence of *G. luxorensis* immediately follows the extinction of *Gavelinella beccariiformis* and associated species. For shallow neritic areas without any deep-sea benthics, such as in Bir Inglisi (Red Sea coast, Egypt), this level can independently be identified by the negative spike in stable carbon isotope values (B. Schmitz pers. communication 1994; Speijer and Van der Zwaan, 1994a). As discussed above, this excursion coincides with the extinction of many deep-sea benthic foraminifera observed in cores recovered by DSDP/ODP. Thus, at least in the circum-Mediterranean region the lowest common occurrence of *G. luxorensis* provides a powerful and easy tool for recognition of the P/E boundary, even within shallow neritic environments where the extinction event is expressed differently.

Conclusions

(1) Transitional forms between *G. chapmani* and *P. wilcoxensis* from the circum-Mediterranean region are regarded as *G. luxorensis* (Nakkady). These taxa are primarily distinguished by their apertural characteristics. Within Zones P4-P6 *G. luxorensis* intergrades with *G. chapmani*. Above the P/E boundary (Zones P5-P6) it also intergrades with *P. wilcoxensis*. Initially, the *P. wilcoxensis* morphology is only attained in large adult specimens; later on, also juvenile specimens show the characteristic features of *P. wilcoxensis* (heterochronic pre-displacement).

(2) In the circum-Mediterranean region the lowest common occurrence of *G. luxorensis* immediately follows the extinction of *Gavelinella beccariiformis* and associated taxa, which coincides with the strong negative excursion in the $\delta^{13}C$ record. From that level onwards, *G. luxorensis* is the dominant species in the *Globanomalina* lineage. Below this level *G. luxorensis* is

very rare and *G. chapmani* is the dominant species in this lineage.

(3) At least in Egypt the lowest common occurrence of *G. luxorensis* provides an excellent independent tool for assigning the P/E boundary in shallow neritic environments, where the benthic extinction event is expressed differently.

(4) In combination, the benthic foraminiferal extinction event, the lowest common occurrence of *G. luxorensis* and the carbon isotope excursion, are powerful tools to recognize a distinct horizon in various marine environments. Therefore, it is strongly recommended that the GSSP of the P/E boundary should be fixed at this horizon.

(5) Some of the Egyptian sections appear good candidates for this GSSP, although other stratigraphic tools still need to be elaborated for these sections.

Acknowledgements

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- CHAPTER IV -

The late Paleocene benthic foraminiferal extinction as observed in the Middle East

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ABSTRACT

The microfossil content of the upper Paleocene parts of the Nahal Avdat section (Negev Desert, Israel) and the Abu Rudeis section (Sinai Desert, Egypt) was studied. Direct correlation of planktonic foraminiferal and calcareous nannofossil zonations results in positioning the NP9/NP10 zonal boundary within the top part of Zone P6a. Benthic foraminiferal assemblages in the two areas are diverse and very similar: 92% of the more abundant species are observed at both sites. These sites were situated in the deeper parts of a NE-SW trending basin at a paleodepth of 500-700 m.

The well-known deep-sea benthic extinction (within Zones P6a, NP9) is easily recognized by the sudden disappearance of *Gavelinella beccariiformis, Angulogavelinella avnimelechi, Pullenia coryelli* and other species within a 50 kyr. timespan. In contrast to deep ocean sites, simple diversity drops only 17%, since the abundant shallow-water species in the assemblages are not affected. Post-extinction faunas are dominated by *Nuttallides truempyi* (up to 29%). In addition to this species a number of other species occur which seem to invade the deeper parts of the basin from shallow waters, immediately after the extinction. Infaunal morphotype abundance does not increase across the extinction level, indicating stable bottom water oxygenation.

On the basis of these data, it is concluded that the hypothesis involving a temporal shift of bottom water formation from high to low latitude, inducing warm saline bottom water to spread through all oceanic basins, is tenable. However, oxygen deficiency of this postulated watermass originating at low latitudes, can not be the controlling factor in the worldwide extinction. A change in other properties, e.g. salinity and/or temperature, must at least have played a role as well.

Introduction

The late Paleocene is characterized by a major turnover in deep-sea benthic foraminiferal assemblages (Tjalsma and Lohmann, 1983). This event was first described by Beckmann (1960) for the Lizard Springs Formation in Trinidad. Subsequently it was recorded in the Alps (Von Hillebrandt, 1962; Braga et al., 1975), in Japan and New Zealand (Kaiho, 1988) and in many deep-sea cores, recovered by the Deep Sea Drilling Project and the Ocean Drilling Program, from all the world's oceans (e.g. Tjalsma, 1977; Schnitker, 1979; Thomas, 1990b; Katz and Miller, 1991; Nomura, 1991). Many cosmopolitan Cretaceous species that apparently easily survived the biotic crisis at the Cretaceous/Paleogene (K/P) boundary (Beckmann, 1960; Webb, 1973; Dailey, 1983), became extinct near the end of the Paleocene (Tjalsma and Lohmann, 1983; Thomas, 1990b; Nomura, 1991). In fact, the late Paleocene extinction can be regarded as the largest turnover in deep-sea benthic foraminifera of the last 90 million years (Tjalsma and Lohmann, 1983). A drop in species diversity of 35-50% has been observed at several locations in the

Southern Ocean (Thomas, 1990b; Katz and Miller, 1991; Nomura, 1991).

Ever since the recognition of this event, it has been difficult to asses its exact timing within a rigid biostratigraphic framework (Tjalsma and Lohmann, 1983). Tjalsma (1977) and Schnitker (1979) observed a post-extinction fauna within the lowermost part of Zone P6a, following the foraminiferal zonal scheme of Berggren (1969). Therefore, Tjalsma and Lohmann (1983) concluded that the faunal turnover coincided with the P5/P6a zonal boundary. Because of the occurence of a pre-extinction fauna within Zone P6a in a Pacific deep-sea core, Miller et al. (1987) suggested that the turnover should be placed within Zone P6a and probably just below the P6a/P6b zonal boundary (Berggren and Miller, 1989), often referred to as the Paleocene/Eocene boundary (Berggren et al., 1985).

Recently, the benthic turnover has been linked to a calcareous nannofossil zonal scheme. Both at Maud Rise, Weddell Sea, (Thomas, 1989) and at Broken Ridge, Indian Ocean (Nomura, 1991) it is placed within the top part of Zone NP9, following the zonal scheme of Martini (1971). Because of the scarcity of the NP10 zonal marker *Tribrachiatus bramlettei* within oceanic sediments, the NP9/NP10 zonal boundary is often drawn at the last occurrence (LO) of *Fasciculithus* (Aubry et al., 1988). This LO is sometimes correlated with the benthic turnover (Katz and Miller, 1991). Of course, the use of this LO should be used with great care because of the easy reworking of *Fasciculithus.*

The benthic extinction event has often been referred to as a Paleocene/Eocene boundary event (Boersma, 1984; Rea et al., 1990). However, Aubry et al. (1988) pointed out that the Paleocene/Eocene boundary, as it was originally defined by Von Koenen (1885), corresponds to the upper part of Zone NP10. Therefore, the extinction is merely a late Paleocene feature. Whatever the exact timing might be, Kennett and Stott (1991) clearly demonstrated, by means of high resolution sampling, that it was a rather rapid event spanning only a few thousand years, at least at Maud Rise. Furthermore, these authors showed that it was accompanied by a sudden decline in carbonate $\delta^{18}O$ values, which is immediately followed by a strong decrease in $\delta^{13}C$ values. These isotopic shifts are superimposed on longer term trends towards lighter values starting in the late Paleocene, which have been observed in many other areas (e.g. Shackleton et al., 1984, 1985; Katz and Miller, 1991; Barrera and Huber, 1991; Nomura, 1991; Hovan and Rea, 1992).

Four main hypotheses have been proposed in explaining stable isotope excursions and the benthic extinction. The first two emphasize excursions of oxygen and carbon stable isotopes, whereas the other two more strongly lean on the change in $\delta^{13}C$ values. Shortly summarized the explanations are:

1 - Rapid global warming would induce intense formation of warm saline bottom water (WSBW), after the model of Brass et al. (1982); the high temperature of this watermass would be lethal to many benthic species (Miller et al., 1987).

2 - In essence the same as mentioned above, but pointing to oxygen deficiency of the WSBW as the lethal factor (Thomas, 1989, 1990b).

3 - In sharp contrast with the previous explanations, this one invokes a cessation of WSBW formation induced by reduction of evaporation in marginal seas (Brass, et al., 1982; Barron et al., 1981); This would lead to aged and oxygen-depleted bottom water causing the extinction (Nomura, 1991).

4 - The strong negative $\delta^{13}C$ excursion has been interpreted as a signal of a global decrease in primary production (Shackleton et al., 1985). This would lead to a decrease in organic carbon flux to the bottom, resulting in starvation for benthic organisms (Miller et al., 1987).

The causal mechanism for the global changes in oceanic chemistry and/or circulation in the first three hypotheses mentioned is still a matter of speculation. It is suggested that a sharp increase in atmospheric CO_2, causing an extreme greenhouse effect, was induced by extensive volcanism and hydrothermal activity at a time of plate-tectonic reorganization (e.g. Rea et al., 1990; Thomas and Varenkamp, 1992).

In order to evaluate the merit of the models for low latitude areas, samples from two sections (Nahal Avdat, Negev Desert, Israel and Abu Rudeis, Sinai Desert, Egypt) have been investigated. Both sections display an almost continuous sequence of Upper Cretaceous through lower Eocene deposits. In this paper some preliminary results concerning the benthic foraminiferal patterns from the upper Paleocene parts of the sections are presented.

Regional geology

The deposits studied, belong to the Taqiye Formation for the Israelian Nahal Avdat section (Romein, 1979a) and to the Esna Shales, first described by Beadnell (1905), for the Egyptian Abu Rudeis section (for location see Fig. 1). Both are however partially lateral equivalents with very similar, predominantly marly, lithologies (Arkin et al., 1972). These deposits are widely distributed all over Egypt (e.g. Leroy, 1953; Nakkady, 1957; Luger, 1985) and within a NE-SW trending area across the central Sinai between the Dead Sea and the Gulf of Suez (Bartov and Steinitz, 1977). This area delineates a basin which developed during the Late Cretaceous Laramide orogeny, creating the Syrian Arc System (Bartov and Steinitz, 1977; El Shazly, 1977). Based on isopach maps, the two sections studied are thought to be situated in the deeper parts of this basin (Bartov and Steinitz, 1977). Small-scale fold structures with the same NE-SW direction are observed in the area around Nahal Avdat causing basinal highs and lows. The upper part of the Taqiye Formation, i.e. the Hafir Member, clearly wedges out against the structural highs (Arkin et al., 1972). Based on lithofacies and clay mineral distributions, these authors argued that, these highs were emerged during late Paleocene-early Eocene time, forming longitudinal peninsulas within a shallow sea.

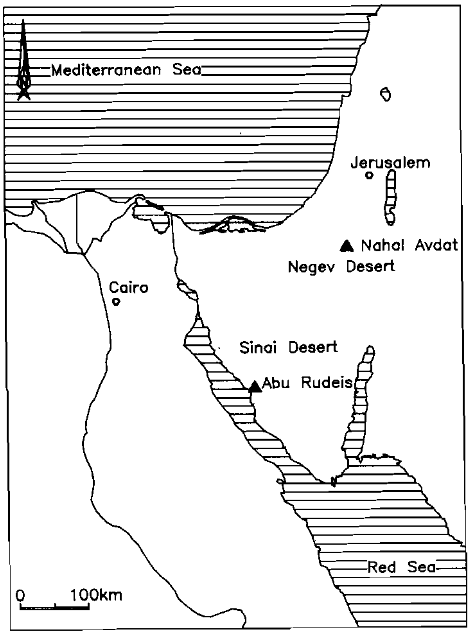

Fig. 1. Location of the two studied sections (triangles) in the Middle East.

Most papers dealing with late Paleocene-early Eocene microfossils, obtained from the Sinai/Negev region, focused on (regional) stratigraphic correlations (e.g.: Reiss, 1952; Said and Kenawy, 1956; Nakkady, 1957; Abdelmalik et al., 1978a,b), of course strongly relying on pelagic fossils. Unfortunately, useful paleoenvironmental analyses based on either benthic and/or pelagic microfossils are extremely scarce. An example is the paper by Shahin (1990) discussing an area somewhat south of Abu Rudeis. More paleoenvironmental studies are needed, however, in order to test the validity of the above-mentioned basin configurations; in that way it would be easier to distinguish local from regional and global events.

Material and methods

Data on calcareous nannofossil distributions of the Nahal Avdat section were obtained from Romein (1979a). For the Abu Rudeis section, analyses on calcareous nannofossils were carried out separately. Special attention was paid to marker species. All samples, except IR106 were disintegrated in water for a few days and were subsequently washed over a 63- and 125-µm mesh sieve. Afterwards samples were dried at 60°c in a stove. Benthic foraminifera showed a reasonabe preservation, whereas in many samples the planktonic foraminifera showed more or less severe signs of dissolution. Because Israelian samples were extremely small, the planktonic foraminiferal assemblages were sometimes rather poor. Only the 125-µm fraction was employed both for planktonic and benthic foraminiferal analyses. For planktonic foraminiferal biostratigraphy the samples were only searched for several marker species. In contrast, all benthic forminiferal specimens (about 200-300) were picked from a split of the sample and were subsequently stored and sorted in a Chapman-slide. These pickings were used in quantative analyses of the benthic assemblages. Most specimens were determined at species level, in closed or open nomenclature; a minor part was assigned to a higher taxonomic level. The standard zonations of Berggren (1969) and Martini (1971), for planktonic foraminifera and calcareous nannofossils respectively, were used for biostratigraphy.

Biostratigraphic results

In figure 2 the ranges of several nannofossil (Romein, 1979a) and planktonic foraminiferal marker species in the Nahal Avdat section are displayed. *Discoaster multiradiatus* is observed in all samples; this implies that the base of Zone NP9 (Martini, 1971) is not encountered in this part of the section. The zonal boundary between NP9 and NP10 which is defined by the first occurrence (FO) of *Tribrachiatus bramlettei* (Martini, 1971) is observed between samples IR106 and IR107. This level coincides with a sharp decrease in *Fasciculithus* spp. Possibly, the *Fasciculithus tympaniformis* found in higher samples are reworked; if so, then the last common occurrence (LCO) of *Fasciculithus* approximates the NP9/NP10

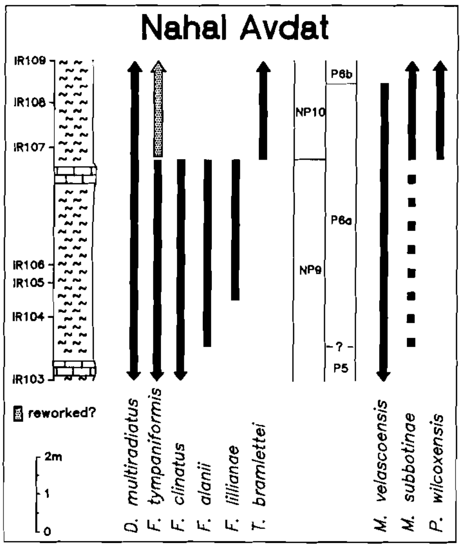

Fig. 2. Lithologic column and studied samples (IR codes) of the Nahal Avdat section; biozonation is based on ranges of selected calcareous nannofossil species (left, after Romein, 1979a) and planktonic foraminifera (right).

zonal boundary (Berggren et al., 1985; Perch-Nielsen, 1985).

In samples IR104 and IR105 only a few specimens resembling *Morozovella subbotinae* were observed; therefore the boundary between Zones P5 and P6a (Berggren, 1969) was tentatively placed between samples IR103 and IR104. The FO of *Pseudohastigerina wilcoxensis* coincides with the FO of *Tribrachiatus bramlettei*. The LO of *Morozovella velascoensis* is encountered in IR108; therefore IR109 belongs to the basal part of Zone P6b. The extinction of many benthic species, e.g. *Gavelinella beccariiformis* and *Pullenia coryelli* falls between IR105 and IR107, thus within Zone P6a and near the NP9/NP10 zonal boundary.

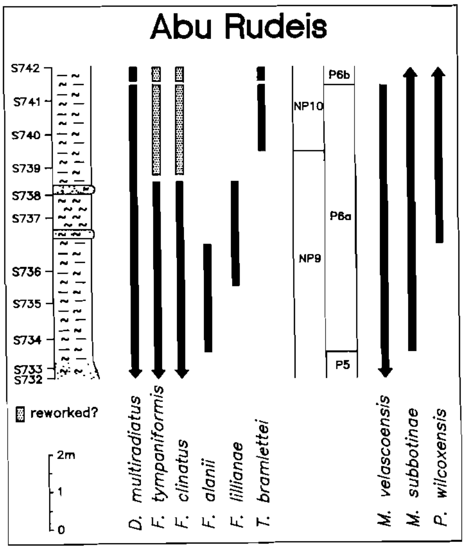

Fig. 3. Lithologic column and studied samples (S codes) of the Abu Rudeis section; biozonation is based on ranges of selected calcareous nannofossil species (left) and planktonic foraminifera (right).

Ranges of marker species in the Abu Rudeis section (Fig. 3) reveal essentially the same pattern as in the Nahal Avdat section; moreover, they add some biostratigraphic resolution. Again, *Discoaster multiradiatus* has been observed in all samples, thus the base of Zone NP9 is not reached. A clear lag separates the LCO of *Fasciculithus* spp. and the FO of *Tribrachiatus bramlettei*. Thus it seems that the probable extinction of *Fasciculithus* is just below the NP9/NP10 zonal boundary.

Distinct *Morozovella subbotinae* appear from sample S734 onwards, defining the P5/P6a zonal boundary just below this sample. *Pseudohastigerina wilcoxensis* appears well below the FO of *Tribrachiatus bramlettei*, at about the same level of the benthic extinction. Based on the LO of *Morozovella velascoensis*, the P6a/P6b zonal boundary is situated near the top of the section. Again the benthic extinction falls within P6a and just below the NP9/NP10 zonal boundary.

Evidently the Abu Rudeis section displays a higher biostratigraphic resolution. This probably results from the better sample coverage in this section. Fig.4 shows that the two sections can easily be correlated using all faunal events. If Fig. 4 is compared with the integrated Paleogene geochronological scheme of Aubry et al. (1988), it appears that these authors propose quite a different sequence of faunal events: they correlated the NP9/NP10 zonal boundary with a level within Zone P6b. Probably the reason for this discrepancy is the scarcity of NP10 zonal marker *Tribrachiatus bramlettei* in oceanic sediments (Aubry et al., 1988) and/or reworking of *Fasciculithus* above its supposed extinction level. These results, however, are not completely new. In fact, the FO of *Tribrachiatus bramlettei* within the *Morozovella velascoensis* Zone (i.e. Zone P5 or P6a, following Berggren, 1969) was already proposed by Hay and Mohler (1969) and Abdelmalik et al. (1978a,b) for some epicontinental deposits exposed in land sections. The latter authors based this idea on studies on a parallel-section of the Abu Rudeis section.

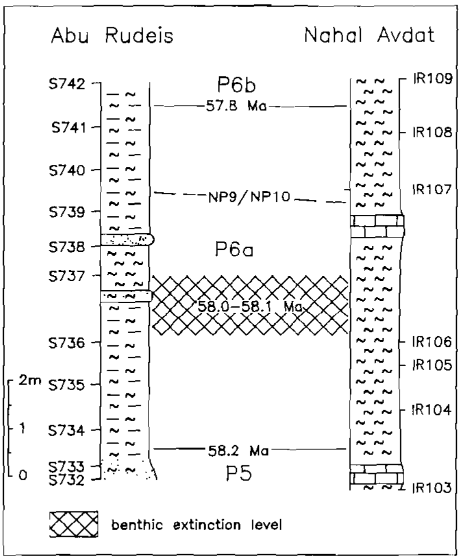

Fig. 4. Correlation of the two sections based on foraminiferal and nannoplankton events, introducing numerical age estimates (after Aubry et al., 1988) for the foraminiferal zonal boundaries. Constant sedimentation rates are assumed for the correlation of the benthic extinction level.

Our study indicates that the extinction event should be placed below the NP9/NP10 zonal boundary (Fig.4), either based on the FO of *Tribrachiatus bramlettei* or approximated by the LCO of *Fasciculithus*. This agrees well with recent ODP data (Thomas, 1989; Katz and Miller, 1991; Nomura, 1991). It is also clearly demonstrated that the benthic extinction occurs within Zone P6a. This is in agreement with the suggestion of Miller et al. (1987). In the study area the FO of *Pseudohastigerina wilcoxensis* is the best coeval faunal event in the pelagic realm to approximate the benthic extinction (Figs. 2,3,4). Whether this is just a local feature, remains to be investigated. However, there is some proof that this is a global feature for (sub-)tropical areas (Berggren and Miller, 1988).

When numerical age estimates for the P5/P6a (58.2 Ma) and P6a/P6b (57.8 Ma) zonal boundaries are used (Aubry et al., 1988), the average sedimentation rates in both sections can be estimated at about 1,75 cm/kyr. By extrapolation this implies that the benthic extinction occurred between 200-300 kyr before the extinction of *Morozovella velascoensis*, thus at 58.1-58.0 Ma. Furthermore, this sedimentation rate implies that in the Abu Rudeis area the turnover in the benthic assemblage took less than 50 kyr. This is not surprising since Kennett and Stott (1991) already denoted a time span of less than 3 kyr(!) for the enormous drop in benthic foraminiferal diversity at Maud Rise. The relative rapidity of this event places constraints on the various hypotheses put forward to explain this extinction.

Quantitative analysis of benthic assemblages

Within the 16 samples treated in this paper, 118 different taxa were encountered; this number would have been much higher if the complete washed residue would have been searched for rare specimens and if certain species (e.g. Nodosariids) were not lumped together.

The taxa found can be grouped into three categories.

- 64 species are more or less common and compose 81-92% of the specimens in each sample.
- 37 species are very scarce and compose up to 5% of the specimens in each sample.
- Other species are lumped into 17 taxa, composing 7-17% of the specimens in each sample.

92% of the common species were encountered in samples from both sections. The quantitative patterns of the 36 most common species are displayed in Fig. 5.

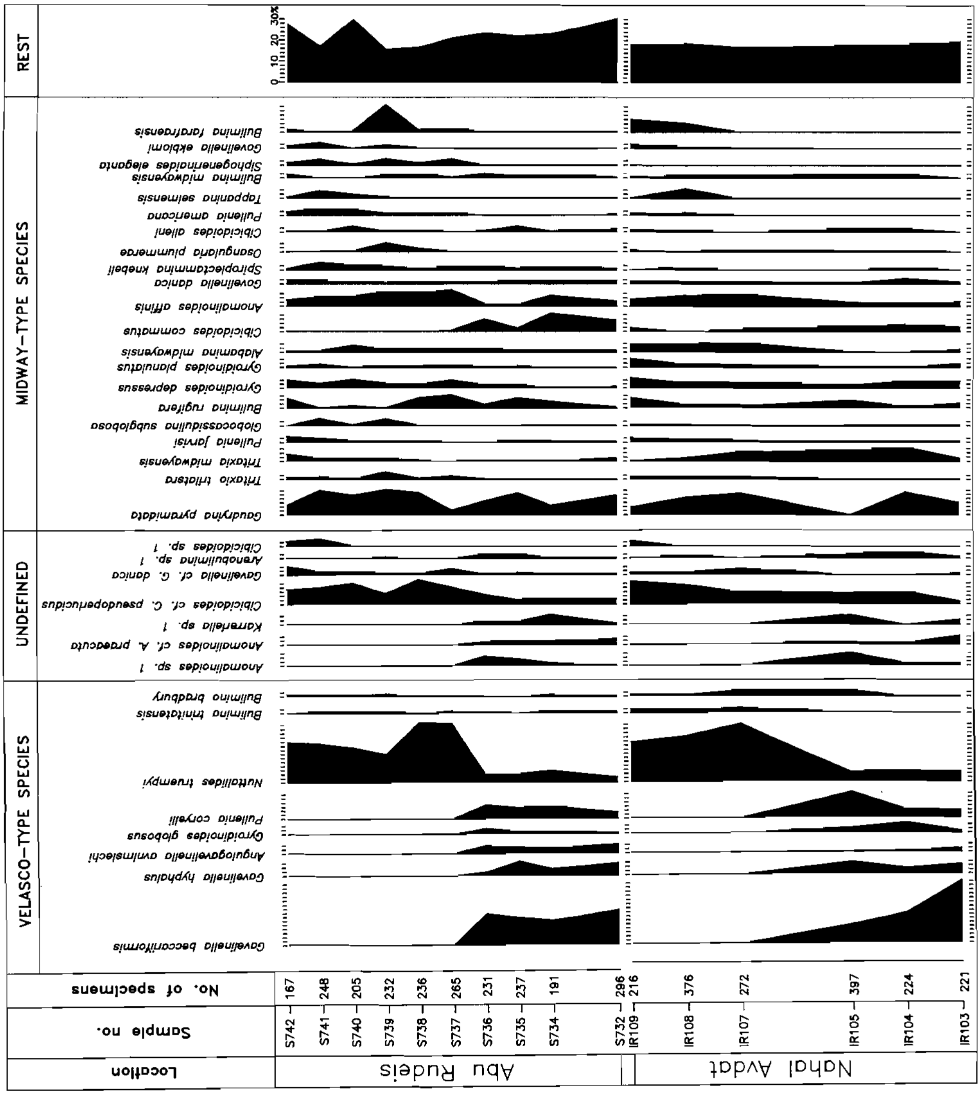

Fig. 5. Frequencies of the 36 most common species in the >125 µm fraction, grouped according bathyal (Velasco-type) and neritic (Midway-type) biofacies. One bar equals 2% of the total assemblage.

The Paleocene (pre-extinction) benthic assemblages are highly diversified: each sample contained about 50 different taxa; 97 taxa were encountered in all samples together (Nahal Avdat: 75; Abu Rudeis: 83). Many common species (Fig. 5) can be regarded as belonging to the Velasco-type fauna (VF) of Berggren and Aubert (1975). This fauna was named after the lower Paleocene Velasco Shale Formation, Mexico; its foraminiferal contents have first been described by Cushman (1925, 1926) and White (1928, 1929). The VF is commonly recognized in bathyal and abyssal deposits (Berggren and Aubert, 1975). Many VF species were cosmopolitans and range from the Campanian or Maastrichtian onward, straddling the K/P boundary into the Paleocene (Tjalsma and Lohmann, 1983). This assemblage is very often easily recognizable by the presence of *Gavelinella beccariiformis*, a very distinct species. In both sections this species dominates (up to 31%) the Paleocene assemblages until its abrupt disappearance.

Many other common species in the assemblages can be regarded as Midway-type fauna (MF) elements (Berggren and Aubert, 1975); this fauna was named after the benthic foraminiferal assemblages observed in the lower Paleocene Midway Formation, Texas (Plummer, 1926; Kellough, 1965). All species commonly occuring in neritic marl/shale deposits in Europe and North Africa (e.g. Brotzen, 1948; LeRoy, 1953; Aubert and Berggren, 1976; Salaj et al., 1976; Luger, 1985; personal observations), are considered to belong to this MF assemblage (Fig. 5), thus using this term in its widest sense.

Having a mixture of VF and MF suggests that the VF and MF are not strictly separate entities, but more the two extremes of a range of different assemblages. Similar mixed MF/VF assemblages were described by earlier workers in Israel (Reiss, 1952) and the Sinai (Said and Kenawy, 1956). In fact, many typical MF species, e.g. *Bulimina midwayensis* and *Coryphostoma midwayensis*, are often observed in bathyal and abyssal deposits (Tjalsma and Lohmann, 1983; Van Morkhoven et al., 1986). In contrast, most VF species never occur in neritic deposits indicating that these species have bathyal upper depth limits (Morkhoven et

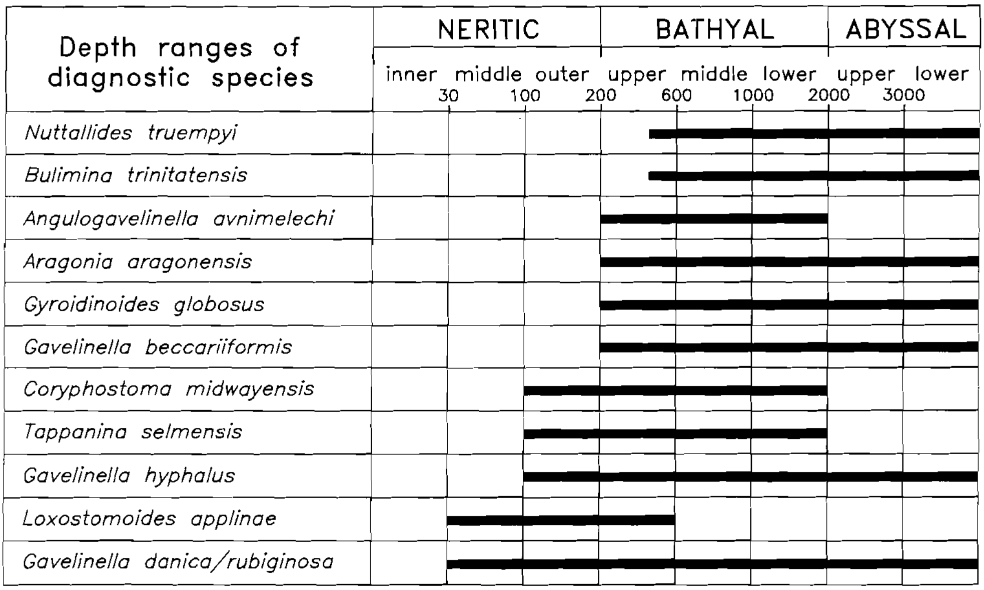

Fig. 6. Paleobathymetric ranges of observed species (modified after Van Morkhoven et al., 1986) indicate an upper to middle bathyal (500-700m) paleodepth for the examined deposits.

al., 1986). This is visualized in Fig. 6: bathymetric ranges of the most common species are displayed. This graph shows that the minimum depth of deposition should have been about 500m, because of the occurrence of *Nuttallides truempyi* and *Bulimina trinitatensis* in both areas.

In all samples planktonic foraminifera dominate the assemblages (50-70 %), despite some loss by dissolution. When this value is compared with regression curves of modern %P versus depth as compiled in Van der Zwaan et al. (1990), the proposed minimum paleodepth appears realistic. However, since the total abundance of MF and VF is about equal (Fig. 7), it seems reasonable to assume that the basin was not much deeper than 500-700m at the two locations studied.

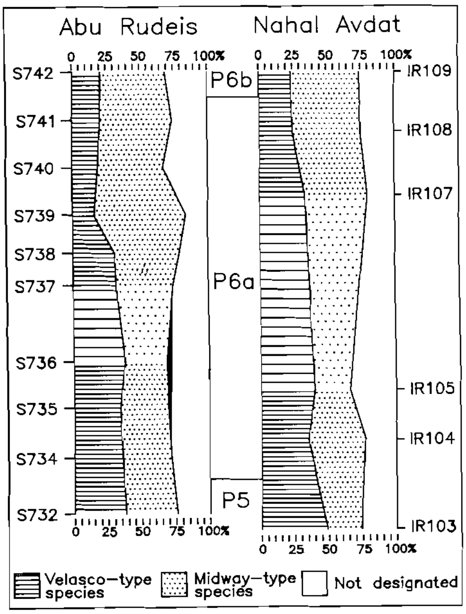

Fig. 7. Total abundances of VF and MF species through the sections. Wider hatching indicates benthic turnover interval. Note the gradual increase in MF species after the benthic extinction.

Latest Paleocene, post-extinction, assemblages differ significantly from the earlier Paleocene ones. They are slightly impoverished; each picking contained about 45 taxa, with a total of 80 recorded taxa (Nahal Avdat: 63; Abu Rudeis: 73). Simple diversity (total number of taxa) drops with 17 %. 14 species have last appearances, whereas 7 common species are newly appearing within the studied interval (Fig. 8). Few common VF species persist in the Eocene assemblages (Fig.5), although *Nuttallides truempyi* is now most dominant (up to 29 %). In contrast many MF species remain or become important constituents, on the average 50 % of the total abundance (figs. 5,7).

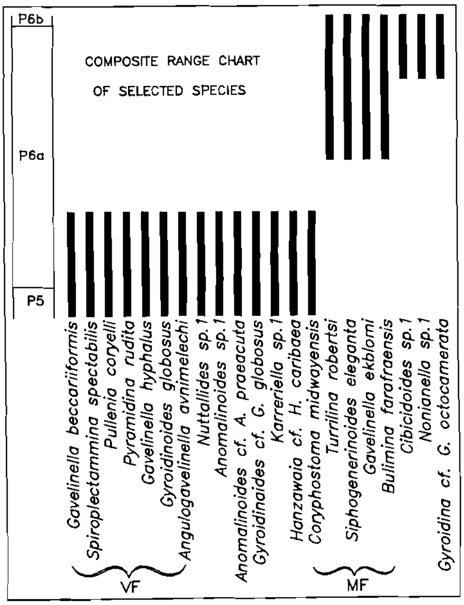

Fig. 8. Ranges of all common species that either appear or disappear in the studied interval. Note the sudden first appearances of several MF species after the extinction of mainly typical VF species.

A similar fauna was described earlier in Israel (Reiss, 1952). Using the paleobathymetric ranges in Fig. 6, it seems that depth of deposition did not change during the late Paleocene i.e. remained at approximately 500-700m, despite the high total abundance of MF. High frequencies of well preserved planktonic foraminifera (> 90 %) could even indicate slightly deeper deposition (Van der Zwaan et al., 1990).

Several ways of quantifying the benthic assemblages have been applied in order to assess what changes took place during the late Paleocene. Fig. 9 shows that a drastic change in the faunal composition occurred in both studied areas. Although only 14 (25%) of the common species disappeared (Fig. 8), they composed almost half of the total assemblage during the Paleocene. During the latest Paleocene their position is primarily taken over by species already extant during the earlier Paleocene. This however, could partly be a closed sum effect. Newly appearing species play a very subordinate, but upward increasing, role. At least 7 disappearing species belong to the VF (Fig. 8). In contrast, only one certain MF species (at least in the early Paleocene), namely *Coryphostoma midwayensis*, died out simultaneously. The remainder cannot be assigned to one of the faunal assemblages. Thus it appears that in particular species restricted to the bathyal/abyssal realm did not survive the late Paleocene event. This idea is substantiated by observations of typical MF assemblages in the uppermost Paleocene and lower Eocene of Egypt (Luger, 1985) and Rockall Bank (Berggren, 1974). Thus the MF remains rather unaffected and lingers on in the early Eocene (Berggren and Schnitker, 1983). I speculate that before the extintion event the paleobathymetric range of *Coryphostoma midwayensis* was restricted to the bathyal/abyssal realm, thus being a VF species in the late Paleocene. The changes in total abundance of VF versus MF (Fig. 7) could of course indicate a rapid shallowing of the basin during the late Paleocene. This seems highly unlikely, as pointed out earlier. The increase of MF abundance

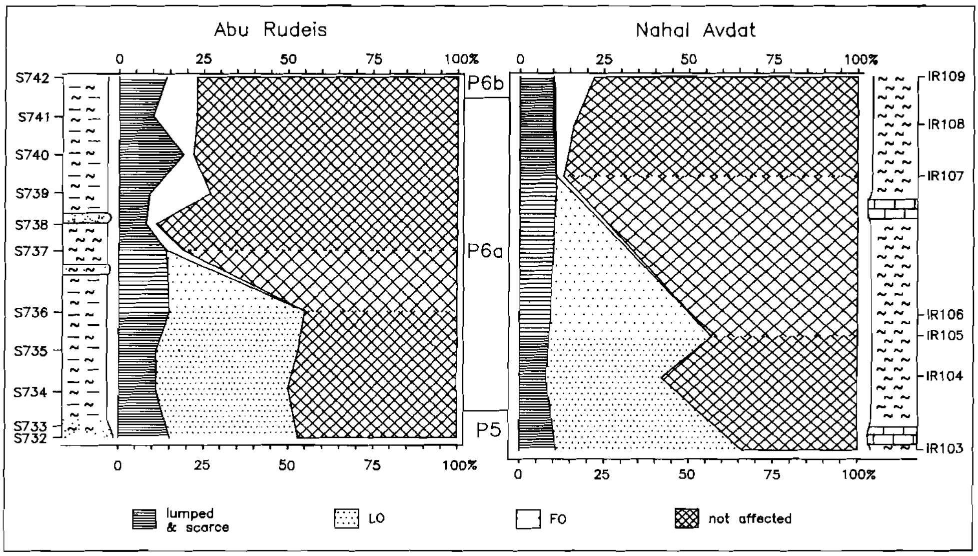

Fig. 9. Total abundance grouping according lumped and scarce taxa, taxa with last occurences (LO), taxa with first occurrences (FO) and not affected taxa, before and after the extinction event. Wider hatching indicates benthic turnover interval.

might again partly be a closed sum effect. On the other hand, the first appearance of *Bulimina farafraensis*, a MF species in the upper Paleocene (P4) of Central Egypt (LeRoy, 1953; Berggren and Aubert, 1975), indicates immigration of bathyal environments from shallower shelf areas. Such a shift might as well be applicable to other MF species, such as *Siphogenerinoides eleganta* and *Gavelinella ekblomi*; further comparison of regional distribution patterns will be needed to confirm this idea.

The quantitative analyses mentioned above unravel the changes in composition clearly, but do not render any clues to the mechanism leading to these changes. An actualistic approach to deduce environmental changes related to oxygen content and organic carbon flux implies the use of benthic morphotype ratios. In general all bottom dwelling benthic foraminifera can be devided into two groups (Corliss, 1985).

1. Epifaunal morphotypes: species living at the sediment-water interface usually having a test morpholgy with a low surface area to volume ratio (plano-, or biconvex trochospiral forms), only able to live within well-oxygenated bottom water.
2. Infaunal morphotypes: species living primarily within the sediment usually having a test morphology with a high surface area to volume ratio (slender uni-, bi- ,triserial and planispiral forms) able to live in an oxygen deficient environment.

The ratio of these morphotypes could reveal paleoxygenation of the bottom environment. Changes in the ratio would then suggest circulation and/or organic carbon flux changes. Although this approach is even in recent environments still controversial and at best simplistic, especially in shallow marine and/or seasonally influenced areas (Wetmore, 1991; Barmawidjaja et al., 1992), it has been applied to Paleogene benthic assemblages (Thomas, 1990b; Kaiho, 1991; Kaminski, pers. comm., 1991). To facilitate an easy comparison with the data of Thomas (1990b), the same morphotype criteria have been applied: cylindrical species are included within the infaunal group, agglutinants are completely excluded. Unfortunately, Thomas analysed the 63-µm fraction, therefore absolute figures cannot directly be compared. Nevertheless observed trends should still be comparable.

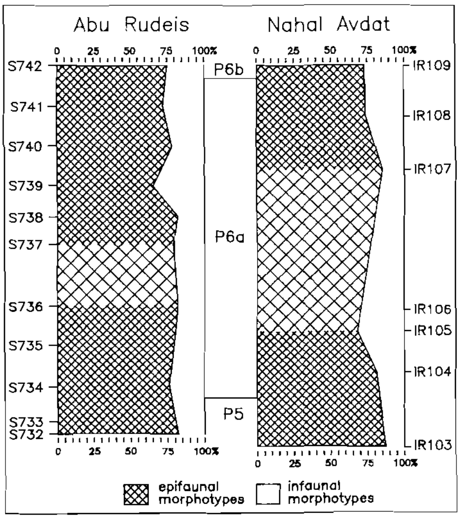

Fig. 10. Total abundances grouped according epifaunal and infaunal morphotypes (same criteria as in Thomas, 1990b). Wider hatching indicates benthic turnover interval. No dramatic change can be observed in the studied sections.

Fig. 10 displays the total abundance of epi- and infaunal morphotypes. The epifaunal group constitutes between 70 and 90 % of the Paleocene pre-extinction assemblages in both studied areas. This value decreases only slightly during the latest Paleocene. To check the pattern, two 63-µm pickings have been performed on samples S736/S737, both showing about 50% infaunal morphotypes. Therefore, in the studied basin no change in bottom water oxygenation can be inferred. This is in sharp constrast with the results from the Weddell Sea (Thomas, 1990b), the Pacific (Kaiho, 1991), the Southern Indian Ocean (pers. obs.) and the Barents Sea (Kaminski, pers. comm., 1991), where infauna dominates latest Paleocene assemblages and indicates low oxygen conditions. Especially at Maud Rise peak values of more than 90% infauna just after the extinction point to oxygen deficiency (Thomas, 1990b).

Discussion

Because of the striking similarity between the faunas in the two studied areas, both before and after the benthic crisis, it seems evident that the two depositional sites were situated in a very similar physical/chemical environmental setting, during the studied part of the Paleocene. Both sites belonged to the deeper part of a NE-SW trending trans-Sinai basin. Little is known about paleogeography of the Abu Rudeis area; the Nahal Avdat area, however, has been studied more extensively in this respect (Arkin et al., 1972). On their paleogeographic maps these authors suggest that the Nahal Avdat section was within 5 km distance from the ancient shoreline of a NE-SW peninsula during the late Paleocene and early Eocene. This idea conflicts with the estimated paleobathymetry and the widespread and rather uniform lithofacies of the Taqiye Formation, pointing at open marine epipelagic sedimentation. Possibly this peninsula was in fact a submerged basinal high, a few hundred meters below sea-surface. Sediment accumulation on top of this elevation could have been stripped of during subsequent regional uplift or sea level lowering. Consequently, only deposits in the structural lows were preserved.

The basin as a whole was probably well connected with the Tethys and other oceans. This can be concluded from the predominance of the cosmopolitan deep-water VF and its successor. A more isolated basin would have shown much more endemic benthic taxa; instead very few such elements have been observed.

The fact that many common Paleocene VF species are cosmopolitans and have large depth ranges (Tjalsma and Lohmann, 1983; Van Morkhoven et al., 1986) could suggest a rather uniform intermediate- and deep watermass, dominating the world's oceans (cf. Thomas, 1992). This watermass may have originated in a single source-area, e.g. at the margins of the Southern Ocean or the Tethys. This idea is substantiated by comparisons of stable isotope values from different oceans (Pak et al., 1991). Late Paleocene $\delta^{18}O$ profiles are very gentle, indicating equable temperature of intermediate and deep waters. In contrast, $\delta^{13}C$ values seem to point to the occurrence of the most nutrient-depleted, young bottomwater in the Southern Ocean, and nutrient contents increasing towards the other oceans. From this it appears that intermediate and deep waters could have originated somewhere around the Austral-Antarctic continent (see also Barrera et al., 1987; Barrera and Huber, 1991).

However, the high amount of infaunal morphotypes at Maud Rise (Thomas, 1990b) and Broken Ridge (pers. obs.) seem to contradict this latter concept. This discrepancy can best be explained when a high latitude strong seasonal cycle in primary production is taken into account. At times of maximum insolation before the seasonal thermocline build-up (Kennett and Barker, 1990), high levels of nutrients are available for primary producers such as diatoms. Subsequently an increased organic carbon flux will reach the seafloor. This organic matter will preferentially be advantageous for infaunal benthics, because at the same time dissolved oxygen is consumed in the process of organic decay. When the thermocline is developed surface water nutrients will soon be depleted and primary production deminishes. As a consequence the normal equilibrium fauna will re-establish until the next surface bloom.

Since a non-laminated sample contains a mixed assemblage of at least a few thousand years, the result will be that infauna is relatively enriched compared with assemblages obtained from low latitude areas where no seasonal bloom occurs. Substantial evidence for (seasonal) high productivity can be found at Broken Ridge site 752 where high amounts of diatoms and radiolarians are preserved (Fourtanier, 1991; pers. obs.). Unfortunately this has not been observed at Maud Rise, which might well be a preservational artifact, because biogenic opal easily dissolves at the seafloor (Broecker and Peng, 1982).

What could have happened to disturb the very stable Paleocene deep-sea benthic foraminiferal composition? Since all well-known late Cenozoic climatic/oceanographic events had only a minor effect on deep-sea benthic foraminifera, a very dramatic but still rather elusive climatic-/oceanographic perturbation must have occurred during the late Paleocene.
The various hypotheses and ideas proposed to solve this problem, should at least account for the following:

1. The importance of *Gavelinella beccariiformis* c.s. in the bathyal environment does not diminish up to the moment of its abrupt disappearance; there is no sign of a gradual restriction to southern high latitudes, as has been suggested by Katz and Miller (1991).
2. Most species becoming extinct were VF deep-sea dwellers; the shallow-water MF biofacies was (almost?) not affected.
3. Diversity decrease in the Middle East is much less than in other areas, because of the richness of MF species during the entire time interval.
4. A temporal oxygen deficiency of bottom water of the Tethys-margin can not be deduced by means of benthic morphotype analyses.
5. Immediately after the extinction at least three common MF species migrated from the neritic to the bathyal environment.

Combining this with data available from various sources and areas I conclude that:

1. It seems unlikely that the benthic extinction was directly caused by a decrease in primary production and restricted food supply to the deep-sea (Miller et al., 1987), mainly because the K/P boundary productivity crisis hardly had any impact on approximately the same benthic fauna (Tjalsma and Lohmann, 1983; Thomas, 1990b; Nomura, 1991), and because the vertical $\delta^{13}C$ gradient does not change (e.g. Stott and Kennett, 1989).
2. Because of $\delta^{13}C$ trends (Pak et al., 1991) it seems unlikely that WSBW originating at the Tethys margin dominated the oceans and that the disappearance of VF was caused by a cessation in WSBW formation (Nomura, 1991).
3. The currently most likely extinction scenario includes a change from high to low latitude domination of bottomwater formation, thus to an initiation, or a major increase in the influence, of WSBW formation (Miller et al., 1987; Thomas, 1990b, 1992).

The last-mentioned scenario would at modern PO_4 nutrient levels and atmospheric oxygen content lead to extensive anoxia (Herbert and Sarmiento, 1991), comparable with the proposed mid-Cretaceous situation (Arthur and Natland, 1979). There are however only few indications of regional dysoxic conditions at the moment of the extinction (Thomas, 1990b; pers. obs.). Probably Paleocene atmospheric oxygen content was slightly higher than at present (Berner, 1989) and possibly more importantly, PO_4 levels were much reduced, because of storage in shallow marginal marine deposits (Oberhänsli and Hsü, 1986). Thus, anoxic bottom waters could be much more constrained to locally high productive areas and/or areas very remote from the source area. Since no indications of temporal dysoxic conditions are found in the studied area, a short term global WSBW oxygen deficiency can not be the sole controlling factor for the benthic extinction. Probably another (combination of) water-mass property(ies) e.g. temperature and/or salinity must be directly responsible for the extinction of many deep-sea benthic foraminifera.

The ultimate cause for high latitude warming and the reversed poleward deep circulation remains elusive, but could be a sudden pulse of atmospheric CO_2 increase through extensive volcanism related to the opening of the North Atlantic (Thomas and Varenkamp, 1992), superimposed on a longer term warming trend. How long this reversed circulation persisted remains unclear, although Thomas (1990b) suggested it to last about 350 kyr. (the period of prevalence of the oxygen deficient benthic assemblage). This however has not been noted elsewhere, whereas the reversal to normal circulation should well be visible from the benthic assemblage. In the studied area this can explained by having a too short post-extinction record of only about 300 kyr. (Fig. 4). Here immigration of newly appearing MF species took place within 50 kyr. after the extinction. Possibly they were accompanied by earlier extant MF species which temporarily disappeared from an inhospitable bathyal environment but were able to sustain at apparently environmentally more stable neritic depths. More detailed records of both bathyal and neritic deposits in the studied basin will result in a more conclusive viewpoint.

Conclusions

Two Middle East sections contain a continuous upper Paleocene sequence. Direct correlation of planktonic foraminiferal and calcareous nannofossil zonal schemes has resulted in the establishment of the NP9/NP10 zonal boundary within the top part of Zone P6a. The deep-sea benthic foraminiferal extinction is observed in the middle part of Zone P6a, and thus does not mark the Paleocene/Eocene boundary. Faunal paleobathymetric analyses leads to a propsed paleodepth of 500-700 m for both depositional sites, which were situated in the deeper parts of a NE-SW trending trans-Sinai basin. The benthic foraminiferal assemblages contain a mixture of shallow- and deep-water species, of which several very common, exclusively bathyal/abyssal species became extinct, whereas none of the neritic/bathyal species were affected. Therefore simple diversity drops only 17%. After the extinction event several neritic species known from surrounding areas, extended their depth range into deeper bathyal environments. This study does not conflict with the hypothesis that the major bottom water source area temporarily shifted from high to low latitude, inducing intensified WSBW formation. However, simple WSBW oxygen-deficiency can not be the sole controlling factor of the worldwide extinction.

Acknowledgements

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- CHAPTER V -

The impact of Paleocene/Eocene boundary events on shallow water benthic foraminiferal assemblages from Egypt

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ABSTRACT

Upper Paleocene to lower Eocene shales and marls of the Esna Formation are well exposed in outcrops near the Red Sea coast of Egypt. These deposits yield rich microfossil assemblages and in some sections the Paleocene/Eocene (P/E) boundary interval is continuously exposed. In this paper, results from the Bir Inglisi I section are reported and the local impact of the sudden global paleoenvironmental perturbations at the P/E boundary, which led to the extinction of many deep-sea benthic foraminifera, is discussed.

The studied benthic foraminiferal assemblages suggest middle neritic deposition throughout the entire time-slice (upper Zone P4 to upper Zone P5) and only minor sea-level variations. Although typical deep-sea taxa are absent, a distinct faunal change marks the P/E boundary. In contrast with known deep-sea records, however, the change at this shallower site appears much less abrupt and is preceded by a gradual diversity decrease starting 4 m below the boundary; only two taxa disappear exactly at the P/E boundary. Most exits are temporal since many taxa start to reappear shortly after the boundary event; moreover, most taxa that do not reappear locally are known from Eocene deposits elsewhere in Egypt.

In general, benthic foraminiferal assemblages are oligotypic and display high dominance values, suggesting high levels of environmental stress. In combination with sometimes very high abundances of planktonic foraminifera and lithological characteristics as laminations and high organic carbon contents, the assemblage characteristics point to a strong influence of frequently occurring dysoxia and/or anoxia. We suggest that these resulted from surface eutrophication by intermittent upwelling and reduced ventilation. These conditions seem to have prevailed during most of the time-slice studied; but during the latest Paleocene upwelling gradually intensified, resulting in longer or more severe anoxia.

In our view enhanced atmospheric contrasts between the Tethys and the African continent may have controlled these changes. At the P/E boundary the bottom environment became minimally ventilated, due to either reduced themoclinal mixing or reduced oxygen advection from deeper waters. Three metres above the boundary a succession of increasingly diverse assemblages indicate a gradual decrease of environmental stress and a return to more normal conditions, although fertility remains high. The implications of these local environmental changes for global P/E boundary scenarios, are briefly discussed.

Introduction

The Paleocene/Eocene (P/E) boundary is marked by the extinction of many cosmopolitan deep-sea benthic foraminifera, many of which had survived since the Cretaceous (e.g. Beckmann, 1960; Tjalsma and Lohmann, 1983; Thomas, 1990b; Nomura, 1991; Kaiho et al., 1993). In the Southern Ocean this sudden extinction event coincides with short (< 10 kyr) but sharp negative excursions in the oxygen and carbon isotope records, together with the near elimination of the vertical temperature and nutrient gradients (Kennett and Stott, 1990, 1991). The P/E boundary $\delta^{13}C$ excursion is superimposed on a gradual decline, following the early late Paleocene $\delta^{13}C$ maximum (e.g. Shackleton et al., 1984, 1985; Shackleton, 1986; Barrera and Huber, 1991; Katz and Miller, 1991; Corfield and Cartlidge, 1992; Pak and Miller, 1992). A similar $\delta^{13}C$ excursion has also been registered in continental deposits (Koch et al., 1992).

The appearance of (sub)tropical pelagic flora and fauna in the Southern Ocean (Haq et al., 1977; Huber, 1991a; Van Eijden and Smit, 1991; Lu and Keller, 1993), and the presence of paratropical rainforests and development of kaolinitic soils on Antarctica (Wolfe, 1985; Robert and Kennett, 1992, 1994) in combination with oxygen isotopic data (Kennett and Barker, 1990; Stott et al., 1990, Barrera and Huber, 1991), suggest that these events occurred within the context of a longer period (late Paleocene-early Eocene) of global warmth and equable climates. It has been suggested that during a short period of maximum polar warmth near the P/E boundary high latitude deep water formation cessated and that during (part of) the early Eocene warm saline deep water (WSDW), generated at low latitudes, was the main deep water-mass (e.g. Miller et al., 1987; Thomas, 1989, 1990b; Rea et al., 1990; Kennett and Stott, 1991; Pak and Miller, 1992; Thomas, 1992; Zachos et al., 1993, 1994).

Although the exact reasons for the abrupt perturbations, particularly in the deep-sea ecosystem, the carbon budget and the thermal balance, are still rather enigmatic (Stott, 1992; Eldholm and Thomas, 1993), increasing interest in these events has led to the rapid accumulation of a considerable amount of data. Unfortunately, most research is focusing on (a)biotic changes in deep-sea records; little has been reported on paleoenvironmental changes in shallow water systems.

It has been argued that the events did not really affect neritic benthic foraminiferal assemblages, since late Paleocene and early Eocene neritic assemblages are very similar (Berggren, 1974; Berggren and Schnitker, 1983; Luger 1985; Speijer, 1994a). Judging from recent studies, however, this view is clearly oversimplified. Gibson et al. (1993) showed gradual but marked changes in late Paleocene-early Eocene middle neritic benthic foraminiferal associations. Unfortunately, lacking isotope stratigraphic data, these authors were unable to exactly correlate the level of the deep-sea extinction event to their record. Also Speijer (1993) reported a clear expression of the benthic extinction event in outer neritic deposits of the Gebel Oweina section in central Egypt. Several species that are often found in bathyal deposits disappear simultaneously and abruptly in the middle part of Zones P5 and NP9. A significant shift in the $\delta^{13}C$ record, superimposed on a gradual decline of bulk carbonate values, coincides with this extinction level (Charisi and Schmitz, 1994). These data strongly suggest that also shallow (sub)tropical epicontinental seas experienced a coeval perturbation of the benthic ecosystem.

In this paper we focus on the question whether similar paleoenvironmental changes can be traced in even shallower neritic assemblages, and if so, whether these occurred as abruptly as noted in all previous studies on bathyal deposits. For this exercise we collected samples from the Bir Inglisi I exposure, situated at the base of Gebel Duwi near the Red Sea coast of Egypt (Fig. 1). Previously, outcrops on the flanks of this conspicuous hill, composed of gently NE dipping Late Cretaceous to Eocene strata, have been extensively studied by various micropaleontologists (Nakkady, 1950, 1957; Krasheninnikov and Abdel-Razik, 1969; El-Dawoody and Barakat, 1972; Abdelmalik, 1982; Faris, 1982; Aboul-Ela, 1989). Despite all (mainly biostratigraphic) research performed earlier, few papers have considered smaller benthic foraminifera to some extent (Nakkady, 1950,

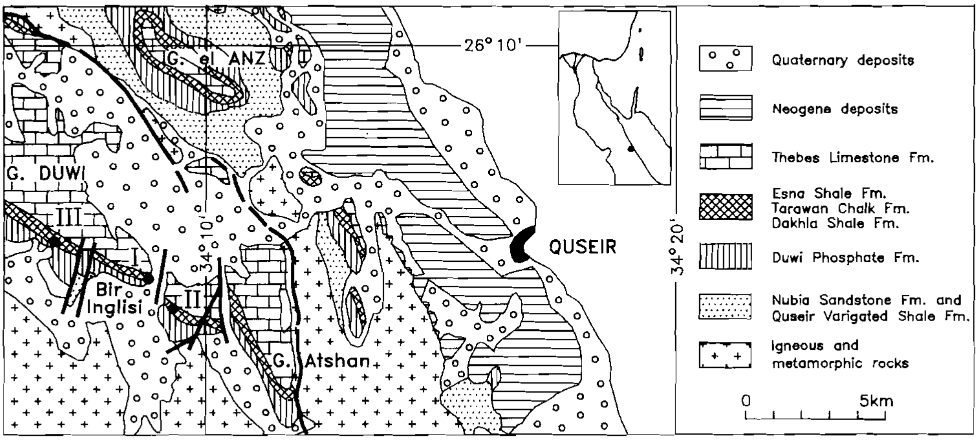

Fig. 1. Geological map of the study area near Quseir at the Red Sea coast (modified from Said, 1960). Roman figures indicate locations of three different outcrops; Bir Inglisi I yields an excellent, easily accessible, exposure of the late Paleocene-early Eocene Esna shales at the base of Gebel Duwi.

1957; Faris, 1982). This paper encompasses the first detailed quantitative paleoenvironmental analysis based on benthic foraminifera from this area. Geochemical and other faunal/floral (planktonic foraminifera, ostracods, nannoplankton, dinoflagellates) studies are still in progress.

Material and methods

Rock samples were dried in a stove at 60°c for at least 24 hours. Fifty gram of dry rock was soaked in a 0.35 mole/l Na_2SO_4 solution. After desintegration, the sample was washed over three sieves of 595, 125 and 63 µm mesh size, respectively. When the residue still contained sediment aggregates, the procedure was repeated. The 125 µm fraction was used for quantitative benthic foraminiferal analysis. With the aid of an Otto microsplitter a suitable split with approximately 200-300 benthic specimens was obtained. From this split the percentage of planktonic foraminifera (%P) and foraminiferal numbers (planktonic and benthic) were calculated. All benthic foraminifera were picked and permanently stored in a Chapman-slide. Most common and/or diagnostic species were, whenever possible, identified at species level, although sometimes placed in open nomenclature. Some taxa displayed such a morphological variability, or such differential preservation, that they were hard to discriminate from each other; these taxa were placed under generic headings. The > 595 µm fraction was scanned for extremely large species and treated qualitatively. Papers by LeRoy (1953) and Aubert and Berggren (1976) were the primary sources for taxonomic classification.

Diversity of the benthic assemblage is expressed as Fisher-α index values (Murray, 1991), dominance was calculated as percentage of the most frequent taxon (Walton, 1964), and foraminiferal number as numbers of foraminifera per gram dry sediment. A statistical evaluation was performed on the species frequency data by means of R-mode Cluster Analysis (unweighted pair group method; Drooger, 1982) and standardized R-mode Principal Component Analysis. The computer program used, Pattern Recognition (PATREC), was developed at the Geology Department, Utrecht University. A BALANC routine (Drooger, 1982) was used to surpress squeeze effects of highly abundant taxa.

Biostratigraphic terminology is adopted from the recently revised Paleocene planktonic foraminiferal biozonation (P-notation; Berggren et al., 1994; see also Berggren, 1994: Fig. 1) and from the nannofloral biozonation of Martini (NP-notation; 1971).

Lithology and stratigraphy

The lithological sequence (Fig. 2) mainly consists of brown-green marls and shales, with two brownish layers of indurated sandy-silty marls: one in the middle and one at the top of the section. The sequence belongs entirely to the upper Paleocene-lower Eocene Esna Formation that is intercalated between the middle Paleocene Tarawan (Chalk) Formation and the lower Eocene Thebes (Limestone) Formation (Fig. 1). These three rock-units are widely distributed (under various names) all over Egypt (Said, 1960; Masters, 1984; Said, 1990d). In this section, the Esna shale is often laminated; the sandy-silty beds are homogeneous and extremely rich in foraminifera. Apart from a few juvenile bivalves, little macrofauna has been observed, but some levels contain abundant fish remains. During grinding of the sediment for stable isotope analysis a strong bituminous smell was noticed (B. Schmitz, pers. comm., 1993). The occurrence of lamination, the near absence of macrofossils and the bitumen strongly suggest that these sediments were generally poorly bioturbated and ventilated, and are rich in organic carbon.

Biostratigraphically, the section covers the upper part of Zone P4 to the uppermost part of Zone P5 and based on correlation with the Bir Inglisi II section, terminating about one metre below the P5/P6a zonal boundary. In terms of nannofossil biozonal schemes, the section covers the upper part of Zone NP8 to the lower part of Zone NP10. Traditionally, the position of the P/E boundary in pelagic sequences has been inferred from several bioevents. Using foraminifera, the boundary is often approximated by the exit of *Morozovella velascoensis* (P5/P6a zonal boundary) or by the entry of *Pseudohastigerina wilcoxensis*. Based on calcareous nannofossils, the boundary is usually equated with the NP9/NP10 zonal boundary, marked by the entry of *Tribrachiatus bramletti* or by the virtually coinciding exit of *Fasciculithus*. However, Aubry et al. (1988) pointed out that the P/E boundary in its type-area correlates with a stratum within

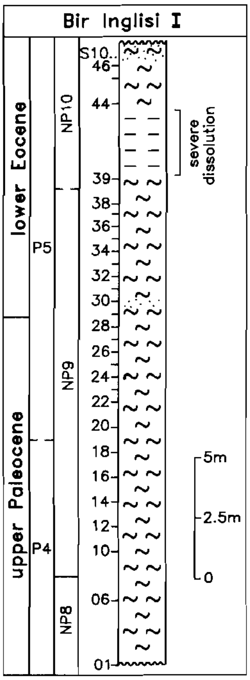

Fig. 2. Lithology and biostratigraphy of the Bir Inglisi I section. For definition of the P/E boundary, see text. The P/E boundary is overlain by a sandy foraminifer-rich marl, intercalated between largely laminated brown-green marls and shales of the Esna Formation.

Zone NP10, rendering the common practice as described above as incorrect.

As for the Cretaceous/Paleogene (K/P) boundary, the aim is now to define a Global Stratotype Section and Point (GSSP) for the P/E boundary within an interval of global environmental change (Aubry et al., 1994). The best suited candidate is the interval that comprises the deep-sea benthic foraminiferal extinction event and the sharp negative excursion in the $\delta^{13}C$ record. In the expectation that the GSSP will eventually indeed be defined at this level, we already use the P/E boundary notation in this sense. In terms of pelagic biozonal schemes, the P/E boundary would then be situated somewhere in the middle part of Zones P5 and NP9, respectively. As in other detailed records, the bulk $\delta^{13}C$ record of Bir Inglisi I shows a negative excursion (sample S 1029) superimposed on a long-term negative trend within Zones P5 and NP9 (B. Schmitz, pers. commun., 1993).

Study of bathyal deposits from the Abu Rudeis and Nahal Avdat sections, revealed that the deep-sea benthic extinction coincided with the entry of *Pseudohastigerina wilcoxensis* (Speijer, 1994a). More detailed observations on the phylogeny of *P. wilcoxensis* now show that the earliest occurring specimens of this taxon are not really belonging to *P. wilcoxensis*, but actually belong to *Globanomalina luxorensis*. This species can be considered as the precursor of *P. wilcoxensis* and differs in its more asymmetric trochospiral mode of coiling (Speijer and Samir, 1994). Although scattered specimens of *G. luxorensis* are encountered already in the middle Paleocene (Zone P4; Nakkady, 1959; Speijer and Samir, 1994), the lowest common occurrence (LCO) of this taxon in many localities in Egypt and in sections in Israel, Tunisia and Spain, is immediately above the extinction of *Gavelinella becariiformis* and associated species. At least for the circum-Mediterranean region the LCO of this taxon is a marker for the P/E boundary (Speijer and Samir, 1994). In Bir Inglisi I the LCO of *G. luxorensis* is in S 1029.

Some features provide possibilities for regional and local correlation of the P/E boundary interval and support the stratigraphic assignment as discussed above. In Wadi Nukhl (= Abu Rudeis of Speijer, 1994a) a sapropelitic bed is intercalated in the marly succession. The extinction of *G. beccariiformis* and associated species is at the base of this bed; the %P is suddenly extremely high (> 98%) and the planktonic assemblage is largely composed of acarininids, whereas especially morozovellids are suddenly extremely scarce; *Anomalinoides aegyptiacus* dominates the benthic associations. All these features are observed within Zone P5 in the Esna shales of the Gebel Qreiya section northeast of Qena as well (cf. Hendriks et al., 1990, p. 91; additional observations by R. Speijer, 1993). In Bir Inglisi, sample S 1029 contains a very similar planktonic assemblage (%P > 98%, see below) with very few morozovellids.

These and abovementioned stratigraphic correlations, justify positioning the P/E boundary between samples S 1028-1029. Unfortunately, most of these criteria are problematic or of no help in assessing the P/E boundary in the field. However, as we investigated the section we noted that the very common large shallow water benthic foraminifer (up to 3 mm in diameter) *Frondicularia phosphatica* disappeared at exactly the same level, providing an excellent field-marker for tracing the P/E boundary in the Bir Inglisi area.

Faunal patterns

Faunal indices

Post-depositional dissolution may severely alter the calcareous faunal composition and in particular the abundance of small aragonitic components. Aragonitic benthic foraminifera were not observed in any sample, whereas such taxa are fairly common in neritic deposits from Europe and North America (Brotzen, 1948; Cushman, 1951; Kellough, 1965). Also aragonitic pteropods are extremely rare, and if present always preserved as pyritic casts; miliolids are usually preserved as calcitic molds. These features point to dissolution of most of the least stable $CaCO_3$ in all samples. In order to obtain an impression of the general paleoenvironmental conditions and possible post-depositional alterations, we calculated foraminiferal numbers, proportion of planktonic foraminifera of the total foraminiferal association, and diversity and dominance of the benthic foraminiferal assemblage (Fig. 3).

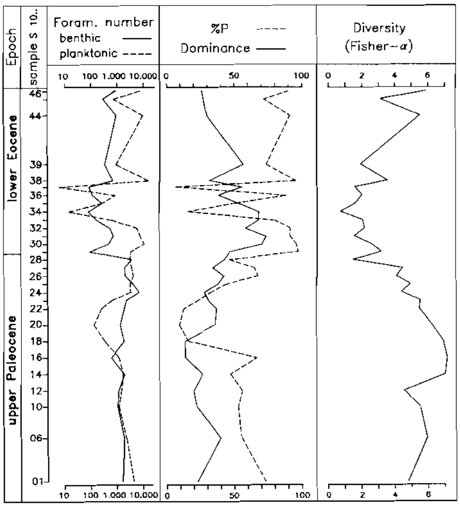

Fig. 3. General faunal indices derived from foraminiferal analysis. Note the gradual trends in benthic foraminiferal dominance and diversity across the P/E boundary, in contrast to the sudden increase in proportion of planktonic foraminifera (%P) and the drop in benthic foraminiferal numbers at the P/E boundary.

Foraminiferal numbers (number of foraminifera in the 125-595 μm size fraction per gram dry sediment) depend on three factors: test production, dilution by other sedimentary particles and post-depositional alteration (mainly dissolution of calcareous components, e.g. foraminifera, nannofossils). The proportion of planktonic foraminifera in the foraminiferal association can be regarded either as a measure for depth of deposition (e.g. Grimsdale and Van Morkhoven, 1955; Van der Zwaan et al., 1990), a paleoproductivity index (Berger and Diester-Haass, 1988; Herguera, 1992) or as measure for preferential loss by dissolution. The latter may occur at the seafloor below lysoclinal depths (e.g. Adelseck and Berger, 1975) or due to diagenesis and outcrop weathering (e.g. Murray, 1991). Provided that dissolution is subordinate, bathyal foraminiferal associations are usually strongly dominated by planktonic foraminifera (> 90%). This dominance decreases towards basin margins, where benthic foraminifera predominate (%P < 20%). However, in case of moderate dissolution even a bathyal foraminiferal association can be dominated by benthic foraminifera, since planktonic foraminifera are much more susceptible to dissolution than most benthic ones. Insufficient paleoxygenation of the seafloor may further inhibit the use of %P for paleodepth reconstructions (Van der Zwaan et al., 1990).

Especially in the Eocene part of the section planktonic foraminiferal numbers strongly covary with %P, suggesting that post-depositonal dissolution has overprinted the primary signal, resulting in decreased planktonic foraminiferal numbers and %P values. Apart from these beds with aberrantly low %P values, %P in Eocene assemblages is generally higher than in the Paleocene ones. This could also partly be a preservational artifact, but high values of > 98%P in the basal Eocene beds, in combination with reduced benthic foraminiferal numbers strongly suggest that bottom stress has played an important role in determining the primary foraminiferal composition. Another striking feature is the occurrence of extremely high foraminiferal numbers in a few samples, especially those from levels that appeared to be silty. This could be the result of increased production rates, but the numbers are so high that decreased dilution by fine-grained sediment, possibly due to winnowing, is a more likely cause. The samples with > 10.000 specimens per gram of sediment are for the latter possibility suspect, although a decreased sediment supply to the basin or even high production can not be ruled out completely.

Diversity (expressed in Fisher-α values) and dominance usually correlate negatively (Murray, 1991 and references therein). These parameters are generally regarded as proxies for ecological stress. High diversity and low dominance correspond to low levels of ecological stress; such circumstances are often met in relatively stable and well ventilated deep-sea environments. Usually, shallow shelf areas are subject to less stable environmental conditions, and therefore display less diversified benthic foraminiferal assemblages characterized by higher dominances (e.g. Boltovskoy and Wright, 1976; Murray, 1991 and references therein). Compared with contemporaneous assemblages from other areas in Egypt (Speijer and Van der Zwaan, 1994b), diversity in this section is low to very low. Highest values are reached in samples S 1014-1018, followed by a gradual but strong decline and a subsequent gradual increase. This curve shows in the upper part some covariance with the %P curve, indicating that the negative peaks could at least partly be the result of taphonomic processes. In the lower part there is no correlation apparent, e.g. the sharp drop in %P values between samples S 1016-1018 that may be due to dissolution, is not reflected in either the diversity or the dominance curve, suggesting that in general diversity and dominance curves are unaffected by dissolution and thus represent primary signals. The curves indicate gradually increasing ecological stress in the uppermost Paleocene, culiminating just above the P/E boundary, followed by a gradual decrease in the lower Eocene. Lowest diversities and highest dominance in the lowermost Eocene correspond to extremely high %P, indicating rather severely restricted bottom life. The whole picture, certainly in combination with the occurrence of bituminous and laminated sediment, strongly suggests that oxygen deficiency could be an important component of this ecological stress.

Paleobathymetry

Figure 4 shows the frequency patterns of the quantitatively most important taxa listed in Table 1. In addition, presence-absence ranges of *Frondicularia phosphatica, F. nakkadyi* and *Dentalina latejugata* are given based on analysis of the > 595 µm fraction, which could not be processed by means of the Otto microsplitter. The taxa are ordered in stratigraphic sense. The first group contains species with exits near the P/E boundary. Most of these exits are merely local disappearances, since those taxa have been observed in younger deposits in other areas in Egypt (Luger, 1985; Speijer, 1993; Speijer and Van der Zwaan, 1994b). A second group is composed of taxa with an absence (Lazarus) interval in the middle part of the section. The third group contains all omnipresent taxa and the fourth group contains taxa that appear above the P/E boundary.

Figure 4 clearly shows the trends in decreasing diversity and increasing dominance in the uppermost Paleocene as discussed earlier, as well as the reverse pattern in the lower Eocene. Apart from two samples (S 1014 and S 1046) all benthic foraminiferal assemblages are dominated by only three species: *Anomalinoides aegyptiacus, A.* cf. *aegyptiacus* (due to the subtle morphological differences, both taxa are combined in the quantitative analyses; see taxonomic

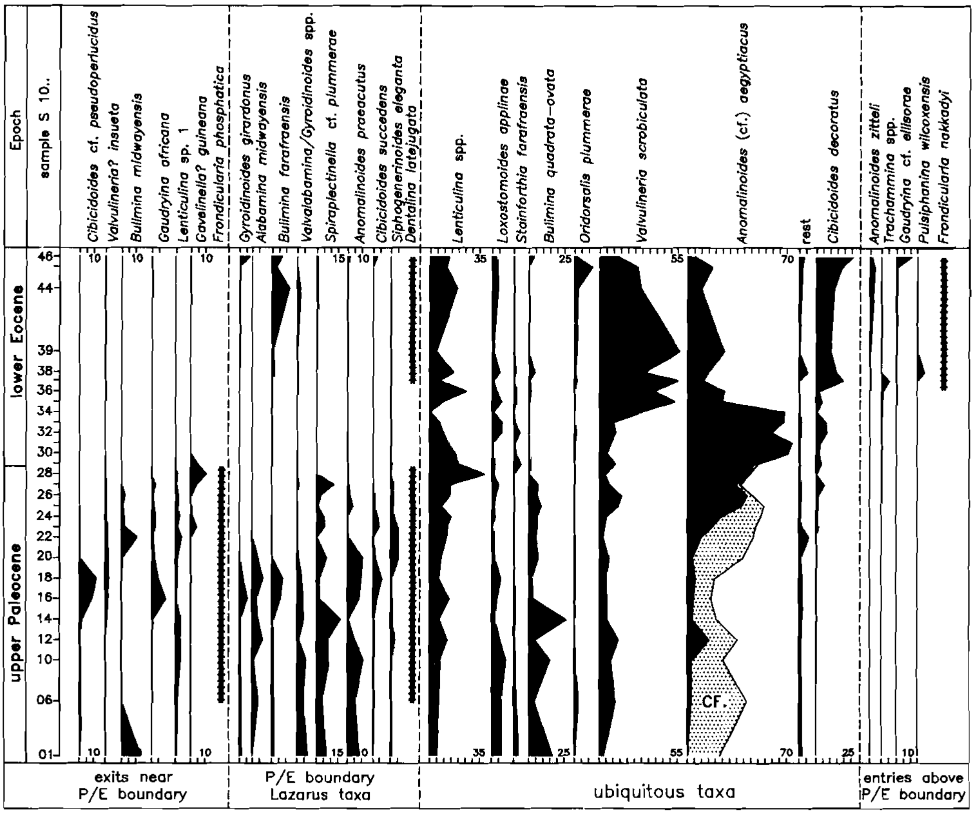

Fig. 4. Frequency chart of the most common taxa, ordered by their stratigraphic distribution (data from Table 1). "Railway"-bars indicate the presence of taxa in the > 595 µm size fraction. Note the gradual impoverishment in the upper Paleocene, the high number of (temporal) exits near the P/E boundary (*Frondicularia phosphatica*!), and the subsequent gradual diversification.

notes) and *Valvulineria scrobiculata*. Peak abundances of *V. scrobiculata* in the Eocene correspond to relative low values of %P and of benthic foraminiferal numbers, possibly indicative of some taphonomic (relative) enrichment of this taxon.

In upper Paleocene-lower Eocene deposits elsewhere in Egypt and Tunisia, similar benthic assemblages as in Bir Inglisi were interpreted to be characteristic of open marine, inner to middle neritic, environments (Aubert and Berggren, 1976; Salaj, et al., 1976; Luger, 1985; Saint-Marc and Berggren, 1988; Van Oosterhout, 1988; Saint-Marc, 1993; Speijer and van der Zwaan, 1994b). Especially very large nodosariids such as *Frondicularia phosphatica*, *F. nakkadyi* and *Dentalina latejugata* are typical for such deposits. Similar assemblages were described from the Uweinat-Aswan High region in southern Egypt (Luger, 1985; Speijer and Van der Zwaan, 1994b) and from the upper Paleocene part of the El Kef section (Salaj et al., 1976; Van Oosterhout, 1988; Saint-Marc, 1993); these were interpreted to be indicative of middle to inner neritic deposition. In deeper areas of the paleoshelf of Egypt, further north and north-

Table 1. Frequency data of the 28 most common taxa in the Bir Inglisi I section; infrequent taxa were lumped into higher order categories.

Paleocene sample S....	1001	1006	1010	1012	1014	1016	1018	1020	1022	1023	1024	1025	1026	1027	1028
Cibicidoides cf. pseudoperlucidus	0	2.1	1.4	0.4	1.7	8.8	12.1	0.4	0	0	0	0	0	0	0
Valvulineria? insueta	0	0.8	0	0	0.9	1.6	2.5	1.4	0.3	0.4	0	0.5	0	0	0
Bulimina midwayensis	13.8	0	0	0	0	0	0	0.7	11.1	2	1.9	0.9	2.4	0	0
Gaudryina africana	0	0	0.5	0	0.9	10	4.6	1.8	1.2	2.5	2.8	1.4	0.7	2.4	0
Lenticulina sp. 1	0.5	1.2	3.3	3.4	3.4	0.4	0.4	1.4	4.2	1.2	2.8	1.4	2.2	0.7	1.1
Gavelinella? guineana	0	0	0	0	0.4	0	0	0	0.3	4.1	0.9	0	0.7	4.1	10.8
Gyroidinoides girardanus	1.5	0.4	0.5	0.4	0.4	5.6	2.5	0.4	0.3	0	0	0.5	0	0	0
Alabamina midwayensis	0	4.2	0.9	7.3	3.8	3.2	7.5	3.9	0.3	0	0	0	0.2	0	0
Bulimina farafraensis	1.5	1.7	0	0	1.3	6	7.5	0.4	0	0	0	0	0	0.3	0
Valvalabamina/Gyroidinoides spp.	7.4	4.2	6.1	1.3	4.7	3.6	3.8	1.1	0	0	0.5	0	0	1.4	0
Spiroplectinella cf. plummerae	6.9	3.7	8.9	7.7	16.6	1.6	2.1	7.1	0	5.3	5.1	0.9	2.9	12	0
Anomalinoides praeacutus	8.4	5.4	11.2	5.1	0.4	8.4	9.6	10.6	0.7	0.4	0	3.7	1.7	0.7	0
Cibicidoides succedens	0	1.2	0.5	0	0.4	2.8	6.3	1.4	0.3	4.5	3.3	0.9	1	0	0
Siphogenerinoides eleganta	1	0.8	0.5	2.6	1.3	1.2	0.4	5.7	5.7	4.9	2.3	1.4	1.7	2.1	0
Lenticulina spp.	4.9	6.2	7	12.4	6.4	13.6	6.3	7.8	11.6	12.2	15	7.9	14.1	14.3	38.6
Loxostomoides applinae	6.9	6.6	9.8	5.6	2.1	3.6	6.3	1.8	2	0	2.3	1.4	2.4	4.8	1.4
Stainforthia farafraensis	3	1.2	1.4	0	1.3	2	0	1.1	1.5	1.2	0.5	0.9	0	0	0
Bulimina quadrata-ovata	16.8	3.7	15	4.3	26.4	2.8	2.1	6.7	5	5.7	5.6	8.9	6	6.5	0
Oridorsalis plummerae	0	2.9	0	0	0	0.8	0.8	0	0	0.4	0	0	0	0	0
Valvulineria scrobiculata	3	11.2	7.9	13.3	5.5	5.2	4.6	6.7	2.5	3.7	4.7	13.1	15.5	7.2	4
Anomalinoides aegyptiacus	0	2.5	2.8	15.4	3	4.4	5.4	3.2	9.7	17.1	23.8	37.9	42.2	33.8	42.6
Anomalinoides cf. aegyptiacus	22.7	39.4	22	19.7	17.5	12	13.3	35.7	36.6	30.6	27.6	16.4	3.8	3.1	1.1
rest	2	0.4	0.5	1.3	1.7	2.8	2.1	1.1	6.9	2	0.5	0.9	1.4	1.4	0.3
Cibicidoides decoratus	0	0	0	0	0	0	0	0	0	1.6	0.5	0.9	1.2	5.5	0
Anomalinoides zitteli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trochammina spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaudryina cf. ellisorae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pulsiphonina wilcoxensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total number of specimens	203	241	214	234	235	251	240	283	404	245	214	214	419	293	352

Eocene sample S....	1029	1030	1031	1032	1033	1034	1035	1036	1037	1038	1039	1044	1045	1046
Cibicidoides cf. pseudoperlucidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Valvulineria? insueta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bulimina midwayensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaudryina africana	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lenticulina sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gavelinella? guineana	4.5	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyroidinoides girardanus	0	0	0	0	0	0	0	0	0	0	0	0.4	0	7
Alabamina midwayensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4
Bulimina farafraensis	0	0	0	0	0	0	0	0	0	1.3	0.5	12.1	3.1	7
Valvalabamina/Gyroidinoides spp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Spiroplectinella cf. plummerae	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0.4
Anomalinoides praeacutus	0	0	0	0	0	0	0	0	0	0	0	0.8	0	1.2
Cibicidoides succedens	0.5	0	0	0	0	0	0	0	0	0	0	0	0	2.9
Siphogenerinoides eleganta	0.9	0	0	0	0	0	0	0.9	0	0.4	0.5	0	0	0
Lenticulina spp.	20.1	18.1	13	9.6	6.6	0	9.3	25.9	6.2	16.7	4.3	19.3	11.7	13.5
Loxostomoides applinae	2.2	0.9	1	6.5	6.9	1	6.6	3.4	0.8	5.3	1	4	4.3	2.9
Stainforthia farafraensis	4.9	1.2	0.7	3.9	1.1	0	1.8	1.7	0	1.3	0	0.8	0.4	0
Bulimina quadrata-ovata	1.3	0.2	0	0.4	0	0	0.4	1.3	0.4	4	0	0.8	0	3.3
Oridorsalis plummerae	0.5	0.2	0.3	1.3	0	0	0	0	1.7	0.4	1.4	2.4	12.5	1.6
Valvulineria scrobiculata	11.2	5.2	7.9	11.3	9.5	29.9	53.1	38.1	55.6	31.3	56.7	29.3	27	13.5
Anomalinoides aegyptiacus	46.9	70.7	73.7	58.3	67.9	68.3	24.3	25.9	10.8	14.1	24.3	9.2	17.2	5.7
Anomalinoides cf. aegyptiacus	2.7	0.2	0	0	0	0	0	0	0	0	1.4	0	0	0
rest	0.9	1.2	0.7	1.3	1.5	0.5	0	0.4	0	5.7	0	1.6	2	3.3
Cibicidoides decoratus	3.6	1.9	2.7	7.4	6.6	0	4	1.7	19.1	14.1	10	12.5	18.4	25.8
Anomalinoides zitteli	0	0.2	0	0	0	0	0	0	0	0	0	2.4	3.1	1.2
Trochammina spp.	0	0	0	0	0	0.5	0.4	0.9	5.4	0	0	0.4	0	0
Gaudryina cf. ellisorae	0	0	0	0	0	0	0	0	0	0.4	0	0.8	0.4	10.3
Pulsiphonina wilcoxensis	0	0	0	0	0	0	0	0	0	4.9	0	0.8	0	0
Total number of specimens	224	426	293	230	274	211	226	236	241	227	210	249	256	244

west (Nile Valley, Wadi Qena and northern Kharga Oasis), some shallow water taxa persist, but many others become very rare or absent, to be replaced by a.o. various common spiroplectamminids, verneuilinids, parrelloidids (Luger, 1985, Speijer and Van der Zwaan, 1994b). Even further north (Sinai), benthic assemblages are dominated by deep-sea taxa (Tjalsma and Lohmann, 1983; Van Morkhoven et al., 1986), such as *Gavelinella beccariiformis*, *Nuttallides truempyi*, *Pullenia coryelli*, and *Cibicidoides hyphalus* indicating paleodepths of 500-700 metres (Speijer, 1994a; Speijer and Van der Zwaan, 1994b). Since there are no occurrences of deeper dwelling taxa, the Bir Inglisi area probably never was deeper than about 100 metres. The absence of larger foraminifera and sedimentological features indicating shallow depths (< 50 m) in combination with the almost continuous common presence of planktonic foraminifera, suggest the area was never shallower than about 50 metres either.

In spite of these rather well constrained and narrow bathymetric limits, the assemblages of Bir Inglisi I display some clear changes. Some of these could be interpreted as related to bathymetric change. Recently, a late Paleocene-early Eocene paleobathymetric model was developed, based on benthic foraminiferal distributions in many Egyptian sequences (Speijer and Van der Zwaan, 1994b). The paleobathymetric ranking of many diagnostic taxa is comparable to that observed in Tunisian deposits (Saint-Marc and Berggren, 1988; Saint-Marc, 1993). Summarizing from Speijer and Van der Zwaan (1994b), we distinguish six paleobathymetric assemblages (PA), each one containing taxa with a common depth preference:
PA 1: taxa restricted to bathyal deposits as

Table 2. Paleobathymetric assemblage assignment (first column), cluster assignment (second column) derived from cluster analysis, and loadings on the first three principal componens for all common taxa of Table 1.

Species	PA	clus.	PC1	PC2	PC3
Valvulineria? insueta	5	A	0.338	-0.175	0.056
Anomalinoides praeacutus	3	A	0.322	-0.04	0.05
Cibicidoides cf. pseudoperlucidus	3	A	0.314	-0.25	-0.037
Alabamina midwayensis	3	A	0.306	-0.086	0.028
Gaudryina africana	6	A	0.27	-0.159	0.082
Valvalabamina/Gyroidinoides spp.	3	A	0.268	0.031	0.029
Cibicidoides succedens	3	A	0.235	-0.209	0.147
Spiroplectinella cf. plummerae	6	A	0.196	0.207	0.209
Bulimina quadrata-ovata	5	A	0.167	0.212	0.24
Lenticulina sp. 1	6	A	0.14	0.258	0.322
Gyroidinoides girardanus	5	C	0.134	-0.337	0.099
Siphogenerinoides eleganta	6	A	0.107	0.196	0.347
Bulimina farafraensis	3	C	0.048	-0.395	0.105
Bulimina midwayensis	3	A	0.031	0.181	0.158
Loxostomoides applinae	5	B	-0.019	-0.039	0.098
rest	3	C	-0.056	-0.076	0.377
Gavelinella? guineana	6	B	-0.079	0.101	0.2
Gaudryina cf. ellisorae	3	C	-0.082	-0.265	0.153
Stainforthia farafraensis	6	B	-0.084	0.105	0.102
Anomalinoides (cf.) aegyptiacus	6	B	-0.111	0.134	0.305
Pulsiphonina wilcoxensis	3	C	-0.126	-0.06	0.075
Trochammina spp.	5	C	-0.136	-0.049	-0.097
Oridorsalis plummerae	3	C	-0.153	-0.225	0.107
Lenticulina spp.	3	B	-0.172	-0.021	0.395
Anomalinoides zitteli	3	C	-0.176	-0.271	0.163
Valvulineria scrobiculata	5	C	-0.232	-0.089	0.086
Cibicidoides decoratus	6	C	-0.254	-0.279	0.237

found in the Sinai.

PA 2: taxa with outer neritic upper depth limits, typical of deposits in northern and central Egypt.

PA 3: taxa without a clear paleobathymetric preference, common in all localities studied.

PA 4: taxa exclusively encountered in the outer neritic deposits of Gebel Oweina.

PA 5: taxa common in neritic deposits of central and southern Egypt.

PA 6: taxa common to abundant in inner-middle neritic deposits of Bir Inglisi and southern Egypt.

In the Bir Inglisi I section, species belonging to only three of these paleobathymetric assemblages (PA 3, PA 5, PA 6) were encountered (see Table 2). Figure 5 shows the relative abundances of these three assemblages in vertical sequence; several taxa which where lumped in a supraspecific category in Table1/Fig. 4 (*Lenticulina* spp., *Trochammina* spp. and "rest") were ommited. The remaining part of the assemblages was normalized to 100 percent. The patterns in Fig. 5 show distinct fluctuations in the relative contribution of the three paleobathymetric assemblages. PA 6 strongly dominates in the middle part of the section and to a lesser degree also in the lower part of the section. In the upper part of the section PA 5 dominates, but decreases upwards. The lower and the uppermost part of the section show a fairly high proportion of PA 3. The near absence of PA 3 and the peak frequency of PA 6 in the P/E boundary interval suggest a relatively low sea-level at that time. Nevertheless, the magnitude of bathymetric changes seems rather small, since the presence of PA 6 remains very persistent over the interval studied. We will return to this issue later.

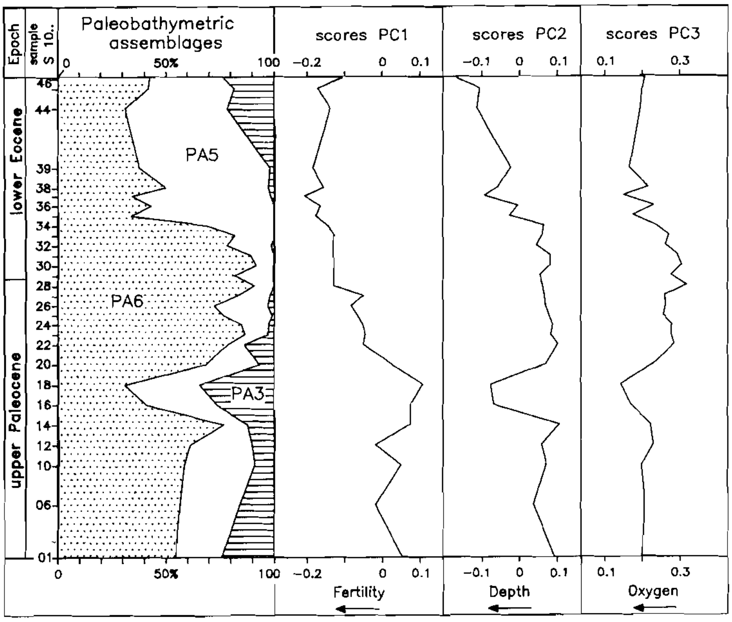

Fig. 5. Relative abundance of the three paleobathymetric assemblages (PA) encountered in Bir Inglisi I and principal component sample scores on the first three components. Note the similarity between the proportion of the shallowest assemblage (PA 6) and the sample scores on PC 2, both suggesting (minor) relative sea-level variations.

Quantitative benthic foraminiferal analysis

The frequency data displayed in Table 1-/Fig. 4 were subjected to cluster and principal component analyses. Cluster Analysis (unweighted pair group method) resulted in three rather well defined clusters A, B and C (Fig. 6). None of the clusters seems to be bathymetrically defined; elements of PA 3-6 are randomly divided between them (Table 2). Cluster A seems to be a "Paleocene" cluster composed of Lazarus taxa and taxa with an exit at or below the P/E boundary. Cluster B contains taxa that proliferate in the middle part of the section; all these taxa, except *Gavelinella? guineana*, also proliferate in the sapropelitic bed at the P/E boundary of Wadi Nukhl (Speijer and Van der Zwaan, 1994b), clearly indicating that this cluster is composed of the most opportunistic, oxygen-stress tolerant taxa. The enormous abundance reached by *Anomalinoides aegyptiacus* is reminiscent of patterns displayed by some modern opportunistic epibenthic taxa as *Epistominella* and *Alabaminella*, taxa with comparable test morphologies, that dominate high productive sites often stressed by oxygen deficiency (Jorissen et al., 1992; Sen Gupta and Machain-Castillo, 1993; Gooday, 1993).

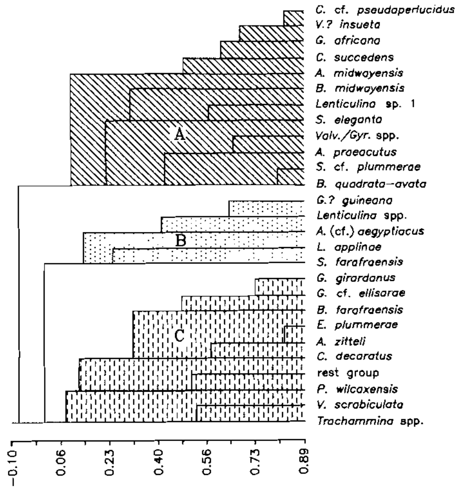

Fig. 6. Dendrogram derived from cluster analysis. Cluster A contains taxa that are most common in the Paleocene; cluster B contains common P/E boundary interval taxa; cluster C contains taxa that are most common in the early Eocene.

Cluster C is composed of "Eocene" taxa, taxa that are more frequent above than below the P/E boundary and taxa that enter the record above the boundary. Most taxa in this cluster have wide bathymetric distribution patterns (PA 3 or PA 5). Most taxa of cluster C have low trochospiral testforms, morphologies often equated with epibenthic living positions (e.g. Corliss, 1985, Corliss and Chen, 1988), although recent work showed that test morphology and living position are not very intimately related (Barmawidjaja et al., 1992; Linke and Lutze, 1993). Yet, in particular the dominance of *Valvulineria scrobiculata* could be taken as indicative of a raised organic flux, in analogy with modern *Valvulineria* which often dominate in high productive areas and river plumes (e.g. Jorissen, 1988; Van der Zwaan and Jorissen, 1992; Murray, 1991).

To provide the relative abundance data with a statistically founded basis, a standardized Principal Component Analysis (PCA) was run. The first axis explains 20% of the variation, the second 16% and the third 9%. The higher order axes explain less than 9% and are regarded as insignificant. Sample scores (Table 3) are plotted along sequence in Fig. 5. In addition we plotted the sample scores in three bivariate plots (Fig. 7).

The first component (PC 1) essentially distinguishes Paleocene from Eocene assemblages, with most taxa of cluster A loading positively and most taxa of clusters B and C loading negatively. Similar to the cluster compositions, PC 1 loadings appear unrelated to paleobathymetric distribution. Since cluster B and in particular cluster C were tentatively interpreted to reflect raised organic fluxes (in combination with oxygen deficiency) the negative scores on PC 1 could well be interpreted to reflect increasing fertility, starting just below the P/E boundary.

Table 3. Sample scores on the first three principal components, based on frequency data listed in Table 1.

Sample	PC1	PC2	PC3
1046	-0.111	-0.167	0.206
1045	-0.174	-0.107	0.2
1044	-0.139	-0.115	0.195
1039	-0.187	-0.024	0.165
1038	-0.157	-0.058	0.215
1037	-0.209	-0.095	0.149
1036	-0.166	-0.005	0.23
1035	-0.179	-0.028	0.175
1034	-0.146	0.064	0.236
1033	-0.128	0.06	0.27
1032	-0.132	0.044	0.261
1031	-0.131	0.081	0.294
1030	-0.128	0.081	0.305
1029	-0.129	0.053	0.276
1028	-0.131	0.06	0.317
1027	-0.051	0.065	0.259
1026	-0.084	0.068	0.261
1025	-0.067	0.077	0.255
1024	-0.053	0.087	0.279
1023	-0.045	0.082	0.277
1022	-0.051	0.102	0.285
1020	0.023	0.07	0.23
1018	0.107	-0.078	0.141
1016	0.074	-0.07	0.168
1014	0.072	0.106	0.222
1012	-0.019	0.058	0.229
1010	0.049	0.071	0.198
1006	-0.019	0.036	0.207
1001	0.052	0.092	0.199

The second axis seems to represent bathymetry, since it is positively loaded by most middle neritic taxa of PA 6 (see Table 2) and negatively by PA 5 and PA 3 taxa. Consequently, there is great similarity between the curve of sample scores on PC 2 and the relative abundance of PA 6. This confirms the earlier paleobathymetric analysis, which suggested a minor and temporal shallowing in the P/E boundary interval. We can not substantiate the magnitude of the shallowing, but we estimate this to be in the order of 20 metres at most; as explained earlier, upper and lower depth of deposition of the sediments is narrowly contrained.

The taxa of the shallow PA 6 yield the highest positive loadings on the third component, and due to the high abundance of these taxa, the sample scores along sequence therefore show a similar pattern as the one on PC 2. On the other hand, PA 3 and PA 5 taxa load randomly along this axis, suggesting that paleobathymetry is not the controling parameter on PC 3. In order to appreciate the difference in paleoenvironmental significance between PC 2 and PC 3 more clearly, we plotted the taxa loadings of these components in a bivariate plot (Fig. 7). In this plot two groups of taxa are widely separated. The largest group (lower left corner) with generally low loadings on PC 3 contains most taxa from clusters A and C, whereas the other group (upper right corner) with high loadings on PC 3 contains taxa from cluster B, the remainder of cluster A, and lumped taxa in "rest" (= mainly *Fursenkoina, Uvigerina,* and *Caucasina*). All taxa in the latter group seem to be indicative of oxygen stress as already discussed for cluster B. The taxa from cluster A now joining this group (*Spiroplectinella* cf. *plummerae, Lenticulina* sp. 1, *Bulimina midwayensis, Bulimina quadrata-ovata,* and *Siphogenerinoides eleganta*), as well as "rest", all have an endobenthic morphology (Corliss, 1985; Corliss and Chen, 1988). In a sense, these taxa seem to represent the "Paleocene" faunal component resistant to oxygen stress, but apparently not able to resist the changing conditions during the P/E boundary interval. In contrast, the first group yields predominantly taxa with an epibenthic morphology that are thought to be least resistant to oxygen stress. From these patterns, we infer that the second component reflects oxygenation, which appears tightly coupled to bathymetry: most severe oxygen stress coincides with slightly lowered sea-levels. Strikingly, the assemblages that suggest lowest oxygen stress and highest sea-level

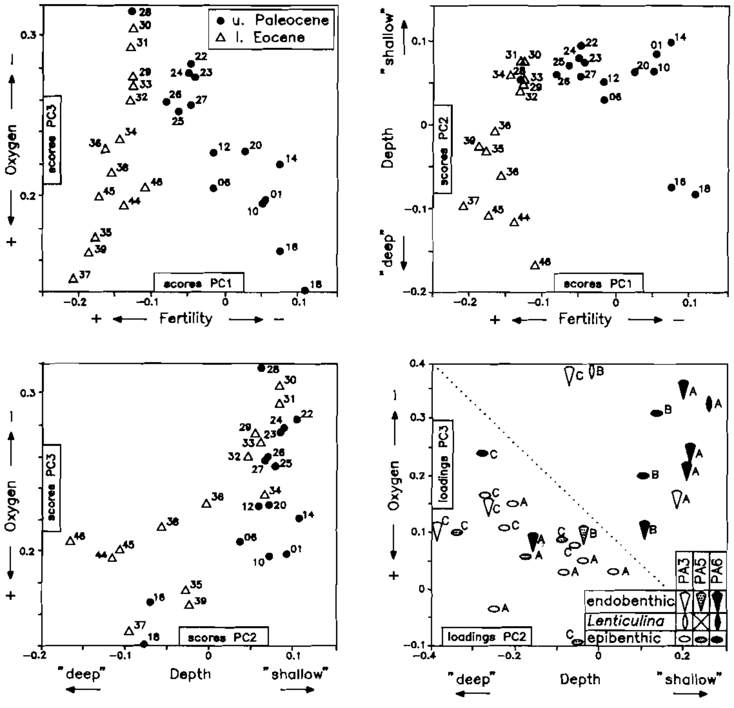

Fig. 7. Bivariate sample score plots of the first three principal components (data from Table 3; numbers 01-46 refer to sample numbers S 1001-1046). In the lower right-hand corner the plot contains taxa loadings on PC 2 and PC 3 (Table 2). For further explanation see text.

(S 1016-18; Fig. 5) are from one of the few non-laminated intervals.

The pattern of sample scores further suggests that organic flux stepped up significantly from a level below the P/E boundary and persisted to be high during the lowermost Eocene. Strikingly, oxygenation and organix flux patterns are not tightly coupled, since organic flux during the early Eocene remained high, whereas oxygenation improved. The total analysis suggests that within the P/E boundary interval, the assemblages indicate relatively shallow and most oxygen deficient conditions. This picture is well supported by the analysis of the faunal indices.

Discussion

Although our database is relatively limited and restricted to one locality, some constraints on P/E boundary events immediately become apparent. The Bir Inglisi I section is located near the margin of the early Paleogene epicontinental Tethys margin. Although precise paleobathymetry, for instance using P/B models, is inhibited due to the sometimes poor preservation of planktonic foraminifera, the composition of the benthic foraminiferal association suggests shallow water conditions during deposition of the entire Bir Inglisi I sequence. Comparison with other localities indicates that the depth of deposition was middle neritic, probably about 75-100 metres. Our data suggest that a short term deepening in the upper Paleocene was followed by a relative sea-level lowstand, that persisted into the early Eocene. Subsequently, the basin deepened again. Total variation was certainly not more than some 10-20 metres. This implies that any model explaining the P/E boundary events can not call upon considerable global sea-level fluctuations, since the effects would almost certainly be traceable in a shallow water locality as Bir Inglisi.

Although dissolution possibly affected planktonic foraminiferal numbers, the general increasing trend is suggestive for increased production. This is supported by the scores on the first principal component, showing that fertility increased rapidly just prior to the P/E boundary and reached highest values during the Eocene. Comparison of foraminiferal numbers with other areas in Egypt indicates that in general feritility in Bir Inglisi was high (Speijer and Van der Zwaan, 1994b). This is well in agreement with the general aspect of the sediment: highly organic rich, green-brown marls and shales which are often laminated. The latter feature suggests that Bir Inglisi also rather continuously experienced bottom water oxygen deficiency, resulting in strongly reduced bioturbation. At times of slightly higher sea-level, oxygenation appears to have ameliorated; this is also reflected in better bioturbated sediments. The faunal patterns and the pattern displayed by the sample scores on the third axis, interpreted to reflect the bottom water oxygen content, suggest that the oxygen content reached lowest values during the earliest Eocene.

Plate-tectonic reconstructions for the late Paleocene show Africa situated some 15° South of its present position (Barron et al., 1981; Smith et al., 1981). In that position North Africa and thus the southern margin of the Tethys seaway would be subject to prevailing NE northern hemisphere tradewinds. The exact position of the late Paleocene-early Eocene Tethyan paleoshoreline running east of Egypt can not be determined; most marginal marine deposits in southeastern Egypt and along the Arabian shield have been eroded due to uplift along the Red Sea rift (Said, 1960; Said, 1990b). But, since in Saudi-Arabia only coastal and lacustrine Paleocene deposits are recovered (Madden et al, 1980; Brown et al., 1989), the paleo-shoreline would have run approximately NE-SW across the Nubian-Arabian shield in the direction of Jordany. Apart from local swells, the basin generally deepened perpendicular to this direction (cf. Luger, 1988; Said, 1990d; Speijer and Van der Zwaan, 1994b). In this configuration longshore tradewinds would have induced offshore Ekman transport of the upper water column, which would have been compensated by upwelling of deeper nutrient-rich waters of the Tethys. The general picture emerging from our faunal analysis of Bir Inglisi I indeed suggests a sequence located in the shallow part of the southern Tethyan shelf, characterized by fairly high production and consequently organic-rich, oxygen deficient sediments during the entire time-slice.

The total setting is reminiscent of the Late Cretaceous, in particular of the Campanian, when upwelling prevailed over vast areas of the southern Tethyan margin (Wiedmann et al., 1978; Bock, 1987; Reiss, 1988; Notholt et al., 1989; Kroon and Nederbragt, 1990; Almogi-Labin et al., 1993; Eshet, 1994). Upwelling has been related to the paleogeographic position of the wide North African shelves within the area of NE trades (Parrish and Curtis, 1982). Global Circulation Model (GCM) studies indicate that during warm equable climates and slightly warmer (sub)tropics, tradewind strenght may have increased due to a stronger atmospheric contrast, resulting from enhanced evaporation in the subtropics and greater latent heat release in the tropics, despite the weaker meridional thermal gradient at the sea-surface (Barron and Washington, 1985; Barron, 1986; Crowley and North, 1991). Significantly, enhanced evaporation may result, at the same time, in deep water formation in the Tethys (Chamberlain, 1906; Brass et al., 1982). Provided that the implications from GCM studies are correct, upwelling intensity should have decreased in the Maastrichtian and early Paleocene, when global and in particular tropical temperatures declined (Douglas and Woodruff, 1981; Gerstel and Thunnell, 1986; Barrera et al, 1987; Kennett and Barker, 1990; Frakes et al., 1992; Lécuyer, 1993). This seems confirmed by the relatively rare occurrence of phosphate and organic rich deposits of late Maastrichtian to early Paleocene age (Said, 1960; Notholt et al., 1989; Hussein and El-Sharkawi, 1990; Almogi-Labin et al., 1993).

Upwelling in the southern Tethys gradually intensified during the late Paleocene, as evidenced by the renewed formation of phosphate deposits in North Africa, in particular in Tunisia and Morocco (Burollet and Oudin, 1980; Busson and Cornee, 1986; Notholt et al., 1989). Significantly, this goes hand in hand with the late Paleocene warming trend up to the early Eocene thermal maximum (Douglas and Woodruff, 1981; Wolfe, 1985; Shackleton, 1986; Corfield et al., 1991; Stott et al., 1990; Lécuyer, 1993; Zachos et al., 1993, 1994). We suggest that these trends are interrelated. Although in Egypt higher productivity did not lead to the formation of phosphorites, the Bir Inglisi I sequence indeed indicates high productivity. Late Paleocene ostracode assemblages from the El Kef section in Tunisia were interpreted as indicating upwelling and high productivity in a middle neritic environment (Peypouquet et al., 1986). Interestingly benthic foraminiferal assemblages from that section bear great similarity with the ones from Bir Inglisi I (Salaj et al., 1976; Van Oosterhout, 1988; Saint-Marc, 1993), thus strengthening our paleoenvironmental interpretations. Furthermore, our data indicate a significant fertility increase just prior to the P/E boundary. Judging from the increasingly large amounts of phosphate and organic rich deposits of early Eocene age in Tunisia (Burollet and Oudin, 1980), upwelling intensified in that region during the same period as well.

Our interpretation of the general setting of the late Paleocene to early Eocene southern Tethys implies strong atmospheric contrast between the subtropical southern Tethys and the African craton, situated within the tropical zone. This scenario is consistent with predictions from GCM simulations (Barron and Washington, 1985; Barron, 1986, 1987; Barron and Peterson, 1991: Crowley and North, 1991). It requires, however, high (sub)tropical temperatures; estimated temperatures from planktonic foraminiferal stable isotopes were considered to be significantly lower than present values (Boersma and Shackleton, 1981). In a recent paper, Zachos et al. (1994) dismissed the latter conclusions and demonstrated that late Paleocene and early Eocene low-latitude $\delta^{18}O$ values fall within the lower (warmer) range of Holocene values (see discussion in Zachos et al., 1994).

Another objection against our scenario could be found in eolian grainsize and flux data from deep-sea deposits in the Pacific and Indian Oceans. These were considered to indicate a decrease in zonal wind strength, related to the warm equable climate during this time-slice (Janecek and Rea, 1983; Miller et al., 1987; Rea et al., 1990; Hovan and Rea, 1992a). However, floral records point at mild seasonality and winter temperatures well above freezing in middle-high latitude continental interiors (MacGinitie, 1969, 1974; Wolfe, 1978; Wing et al., 1991), a situation that is incompatible with weaker zonal winds (Barron, 1987). A clue for this apparent paradox is provided by Hovan and Rea (1992b), who reinterpreted the Indian Ocean eolian dust record in terms of changing aridity in the source area and a decrease in dust supply.

Possibly, such an interpretation might well be applicable to the Pacific Ocean records, that show reduced grain sizes during the entire Eocene and Oligocene (Janecek and Rea, 1983), long after warm equable climates had ended (Crowley and North, 1991; Frakes et al., 1992).

The high production at the Tethys margin evidently affected bottom water oxygen contents. However, the presence of ample benthic fauna proves that anoxia and/or dysoxia had a temporal, possibly seasonal, nature and alternated by periods of ventilation. In shallow seas, like the one represented by the Bir Inglisi I sequence, seasonal mixing is able to ventilate the basin fully and can lead to rapid restorement of benthic fauna. However, the patterns of sample scores on the first and third axis show that oxygen contents were not determined by organic flux alone.

At the P/E boundary oxygen contents dropped significantly further; %P increased enormously due to sharp drop in benthic foraminiferal test production. Yet, planktonic foraminiferal numbers, nor the nature of the faunal assemblages, indicate increased production at the P/E boundary. Therefore, the most likely scenario is that the rather sharp drop in oxygen content was caused by reduced ventilation; with a constant consumption rate this would have led to a stronger oxygen deficiency at the bottom than before and after. Our data are insufficient to unravel the exact nature of this event. Decreased ventilation could have been caused by increasing development of the seasonal thermocline, leading to reduced thermocline mixing. On the other hand, the same effect can be generated by reduced oxygen advection from deeper waters, due to decreased intermediate and deep water formation. The latter alternative would have far-reaching implications, if we consider that these intermediate and deep waters could have been formed at high southern latitudes (Thomas, 1992). A more comprehensive analysis of late Paleocene-early Eocene benthic foraminiferal distribution patterns in Egypt (Speijer and Van der Zwaan, 1994b), indeed suggests that during the late Paleocene this part of the Tethys was ventilated by intermediate water from a high latitude source, and that the P/E boundary oxygen deficiency is a widespread phenomenon, as in other parts of the Tethys.

Conclusions

The P/E boundary sequence of Bir Inglisi I at the Red Sea coast shows that the boundary events, leading a.o. to extinction of deep-sea benthic foraminifera and a strong perturbation of the global carbon cycle, also affected shallow water sites. Although the database discussed is not comprehensive enough to draw far-reaching conclusions from, the faunal data provide some further constraints on the nature of the boundary events.

We firmly established that a significant global sea-level change at the P/E boundary seems to be highly unlikely; we detected only minor sea-level changes at this shallow site. In general, the area appears to have been highly productive probably due to (intermittent) tradewind-induced coastal upwelling. Moreover, organic flux seems to have stepped up significantly just prior to the P/E boundary. We attribute this to the re-establishment of strong atmospheric contrasts between the tropical and subtropical zone, leading to intensified trade winds, induced by the establishment of the early Eocene thermal maximum.

The P/E boundary is characterized by minimal average sea-floor oxygenation, superimposed on a gradual decrease that started below the boundary. The cause of the gradually decreasing oxygenation may be the increasing organic loading at the sea-floor, but the distinct drop in ventilation at the P/E boundary was probably due to either reduced thermocline mixing or reduced oxygen advection from deeper waters, resulting from decreased (possibly high latitude) intermediate and deep water formation.

Acknowledgements

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Appendix - Taxonomic notes

We largely adopted species concepts used by LeRoy (1953) and Aubert and Berggren (1976), but in some instances we deviated from these and used additional documentation. As far as possible, we refer to earlier studies on Egyptian material. For (supra-)generic classification we largely followed Loeblich and Tappan (1988).

Spiroplectamminacea
Spiroplectamminidae
Spiroplectinella* cf. *plummerae (Cushman)
(Pl. I, Fig. 1)

cf. 1926 *Textularia carinata* d'Orbigny var. *expansa* Plummer: p. 67, pl. 3, fig. 3
cf. 1948 *Spiroplectammina plummerae* Cushman: p. 226, pl. 16, fig. 2
cf. 1951 *Spiroplectammina plummerae* Cushman. Cushman: p. 5, pl. 1, figs. 19-20
Remarks: in side view this species seems very similar to the type species, although it is probably more compressed. Unfortunately no apertural view was given for the holotype, but Cushman (1948) mentions a broad aperture, whereas the Egyptian specimens have a very narrow aperture and apertural face. The presence of depressed sutures makes this species easily distinguishable from other species occurring in Egypt.

Verneuilinacea
Verneuilinidae
Gaudryina africana LeRoy
(Pl. I, Fig. 2)

1953 *Gaudryina africana* LeRoy: p. 30, pl. 1, figs. 7-8
Remarks: the strongly inflated later chambers of the biserial part distinguish this species from *G. pyramidata*.

Gaudryina* cf. *ellisorae Cushman
(Pl. I, Fig. 3)

cf. 1936 *Gaudryina (Pseudogaudryina) ellisorae* Cushman: p. 13, pl. 2, fig. 12

cf. 1946 *Gaudryina (Pseudogaudryina) ellisorae* Cushman. Cushman: p. 35, pl. 8, figs. 12, 13
Remarks: the carinate ribs are very distinct in this species; the outer test wall is built of much coarser grains than in the type specimen.

Nodosariacea

Nodosariidae

Dentalina latejugata (Gümbel)

1870 *Nodosaria latejugata* Gümbel: p.169, pl. 1, fig. 32
1976 *Nodosaria latejugata* Gümbel. Aubert and Berggren: p. 412, pl. 2, fig. 4
Remarks: a very large costate species; usually only fragments (single chambers) are encountered.

Frondicularia nakkadyi Futyan

1976 *Frondicularia nakkadyi* Futyan: p. 528, pl. 82, fig. 1
1985 *Frondicularia nakkadyi* Futyan. Luger: p. 80, pl. 4, fig. 3
Remarks: a smooth large palmate *Frondicularia*, without any ornamentation.

Frondicularia phosphatica Russo
(Pl. I, Fig. 4)

1934 *Frondicularia phosphatica* Russo: p. 358, pl. 16, figs. 6-8, 12
1950 *Frondicularia wanneri* Nakkady: p. 685, pl. 89, fig. 23
1976 *Frondicularia phosphatica* Russo. Aubert and Berggren: p. 414, pl. 2, fig. 12
1985 *Frondicularia wanneri* Nakkady. Luger: p. 80, pl. 4, fig. 2
Remarks: the elevated central ridge(s) on both sides of the test and occasionally oblique costae lead to easy identification of this large species. *Frondicularia wanneri* Nakkady is considered to be a junior synonym. Due to its large size, it is an excellent field marker for the P/E boundary in Bir Inglisi.

Vaginulinidae

***Lenticulina* sp. 1**
(Pl. I, Fig. 5)

Remarks: the compressed to moderately compressed test with the sharp sutural costae, the spiral structure, and the marginal carina are very characteristic for this taxon. It does not seem to have been described earlier from Egypt.

Bolivinacea

Bolivinidae

Loxostomoides applinae (Plummer)
(Pl. I, Fig. 11)

1926 *Bolivina applini* Plummer: p. 69, pl. 4, fig. 1
1953 *Loxostomum applinae* (Plummer). LeRoy: p. 37, pl. 8, fig. 1
1956 *Loxostomum clavatum* (Cushman). Said and Kenawy: p. 144, pl. 4, fig. 21
1959 *Loxostomum applinae* (Plummer). Nakkady: p. 459, pl. 2, fig. 1
1976 *Loxostomoides applinae* (Plummer). Aubert and Berggren: p. 420, pl. 4, fig. 11
1982 *Loxostomoides applinae* (Plummer). Faris: p. 211, pl. 5, fig. 2
1985 *Loxostomoides applinae* (Plummer). Luger: p. 106, pl. 7, fig. 1
Remarks: this species is characterized by the crenulated base of the biserially arranged chambers and the longitudal striae, fusing into low costae on the initial part of the test.

Turrilinacea

Stainforthiidae

Stainforthia farafraensis (LeRoy)
(Pl. I, Fig. 7)

1953 *Neobulimina farafraensis* LeRoy: p. 39, pl. 8, figs. 3-4
Remarks: this smooth species has a very short triserial part and rather straight horizontal sutures. Specimens are often compressed due to sediment compaction.

Buliminacea
Siphogenerinoididae
Siphogenerinoides eleganta (Plummer)
(Pl. I, Fig. 6)

1926 *Siphogenerina eleganta* Plummer: p. 126, pl. 8, fig. 1
1953 *Siphogenerinoides eleganta* (Plummer). LeRoy: p. 49, pl. 2, figs. 20-21
1976 *Siphogenerinoides eleganta* (Plummer). Aubert and Berggren: p. 421, pl. 5, fig. 3

Remarks: in large specimens the biserial arrangement is followed by a uniserial part. Surface ornamentation in the specimens from Bir Inglisi is coarsely punctate and slightly rugose. This ornamentation might be more pronounced than in the type species.

Buliminidae
Bulimina farafraensis LeRoy
(Pl. I, Fig. 8)

1953 *Bulimina farafraensis* LeRoy: p. 21, pl. 7, figs. 26-27
1982 *Bulimina* cf. *instabilis* Cushman and Parker. Faris (partim): p. 212, pl. 5, fig. 6 (not fig. 7)

Remarks: very distinct rounded triangular species with large branching costae over the entire test and with distinct pores except in the upper part of the chambers of the last whorl.

Bulimina midwayensis Cushman and Parker
(Pl. I, Fig. 9)

1926 *Bulimina aculeata* d'Orbigny. Plummer: p. 73, pl. 4, fig. 3
1936a *Bulimina arkadelphiana* Cushman and Parker var. *midwayensis* Cushman and Parker: p. 42, pl. 7, figs. 9-10
1953 *Bulimina inflata* Seguenza. LeRoy: p. 21, pl. 8, fig. 25
1956 *Bulimina arkadelphiana midwayensis* Cushman and Parker. Said and Kenawy: p. 142, pl. 4, fig. 11
1959 *Bulimina arkadelphiana* Cushman and parker var. *midwayensis* Cushman and Parker. Nakkady: p. 458, pl. 1, fig. 9
1976 *Bulimina midwayensis* Cushman and Parker. Aubert and Berggren: p. 422, pl. 5, fig. 7
1982 *Bulimina midwayensis* Cushman and Parker. Faris: p. 213, pl. 5, figs. 3-5
1985 *Bulimina midwayensis* Cushman and Parker. Luger: p. 106, pl. 7, fig. 7

Remarks: the ornamentation of this species is subject to a considerable amount of variation; often only short spines at the base of the chambers are formed, whereas in other specimens they merge into short irregular costae on the chambers.

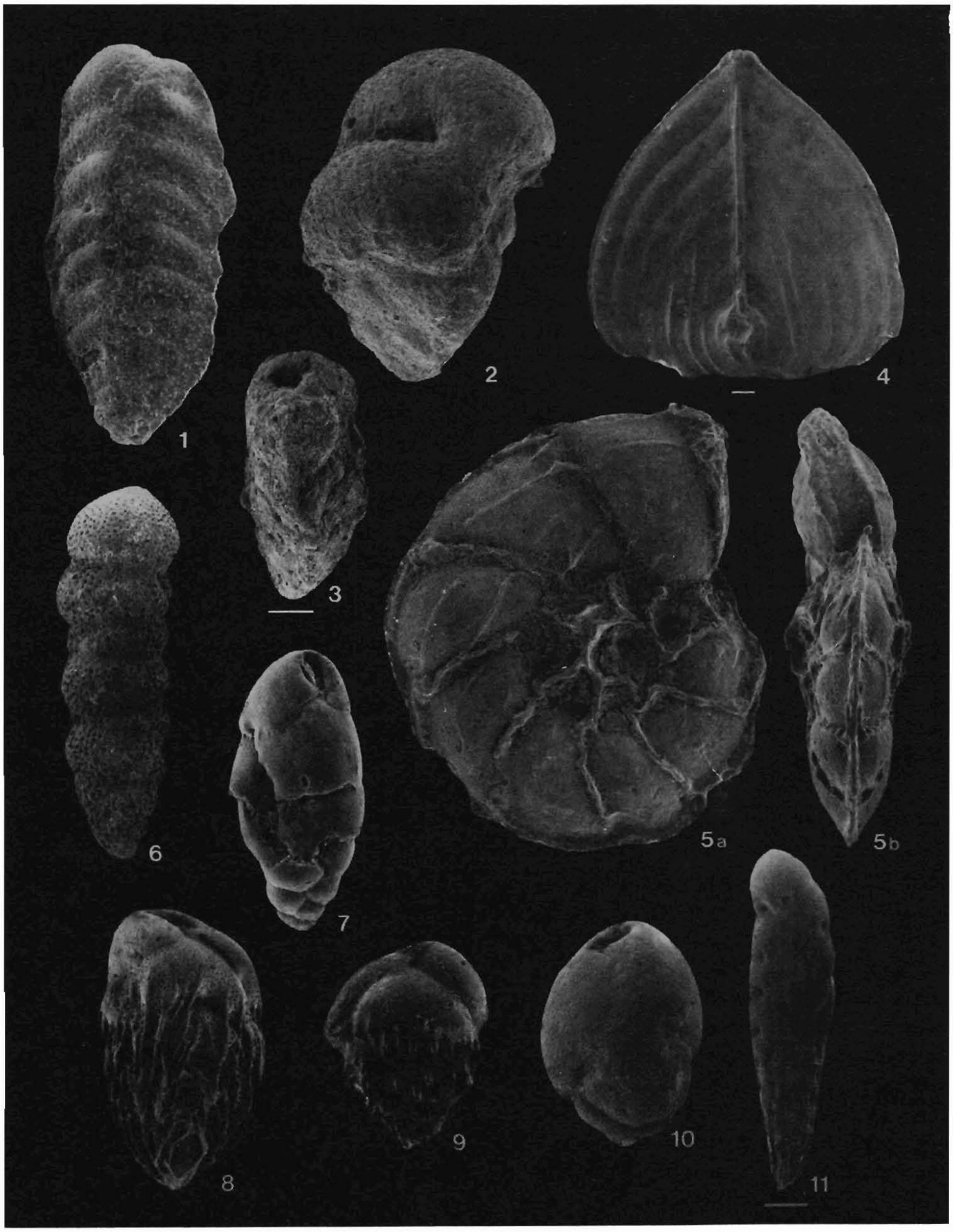
Bulimina quadrata-ovata plexus
(Pl. I, fig. 10)

1926 *Bulimina quadrata* Plummer: p. 72, pl. 4, figs. 4, 5

Plate I

Fig. 1 *Spiroplectinella* cf. *plummerae* (Cushman), sample S 1024 (X 60)
Fig. 2 *Gaudryina africana* LeRoy, sample S 1016
Fig. 3 *Gaudryina* cf. *ellisorae* Cushman, sample S 1046 (X 60)
Fig. 4 *Frondicularia phosphatica* Russo, sample S 1025 (X 30)
Fig. 5 *Lenticulina* sp. 1, sample S 1025
Fig. 6 *Siphogenerinoides eleganta* (Plummer), sample S 1025
Fig. 7 *Stainforthia farafraensis* (LeRoy), sample S 1032
Fig. 8 *Bulimina farafraensis* LeRoy, sample S 1016
Fig. 9 *Bulimina midwayensis* Cushman and Parker, sample S 1025
Fig. 10 *Bulimina quadrata-ovata* plexus, sample S 1025
Fig. 11 *Loxostomoides applinae* (Plummer), sample S 1025 (X 60)
All magnifications X 120 unless indicated otherwise (bar = 100 µm).

PLATE I



1953 *Bulimina pupoides* d'Orbigny. LeRoy: p. 22, pl. 8, fig. 21
1956 *Bulimina kickapooensis* Cole. Said and Kenawy: p. 142, pl. 4, fig. 12
1976 *Bulimina quadrata* Plummer. Aubert and Berggren: p. 422, pl. 5, fig. 91982 *Bulimina quadrata* Plummer. Faris: p. 214, pl. 5, fig. 8
1985 *Bulimina quadrata* Plummer. Luger: p. 107, pl. 7, fig. 6
1985 *Bulimina reussi* Morrow. Luger: p. 107, pl. 7, fig. 7
Remarks: this plexus comprises all smooth, finely perforate species with a "globular" shape. It appeared to be rather difficult to assign all encountered specimens within this group to various species in a consistent way, since the specimens are often compressed and poorly preserved.

Discorbacea

Bagginidae

Valvulineria? Insueta Cushman and Bermúdez
(Pl. III, Fig. 4)

1951 *Valvulineria insueta* Cushman and Bermúdez. Cushman: p. 51, pl. 23, figs. 2-4
Remarks: this species is tentatively placed in *Valvulineria*. In spiral view this species resembles *Alabamina creta*. Apertural features, however, are quite different and better fit the concept of *Valvulineria*.

Valvulineria scrobiculata (Schwager)
(Pl. IV, Figs. 1-3)

1883 *Anomalina scrobiculata* Schwager: p. 129, pl. 29, fig. 18
1950 *Anomalina scrobiculata* Schwager var. *esnehensis* Nakkady: p. 691, pl. 90, figs. 33, 34
1953 *Valvulineria scrobiculata* (Schwager). LeRoy: p. 53, pl. 9, figs. 18-20
1959 *Valvulineria scrobiculata* (Schwager). Nakkady: p. 460, pl. 2, fig. 5
1985 *Gavelinella scrobiculata* (Schwager). Luger: p. 112, pl. 9, figs. 9, 10
Remarks: a very distinct, large species with large pores on both sides, except around the umibilicus, which is surrounded by nodes of clear shell material. The umbilical flaps do not entirely cover the umbilicus. In Tunisia two different species are recorded under the same name (Aubert and Berggren, 1976; Salaj et al., 1976). It is rather difficult to decide which species fits better with the type specimen. The Tunesian specimens of Aubert and Berggren (1976; lower Paleocene) appear much more compressed, whereas the Egyptian specimens (upper Paleocene-lower Eocene) are more inflated than Schwager's holotype. The specimens referred to as this species in Salaj et al. (1976), are regarded in this paper as *Anomalinoides aegyptiacus* (LeRoy). Schwager described this species from the Eocene of the Libyan Desert

Siphoninacea

Siphoninidae

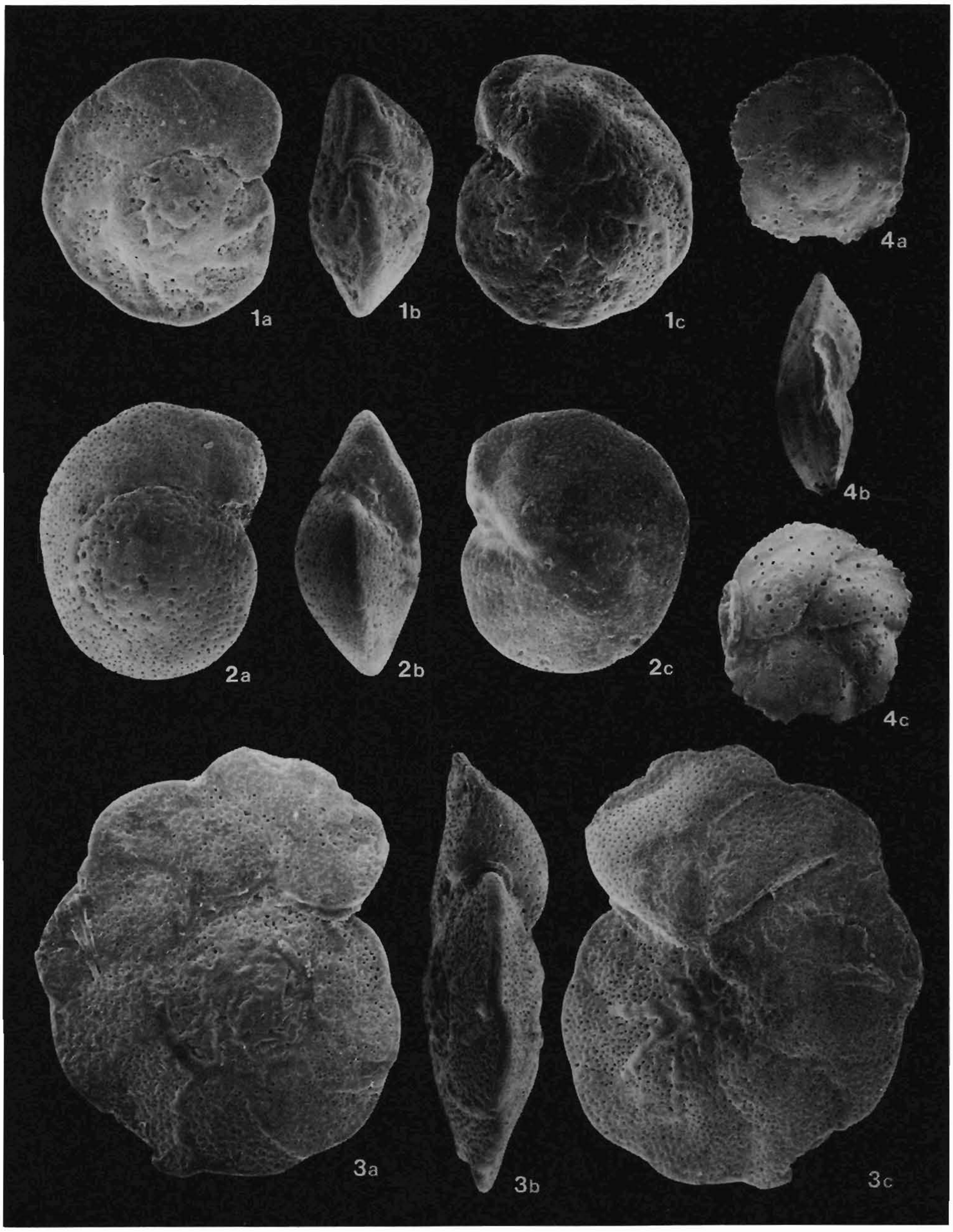
Pulsiphonina wilcoxensis (Cushman)
(Pl. II, Fig. 4)

1951 *Siphonina wilcoxensis* Cushman. Cushman: p. 56, pl. 15, fig. 10
Remarks: this rather small species differs from its ancestor *P. prima* in the development of a more protruding apertural lip, also visible from the spiral side and the much more depressed sutures on the spiral side.

Plate II

Fig. 1 *Cibicidoides succedens* (Brotzen), sample S 1016
Fig. 2 *Cibicidoides* cf. *pseudoperlucidus* (Bykova), sample S 1016
Fig. 3 *Cibicidoides decoratus* (LeRoy), sample S 1026
Fig. 4 *Pulsiphonina wilcoxensis* (Cushman), sample S 1038
All magnifications X 120.

PLATE II



Discorbinellacea

Parrelloididae

Cibicidoides decoratus (LeRoy)

(Pl. II, Fig. 3)

1953 *Cibicides decoratus* LeRoy: p. 23, pl. 6, figs. 15-17

Remarks: a large strongly compressed species, with a thin marginal keel and large pores on both sides. The spiral side is almost entirely evolute and does not develop a spiral slit. Clear shell material thickens the center of both sides slightly.

Cibicidoides cf. *pseudoperlucidus* (Bykova)

(Pl. II, Fig. 2)

1983 *Cibicidoides* cf. *pseudoperlucidus* (Bykova). Tjalsma and Lohmann: p. 9, pl. 6 , fig. 9

Remarks: since most *Cibicidoides* species are slightly transparent and dull, this species is very characteristic due to its smooth, glossy, white appearance. The test is usually equally convex and perforate on both sides. The spiral side is almost entirely evolute and possesses a short spiral slit. Sutures on both sides are flush with the test surface. The test is also smaller than many other *Cibicidoides.*

Cibicidoides succedens (Brotzen)

(Pl. II, Fig. 1)

1948 *Cibicides succedens* Brotzen: p. 80,pl. 12, figs. 1, 2

1976 *Cibicidoides succedens* (Brotzen). Aubert and Berggren: p. 432, pl. 11, fig. 1

Remarks: a concavo-convex to plano-convex species with large pores on both sides. Sutures are thickened, oblique, and curved on the spiral side. Approximately semi-involute on the spiral side, although this character may vary. Variability in test shape might be due to an attached epibenthic mode of life. In view of this morphological variability, a rather wide taxonomic concept is employed.

Chilostomellacea

Alabaminidae

Alabamina midwayensis Brotzen

(Pl. III, fig. 2)

1926 *Pulvinulina exigua* H.B. Brady. Plummer: p. 150, pl. 11, fig. 3

1948 *Alabamina midwayensis* Brotzen: p. 99, pl. 16, figs. 1, 2

1956 *Alabamina wilcoxensis* Toulmin. Said and Kenawy: p. 152, pl. 6, fig. 18

1959 *Alabamina midwayensis* Brotzen. Nakkady: p. 460, pl. 2, fig. 2

1976 *Alabamina midwayensis* Brotzen. Aubert and Berggren: p. 428, pl. 8, fig. 3

1985 *Alabamina midwayensis* Brotzen. Luger: p. 110, pl. 7, figs. 17, 18

Remarks: convexity of the spiral side is rather variable. In specimens with a clean aperture without sediment infill, an apertural lip as well as a rim erecting from the previous whorl below the aperture are visible.

Valvalabamina depressa (Alth)

(Pl. III, fig. 1)

1850 *Rotalina depressa* Alth: p. 266, pl. 13, fig. 21

1946 *Gyroidina depressa* (Alth). Cushman: p. 139, pl. 58, figs. 1-4

1953 *Gyroidina orbicularis* d'Orbigny. LeRoy: p. 35, pl. 7, figs. 12-14

Remarks: we are uncertain whether Alth's species is the same as ours; the specimens depicted by Cushman (1946) bear great similarity. This species is characterized by its entirely evolute spiral side with slightly raised oblique, curved sutures; the umbilical sutures are almost straight and sometimes slightly incised

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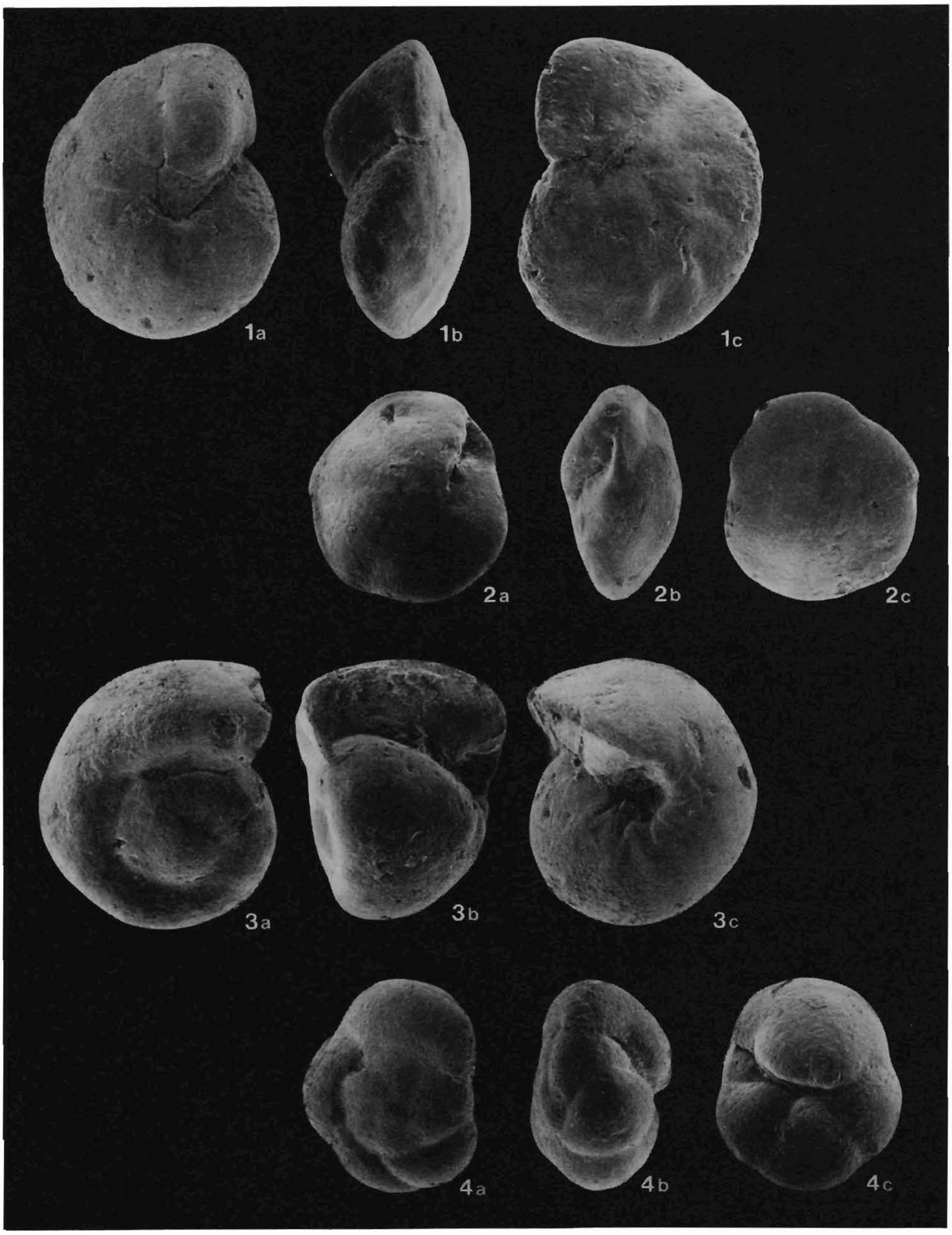
Plate III

Fig. 1 *Valvalabamina depressa* (Alth), sample S 1016
Fig. 2 *Alabamina midwayensis* Brotzen, sample S 1016
Fig. 3 *Gyroidinoides girardanus* (Reuss), sample S 1016
Fig. 4 *Valvulineria? insueta* Cushman and Bermúdez, sample S 1016
All magnifications X 120.

PLATE III



around the umbilicus, which is covered by an umbilical flap in well preserved specimens. The apertural face is inflexed.

Oridorsalidae

Oridorsalis plummerae (Cushman)

(Pl. IV, figs. 5-7)

1926 *Truncatulina tenera* H. B. Brady. Plummer: 146, pl. 9, fig. 5
1948 *Eponides plummerae* Cushman: p. 44, pl. 8, fig. 9
1951 *Eponides plummerae* Cushman. Cushman: p. 52, pl. 14, figs. 20, 23
1953 *Eponides lunatus* (Brotzen). LeRoy: p. 30, pl. 9, figs. 24-26
1956 *Eponides lunatus* (Brotzen). Said and Kenawy: p. 148, pl. 5, fig. 3
1956 *Eponides mariei* Said and Kenawy: p. 148, pl. 5, fig. 2
1956 *Eponides sigali* Said and Kenawy: p. 148, pl. 5, fig. 6
1976 *Eponides plummerae* Cushman. Aubert and Berggren: p. 426, pl. 7, fig. 4
1985 *Alabamina obtusa* (Burrows and Holland). Luger: p. 110, pl. 8, figs. 4, 5
Remarks: we believe this species shows a high degree of morphological variability with respect to size, convexity of both sides, angularity of the margin, and the shape of the sutures. Apertural features (sometimes supplementary apertures visible on the spiral side) point to an assignment of this species to *Oridorsalis* and not to *Eponides* (see also Hauser and Grünig, 1993).

Heterolepidae

Anomalinoides aegyptiacus (LeRoy)

(Pl. V, fig. 3)

1953 *Anomalina aegyptiaca* LeRoy: p. 17, pl. 7, figs. 21-23
1976 *Valvulineria scrobiculata* (Schwager). Salaj et al.: p. 156, pl. 8, figs. 1, 2
Remarks: a flattened bi-umbilicate species; both sides are partially involute, the umbilical side slightly more than the spiral side. In apertural view the periphery is rounded to bluntly acute. The suture between the last two chambers is depressed, the earlier sutures are usually flush, but may also be distinctly raised (see also discussion of *V. scrobiculata*).

Anomalinoides* cf. *aegyptiacus (LeRoy)

(Pl. V, fig. 2)

cf. 1953 *Anomalina aegyptiaca* LeRoy: p. 17, pl. 7, figs. 21-23
Remarks: differs from *A. aegyptiacus* in its larger, more robust and less flattened test, and the higher degree of morphological variability; large plano-convex specimens are also included into this concept. It seems, however, to be intergrading with *A. aegyptiacus*.

Anomalinoides praeacutus (Vasilenko)

(Pl. V, figs. 4-6)

1950 *Anomalina praeacuta* Vasilenko: p. 208, pl. 5, figs. 2, 3
1976 *Anomalinoides praeacuta* (Vasilenko). Aubert and Berggren: p. 430, pl. 9, fig. 2; pl. 12, fig. 5
Remarks: A very distinct species with considerable morphological variability. The spiral side is always semi-involute and may develop a transparent plug which covers the earlier whorls. The sutures on this side are flush to strongly raised and large pores are confined to the the later half of the last whorl. The umbilical side has a distinct irregular plug surrounded by umbilical flaps. The sutures on this side are flush to slightly raised and large pores are evenly distri-

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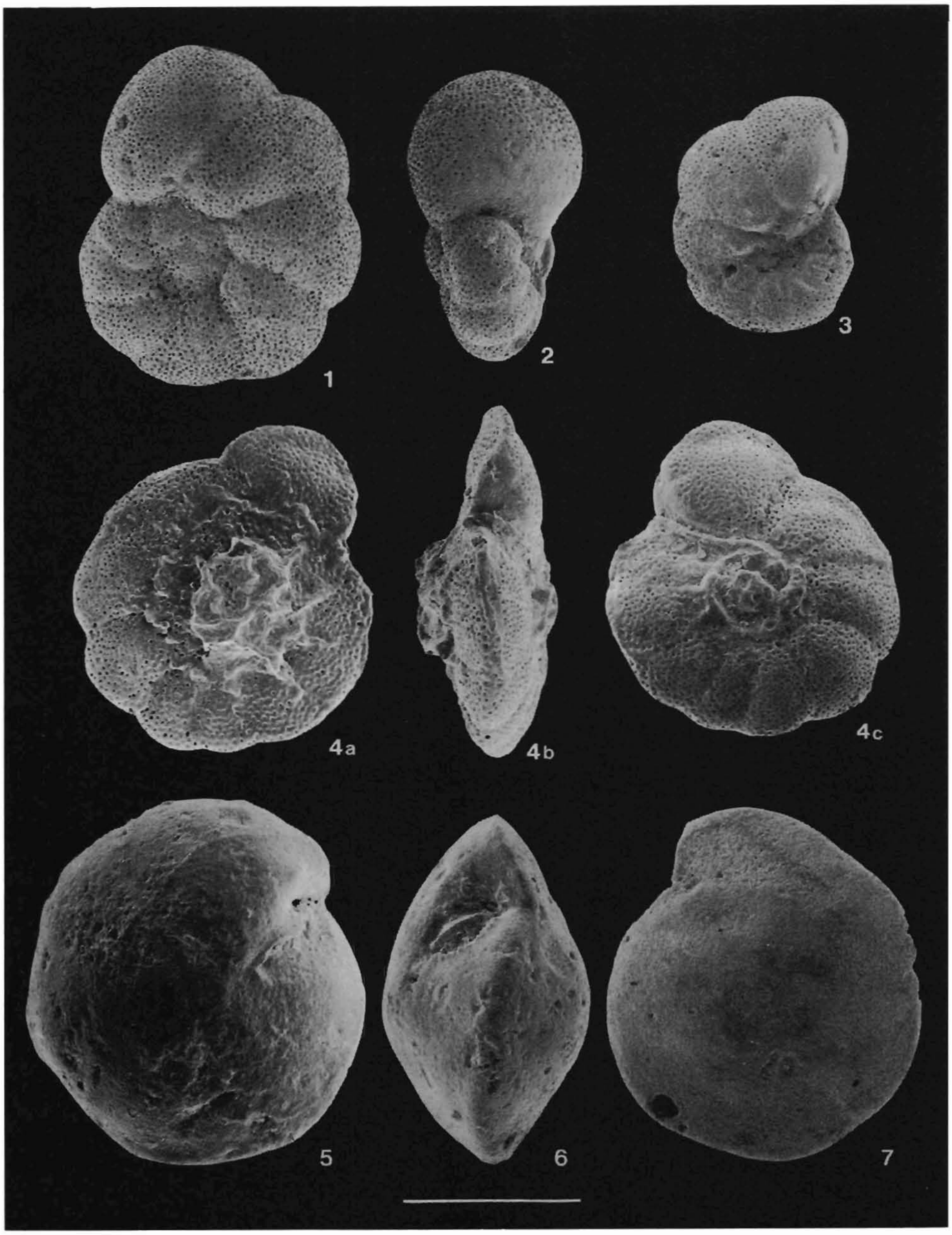
Plate IV

Figs. 1-3 *Valvulineria scrobiculata* (Schwager), sample S 1025
Fig. 4 *Gavelinella? guineana* Petters and Adegoke, sample, S 1028
Figs. 5, 6 *Oridorsalis plummerae* (Cushman), sample S 1006 (X 240)
Fig. 7 *Oridorsalis plummerae* (Cushman), sample S 1039 (X 240)
All magnifications X 120 unless indicated otherwise (bar = 100 μm).

PLATE IV



buted over the entire surface. The aperture is extra-umbilical to peripheral and is covered by a distinct lip.

Anomalinoides zitteli (LeRoy)
(Pl. V, fig. 1)

1953 *Cibicides zitteli* LeRoy: p. 25, pl. 6, figs. 20-22

Remarks: this species has a compressed, bi-umbilicate test. Both sides are slightly evolute. Sutures on both sides are limbate, raised and strongly curved. The periphery is (sub)acute and has a narrow imperforate keel.

Gavelinellidae

Gyroidinoides girardanus (Reuss)
(Pl. III, fig. 3)

1851 *Rotalina girardana* Reuss: p. 73, pl. 5, fig. 34

1953 *Gyroidina girardana* (Reuss). LeRoy: p. 35, pl. 5, figs. 10-12

1956 *Gyroidina girardana* (Reuss). Said and Kenawy: p. 148, pl. 5, fig. 7

1959 *Gyroidina aegyptiaca* Nakkady and Talaat. Nakkady: p. 459, pl. 6, fig. 7; pl. 7, fig. 1

1959 *Gyroidina girardana* (Reuss). Nakkady: p. 460, pl. 3, fig. 1

1976 *Gyroidinoides subangulata* (Plummer). Aubert and Berggren: p. 429, pl. 8, fig. 6

1982 *Gyroidinoides subangulata* (Plummer). Faris: p. 215, pl. 6, figs. 1, 2, 4

1982 *Anomalinoides acuta* (Plummer). Faris (partim): p. 216, pl. 6, fig. 7 (not figs. 8, 10)

1985 *Gyroidinoides girardanus* (Reuss). Luger: p. 110, pl. 8, figs. 2, 3

Remarks: a very distinct plano-convex species. The umbilical side is high conical and has a deep open umbilicus, which may be partly covered by umbilical flaps. The central part of the sutures on this side are slightly incised and bordered by an elevated tapering rim of clear shell material. The sutures on the spiral side are straight and flush to slightly depressed. The chambers on the spiral side are slightly concave and the spiral suture is depressed. The periphery is angular. The aperture may extend from the umbilicus to the periphery, but it may also terminate well before the peripheral margin.

Gavelinella? guineana Petters and Adegoke
(Pl. IV, fig. 4)

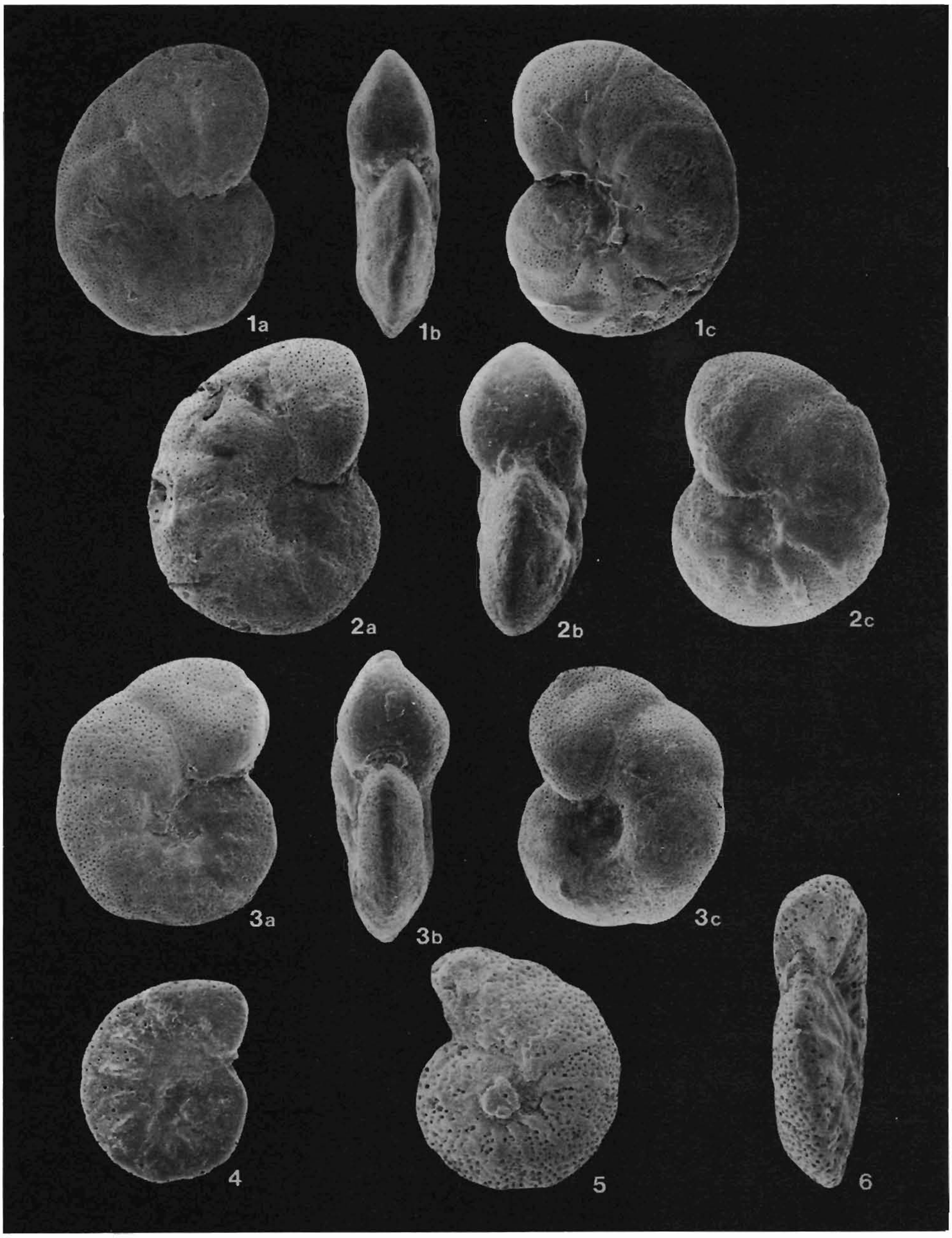
1982 *Gavelinella guineana* Petters and Adegoke. Petters: p. 83, pl. 15, figs. 1, 2

Remarks: a very distinct taxon, referred to as *Eponides elevatus* by Luger (1985), with which it may be related; therefore the tentative generic assignment. The umbilical side is slightly evolute and develops an irregular central plug. The umbilical sutures are depressed to raised near the central plug. The spiral side is entirely evolute and the earlier whorls are decorated by a reticulate pattern which develops from short costae on the inner part of the sutures. Both sides, as well as the sharp margin (in adult specimens) are coarsely perforate.

Plate V

Fig. 1 *Anomalinoides zitteli* (LeRoy), sample S 1044
Fig. 2 *Anomalinoides* cf. *aegyptiacus* (LeRoy), sample S 1006
Fig. 3 *Anomalinoides aegyptiacus* (LeRoy), sample S 1020
Figs. 4-6 *Anomalinoides praeacutus* (Vasilenko), sample S 1025
All magnifications X 120.

PLATE V



- CHAPTER VI -

The differential effect of the P/E boundary event on extinction and survivorship in shallow to deep water Egyptian benthic foraminiferal assemblages

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ABSTRACT

We performed a quantitative study on late Paleocene to early Eocene benthic foraminiferal distribution patterns, in particular focussing on differential effects of the terminal Paleocene extinction event on deep to shallow water ecosystems. Three Egyptian localities were selected, aligned along a paleobathymetric gradient (middle neritic to upper bathyal), to track the progradation of faunal extinction and recovery through the system. First a foraminifera-based paleobathymetric framework of the sections is treated in detail. Two biofacial end-members could be distinguished: a deep water end-member (500-700 m paleodepth), largely consisting of deep-sea taxa and a shallow one (75-100 m). Assemblages from intermediate depths consist of a mixture of both end-members. Comparison with assemblages from many other localities, combined with literature data, revealed wide recognizability of the main assemblages.

Analysis of general faunal and sedimentary characteristics (diversity, dominance, proportion of planktonic foraminifera, PFAR, BFAR, lamination, and organic carbon content) reveals distinct trends of increasing diversity and oxygenation with depth as well as decreasing dominance and productivity. These trends were analogous with the modern situation going from fertile coastal waters to nutrient poor bathyal environments. This pattern is confirmed by benthic foraminiferal morphotype predominance: potentially endobenthic taxa (e.g. *Bulimina*) dominate at intermediate depths, whereas epibenthic taxa are dominant in shallower and deeper environments.

As expected, faunal turnover at the P/E boundary is most prominent at the deepest locality; at the shallow site faunal change is much more gradual, starting earlier, ending later and less severe in terms of the number of extintions. The forcing parameter for the extinctions appears to be oxygen deficiency. Opportunistic low oxygen tolerant shallow water taxa temporarily occupied the ecological vacuum of the deepest locality just after the onset of severe short-term (< 50 kyr) oxygen deficiency at the P/E boundary. Although the shallow water ecosystem was almost as severely affected at the P/E boundary, this did not result in a major faunal turnover. This is related to the capability of many shallow water taxa to cope with highly variable environmental conditions (e.g. in oxygenation and food supply), that apparently typified the shallower parts of the basin.

Early Eocene foraminiferal associations indicate an increase in productivity, especially at the shallower sites. The total paleoenvironmental picture that emerges from our data is complementary to deep-sea studies wherein a reversed ocean circulation is suggested for some time during the early Eocene. We envisage a time of punctuated global warming leading to stronger atmospheric contrasts within the (sub)tropics. Stronger tradewinds resulted in enhanced evaporation and warm saline deepwater formation. At the same time high latitude deep water formation was largely sealed off because of very mild climates at the poles. For a short period ocean circulation would have been minimized, resulting in widespread anoxia until halothermal circulation took over and was in full swing during the early Eocene.

Introduction

The paleoenvironmental perturbation that caused the extinction of many deep-sea benthic foraminifera at the Paleocene/Eocene (P/E) boundary (e.g. Beckmann, 1960; Tjalsma and Lohmann, 1983; Miller et al., 1987; Thomas, 1990b; Katz and Miller, 1991; Nomura, 1991; Thomas, 1992 and references therein) is growing into a well-documented but still poorly understood event. By now it is evident that also other marine as well as terrestrial faunal groups underwent substantial changes (Hooker, 1991; Schneider, 1991; Canudo and Molina, 1992; Koch et al., 1992; Lu and Keller, 1993). Moreover, the abiotic record shows a rather dramatic perturbation as indicated by detailed stratigraphic, geochemical and sedimentological analyses performed by various research groups (e.g. Rea et al., 1990; Kennett and Stott, 1991; Pak and Miller, 1992; Robert and Kennett, 1994).

Much of the effort is devoted to the analysis of deep-sea sequences based on DSDP/ODP material; relatively few papers deal with faunal and geochemical changes across the P/E boundary in shallower water. Recent studies show that although the P/E event is commonly regarded as a deep-sea event, it is also a distinct phenomenon with a similar expression in bathyal continental margin deposits (Kaiho, 1988; Benjamini, 1992; Kaiho, 1993; Molina et al., 1994; Speijer, 1994a). But also shallow neritic sites experienced simultaneous paleoenvironmental perturbations (Gibson et al., 1993; Speijer, 1993; Speijer and Van der Zwaan, 1994a). The main difference between deep water and shallow water ecosystem response is that at shallow water sites the changes proceeded in a more gradual way and the rate of extinction was significantly lower (Gibson et al., 1993; Speijer and Van der Zwaan, 1994a).

A major drawback of many studies is that they often deal with only one isolated locality instead of studying the effects of the P/E boundary event along an environmental gradient. It seems crucial to the understanding of the event to trace the effects throughout the system, for instance along well-constrained bathymetric or latitudinal gradients. In this paper we present quantitative benthic foraminiferal records of a 2 Ma time-slice across the P/E boundary retrieved from three localities, that were arranged along a paleobathymetric gradient (middle neritic to upper bathyal) in the eastern part of the Paleogene Egyptian epicontinental basin. We compare the patterns found with those from 18 other localities in Israel and Egypt (literature data and personal observations), all located on the southern shelf and slope of the former Tethys. In this way we hope to assemble a coherent picture of the progradation of the effects of the P/E boundary event through the system and to constrain in a more precise manner the mechanisms of the faunal turnover.

This paper is divided into two parts. We first discuss distributional patterns of the most common taxa and discriminate six paleobathymetric assemblages. Then we discuss the changes in the composition of the benthic foraminiferal assemblages across the P/E boundary in order to elucidate the paleoecological and paleoenvironmental sequence. We will try to assess extinction selectivity and survivorship along a paleobathymetric gradient; this will provide insight into the sequence of ecosystem destruction and recovery. Next we will attempt to explain this sequence in terms of changes in paleocirculation and paleoproductivity. Finally we will discuss earlier proposed global P/E boundary scenarios in view of these results.

Material and methods

The benthic foraminiferal assemblages were extracted from marine marls and shales of the upper Paleocene to lower Eocene Esna Formation. The sediments of this formation were deposited over vast areas in an epicontinental basin on the gently north-dipping Egyptian paleoshelf (e.g. Beadnell, 1905; LeRoy, 1953; Nakkady, 1957; Said, 1960; Said, 1990d). The Esna Formation laterally grades into more calcareous deposits in the south and southwest (e.g. Ain Dalla Formation near Ain Dalla and Garra Formation in the Aswan-Uweinat area) at the basin margins and near the basinal carbonate platforms of Abu Tartur and Galala (Said, 1960; Barthel and Herrmann-Degen, 1981; Luger, 1985; Bandel and Kuss, 1987; Hermina, 1990). Unfortunately, a marginal facies of the eastern margin of the basin has not been preserved either in Egypt or on the northern part of the Arabian shield, due to Oligocene-Neogene uplift along the Red Sea rift (Said, 1990b; Brown et al., 1989). Nevertheless, the wide distribution and preservation of deposits of this time-slice in other parts of Egypt enable rather detailed basin-wide paleoenvironmental reconstructions.

Paleobotanical and palynological data suggest subtropical to tropical conditions onshore (Aboul-Ela, 1989). Clay mineral composition, the absence of coarse grained terrigeneous clastics and the presence of bauxitic soils indicate prevailing tropical chemical weathering of a denudated North African craton at the time of deposition of the Esna Formation (Hendriks et al., 1990; Strouhal, 1993) This paleoclimatic interpretation is compatible with plate-tectonic reconstructions, wherein North Africa lies within the tropical-subtropical zone, 15° south of its present position (Barron et al., 1981; Smith et al., 1981).

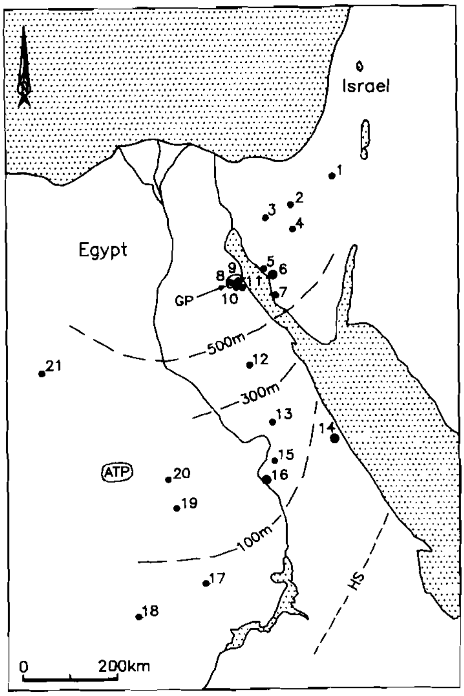

Fig. 1. Provenance of the studied late Paleocene-early Eocene foraminiferal assemblages. Large dots indicate sequences studied in detail; smaller dots are qualitatively investigated for recognition of lateral biofacial distribution. Dashed lines indicate tentative paleobathymetric contour lines. GP and ATP stand for Galala and Abu Tartur carbonate platforms, HS indicates hypothetical shoreline (see text for discussion).
1: Nahal Avdat (Speijer, 1994a), 2*: El Minshera (Ansary and Emara, 1962), 3*: Giddi, 4*: Nekhl (both: Said and Kenawy, 1956), 5: Hamman-Faroun, 6: Wadi Nukhl (Speijer, 1994a), 7: Gebel Ekma, 8: St. Anthony, 9: Gebel Thelmet, 10: St. Paul, 11*: Ezz El Orban (Ansary and Fahmy, 1969), 12: Masak El Sharif, 13: Gebel Qreiya, 14: Bir Inglisi I, 15: Gebel Nezzy, 16: Gebel Oweina, 17: Bir Dungul, 18: Bir Abu El Husein, 19: Darb Gaga, 20: Pyramidal Hill (17-20: see also Luger, 1985), 21*: Maqfi (LeRoy, 1953). Paleobathymetric interpretations of localities marked by an * are solely based on literature data.

The three localities (Fig. 1) were sampled during several field trips. Samples S 732-741 from the Wadi Nukhl section (or "Abu Rudeis" section in Speijer, 1994a), in the Western Sinai, were collected during a field trip in 1984; the P/E boundary interval (S 1371-74) was resampled in more detail (25 cm intervals) during a field trip in 1993. The Bir Inglisi I section, near Quseir at the Red Sea coast, was also sampled (S 1010-1046) during the latter field trip. In 1992, a team of Swedish geologists from Göteborg sampled the Gebel Oweina section, situated along the Nile Valley near Esna (sample notation in metres above the Cretaceous-Tertiary boundary). Unfortunately, a box with some of their samples was stolen before shipping, including the sample nearest to the P/E boundary.

Samples from these three localities were treated quantitatively; in addition, benthic foraminiferal assemblages as well as literature data from many other localities in Egypt (Fig. 1) were qualitatively examined, in order to investigate the lateral distribution of the assemblages encountered in the three main sections.

To extract the foraminifera, the samples were dried in a stove at 60°c for at least 24 hours. From each sample, 50 gr of dry rock was soaked in a 0.35 mole/l Na_2SO_4 solution. After disintegration it was washed over three sieves of 595, 125 and 63 μm mesh size, respectively. If necessary, this procedure was repeated until the residue was free of sediment aggregates. Some levels in the Gebel Oweina and Bir Inglisi I sections did not yield any calcareous foraminifera, due to severe carbonate dissolution (e.g. S 1040-43). Only the 125 μm size fraction was used for quantitative benthic foraminiferal analysis. With the aid of an Otto microsplitter a suitable split, containing approximately 200-300 benthic specimens, was obtained. From this split the proportion of planktonic foraminifera (%P) and foraminiferal numbers (N/gr = number of specimens per gram dry weight, both for benthic and planktonic foraminifera) were calculated. Planktonic and benthic foraminiferal accumulation rates (PFAR and BFAR; $N/cm^2/kyr$) were calculated from foraminiferal number counts, multiplied with estimated average sedimentation rates and with the specific weight of the sediment (approximately 2 gr/cm^3), assuming continuous sedimentation throughout the sections.

All benthic foraminifera in the split were picked and permanently stored in a Chapman-slide. Most specimens were, whenever possible, identified at species level although sometimes placed in open nomenclature. Papers by LeRoy (1953), Aubert and Berggren (1976), Tjalsma and Lohmann (1983) and Van Morkhoven et al. (1986) provided the main taxonomic basis, although numerous other papers were used as well. The initial dataset, containing about 200 different taxa, was condensed to only 56 most common ones; rare taxa were assembled into higher order lump categories. Diversity of the benthic assemblages, expressed as Fisher-α values (Murray, 1991), is based on the initial dataset. We performed a statistical analysis on the frequency data by means of R-mode Cluster Analysis (Unweighted Pair Group Method) and a standardized Principal Component Analysis (Davis, 1985). The computer program used, Pattern Recognition (PATREC), was developed at the Geology Department, Utrecht University. A BALANC routine (Drooger, 1982) was used to surpress possible squeeze effects of highly abundant taxa.

Lithology, stratigraphy, and age model

The Esna Formation is predominantly composed of grey, green or brownish marls and shales (Fig. 2). In Gebel Oweina and Bir Inglisi I the sediments generally are laminated, and in Bir Inglisi I also strongly bituminous. In Wadi Nukhl the sediment is usually not laminated except for a dark sapropelitic bed that marks the P/E boundary; this bed is distinctly laminated (light and dark coloured laminae) and evidently has a high organic carbon content (a.o. abundant fish remains). In Gebel Oweina such a bed was not noticed (B. Schmitz, pers. commun., 1993), but also in Bir Inglisi I we noted a somewhat similar bed, albeit less dark and lacking distinct light-dark laminae. All three sections show a more calcareous sandy bed just above the P/E boundary, whereby much of the sandy character is caused by abundant foraminifera in the sand size class.

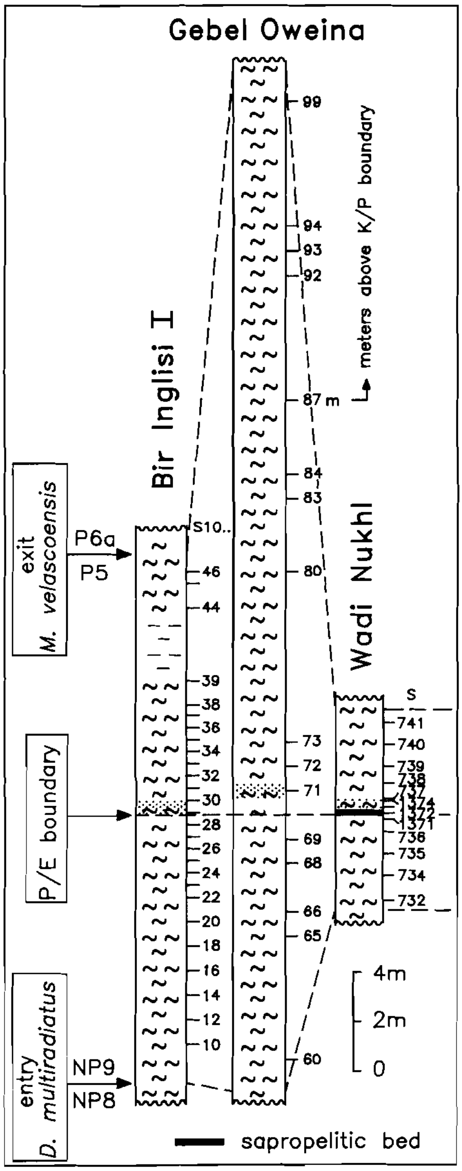

Fig. 2. Lithology and stratigraphy of the studied sequences. The levels of the entry of *Discoaster mulitradiatus* and the exit of *Morozovella velascoensis* bracket the studied late Paleocene-early Eocene interval. The P/E boundary is recognized by the first common occurrence of *Globanomalina luxorensis* (all three sections), the extinction of deep-sea benthic foraminifera (only in Gebel Oweina and Wadi Nukhl) and the carbon isotope excursion (Gebel Oweina: Charisi and Schmitz, 1994; Bir Inglisi I: Schmitz, pers. commun., 1993).

In each section the entry of *Discoaster multiradiatus* (NP8/NP9 zonal boundary; Martini, 1971) marks the base of the interval as discussed in this paper, whereas the exit of *Morozovella velascoensis* (P5/P6a zonal boundary; Berggren, 1994) marks the top. Correlation based on these taxa is preferred, because both are very common in Egypt, and generally accepted as reliable biomarkers for correlations in (sub)tropical areas (Martini, 1971; Aubry et al., 1988; Berggren and Miller, 1988). The exit of *Globanomalina pseudomenardii* (P4/P5 zonal boundary; Bergrren, 1994) is not used as an alternative correlation tool, because of its rareness in the sections studied. The P/E boundary can be pinpointed by a combination of markers: the extinction of several benthic deep-sea taxa, the first common occurrence of *Globanomalina luxorensis* (Speijer and Samir, 1994), and the negative spike occurring in the $\delta^{13}C$ record (Kennett and Stott, 1991; Aubry et al., 1994).

Numerical ages are based on the new Paleogene time-scale (see Fig. 1 in Berggren, 1994; adopted from Berggren et al., 1994). The age of the P5/P6a zonal boundary (54.3 Ma) is retrieved directly from this time-scale; the age of the NP8/NP9 zonal boundary (56.3 Ma) is arrived at through correlation via the magnetic polarity scale (base C25n; Aubry et al., 1988). The age of the P/E boundary is approximated at 55.3 Ma, since the NP9/NP10 zonal boundary (55.0 Ma) is somewhat above the P/E boundary (Berggren et al., 1994). This age estimate is in good agreement with the revised age (55.33 Ma) of the initiation of the isotopic excursion in the ODP Site 690B sequence (Robert and Kennett, 1994).

Calculated sedimentation rates show considerable variation: lowest (4 m/Ma) in Wadi Nukhl, followed by Bir Inglisi I (11 m/Ma). In both areas the average sedimentation rate is constant over the entire timeslice studied. In Gebel Oweina average sedimentation rate increased from 12 m/Ma during the latest Paleocene to 31 m/Ma during the earliest Eocene. The estimated sedimentation rate of Wadi Nukhl differs significantly from a previous estimate (16 m/Ma; reported in Speijer, 1994a). This is due to the longer timespan assigned to the new Zone P5 (formerly Zones P5-P6a; Berggren and Miller, 1988), and due to the fact that the entry of *Morozovella subbotinae* is not longer used as a biostratigraphic marker because of its presumed diachronous distributional pattern (Berggren et al., 1994).

Faunal results

On the basis of the initial quantitative dataset, Fisher-α diversity values were calculated for all samples (Fig. 3). Diversity is highest in Wadi Nukhl, intermediate in Gebel Oweina and lowest in Bir Inglisi I. At all localities diversity decreased in the uppermost Paleocene, reaching minimum values at, or just above, the P/E boundary. Subsequently, diversity gradually increased, but remained below Paleocene values. In Bir Inglisi I the pattern of diversity decrease and increase is rather gradual and smooth; in the other sections it is much more irregular. Dominance curves (Fig. 3) essentially mirror the diversity patterns. Dominance is highest in the basal Eocene of each section; in Gebel Oweina, where a potential P/E boundary event bed has not been sam-

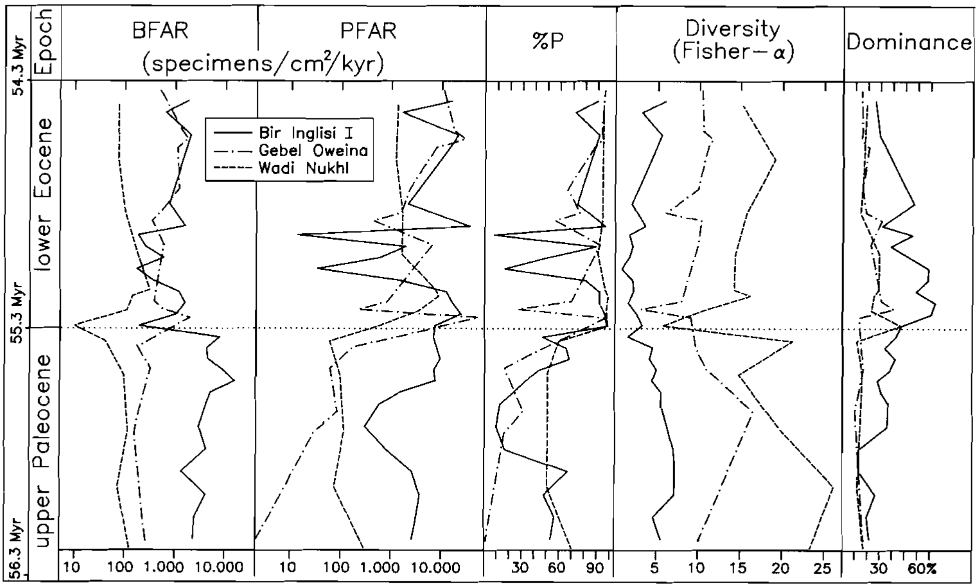

Fig. 3. General faunal characteristics (data in Table 3) for the three sections plotted against a time axis; NP8/NP9 zonal boundary at 56.3 Ma, P5/P6 zonal boundary at 54.3 Ma (time scale based on Berggren et al., 1994, see discussion in text). Note that a P/E event bed is not present in the Gebel Oweina record (wide sample spacing), resulting in deviating patterns above that level (for discussion see text).

pled, the lowest Eocene sample yields a rather low dominance value. Highest dominance and lowest diversity values are here found in the next higher sample, thus clearly above the P/E boundary.

The condensed dataset contains only the 56 most common taxa; 54 of these were observed in at least one of the Paleocene samples. Of these most common taxa, 39 occur in Wadi Nukhl, 38 in Gebel Oweina and 30 in Bir Inglisi I. Only 44 out of the 56 most frequent taxa occur in at least one of the Eocene samples (of these 44, 39 occur in Wadi Nukhl, 35 in Gebel Oweina and 26 in Bir Inglisi I). The relative frequencies of the 56 taxa (Table 1) are displayed in Figure 4. If we compare the three sections, some striking differences can be noted. In the Wadi Nukhl section, *Gavelinella beccariiformis* is the dominant taxon in all Paleocene samples, whereas *Nuttallides truempyi* dominates the Eocene assemblages except in the two basal Eocene samples. Apart from the distinct change observed in the two samples overlying the P/E boundary, frequencies of most taxa are fairly constant; greatest frequency variation is seen in *Bulimina farafraensis*. All dominant taxa are biconvex and have a test morphology suggestive for an epibenthic mode of life (Corliss, 1985; Corliss and Chen, 1988; Corliss, 1991; but see Barmawidjaja et al., 1992). This contrasts strongly with Gebel Oweina, where most samples are dominated by a buliminid (e.g. *Bulimina callahani, B. farafraensis, B. midwayensis* and *Turrilina brevispira*). Judging by their morphology, most of these taxa could have had an endobenthic mode of life (Corliss, 1985; Corliss and Chen, 1988; Corliss, 1991). In Gebel Oweina, frequency patterns fluctuate rather strongly, another feature in contrast with the patterns of Wadi Nukhl. Also in Bir Inglisi I relative frequencies of many taxa strongly fluctuate. Only three species (*Anomalinoides aegyptiacus, A.* cf. *aegyptiacus* and *Valvulineria scrobiculata*) dominate all but two samples; thus, as in Wadi Nukhl, the assemblages are dominated by taxa with a test morphology suggesting an epibenthic mode of life.

Benthic foraminiferal paleobathymetry

It is evident from the paleogeographic setting (Fig. 1; cf. Fig. 3B in Luger, 1988 and Fig. 24.6 in Said, 1990d) that during late Paleocene-early Eocene times the sections were aligned along a bathymetric gradient. The Bir Inglisi I section was the shallowest locality, whereas the Wadi Nukhl section was located farthest offshore. This picture is supported by the distribution of typical deep water taxa, which are almost exclusively confined to Wadi Nukhl. In that section the most common taxa are cosmopolitan deep-sea species as *Gavelinella beccariiformis, Nuttallides truempyi, Cibicidoides hyphalus* and *Pullenia coryelli* (Tjalsma and Lohmann, 1983; Van Morkhoven, 1986). In combination with some taxa with a shallower distribution, this would indicate an upper bathyal position (about 500-700 m; Speijer, 1994a). Assemblages from Gebel Oweina are predominantly composed of middle-outer neritic (about 150-200 m) taxa (e.g. *Spiroplectinella* spp., *Bulimina* spp. and *Cibicidoides* spp.; cf. Saint-Marc and Berggren, 1988), together with a minor proportion of bathyal taxa (e.g. *Angulogavelinella avnimelechi*). Species known from inner neritic environments elsewhere (Aubert and Berggren, 1976; Luger, 1985; Saint-Marc and Berggren, 1988) are rare in Gebel Oweina, which constrains the upper depth limit. Assemblages from Bir Inglisi I contain diagnostic inner-middle neritic (about 50-100 m) taxa (*Frondicularia phosphatica, Lenticulina* spp, and *Gavelinella? guineana*; Aubert and Berggren, 1976; Luger, 1985; Saint-Marc and Berggren, 1988); bathyal taxa are entirely absent.

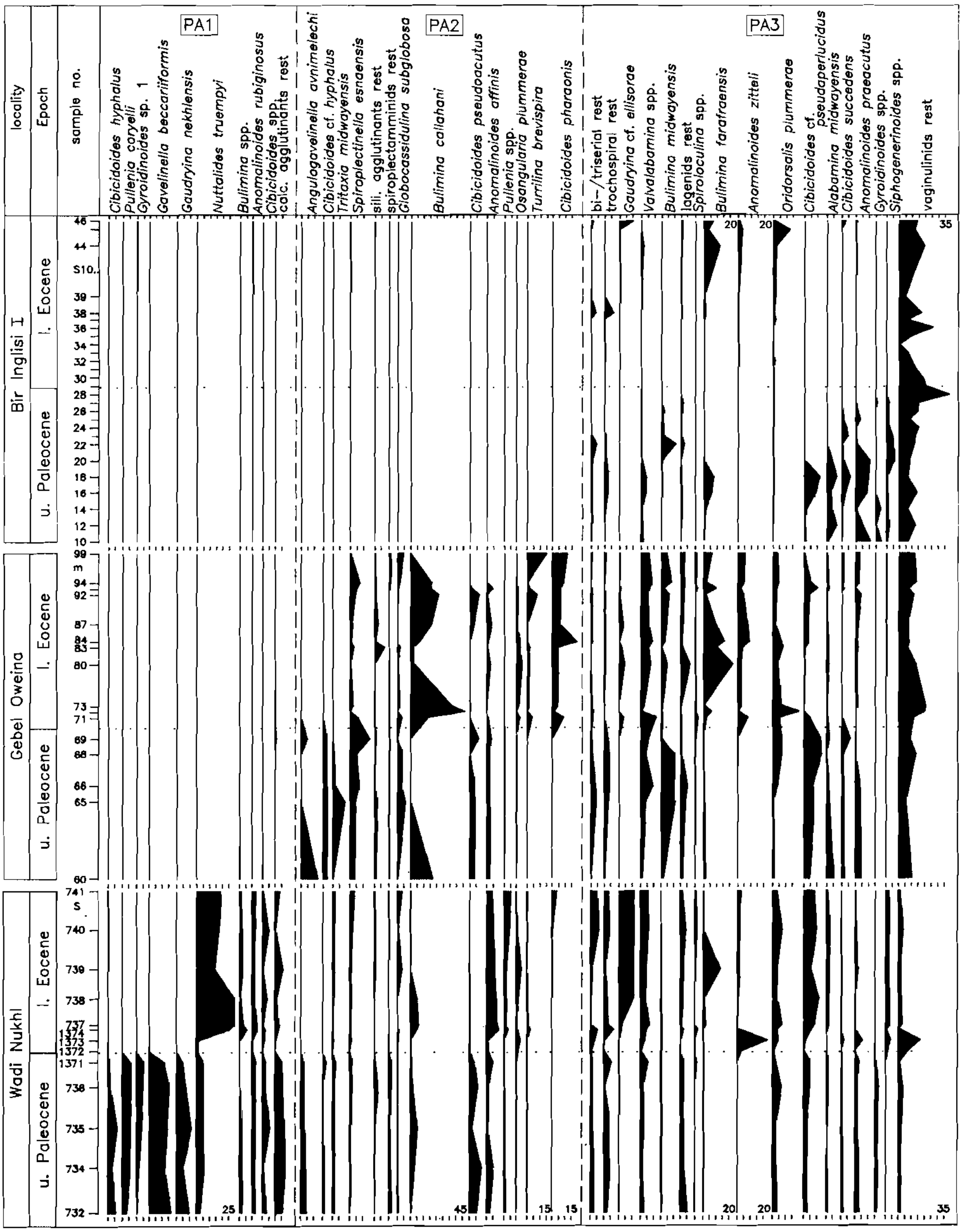

Fig. 4. Frequency patterns of taxa from the condensed data set (Table 1); samples are spaced along a time axis (see caption of Fig. 3). Taxa are arranged according paleobathymetric distribution: PA 1 (upper bathyal) to PA 6 (middle neritic). Note the extinction of several very common deep-sea taxa (PA 1) in Wadi Nukhl at the base of the sapropelitic P/E bed and their temporal replacement by neritic taxa of PA 5-6. The range of *F. phosphatica* is not quantified due to its large size. Its (local) extinction is an excellent field marker to delineate the P/E boundary in the Bir Inglisi area.

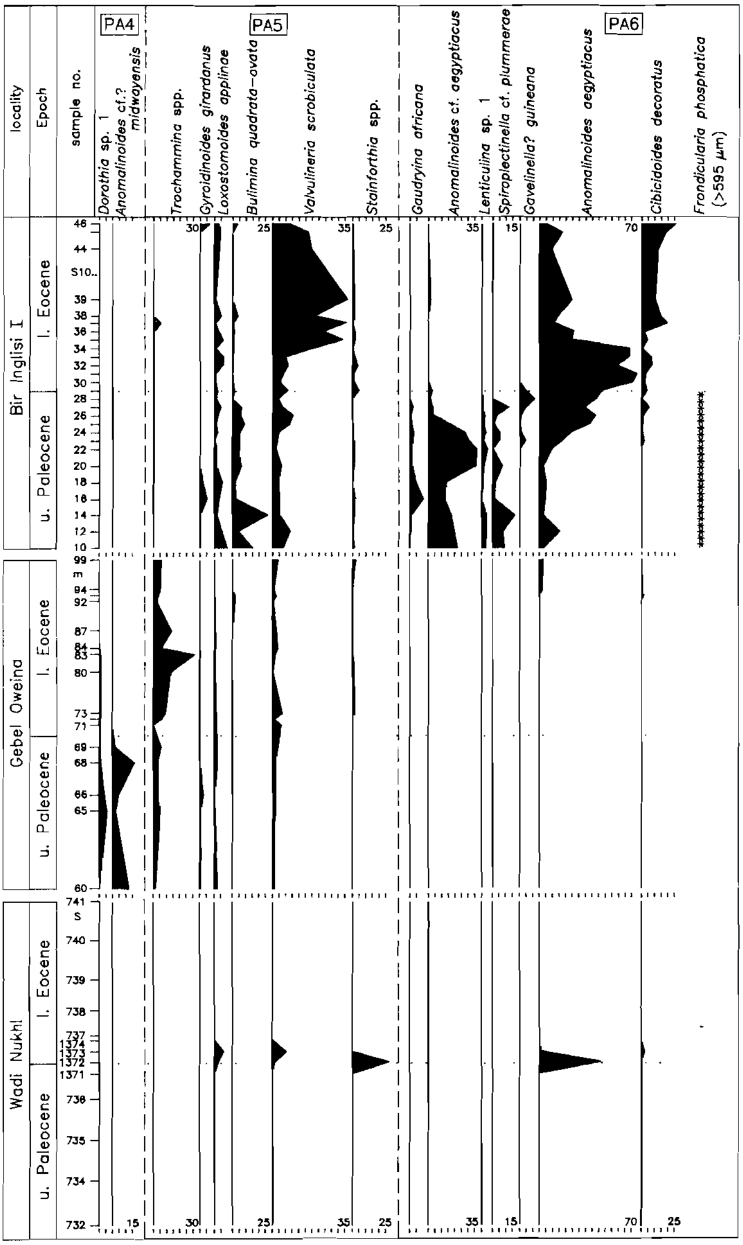

Fig. 4. (Continued)

In Figure 4 the taxa are arranged according to their stratigraphic presence in the three sections, from deepest to shallowest locality. In this way six paleobathymetric assemblages (PA) can be discriminated (compare Table 2), assuming that the distri-

Table 1. Frequency data of the 56 most common taxa of the condensed dataset (Wadi Nukhl and Gebel Oweina).

Sample Nukhl / Oweina	732	734	735	736	1371	1372	1373	1374	737	738	739	740	741	60	65	66	68	69	71	72	73	80	83	84	87	92	93	94	99
Cibicidoides hyphalus	5.7	3.1	6.9	1.7	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pullenia coryelli	3	6.3	5.6	8.9	6.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyroidinoides sp. 1	0	1.6	3.5	4.8	5.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gavelinella beccariiformis	17.2	12	13.9	15.6	11.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaudryina nekhlensis	9.8	4.7	11.3	6.9	4.5	0	0	0	0	0	0	0	0	0	0	0	0.9	0	0	0	0	0	0	0	0	0	0	0	0
Nuttallides truempyi	2.4	5.8	4.3	3.9	5	1	1.4	25.1	28.8	29.2	13.9	17.1	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bulimina spp.	1.7	2.6	0.4	0.4	0	0	0	5.4	2.7	0.4	2.6	1	1.6	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides rubiginosus	2.4	2.1	2.6	1.3	3	0.5	0.5	3.9	3.8	1.7	1.3	2.4	3.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0
Cibicidoides spp.	3	1	5.6	2.2	2.5	0	1.4	2	0.4	3.8	0.4	4.9	0.8	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0
calc. agglutinants rest	4.4	2.8	3	3.9	2	0	0	0	0	0	0	0	0	12.8	0	0.4	0	4.7	0	0	0	0	0	0	0	0	0	0	0
Angulogavelinella avnimelechi	1.3	1	0	0	2.5	0	0	0	0	0	0	0	0	3.4	3.2	3.5	2.2	2.9	0	0	0	0	0	0	0	0	0	0	0
Cibicidoides cf. hyphalus	2	0.5	1.3	0.9	2.5	0	1	0	0	0.8	1.3	1.5	1.6	0.4	9.2	2.2	1.3	0	0	0	0	0	0	0	0	0	0	0	0
Tritaxia midwayensis	5.7	8.4	6.9	6.1	5.4	0	0.5	2.5	3.4	1.3	6.1	0.5	3.6	0	0.5	0	0	1.1	0	0	0	0	0	0	0	0	0	0	0
Spiroplectinella esnaensis	0	1.6	0.9	1.7	2	0	1.4	0.5	1.1	0.8	1.3	2	3.6	3.8	4.1	7.1	4.9	15	5.6	0	2.5	0.5	2.6	0.7	1.5	3.9	5	7.4	0.5
sili. agglutinants rest	0	0.5	0.4	3	1	0	0	0	0	0	1.3	0	0.4	0.9	2.3	0.4	0.4	1.1	0	0	0.5	0	7.1	0.7	2.8	0.9	0.4	0.4	0
spiroplectamminids rest	1.7	2.8	0.4	2.2	2	0	0	0.5	0.4	0	0	0.5	0	0.4	0.5	0	0.9	0.4	0.5	0	0	0	0.4	0	0	0	0.8	0.9	1.8
Globocassidulina subglobosa	0.7	0.5	0	0	0	0.5	0.5	1	0	0.4	3.5	0.5	3.6	0	6	3.1	3.6	0	3.3	0	1.5	0	1.9	0	0	0	0.4	1.3	4.6
Bulimina callahani	0.3	3.1	5.2	1.7	0.5	0.5	0	4.9	6.4	5.1	0	1	0	17.1	0	0	0.4	0	13	41.3	31	2.7	1.9	6.4	15.6	21.1	15.1	16	0
Cibicidoides pseudoacutus	5.4	8.9	1.7	6.1	3.5	0.5	1	0.5	0.8	0	0	0.5	0	3.8	4.1	4	0	6.6	0	0	0.5	0	0	0	2.8	7	1.3	0	0
Anomalinoides affinis	2.4	5.2	0.9	1.3	5	1.5	1	9.4	8	6.8	6.9	4.9	4.4	2.6	3.2	3.1	2.2	3.3	0.9	0	0	2.7	0.4	0.7	3.7	0.4	4.6	0.4	0
Pullenia spp.	1.3	0.5	1.3	0	0	0	0	3	1.5	1.7	1.7	3.9	5.2	0	0.9	0.4	0	0.4	0	0	0	0	0	0	0	0.4	0.8	0	0
Osangularia plummerae	0	0.5	0	0	0.5	1.5	3.3	1	0.4	1.7	4.3	0.5	0.4	0	1.4	0	0	0	2.8	0	2	4.5	2.6	3	0.9	1.3	1.7	0	0
Turrilina brevispira	0	0.5	0.4	0	0	0	0	2.5	1.1	1.3	0	0	0.8	0	0	0	0	0	3.7	0	1.5	0.5	1.9	0	0.3	7.5	1.7	0	15.1
Cibicidoides pharaonis	0	0	0	0	0.5	0	0	0	0	0	0	0.5	3.6	0	0	0	0	0	8.8	1	4	4.5	4.5	18.7	5.8	6.1	6.3	8.7	11.5
bi-/triserial rest	2.7	1.6	0.4	0.9	1.5	1	3.3	5.4	0.4	0.4	1.3	6.3	4.4	0.4	4.1	4	1.3	0.7	1.4	1.9	1	0.9	0	1.1	0.3	1.3	0.8	0	0.9
trochospiral rest	2.4	4.7	5.6	0.4	5.9	0	0.5	7.4	3.4	2.1	1.3	4.4	3.2	0.4	2.8	4.4	4	2.9	0	0	0	1	1.1	0	0.6	0.9	0	0.4	1.4
Gaudryina cf. ellisorae	0	0	0	0	0	0	0.5	2	2.3	11	12.6	9.8	12.1	0	0	0	0	0	3.3	0	0	4.1	1.9	0	3.4	0.4	1.3	0.4	0.5
Valvalabamina spp.	2.7	1	3	2.2	5.9	0.5	3.3	4.4	6.8	3.8	4.3	5.9	6	1.3	3.7	9.3	3.6	5.8	11.6	0.5	2.5	7.2	5.6	9	6.1	5.3	6.7	8.2	6
Bulimina midwayensis	0.3	1.6	0.9	2.2	0.5	0.5	1.4	1	0.4	2.1	1.3	0	0	1.7	11	9.7	10.3	0.4	1.4	0.5	1	4.5	0.4	3	4.3	6.1	1.7	7.8	4.6
lagenids rest	5.7	2.6	1.7	3	2.5	0	0.5	2.5	1.1	2.5	1.7	4.4	1.6	1.3	3.7	5.3	0.9	1.1	0.9	0	0.5	7.2	1.5	1.1	1.8	2.6	2.5	2.6	3.2
Spiroloculina spp.	0	0	0.4	0	1.5	0	0	2.5	0	0.4	0	2	0.8	0	0.5	0.9	0	0.7	2.3	0.5	0.5	0	0	0	0	0	1.7	0.9	1.4
Bulimina farafraensis	0.3	0	0	0	0.5	0	0	0.5	1.9	0.8	13	0.5	0	1.7	0.9	0.4	0	0	1.9	5.8	0	22.2	10	15.7	9.2	1.3	9.7	2.2	6.4
Anomalinoides zitteli	0	0	0	0	0	3	22.9	0.5	0	0.4	1.7	0	2.8	0	0	0	0	0	7.4	0.5	2.5	2.3	3.3	8.6	7.4	4.4	2.1	4.8	5.5
Oridorsalis plummerae	3.4	3.1	2.2	8.9	2.5	1	4.3	3.4	7.2	3.8	3.5	7.3	3.6	1.3	0.5	3.5	6.7	6.9	5.1	19.9	6.5	3.2	7.4	6.4	2.1	2.6	2.9	4.3	3.2
Cibicidoides cf. pseudoperlucidus	2.4	3.1	2.2	4.8	5	0	1.4	5.9	8.3	11.9	5.2	10.2	8.1	4.3	8.3	6.6	13.5	12.8	4.2	0	0	0	1.1	3.7	3.1	3.9	10.5	4.8	0.5
Alabamina midwayensis	1.3	1	0.9	1.7	2	0.5	0	1	2.3	2.1	1.7	3.4	0.8	5.6	1.8	1.8	0	2.2	0.9	0	0	1.8	0.7	0.7	0.9	0.4	1.7	1.7	0.5
Cibicidoides succedens	2	0	0	0	0	0	2.4	0	0.4	0.8	1.3	0	0	2.1	0	0	1.3	6.6	0.5	0	0	0	0.4	0	0.3	0	1.7	1.3	1.4
Anomalinoides praeacutus	3.4	1.6	2.2	1.3	3	0	5.7	0	0.8	0	2.2	0.5	0.4	4.7	4.1	4	0.4	0	0.9	0	1.5	0.5	1.9	1.1	1.8	4.4	0	2.6	3.2
Gyroidinoides spp.	1.3	2.1	1.7	2.6	1	0	0	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphogenerinoides spp.	0	0	0	0	0	1.5	3.8	0.5	3	1.3	3	0.5	2.8	0	0	0	0	0	0.5	0	0.5	0	0.4	0	0.3	0.9	0.8	0	0
vaginulinids rest	1.7	1.6	2.2	3.5	1	7.4	16.7	0	3	1.3	1.3	3.4	1.2	10.3	5.5	8	13	8.4	11.6	19.9	20.5	12.7	6.3	7.9	7.1	11.4	7.1	13.4	11.9
Dorothia sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	4	1.3	0.7	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides cf.? midwayensis	0	0	0	0	0	0	0	0	0	0	0	0	0	12.4	2.3	4.4	16.6	2.2	0	0	0	0	0	0	0	0	0	0	0
Trochammina spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1.3	5	3.1	3.1	5.8	0	6.3	9	13.1	31.2	5.6	13.8	2.6	3.4	5.2	6
Gyroidinoides girardanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9	0.9	2.7	0.4	0.4	0	0	0	0	0	0	0	0	0	0	0
Loxostomoides applinae	0	0	0	0	0.5	3	7.1	0.5	0	0	0	0	0	2.6	0.5	0.4	2.7	2.2	0.9	1	1	1.4	0.4	1.1	0.6	0.4	0.8	0.4	0.5
Bulimina quadrata-ovata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.4	0.9	0.4	0.7	0	0	0.5	0.5	0.7	0.4	0	1.8	2.1	0	0.5
Valvulineria scrobiculata	0	0	0	0	0	1.5	10.5	0.5	0	0	0	0	0	1.7	1.8	2.2	2.2	4	6.5	1	7.5	0.5	2.2	4.1	3.4	0.4	2.5	0.9	4.1
Stainforthia spp.	0	0	0	0	0	27.2	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	1.5	1.8	0.4	0	0	0	0	0.4	2.3
Gaudryina africana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides cf. aegyptiacus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lenticulina sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spiroplectinella cf. plummerae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gavelinella? guineana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides aegyptiacus	0	0	0	0	0	46.5	1.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.2	2.8
Cibicidoides decoratus	0	0	0	0	0	0.5	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.3	0.4	0
No. specimens	297	191	231	231	202	202	210	203	264	236	231	205	248	234	218	226	223	274	215	206	200	221	269	267	326	228	238	231	218
No. taxa in non-condensed dataset	59	53	49	42	48	21	31	42	42	42	41	45	43	32	42	43	33	34	28	13	26	30	33	23	36	34	36	33	32

butional patterns have paleobathymetric meaning:

PA 1: containing upper bathyal taxa confined to Wadi Nukhl;

PA 2: an upper bathyal-outer neritic assemblage containing taxa occurring both in Wadi Nukhl and Gebel Oweina;

PA 3: containing taxa without any clear paleobathymetric preference and present in all sections;

PA 4: a shallower, outer neritic assemblage consisting of taxa confined to Gebel Oweina;

PA 5: containing neritic taxa confined to Gebel Oweina and Bir Inglisi I;

Table 1. (Continued) Frequency data of Bir Inglisi I

Sample Inglisi	1010	1012	1014	1016	1018	1020	1022	1023	1024	1025	1026	1027	1028	1029	1030	1031	1032	1033	1034	1035	1036	1037	1038	1039	1044	1045	1046
Cibicidoides hyphalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pullenia coryelli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyroidinoides sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gavelinella beccariiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaudryina nekhlensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuttallides truempyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bulimina spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides rubiginosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cibicidoides spp.	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
calc. agglutinants rest	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Angulogavelinella avnimelechi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cibicidoides cf. hyphalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tritaxia midwayensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0
Spiroplectinella esnaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sili. agglutinants rest	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
spiroplectammids rest	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Globocassidulina subglobosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bulimina callahani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cibicidoides pseudoacutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pullenia spp.	0	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osangularia plummerae	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turrilina brevispira	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cibicidoides pharaonis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
bi-/triserial rest	0.5	0.9	0.4	0	0	1.1	4	0.8	0	0.5	0	0	0	0	0	0	0	0.7	0.5	0	0	0	3.5	0	0	0	1.6
trochospiral rest	0	0	0.9	2.4	2.9	1.4	0.2	0.8	0	0.5	0	0	0	0.4	0	0	0	0	0	0	0.4	0	6.6	0	0.8	0.4	0
Gaudryina cf. ellisorae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0.8	0.4	10.2
Valvalabamina spp.	1.9	0.9	0.9	3.6	3.8	0.7	0	0	0.5	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Bulimina midwayensis	0	0	0	0	0	0.7	11.1	2	1.9	0.9	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
lagenids rest	0	0.4	1.3	1.6	1.3	0	2.5	0.8	0.5	0	1.2	1.4	0.3	0	0.2	0	0.4	0	0	0	0	0	0	0	0.8	1.2	0.8
Spiroloculina spp.	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0.4	0.7	0.7	0.9	0.4	0	0	0	0	0.4	0	0.4	0	0
Bulimina farafraensis	0	0	1.3	6	7.5	0.4	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0	1.3	0.5	12	3.1	7
Anomalinoides zitteli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	2.4	3.1	1.2
Oridorsalis plummerae	0	0	0	0.8	0.8	0	0	0.4	0	0	0	0	0	0.4	0.2	0.3	1.3	0	0	0	0	1.7	0.4	1.4	2.4	12.5	1.6
Cibicidoides cf. pseudoperlucidus	1.4	0.4	1.7	8.8	12.1	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alabamina midwayensis	0.9	7.3	3.8	3.2	7.5	3.9	0.2	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4
Cibicidoides succedens	0.5	0	0.4	2.8	6.3	1.4	0.2	4.5	3.3	0.9	1	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	2.9
Anomalinoides praeacutus	11.2	5.1	0.4	8.4	9.6	10.6	0.7	0.4	0	3.7	1.7	0.7	0	0	0	0	0	0	0	0	0	0	0	0	0.8	0	1.2
Gyroidinoides spp.	4.2	0.4	3.8	0	0	0.4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphogenerinoides spp.	0.5	2.6	1.3	1.2	0.4	5.7	5.7	4.9	2.3	1.4	1.7	2	0	0.9	0	0	0	0	0	0	0.8	0	0.4	0.5	0	0	0
vaginulinids rest	7	12.4	6.4	13.5	6.3	7.8	11.6	12.2	15	7.9	14.1	14.3	38.6	20.1	18.1	13	9.6	6.6	0	9.3	25.8	6.2	16.7	4.3	19.3	11.7	13.9
Dorothia sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides cf.? midwayensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trochammina spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0.4	0.8	5.4	0	0	0.4	0	0
Gyroidinoides girardanus	0.5	0.4	0.4	5.6	2.5	0.4	0.2	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	7
Loxostomoides applinae	9.8	5.6	2.1	3.6	6.3	1.8	2	0	2.3	1.4	2.4	4.8	1.4	2.2	0.9	1	6.5	6.9	0.9	6.6	3.4	0.8	5.3	1	4	4.3	2.9
Bulimina quadrata-ovata	15	4.3	26.4	2.8	2.1	6.7	5	5.7	5.8	8.9	6	6.5	0	1.3	0.2	0	0.4	0	0	0.4	1.3	0.4	4	0	0.8	0	3.3
Valvulineria scrobiculata	7.9	13.2	5.5	5.2	4.6	6.7	2.5	3.7	4.7	13.1	15.5	7.2	4	11.2	5.2	7.8	11.3	9.5	29.9	53.1	38.1	55.6	31.3	56.7	29.3	27	13.5
Stainforthia spp.	1.4	0	1.3	2	0	1.1	2	1.2	0.5	0.9	0	0	0	4.9	1.2	0.7	3.9	1.5	0	1.8	1.7	0	1.3	0	1.2	0.8	0.4
Gaudryina africana	0.5	0	0.9	10	4.6	1.8	1.2	2.4	2.8	1.4	0.7	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides cf. aegyptiacus	22	19.7	17.4	12	13.3	35.7	36.6	30.6	27.6	16.4	3.8	3.1	1.1	2.7	0.2	0	0	0	0	0	0	0	0	1.4	0	0	0
Lenticulina sp. 1	3.3	3.4	3.4	0.4	0.4	1.4	4.2	1.2	2.8	1.4	2.1	0.7	1.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spiroplectinella cf. plummerae	8.9	7.7	16.6	1.6	2.1	7.1	0	5.3	5.1	0.9	2.9	11.9	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0.4
Gavelinella? guineana	0	0	0.4	0	0	0	0.2	4.1	0.9	0	0.7	4.1	10.8	4.5	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalinoides aegyptiacus	2.8	15.4	3	4.4	5.4	3.2	9.7	17.1	23.8	37.9	42.2	33.8	42.6	46.9	70.7	73.7	58.3	67.9	68.2	24.3	25.8	10.8	14.1	24.3	9.2	17.2	5.7
Cibicidoides decoratus	0	0	0	0	0	0	0	1.6	0.5	0.9	1.2	5.5	0	3.6	1.9	2.7	7.4	6.6	0	4	1.7	19.1	14.1	10	12.4	18.4	25.8
No. specimens	214	234	235	251	240	283	404	245	214	214	419	293	352	224	426	293	230	274	211	226	236	241	227	210	249	256	244
No. taxa in non-condensed dataset	20	18	25	26	24	24	24	21	17	19	19	19	8	14	13	8	10	8	5	8	10	8	15	9	21	14	22

PA 6: the shallowest assemblage containing middle neritic taxa confined to Bir Inglisi I.

It should be noted that these assemblages are based on the more common occurrences, since scattered and infrequent occurrences (less than 3% and isolated in only one or two samples) are disregarded in this respect. Therefore, we do not suggest that the taxa assigned to a certain assemblage are exclusive to the bathymetric zone involved. If all scattered occurrences were taken into consideration as well, many taxa would yield wider ranges. For example, *Anomalinoides aegyptiacus* is observed in all localities, but it is only a diagnostic species for middle neritic environments where it can be extremely abundant (Table 1; Fig. 4). The faunal

Table 2. Composition of the paleobathymetric assemblages (PA 1-6), based on common presence in the three main sections (presence of taxa < 3% in only one or two samples are excluded from this scheme). The column with remarks gives additional information on specific distribution patterns (see also Fig. 4 and Table 1): P = exit near P/E boundary; E = entry near P/E boundary; L = Lazarus taxon; D = disaster taxon (only for Wadi Nukhl); i = Eocene increase in relative abundance; d = Eocene decrease in relative abundance; (N) = exclusively in Wadi Nukhl; (O) = exclusively in Gebel Oweina; (I) = exclusively in Bir Inglisi I; (global) = global extinction; (local;....) = local extinction, taxon observed elsewhere in the Eocene of Egypt (name = locality of observation; numbers refer to localities in Fig. 1).

PA	Species	remarks
1	Cibicidoides hyphalus	P(global)
	Pullenia coryelli	P(global)
	Gyroidinoides sp. 1	P
	Gavelinella beccariiformis	P(global)
	Gaudryina nekhlensis	P
	Nuttallides truempyi	i
	Bulimina spp.	
	Anomalinoides rubiginosus	
	Cibicidoides spp.	L
	calc. agglutinants rest	L
2	Angulogavelinella avnimelechi	P(global)
	Cibicidoides cf. hyphalus	P
	Tritaxia midwayensis	L, P(O)
	Spiroplectinella esnaensis	L
	sili. agglutinants rest	L
	spiroplectamminids rest	L
	Globocassidulina subglobosa	
	Bulimina callahani	i(O)
	Cibicidoides pseudoacutus	d(N)
	Anomalinoides affinis	
	Pullenia spp.	
	Osangularia plummerae	i
	Turrilina brevispira	i(N), E(O)
	Cibicidoides pharaonis	i(N), E(O)
3	bi-/triserial rest	
	trochospiral rest	L
	Gaudryina cf. ellisorae	E
	Valvalabamina spp.	L(I)
	Bulimina midwayensis	P(I)
	lagenids rest	L
	Spiroloculina spp.	
	Bulimina farafraensis	L(I), i
	Anomalinoides zitteli	E
	Oridorsalis plummerae	
	Cibicidoides cf. pseudoperlucidus	L(N), P(I)
	Alabamina midwayensis	L(I)
	Cibicidoides succedens	
	Anomalinoides praeacutus	L
	Gyroidinoides spp.	P
	Siphogenerinoides spp.	E(N,O)
	vaginulinids rest	
4	Dorothia sp. 1	P
	Anomalinoides cf.? midwayensis	P
5	Trochammina spp.	E(I)
	Gyroidinoides girardanus	P(O), L(I)
	Loxostomoides applinae	D
	Bulimina quadrata-ovata	
	Valvulineria scrobiculata	D, i(I)
	Stainforthia spp.	D
6	Gaudryina africana	P
	Anomalinoides cf. aegyptiacus	d
	Lenticulina sp. 1	P(local; G. Gumah)
	Spiroplectinella cf. plummerae	L
	Gavelinella? guineana	P(local; 10, 13)
	Anomalinoides aegyptiacus	D
	Cibicidoides decoratus	D, i
	Frondicularia phosphatica	P(local; 20)

contents of the two lowermost Eocene samples from Wadi Nukhl are also omitted from the ranking, since their faunal contents appear rather anomalous for an upper bathyal locality (see discussion below).

The application of the paleobathymetric assemblages as given in Table 2, is evidently hampered by the fact that many taxa do not have a continuous distribution across the Paleocene/Eocene boundary. Actually, we could have presented two paleobathymetric models, one for the latest Paleocene and a different one for the earliest Eocene. For the sake of saving space, we confine ourselves to one model and we highlight the dissimilarities between the latest Paleocene and earliest Eocene distribution (see also remarks in Table 2). This boundary effect is greatest in deep water; the bathyal assemblages of Wadi Nukhl show the largest faunal turnover, mainly due to the extinction of some of the most common species (e.g. *Gavelinella beccariiformis, Gaudryina nekhlensis, Pullenia coryelli* and *Cibicidoides hyphalus*) and due to the increase in relative abundance of *Nuttallides truempyi* and the entry of *Gaudryina* cf. *ellisorae.* In shallower water (Gebel Oweina) the faunal turnover is somewhat less prominent, although the extinctions of e.g. *Angulogavelinella avnimelechi*, *Cibicidoides* cf. *hyphalus*, and *Anomalinoides* (cf.?) *midwayensis* are very striking, as are the entries and/or the increases in relative abundance of *Anomalinoides zitteli*, *Turrilina brevispira*, *Cibicidoides pharaonis*, *Bulimina farafraensis*, *B. callahani*, and *Trochammina* spp. The effect of the P/E boundary event seems to diminish even further in the shallowest sequence, the one of Bir Inglisi I. Many species that disappear near the P/E boundary, reappear in the Eocene. A few species, however, go locally extinct (see Table 2).

Qualitative examination of assemblages and literature data from various localities (Fig. 1) reveals continuity in the lateral distribution of the assemblages. Upper bathyal assemblages similar to the ones in Wadi Nukhl (PA 1-2) are observed in various localities (Nos. 1-7) on the Sinai peninsula. In the northern Wadi Qena (No. 12) Paleocene-Eocene assemblages are transitional between the ones from Wadi Nukhl and Gebel Oweina, deep-sea taxa are more common than in the latter locality. Outer neritic assemblages similar to the ones in Gebel Oweina are found in central and central eastern Egypt (Nos. 13, 15, 19, 21). Middle neritic assemblages, similar to the ones from Bir Inglisi I, are typical of southern Egyptian localities (Nos. 17, 18). Benthic foraminiferal assemblages confirm that near the two carbonate platforms of Galala and Abu Tartur, the gradual N to NW deepening trend was interrupted (Nos. 8-11, 20). Thus, the assemblages discriminated in the three sections appear to have a wide lateral distribution within the Egyptian basin and most likely represent distinct paleobathymetric zones (Fig. 1).

Apart from using foraminiferal assemblage patterns or species depth limits, one can attempt to reconstruct paleobathymetry using the ratio between planktonic and benthic foraminifera (e.g. Grimsdale and Van Morkhoven, 1955; Van der Zwaan et al., 1990). The plots of the proportion of planktonic foraminifera of the total assemblage (%P, Fig. 3) show strong fluctuations in each section. If taken as a measure for paleobathymetric changes, the patterns are certainly incompatible with the lithological uniformity observed in the sections and the benthic foraminiferal assemblage patterns as discussed above. Selective dissolution of the more susceptible planktonic foraminifera (Murray, 1991) is a likely cause for many negative excursions in %P. Indeed, especially in the Paleocene of Wadi Nukhl and Gebel Oweina planktonic foraminifera appear strongly corroded and are often indeterminable. Eocene assemblages are generally much better preserved, although at some levels dissolution has been severe. It is important to note, that none of the samples contained aragonitic benthic foraminifera or pteropods and that tests of the miliolid *Spiroloculina* spp. are often preserved as calcitic molds. These features together suggest that dissolution could have influenced the %P patterns, especially in those samples where unexpected (and out of pattern) low %P values occur.

Paleoproductivity proxies

In oligotrophic to mildly eutrophic environments PFAR (planktonic foraminiferal accumulation rates N/cm^2/kyr) can roughly be considered as proxies for primary production (Berger and Diester-Haass, 1988; Brummer and Van Eijden, 1992; Herguera, 1992), increasing numbers resulting from increasing primary production. Yet, in truly eutrophic areas with short-chained diatom-based food webs, few competitive taxa may sustain and dominate a low diversity, low abundance planktonic foraminiferal assemblage. Therefore, more diverse assemblages of planktonic foraminifera are usually indicative for oligotrophic to mildly eutrophic conditions (Hallock et al., 1991). A major problem with the use of PFAR is the susceptibility to dissolution of planktonic foraminifera, as noted before. In deep-sea environments below the lysocline, BFAR

Table 3. General faunal data as figured in Fig. 3 (top: Bir Inglisi I; bottom: Wadi Nukhl). Ages are obtained from interpolation between three biostratigraphic tie-points, assuming constant sedimentation rates in between the tie-points. BFAR and PFAR are benthic and planktonic foraminnferal accumulation rates, respectively. %P is the proportion of planktonic foraminifera in the assciations. Alpha and dom. represent diversity and dominance. Boldface figures indicate the samples that are the least suspect of major dissolution and therefore the ones most suitable to determine reliable PFAR values.

sample	age	BFAR	PFAR	%P	alpha	dom.
1046	54.392	1801	15801	89.8	5.9	25.8
1045	54.438	630	1620	72	3.1	27
1044	54.529	**2054**	**21288**	**91.2**	5.5	29.3
1039	54.805	754	2097	73.6	1.9	56.7
1038	54.896	**1567**	**36177**	**95.9**	3.6	31.3
1037	54.933	183	13	6.9	1.6	55.6
1036	54.979	253	1951	88.5	2	38.1
1035	55.025	595	595	50	1.6	53.1
1034	55.071	172	33	15.6	0.7	68.3
1033	55.117	362	1458	80.2	2	67.9
1032	55.162	**1192**	**12454**	**91.3**	2.1	58.3
1031	55.208	**1589**	**16614**	**91.3**	1.5	73.7
1030	55.254	1077	24588	95.8	2.6	70.7
1029	55.3	196	7379	97.4	3.2	46.9
1028	55.345	7858	6785	46.3	1.5	42.6
1027	55.391	4294	8023	65.1	4.5	33.8
1026	55.436	4521	9425	67.6	4.1	42.2
1025	55.482	9038	6983	43.6	4.9	37.9
1024	55.527	15728	7531	32.4	4.4	27.6
1023	55.573	5058	1463	22.4	5.5	30.6
1022	55.618	4151	572	12.1	5.5	36.6
1020	55.709	2961	295	9	6.2	35.7
1018	55.8	4162	792	16	6.9	13.3
1016	55.891	1331	2644	66.5	7.2	13.6
1014	55.982	4147	3705	47.2	7	26.4
1012	56.073	2475	3144	56	4.5	19.7
1010	56.164	2330	2614	52.9	5.5	22
99	54.349	**506**	**11004**	**95.6**	10.3	15.1
94	54.513	**1379**	**17977**	**92.9**	10.5	16
93	54.546	**1806**	**29933**	**94.3**	11.7	15.1
92	54.579	1129	7692	87.2	11	21.1
87	54.743	1202	2336	66	9.9	15.6
84	54.841	506	1580	75.7	6	18.7
83	54.874	342	433	55.8	10.3	31.2
80	54.972	**592**	**6588**	**91.8**	9.9	22.2
73	55.202	384	848	68.9	7.9	31
72	55.234	586	214	26.6	3	41.3
71	55.267	2019	54131	96.4	9	13
69	55.387	177	170	49	9.6	15
68	55.474	324	60	15.5	10.8	16.6
66	55.648	189	85	30.8	16.5	9.7
65	55.735	154	28	15.4	15.4	11
60	56.17	258	2	1	10	17.1
741	54.408	**75**	**1309**	**94.6**	15.1	19
740	54.625	**73**	**1208**	**94.3**	19	17.1
739	54.842	**102**	**1658**	**94.2**	15.7	13.9
738	55.011	**181**	**1628**	**90**	14.3	29.2
737	55.155	316	7590	96	14.2	28.8
1374	55.18	144	8893	98.4	16.1	25.1
1373	55.24	110	3541	97	10.4	22.9
1372	55.3	10	566	98.2	5.6	46.7
1371	55.363	41	59	59.2	21.2	11.4
736	55.5	96	96	50	14.7	15.6
735	55.725	116	117	50.2	19.8	13.9
734	55.95	73	73	50	26.2	12
732	56.2	126	293	70	23.3	17.2

(benthic foraminiferal accumulation rates) have been considered as an alternative proxy for productivity (Herguera and Berger, 1991; Herguera, 1992), since benthic foraminifera are generally much less prone to dissolution. In using BFAR, the additional underlying assumption is that the production of benthic tests primarily depends on the organic carbon flux out of the mixed layer reaching the seafloor (e.g. Van der Zwaan et al., 1990). Since the organic carbon flux is depth-dependent (e.g. Suess et al., 1980), one has to account for depth differences in using BFAR to reconstruct paleoproduction. It should further be noted that a strong disadvantage of BFAR is that it is strongly affected by lowering of the bottom water oxygenation (e.g. Van der Zwaan et al., 1990).

In the Egyptian material PFAR appears highly variable (Fig. 3; Table 3), for which post-depositional dissolution is probably the main cause. This pertains in particular to the Paleocene samples of Gebel Oweina and Wadi Nukhl, but also some aberrantly low values of Bir Inglisi I are suspect in this respect. The sometimes close correlation between negative peaks in PFAR and %P, strongly suggest enhanced dissolution of the planktonic foraminifera for those levels. However, it seems unlikely that general trends occurring in all three sections could have been caused solely by dissolution. Therefore, we take the general tendency of PFAR being considerably higher in the Eocene samples as a genuine expression of raised surface production.

All sections show a corresponding trend across the P/E boundary; highest values are reached slightly above the boundary. As mentioned earlier, the lithology is somewhat coarser here in all three sections, and winnowing can not be excluded. At the P/E boundary itself (thus excluding Gebel Oweina of which we have no event bed sample) PFAR values are the lowest of all Eocene values (disregarding the samples that are most likely affected by dissolution), despite the extremely high %P in the event beds. Clearly, it was the benthic production at those two localities that suddenly failed.

If one compares absolute values instead of trends, it is vital to scrutinize the samples in an attempt to exclude the ones affected most by dissolution. Samples with %P > 90% are probably the ones least altered. In this way we can only discuss the paleoproductivity of the early Eocene in absolute terms, since such high proportions of planktonic foraminifera are not encountered in any late Paleocene sample. Several more samples are excluded from the comparison of PFAR values: these are the P/E event bed samples (S 1372 and S 1029), and samples from the sandy beds above the P/E boundary that may show signs of winnowing (S 1373-74, S 737, K/P+71 m and S 1030). For each locality four more or less reliable PFAR values remain (Table 3): they average 1,450 specimens/cm^2/kyr for Wadi Nukhl, 16,000 for Gebel Oweina and 22,000 for Bir Inglisi I. PFAR values of Bir Inglsi I and Gebel Oweina are thus more than one order of magnitude higher than the ones from Wadi Nukhl. PFAR values for the event beds are about a factor three lower than these average Eocene values: 550 for Wadi Nukhl and 7,000 for Bir Inglisi I. At this point it should be noted that the event bed samples contain a very peculiar planktonic fauna: whereas all samples yield fairly diversified planktonic assemblages with abundant morozovellids, these two samples are fully dominated by acarininids and some *Globanomalina* and *Subbotina*, but virtually no *Morozovella*. In our view, the combination of lower PFAR values and this aberrant composition suggest that not only benthic production failed, but that at the same time surface conditions deteriorated, preventing full niche occupation. A very similar planktonic fauna was also observed in the P/E boundary bed of Gebel Qreiya; apparently, stressed pelagic conditions occurred basin-wide.

In contrast with PFAR values, BFAR values generally do not covary with %P, suggesting that these values are not considerably taphonomically depressed. Two samples are suspect of significant taphonomic impoverishment (S 1034 and S 1037). These samples as well as the ones supect of winnowing are disregarded in the following discussion. BFAR values of Wadi Nukhl show a sharp drop at the P/E boundary, followed by a return to Paleocene levels. Gebel Oweina clearly shows an average fourfold increase in BFAR values across the P/E boundary. Bir Inglisi I BFAR values also display a sharp drop at the P/E boundary, but remain relatively low in the Eocene. If we compare the absolute values for the three sections, than a clear trend of productivity increase can be observed going from the deep water site of Wadi Nukhl via the shallower Gebel Oweina section to the shallowest locality of Bir Inglisi I.

Summarizing, it seems safe to conclude that pelagic productivity increased in the early Eocene. We can not, however, assess the magnitude of increase due to taphonomic processes that to some extent altered the Paleocene associations. At the P/E boundary itself surface conditions temporarily deteriorated, leading to relatively depressed surface productivity compared with the subsequent period. Also benthic production failed at the P/E boundary in Wadi Nukhl and Bir Inglisi I. Wadi Nukhl shows full recovery, whereas production remains relatively depressed in Bir Inglisi I.

We lack information on benthic production at the P/E boundary of Gebel Oweina, but in general production increased significantly during the early Eocene. These patterns indicate a differential benthic response to the pelagic productivity increase.

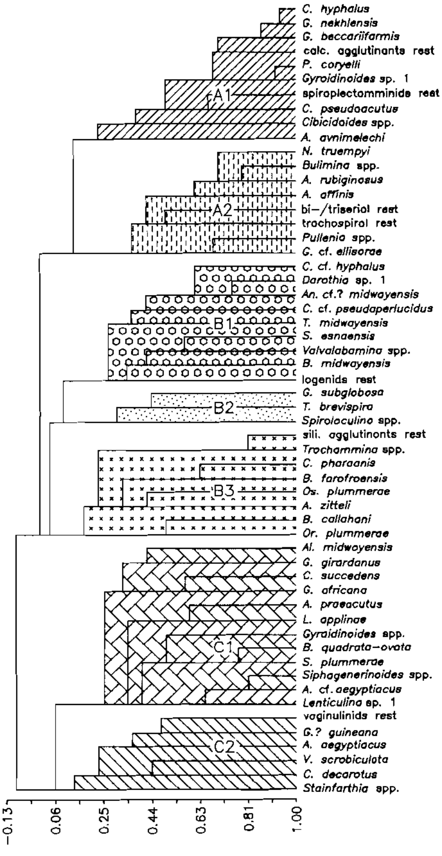

Fig. 5. Dendrogram resulting from cluster analysis; each of the three main clusters (A-C) characterizes one of the localities studied. Subclusters of A and B essentially distinguish "Paleocene" from "Eocene" taxa, whereas the subclusters of the shallow water cluster C separates the most opportunistic taxa frequent around the P/E boundary interval from the less opportunistic ones. Note that all but one of these opportunistic taxa show peak abundances in the basal Eocene of Wadi Nukhl (Fig. 4).

Quantitative faunal analysis

The dendrogram resulting from the cluster analysis (Fig. 5) shows three main clusters (labelled A, B and C). As could be expected, each cluster is more or less made up of taxa characteristic for the respective paleobathymetric zones the sections are located in. The upper bathyal cluster A contains taxa of PA 1-3. The outer neritic cluster B contains taxa of PA 2-5. The middle neritic cluster C contains taxa of PA 3, 5 and 6. The three main clusters can be divided into seven subclusters. This subdivision is mainly the consequence of the faunal changes at or near the P/E boundary. Subcluster A1 ("*Gavelinella beccariiformis assemblage*") consists of bathyal and bathyal-outer neritic taxa of the late Paleocene; six out of ten taxa are not observed in any of the Eocene samples (e.g. *G. beccariiformis, Pullenia coryelli*, and *Angulogavelinella avnimelechi*), whereas the other are more common in the Paleocene than in the Eocene (e.g. *Cibicidoides pseudoacutus*). Subcluster A2 ("*Nuttallides truempyi* assemblage") is made up of bathyal taxa and taxa with a wider paleobathymetric range; most of these are observed over the entire time-slice but are more common in the Eocene (e.g. *N. truempyi, Pullenia* spp.).

Subcluster B1 ("*Bulimina midwayensis* assemblage") is made up of outer neritic taxa and taxa with a wider paleobathymetric range; three out of nine are not observed in any of the Eocene samples (*Dorothia* sp. 1, *Anomalinoides* (cf.?) *midwayensis*, and *Cibicidoides* cf. *hyphalus*), most of the others are more common in the Paleocene (e.g. *Tritaxia midwayensis* and *B. midwayensis*). Subclusters B2 and B3 ("*Bulimina farafraensis* assemblage") are made up of taxa with a wide paleobathymetric range; one species is restricted to the Eocene (*Anomalinoides zitteli*), whereas most of the others are (much) less common in the Paleocene than in the Eocene (e.g. *Turrilina brevispira, Bulimina callahani, B. farafraensis*, and *Cibicidoides pharaonis*).

Subcluster C1 ("*Spiroplectinella* cf. *plummerae* assemblage") is made up of middle neritic taxa and taxa with a wider paleobathymetric range; three out of twelve taxa are restricted to the Paleocene (*Gaudryina africana*, *Lenticulina* sp. 1, and *Gyroidinoides* spp.), whereas most of the others occur both in the Paleocene and the Eocene (e.g. *Loxostomoides applinae*, *Alabamina midwayensis*, and *Anomalinoides praeacutus*). Most of these taxa are absent or much less common in the interval around the P/E boundary of Bir Inglisi I. Subcluster C2 ("*Anomalinoides aegyptiacus* assemblage") is made up of a highly interesting suite of taxa. Three out of six taxa are restricted to middle neritic depths (*Cibicidoides decoratus*, *A. aegyptiacus*, and *Gavelinella? guineana*), two are also observed in outer neritic deposits (*Stainforthia* spp. and *Valvulineria scrobiculata*) and only one is also present in bathyal deposits (*Lenticulina* spp.). All these taxa are common or abundant in the P/E boundary interval in Bir Inglisi I and also, except for *Gavelinella? guineana*, unexpectedly in the basal Eocene beds of Wadi Nukhl.

Paleobathymetry appears to be the prime paleoenvironmental parameter separating the main clusters. The subclusters within clusters A and B are reflection of the faunal changes that occurred at the P/E boundary. These changes are clearly more pronounced in the bathyal cluster A than in the outer neritic cluster B. In contrast, the middle neritic cluster C does not show a similar Paleocene versus Eocene separation. This suggests no major overall Paleocene to Eocene faunal break in the shallowest site, but a gradual and temporal faunal transition.

The first three standardized Principal Component axes explain 35% of the total variation (16%, 11% and 8%, respectively). Taxa loadings as well as sample scores are listed in Table 4; the use of PCA in this case is limited, because the heterogeneity of the sample set precludes assignment of an environmental parameter to each component. In figure 6 only the sample scores on the first and third components are visualized in a bivariate plot; the other bivariate plots did not reveal particularly usefull patterns. The bivariate plot displays six distinct sample clusters, for each locality a Paleocene and an Eocene one. Sample clusters for the three localities are arranged along the first axis: highest values for Wadi Nukhl, intermediate for Gebel Oweina, and lowest for Bir Inglisi I. The taxa loadings are arranged accordingly: highest positive loadings for PA 1-2 and cluster A taxa and most negative loadings for PA 5-6 and cluster C taxa.This arrangement reflects gradients in depth, fertility (decreasing with depth), and oxygenation (increasing with depth), as indicated in earlier discussions. Sample scores of the two lowermost Eocene samples of Wadi Nukhl show a pecu-

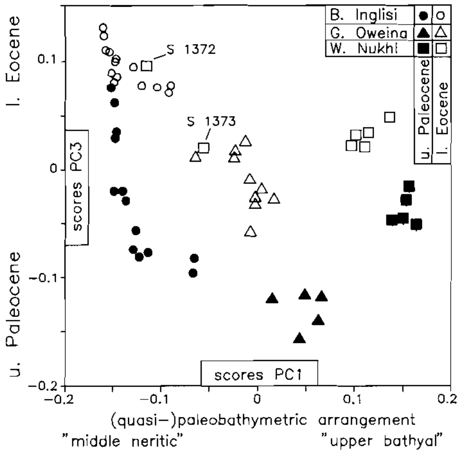

Fig. 6. Bivariate plot of sample scores on the first and third principal component (data from Table 4), showing the sample clusters, corresponding to the six main assemblages in the cluster analysis dendrogram. Note the position of the two lowermost Eocene samples (indicated) from Wadi Nukhl (for discussion see text).

Table 4. Taxa loadings on the first three principal components, together with cluster (CL) and paleobathymetric assemblage (PA) assignment of the taxa. On the right hand side of the table sample scores on the three components are given (top: Bir Inglisi I; bottom: Wadi Nukhl).

Species	PC 1	PC 2	PC 3	Cl	PA	Sample	PC 1	PC 2	PC 3
calc. agglutinants rest	0.267	-0.172	0.031	A1	1	**1046**	-0.091	-0.027	0.071
Anomalinoides rubiginosusa	0.229	-0.064	0.157	A2	1	**1045**	-0.089	-0.016	0.077
Gaudryina nekhlensis	0.216	-0.234	-0.041	A1	1	**1044**	-0.119	-0.04	0.077
trochospiral rest	0.209	-0.078	-0.036	A2	3	**1039**	-0.147	-0.078	0.103
Anomalinoides affinis	0.203	0.103	0.024	A2	2	**1038**	-0.103	-0.058	0.075
Pullenia coryelli	0.203	-0.218	-0.035	A1	1	**1037**	-0.129	-0.053	0.095
Cibicidoides pseudoacutus	0.201	-0.123	-0.164	A1	2	**1036**	-0.148	-0.067	0.081
Cibicidoides hyphalus	0.2	-0.223	-0.014	A1	1	**1035**	-0.15	-0.079	0.089
Gavelinella beccariiformis	0.199	-0.225	-0.039	A1	1	**1034**	-0.158	-0.098	0.123
spiroplectamminids rest	0.187	-0.068	-0.075	A1	2	**1033**	-0.154	-0.094	0.109
Gyroidinoides sp. 1	0.18	-0.2	-0.037	A1	1	**1032**	-0.147	-0.084	0.101
Cibicidoides spp.	0.179	-0.12	0.059	A1	1	**1031**	-0.159	-0.101	0.13
Bulimina spp.	0.177	-0.023	0.147	A2	1	**1030**	-0.156	-0.086	0.11
Pullenia spp.	0.153	0.046	0.116	A2	2	**1029**	-0.146	-0.078	0.086
Nuttallides truempyi	0.146	0.011	0.157	A2	1	**1028**	-0.151	-0.068	0.075
bi-/triserial rest	0.145	0.036	0.075	A2	3	**1027**	-0.146	-0.099	0.034
lagenids rest	0.14	0.083	-0.11	B1	3	**1026**	-0.148	-0.086	0.061
Tritaxia midwayensis	0.122	0.052	-0.168	B1	2	**1025**	-0.147	-0.104	0.029
Cibicidoides cf. pseudoperlucidus	0.113	0.132	-0.216	B1	3	**1024**	-0.148	-0.119	-0.021
Cibicidoides cf. hyphalus	0.105	0.066	-0.335	B1	2	**1023**	-0.139	-0.107	-0.02
Valvalabamina spp.	0.087	0.198	-0.147	B1	3	**1022**	-0.125	-0.081	-0.057
Spiroloculina spp.	0.085	0.094	0.061	B2	3	**1020**	-0.128	-0.114	-0.074
Angulogavelinella avnimelechi	0.083	-0.066	-0.178	A1	2	**1018**	-0.067	-0.037	-0.096
Spiroplectinella esnaensis	0.073	0.228	-0.204	B1	2	**1016**	-0.065	-0.027	-0.083
Gaudryina cf. ellisorae	0.065	0.107	0.171	A2	3	**1014**	-0.122	-0.122	-0.08
Globocassidulina subglobosa	0.063	0.219	-0.036	B2	2	**1012**	-0.136	-0.103	-0.029
Oridorsalis plummerae	0.061	0.112	0.044	B3	3	**1010**	-0.113	-0.113	-0.077
Dorothia sp. 1	0.042	0.134	-0.299	B1	4	**99**	-0.025	0.073	0.012
Osangularia plummerae	0.034	0.165	0.089	B3	2	**94**	-0.008	0.1	-0.057
sili. agglutinants rest	0.026	0.139	-0.072	B3	2	**93**	0.017	0.085	-0.026
Anomalinoides cf.? midwayensis	0.023	0.112	-0.284	B1	4	**92**	-0.003	0.082	-0.029
Bulimina callahani	0.014	0.072	0.028	B3	2	**87**	0.004	0.097	-0.016
Turrilina brevispira	0.006	0.112	0.068	B2	2	**84**	-0.023	0.104	0.018
Gyroidinoides spp.	0.004	-0.231	-0.099	C1	3	**83**	-0.003	0.119	-0.025
Bulimina midwayensis	-0.004	0.136	-0.205	B1	3	**80**	-0.008	0.103	-0.008
Cibicidoides pharaonis	-0.016	0.175	0.053	B3	2	**73**	-0.063	0.037	0.014
Trochammina spp.	-0.021	0.162	-0.038	B3	5	**72**	-0.013	0.072	0.028
Bulimina farafraensis	-0.037	0.126	0.034	B3	3	**71**	0	0.104	-0.012
Anomalinoides zitteli	-0.04	0.136	0.088	B3	3	**69**	0.049	0.046	-0.114
Alabamina midwayensis	-0.041	-0.054	-0.211	C1	3	**68**	0.043	0.104	-0.155
Gyroidinoides girardanus	-0.063	-0.007	-0.222	C1	5	**66**	0.062	0.105	-0.138
Stainforthia spp.	-0.068	-0.028	0.066	C2	5	**65**	0.066	0.052	-0.116
Cibicidoides succedens	-0.089	-0.021	-0.194	C1	3	**60**	0.015	0.03	-0.118
Gavelinella? guineana	-0.095	-0.076	0.044	C2	6	**741**	0.099	0.069	0.019
Anomalinoides praeacutus	-0.095	-0.113	-0.182	C1	3	**740**	0.111	0.05	0.018
Cibicidoides decoratus	-0.096	-0.042	0.125	C2	6	**739**	0.102	0.061	0.028
Siphogenerinoides spp.	-0.12	-0.092	-0.022	C1	3	**738**	0.111	0.051	0.018
Bulimina quadrata-ovata	-0.139	-0.139	-0.1	C1	5	**737**	0.115	0.042	0.031
Valvulineria scrobiculata	-0.146	-0.075	0.102	C2	5	**1374**	0.137	0.036	0.045
vaginulinids rest	-0.151	-0.013	0.033	C2	3	**1373**	-0.056	0.024	0.017
Gaudryina africana	-0.154	-0.148	-0.127	C1	6	**1372**	-0.115	-0.061	0.092
Anomalinoides cf. aegyptiacus	-0.16	-0.158	-0.092	C1	6	**1371**	0.165	-0.084	-0.054
Spiroplectinella cf. plummerae	-0.16	-0.19	-0.108	C1	6	**736**	0.141	-0.089	-0.049
Loxostomoides applinae	-0.164	-0.121	-0.084	C1	5	**735**	0.158	-0.114	-0.019
Anomalinoides aegyptiacus	-0.167	-0.111	0.136	C2	6	**734**	0.154	-0.06	-0.031
Lenticulina sp. 1	-0.169	-0.187	-0.107	C2	6	**732**	0.153	-0.091	-0.048

liar deviating pattern: sample S 1372 (from the sapropelitic bed) plots in the field of Bir Inglisi I samples, whereas the next sample (S 1373) falls in between the Bir Inglisi I and Gebel Oweina samples. This pattern results from the sudden extinction or temporal disappearance of most bathyal taxa and their replacement by shallow water taxa (see Fig. 4).

Along the third axis a separation between Paleocene and Eocene samples is apparent. The Paleocene and Eocene sample clusters of Wadi Nukhl and Gebel Oweina fall widely apart; the clear separation corresponds with the abrupt faunal turnover at the P/E boundary in these localities. By contrast, Paleocene sample scores from Bir Inglisi I gradually pass into Eocene ones, corresponding to the gradual faunal transition in this section (see also Speijer and Van der Zwaan, 1994a). The separation along the third axis corresponds with the distinction between the *G. beccariiformis* and *N. truempyi* assemblages in Wadi Nukhl, the *B. midwayensis* and *B. farafraensis* assemblages in Gebel Oweina, and the *S.* cf. *plummerae* and *A. aegyptiacus* assemblages in Bir Inglisi I.

In Wadi Nukhl the *G. beccariiformis* assemblage is replaced by the *N. truempyi* assemblage during the earliest Eocene, a pattern that is commonly observed in many other areas (Tjalsma and Lohmann, 1983; Miller et al., 1987; Kaiho, 1991; Katz and Miller, 1991; Nomura, 1991; Pak and Miller, 1992; Thomas, 1992; Speijer, 1994a). Data from Tjalsma and Lohmann (1983), Katz and Miller (1991), Kaiho (1991), Nomura (1991), Pak and Miller (1992), and Thomas (1992) strongly suggest that *N. truempyi* is primarily a low latitude species and usually much less frequent at high latitudes. For instance, at Maud Rise Thomas (1992) found that the species disappeared or became reduced in the P/E boundary sequence, whereas at lower latitudes *N. truempyi* substantially increased. Data from Tjalsma and Lohmann (1983) show that after the P/E boundary event *N. truempyi* in particular increased at low latitudes and remained rather persistantly frequent at northern subtropical latitudes after a phase of maximum southward distributional extension in the early Eocene. The total pattern is suggestive for a species that prefers tropical-subtropical latitudes, which were possibly dominated at that time by deep or intermediate water locally formed (Miller et al., 1987; Thomas, 1989, 1990b, 1992). That water would be warm and saline, and lower in oxygen content than cooler polar waters. Therefore, we consider *N. truempyi* as a bathyal species indicative of saline, less well oxygenated waters.

Distributional patterns of *G. beccariiformis* roughly mirror the patterns of *N. truempyi*. Katz and Miller (1991) argue in a similar way as we do for *N. truempy*, that *G. beccariiformis* is a southern species, most frequent in deep water polar areas, a situation that already existed in the Late Maastrichtian (Widmark, in prep.). In our view that would point to a preference for young, cool and oxygen rich waters.

As indicated earlier, cosmopolitan deep water taxa are much less common in Gebel Oweina than in Wadi Nukhl. Yet, also in this locality the *B. midwayensis* and *B. farafraensis* assemblages are easily distinguished due to extinctions and appearances various (local) species at the P/E boundary (see below). As indicated by the names, the assemblages are dominated by several buliminids. In modern environments such dominance would be indicative of oxygen deficiency (e.g. Van der Zwaan, 1982; Murray, 1991; Sen Gupta and Machain-Castillo, 1993). Increasing numbers of *B. callahani*, *B. farafraensis* and *T. brevispira* may indicate slightly increasing oxygen deficiency during the early Eocene. In both instances, however, diversity remains fairly high, suggesting that oxygen stress was not particularly severe.

In Bir Inglisi I the faunal turnover progressed more gradually. In a separate paper (Speijer and Van der Zwaan, 1994a) we demonstrated that this site was generally subject to a high nutrient supply and oxygen deficiency. These conditions favoured highly opportunistic epibenthic taxa as *A.* (cf.) *aegyptiacus* and *V. scrobiculata*, a pattern similar to modern representatives of *Valvulineria, Alabaminella*, and *Epistominella* that thrive in high productive sites (Jorissen et al., 1992; Sen-Gupta and Machain-Castillo, 1993; Gooday, 1993). Bottom conditions became more severe during the latest Paleocene (about 400 kyr before the end of the Paleocene) as evidenced by successive exits of particularly PA 3 taxa, gradually increasing dominance of *A. aegyptiacus*, and decreasing diversity, reaching maximum levels in the earliest Eocene. These deteriorating bottom conditions were ascribed to increasing fertility across the P/E boundary and to reduced ventilation (at the boundary in particular) by advection from deeper waters or thermoclinal mixing (Speijer and Van der Zwaan, 1994a).

Abundance patterns, Lazarus taxa, disaster taxa and extinctions.

Thusfar, we discussed the general faunal composition and the quantitative assemblage changes across the P/E boundary. In this section we will focus on faunal changes at taxon level, in particular definitive, temporal and local extinctions. In general, a faunal turnover consists of several components. The most conspicuous features are extinctions (if temporal called "Lazarus taxa") and entries (if temporal called "disaster taxa"), which can easily be assessed in a qualitative way. Often less conspicuous, but similarly interesting are the accessory components of in- and decreases in relative abundance, which of course can only be adressed in a (semi)quantitative way.

In the sections studied, eighteen Paleocene taxa disappear permanently at or very near the P/E boundary in one or more sections (see Table 2). At least seven of these taxa persist into the Eocene in either one of the other sections (*Tritaxia midwayensis, Bulimina midwayensis, Cibicidoides* cf. *pseudoperlucidus*, and *Gyroidinoides girardanus*), or in any of the other Egyptian localities studied (Fig. 1; *Lenticulina* sp. 1, *Gavelinella? guineana*, and *Frondicularia phosphatica*), and thus become only locally extinct. At least four of the remaining eleven taxa certainly became globally extinct at the P/E boundary (*Gavelinella beccariiformis, Pullenia coryelli, Cibicidoides hyphalus*, and *Angulogavelinella avnimelechi*), whereas this is uncertain for the other seven. It is evident that the deeper water assemblages were affected most severely: 50% (5 taxa) of the bathyal PA 1 became extinct, 100% (2 taxa) of the exclusively outer neritic PA 4, and only 14% (1 taxon) of the shallow PA 1. The number of extinctions of taxa with a broader paleobathymetric range is much lower: for PA 2, 3 and 5 the figures are 14% (2 taxa), 6% (1 taxon) and 0%, respectively. Although it remains uncertain that all these P/E boundary extinctions are true extinctions, it is evident that bathyal taxa or taxa with a narrow paleobathymetric range were more severely affected than neritic ones or taxa with a wider paleobathymetric range. In addition to these disappearances, we have observed for only two taxa that they became much less abundant in the Eocene (*Cibicidoides pseudoacutus*, and *Anomalinoides* cf. *aegyptiacus*).

As implied by the name, many Lazarus taxa temporarily disappeared at the P/E boundary. In a purely quantitative analysis it is not possible to establish whether taxa are really absent or merely extremely rare. We have refrained from scanning the remaining sample residue for extremely rare specimens, since such approach would almost certainly result in introducing rare reworked specimens. Especially at turnover levels such artifacts can strongly interfere with the interpretation of faunal patterns (as in the K/P boundary discussion, ranging from nannofossils up to dinosaur bones). In Wadi Nukhl, ten Lazarus taxa that are consistently present in all Paleocene samples disappear at the P/E boundary. This group is made up of five arenaceous taxa and several lumped categories in which many rare taxa are combined. They are evenly distributed over PA 1-3. Most Lazarus taxa reappear immediately above the P/E boundary bed; a few reappear somewhat higher. For Gebel Oweina a Lazarus effect could not be established, since a potential P/E boundary event bed was not sampled. In Bir Inglisi I six taxa are absent around the P/E boundary. Only one of them (*Spiroplectinella* cf. *plummerae*) occurs exclusively in this section. All others have wider paleobathymetric ranges.

Despite the high number of disappearances at the P/E boundary, there are only a few new taxa to compensate for the loss. Only *Gaudryina* cf. *ellisorae* and *Anomalinoides zitteli* were not observed in any of the Paleocene samples; both belong to PA 3. Apart form these two entries, the loss of common taxa at the P/E boundary is mainly compensated for by increasing abundances of surviving taxa. The following taxa show a clear abundance increase in one or more sections: *Nuttallides truempyi*, *Pullenia* spp., *Osangularia plummerae, Turrilina brevispira, Cibicidoides pharaonis, C. decoratus, Bulimina farafraensis, B. callahani, Trochammina* spp., *Vavulineria scrobiculata*, and *Anomalinoides aegyptiacus.*

Disaster taxa primarily occur in Wadi Nukhl; these are taxa which only are frequent in the basal Eocene and mostly belong to taxa cluster C2 and to PA 5-6 (see Table 2). These are primarily *A. aegyptiacus* and *Stainforthia farafraensis*, accompanied by *V. scrobiculata, A. zitteli* and *C. decoratus.* These typically (middle) neritic taxa were quickly replaced by a normal early Eocene upper bathyal assemblage.

Discussion

The Paleocene-Eocene boundary marks a period of sudden and global environmental change, superimposed on longer-term trends (particularly global warming, e.g. Kennett and Stott, 1991; Frakes et al., 1992; Zachos et al., 1994). The cause and even the exact nature of the changes are still subject of growing interest and debate. It is important to notice that although the event was global, it particularly affected one ecological compartment, the deep-sea. In this sense it mirrors the K/T boundary. The latter was limited mainly to the continental, shallow marine and pelagic compartments of the global ecosystem (Sharpton and Ward, 1990, and references therein; Speijer and Van der Zwaan, 1994c); the deep-sea ecosystem, of which benthic foraminifera are important constituents remained largely unaffected (Beckmann, 1960; Dailey, 1983; Thomas, 1990a; Nomura, 1991). The selectivity of both the extinction events puts important constraints on the respective causes. In the case of the P/E boundary event, a number of features underline the global character. For both the oxygen and carbon isotope records, the P/E boundary acts as a level where long-term trends were abruptly punctuated (Shackleton et al., 1984, 1985; Stott et al., 1990; Barrera and Huber, 1991; Pak and Miller, 1992). The oxygen record shows that the temperatures of high latitude surface and deep waters sharply increased, whereas the global carbon spike gives evidence of a major perturbation of the carbon reservoir (Stott et al., 1990; Kennett and Stott, 1991); as far as could be established, there is evidence of a really synchronous isotope event (Kennett and Stott, 1991; Katz and Miller, 1991; Pak and Miller, 1992; Koch et al., 1992; Thomas, 1992).

The late Paleocene-early Eocene negative trend in the carbon isotope record has been interpreted as indicating a decrease in primary production (e.g. Shackleton et al., 1985; Shackleton, 1987; Katz and Miller, 1991), a view that concurs with foraminiferal evidence (Boersma and Premoli-Silva, 1991; Hallock et al., 1991). The significance of the sharp carbon isotope excursion at the P/E boundary is much more controversial: higher or lower atmospheric CO_2, enhanced carbon burial or not, and failing primary production were put forward as explanation (Kennett and Stott, 1991; Stott, 1992; Zachos et al., 1994; Thomas and Shackleton, 1994). The oxygen isotope evidence of a global warming trend reaching peak values in the early Eocene, is collaborated by high latitude faunal and floral records (Haq et al., 1977; Estes and Hutchison, 1980; Wolfe, 1985; Boersma and Premoli-Silva, 1991; Huber, 1991a; Lu and Keller, 1993) and clay mineral distribution (Robert and Chamley, 1991; Robert and Kennett, 1992, 1994).

There is additional evidence of drastic environmental change: in the deepsea, but also elsewhere, there are clear signs of oxygen deficiency, exemplified by dark brown or black clay layers (e.g. Egypt: Hendriks et al., 1990; Maud Rise: Thomas, 1992; Spain: Molina et al., 1994), or even widespread occurrences of sapropels (e.g. Caucasian Basin: Muzylov, pers. commun., 1991), and increase of so-called endobenthic foraminifera (Kaiho, 1991; Thomas, 1992; Kaiho et al., 1993; Molina et al., 1994; unpubl. data of Caucasian sections). Finally and perhaps most importantly, it should be kept in mind that the P/E boundary marks a period of significant changes in the global plate tectonic configuration, (e.g. North Atlantic: Vogt and Avery, 1974; Williams, 1986; Eldholm, 1990; Indian Ocean: McGowran, 1989, 1991; Klootwijk et al., 1991), leading a.o. to increased hydrothermal activity and massive eruption of flood basalts (Rea et al., 1990; Varekamp and Thomas, 1992; Eldholm and Thomas, 1993). Somehow these changes must have had a profound impact on geochemical cycles and the evolution of the biosphere.

Although many issues remain as yet unsolved, probably the most powerful explanation of the P/E boundary events is provided by assuming that during an already warm time interval a climatic perturbation was generated by a sharp CO_2 increase at a time of massive flood basalt expulsion (e.g. White and McKenzie, 1989; Varenkamp and Thomas, 1992; Eldholm and Thomas, 1993). Such a climatic change may well have generated the changes as observed on the continents and in the clay mineral record, but does not directly explain the marine patterns, in particular the extinction event. One suggested cause for that particular part of the complex problem is a (temporal) reversal of the oceanic circulation patterns (Miller et al., 1987; Katz and Miller, 1991; Kennett and Stott, 1991; Thomas, 1990b, 1992; Pak and Miller, 1992). In this scenario the Southern Ocean deep source was effectively eliminated by sudden polar warming; the deep water supply would have been taken over by another, probably low latitude source. Kaiho (1991) and Thomas (1992) related the sharp oxygen decrease at the P/E boundary to such a change of deep water sources and the consequent change in oxygen content of deep and intermediate watermasses.

The faunal data from the Egyptian assemblages show that at the time of the P/E boundary events, the southern Tethys margin was characterized by a wide, highly productive shelf. Our data suggest that the shallowest site was the most productive one, even characterized by intermittent upwelling. This is exemplified by the high organic carbon content of the sediments, and the persistence of dysoxic conditions as suggested by the virtually continuous occurrence of lamination (Speijer and Van der Zwaan, 1994a). Going to deeper water, average oxygen contents slightly increased, although laminated sediments suggest a combination of high production and poor ventilation. At the deep water site of Wadi Nukhl a low organic carbon flux reaching the seafloor led to a low benthic production and was apparently inadequate to cause dysoxic conditions. Clearly, the Paleocene of Wadi Nukhl contains assemblages indicative of a rather good ventilation.

The P/E boundary events clearly affected all sites, although the events were different from place to place. The faunal patterns of the P/E boundary of Wadi Nukhl, show the temporal increase of shallow water ("disaster") taxa into this deep water setting. At first sight, this might be interpreted as a significant sea-level drop. An important reason to reject a substantial sea-level drop is that in the shallow water Bir Inglisi I section such a drop would have had marked effects. In another paper (Speijer and Van der Zwaan, 1994a) we conclude that at this site there is only evidence for a minor sealevel drop of maximally 10-20 meters some 400 kyr prior to the P/E boundary. Therefore, the shallowing in Wadi Nukhl, appears to be apparent. The explanation is that primarily bathyal-outer neritic taxa disappeared or became extinct at the P/E boundary; they were replaced by taxa normally occurring in middle neritic environments and taxa with very wide (neritic-bathyal) paleobathymetric ranges, thus suggesting a shallowing but in fact only filling a (temporal) ecological vacuum.

The invasion of shallow water taxa into deeper waters shows again that the event affected in particular deep water taxa. Our data show that going from bathyal to inner neritic environments the faunal effects of the event diminished considerably; in shallow water the faunal patterns display gradual change and the extinction rate dropped markedly.

As elsewhere in the oceans, but especially typical for deposits along the Tethys' margins (Spain, Caucasus), the extinction event in the deep water section of Wadi Nukhl is marked by a sapropelitic layer which provides clear evidence for a lack of ventilation. In this case we have rather strong evidence that increase of surface water productivity is not the cause: the most marked surface productivity increase is recorded only shortly above the P/E boundary. Judging from the peculiar planktonic assemblage and the relatively low PFAR value, surface conditions deteriorated at the P/E boundary, a pattern seen also in other parts of the basin. The lack of ventilation in deep water is not easily explained by water column stratification either since the development of a seasonal thermocline would only affect the uppermost part of the watercolumn and not the deep water domain. Therefore, we conclude that oxygen advection from the intermediate and deep water decreased, which in turn could only have been caused by decrease of intermediate and deep water formation.

In the Bir Inglisi I sequence, the enormous dominance of two epibenthic species (*A. aegyptiacus* and *V. scrobiculata*) and the disappearance of many other taxa was taken in another paper (Speijer and Van der Zwaan, 1994a) as indication of increasing fertility and decreasing oxygenation during the latest Paleocene and in particular during the early Eocene. It was concluded that from that time on, upwelling intensified and surface water production increased, leading to periodic high food supply. During the early Eocene the total benthic production however, was apparently restrained by decreasing oxygen contents. Basically, that is the pattern found also in the two other sections. From the P/E boundary onward, we find an increase in pelagic production and a less well ventilated benthic environment, although much better aerated than at the P/E boundary itself.

The key elements of the Egyptian patterns thus are a sharp and short period of dysoxic conditions, failure of benthic production at the boundary, and overall pelagic production increase after the event. The duration of the event is difficult to assess. In Wadi Nukhl the event can be estimated based on the sapropel thickness, and would be 25-50 kyr. From the base of the sapropel to the re-establishment of a bathyal assemblage, the event took about 100-200 kyr. In the shallower site of Gebel Oweina we lack the boundary sequence proper, but a rather comparable timespan seems to be involved. However, at the shallow site of Bir Inglisi I the first faunal change started already at about 400 kyr before the boundary; faunal recovery took place at about 400 kyr after the boundary. These time spans are well comparable with those found in the open ocean, where the peak event took less than several 100,000 years (Miller et al., 1987; Katz and Miller, 1991; Thomas, 1992). However, in our dataset it is remarkable that the event definitely started earlier and lasted longer in the shallowest and highest productive site.

Summarizing, we have evidence that following the event primary production intensified, and that less well oxygenated waters resided in the entire basin. In the deep water section of Wadi Nukhl, the pattern is completely similar to that in various open ocean sites: the "Southern Ocean" species *G. beccariiformis* (Katz and Miller, 1991) is replaced by the tolerant and low latitude *N. truempyi.* Taken together, there seems to be clear evidence that penetration in the Tethys of well oxygenated intermediate or deep water, possibly from higher latitudes, came abruptly to an end at the P/E boundary. Instead, together with intensified upwelling at the margin, intermediate and deep waters became less well oxygenated possibly indicating formation in the Tethys itself. Being generated in the tropical and subtropical belt, the oxygen contents certainly would be lower than in higher latitude water.

The co-occurrence of upwelling and low latitude deep water formation is not surprising. Such a situation was normal during the Late Cretaceous, when strong atmospheric contrasts were generated by high latent tropical heat release (Barron, 1985; Barron and Washington, 1985; Barron, 1986; Crowley and North, 1991). The warm tropical conditions caused at the same time strong evaporation and tropical (Tethyan) deep water formation, whereas the high polar temperatures prevented substantial high latitude deep water formation. There is thus a causal link between tropical-subtropical upwelling and low latitude deep water formation. We argued in a separate paper (Speijer and Van der Zwaan, 1994a) that the strong atmospheric constrasts resulted in intensified NE winds in the northern hemisphere tropical-subtropical belt, leading to upwelling due to Ekman transport along the southern Tethys rim. This concurs with scenarios for the Late Cretaceous as outlined by Parrish and Curtis (1982) and Barron (1985). During that time, the "Cretaceous climatic mode" resulted in upwelling, and often in extensive phosphate deposition along the Tethys margin (Wiedmann et al., 1978; Bock, 1987; Reiss, 1988; Notholt et al., 1989; Kroon and Nederbragt, 1990; Almogi-Labi et al., 1993; Eshet et al., 1994).

Upwelling intensity and phosphate deposition decreased when global, and in particular tropical, temperatures declined in the Maastrichtian (Douglas and Woodruff, 1981; Gerstel et al., 1986; Barrera et al., 1987; Kennett and Barker, 1990; Frakes et al., 1992; Lécuyer, 1993) and terminated at the end of the Cretaceous. In the late Paleocene widespread upwelling-induced phosphate deposition re-initiated along the southern Tethyan margin (Burollet and Oudin, 1980; Busson and Cornee, 1986; Peypouquet et al., 1986; Notholt et al., 1989), parallel to the Paleocene warming trend up to the early Eocene thermal maximum (Douglas and Woodruff, 1981; Wolfe, 1985; Shackleton, 1986; Corfield et al., 1991; Stott et al., 1990; Frakes et al., 1992; Lécuyer, 1993, Zachos et al., 1993, 1994). We suggest that in the late Paleocene the

"Cretaceous mode", including low latitude deep water formation, gradually returned, and intensified in the earliest Eocene. Initially, the buoyancy flux of these deep waters may have been to low to produce a significant watermass. But the situation changed at the P/E boundary, when the buoyancy flux increased due to enhanced evaporation and deep water formation at high latitudes stopped at the same time (Kennett and Stott, 1991). In this way our data from the low latitude Egyptian sections complement the scenario of oceanic circulation reversal, earlier proposed by Miller et al. (1987) and Thomas (e.g. 1992).

We suggest the following, comprehensive scenario, which seems to explain our shallow and deep water low latitude patterns as well as the deep water higher latitude data: at the P/E boundary sudden rise of temperatures caused the blockage of deep water sources in the Southern Ocean. Since modelling experiments have shown the climatic sensitivity for CO_2 during the Cretaceous (cf. overview in Crowley and North, 1991), we share the suggestion of Eldholm and Thomas (1993) that the eruption of flood basalt could well have been the ultimate cause of this sharp and sudden temperature rise. The subsequent elimination of the Southern Ocean deep water sources led to a time span of extremely poor oceanic circulation. In our view, this would have resulted in ocean-wide and synchronous dysoxic to anoxic conditions, except perhaps for extreme southern localities still under influence of a slightly better ventilation due to marginal seasonal deep water formation. In this model oxygen deficiency should have been most severe in the tropical-subtropical belt, which indeed seems to have been the case.

The temperature rise was instrumental in the re-establishment of the "Cretaceous mode", i.e. low latitude deep and intermediate water formation in the Tethys in combination with upwelling along the southern Tethys rim. Our evidence here is circumstantial indeed, since we have only evidence for upwelling intensification starting during the earliest Eocene. As remarked earlier, we explain this with enhanced tropical latent heat release which caused strong atmospheric contrasts. Since during the Cretaceous this went hand in hand with low latitude deep water formation, it seems logical to infer this for the early Eocene as well. Indeed, the fauna after the P/E boundary event is indicative of less well oxygenated waters, as would fit deep water generated at low latitudes. At the same time, it would very well explain why the extinctions were preferential in the deeper water assemblages. Provided that some species survived the anoxic-dysoxic event, they were subsequently subjected to a large change from well ventilated deep water with a Southern Ocean origin to salty and less oxygenated waters with a Tethys origin. It also provides the reason why shallow Tethyan assemblages were not affected: here such assemblages were well adapted to the new oceanographic regime.

We think that there has been a very short period of oceanic circulation "still-stand", caused by the severance of Southern Ocean deep water sources whereas low latitude deep water formation was still not in full swing. The data from the shallow Bir Inglisi I section show that the event started earlier and lasted longer there than in deeper waters. This indicates that upwelling intensification, caused indirectly by temperature change, started earlier than the deep water stagnation event signifying the decrease of deep water formation. Important is that the consequence of such a severance of deep oceanic circulation is the rapid diminution of the surface water nutrient reservoir over deeper waters. Depending on the actual situation, about 90% of the trophic resources in the surface layer, are re-generated via vertical reflux (Broecker and Peng, 1982). Over longer time scales, the deep oceanic circulation is essential in this respect; hampering this circulation would eventually lead (over some thousands of years) to severe reduction of "blue ocean" productivity. This could explain the drop in production at deep water sites.

Following the stagnation, low latitude deep waters penetrated extremely far southward if the distribution of *N. truempyi* would be a reliable marker of this. After the P/E boundary maximum extension of the low latitude deep water gradual lowering of the polar temperatures caused equally gradual but certain growth of the importance of southem polar deep and intermediate water formation. Basically, this could be exemplified by the steady decrease in numbers and retraction to low latitudes of *N. truempyi* during the early and middle Eocene (Tjalsma and Lohmann, 1983). At the same time we see that at the southern Tethys rim the high production lasted till the middle Eocene before deposition of chalks, with extremely high amounts of pelagic organisms, ended.

Conclusions

In the southern Tethys, as in many other areas, the terminal Paleocene benthic foraminiferal extinction resulted primarily from a sudden and brief dysoxic-anoxic event. In Egypt this event was felt in the entire range between upper bathyal and middle neritic environments. Although the number of extinctions is highest in the deepest locality, shallow water ecosystems were equally perturbed. The better adaptation of many opportunistic shallow water species to sustain repeated and variable oxygen deficient conditions, apparently enabled most of them to survive the crisis. Some of these organisms temporarily colonized the ecological vacuum at the deepest locality immediately after the P/E event, when conditions ameliorated. At the deepest locality, as in other deep-sea sites, the event progressed very rapidly, resulting in simultaneous extinctions of deep water taxa. At the shallowest locality environmental deterioration, faunal impoverishment, and recovery proceeded much more gradual, starting earlier and lasting longer.

Our data suggest intensified wind-induced upwelling as well as deep water formation along the Tethyan margin, starting in the latest Paleocene and stepping up in the earliest Eocene. This may have resulted from enhanced atmospheric contrasts related to the early Eocene thermal maximum.

Our data are in accordance with the hypothesis of an ocean circulation reversal approximately coinciding with the P/E boundary, from predominantly high to low latitude deep water formation. The switch in circulation appears to have progressed relatively slowly (up to 50 kyr) and resulted in widespread dysoxic-anoxic conditions, particularly at low latitude sites.

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Appendix - Taxonomic notes

We largely adopted species concepts as used by LeRoy (1953), Aubert and Berggren (1976), Tjalsma and Lohmann (1983), and Van Morkhoven et al. (1986), but in some instances we deviated from these. As far as possible, we refer to earlier studies on Egyptian material. For (supra-)generic classification we largely followed Loeblich and Tappan (1988).

Spiroplectamminacea

Spiroplectamminidae

Spiroplectinella esnaensis (LeRoy)
(Pl. III, Fig. 1)

1953 *Spiroplectammina esnaensis* LeRoy: p. 50, pl. 1, figs. 11-12
1976 *Spiroplectammina knebeli* LeRoy. Aubert and Berggren: p. 409, pl. 1, fig. 7
1982 *Spiroplectammina plummerae* Cushman. Faris: p. 200, pl. 1, fig. 10
1990 *Spiroplectammina esnaensis* LeRoy. Shahin: p. 498, pl. 1, fig. 10
Remarks: this species has a poorly developed carina without dentations; most characteristic are the slightly to highly raised sutures and the broad apertural face.

Spiroplectinella* cf. *plummerae (Cushman)
(Pl. IX, Fig. 1)

cf. 1926 *Textularia carinata* d'Orbigny var. *expansa* Plummer: p. 67, pl. 3, fig. 3
cf. 1948 *Spiroplectammina plummerae* Cushman: p. 226, pl. 16, fig. 2
cf. 1951 *Spiroplectammina plummerae* Cushman. Cushman: p. 5, pl. 1, figs. 19-20
Remarks: in side view this species seems very similar to the type species, although it is probably more compressed. Unfortunately no apertural view was given for the holotype, but Cushman (1948) mentions a broad aperture, whereas the Egyptian specimens have a very narrow aperture and apertural face. The presence of depressed sutures makes this species easily distinguishable from other species occurring in Egypt.

Verneuilinacea

Verneuilinidae

Gaudryina africana LeRoy
(Pl. IX, Fig. 3)

1953 *Gaudryina africana* LeRoy: p. 30, pl. 1, figs. 7-8
Remarks: the strongly inflated later chambers of the biserial part distinguish this species from *G. pyramidata*.

Gaudryina* cf. *ellisorae Cushman
(Pl. V, Fig. 1)

cf. 1936 *Gaudryina (Pseudogaudryina) ellisorae* Cushman: p. 13, pl. 2, fig. 12
cf. 1946 *Gaudryina (Pseudogaudryina) ellisorae* Cushman. Cushman: p. 35, pl. 8, figs. 12, 13
Remarks: the carinate ribs are very distinct in this species. Specimens from the deeper localities have smooth tests; shallow water specimens are more coarse grained.

Gaudryina nekhlensis Said and Kenawy
(Pl. I, Fig. 1)

1956 *Gaudryina nekhlensis* Said and Kenawy: p. 124, pl. 1, fig. 24
1990 *Gaudryina laevigata* Franke. Shahin: p. 499, pl. 1, fig. 29
Remarks: this species has a very large robust test; the aperture is placed in the upper part of the apertural face. It is easily distinguished from other species occurring in Egypt.

Tritaxia midwayensis (Cushman)
(Pl. III, Fig. 2)

1926 *Clavulina angularis* d'Orbigny. Plummer: p. 70, pl. 3, figs. 4, 5
1936 *Clavulinoides midwayensis* Cushman: p. 21, pl. 3, figs. 9, 15
1951 *Clavulinoides midwayensis* Cushman. Cushman: p. 8, pl. 2, figs. 10-16
1976 *Tritaxia midwayensis* (Cushman). Aubert and Berggren: p. 411, pl. 1, fig. 16
1982 *Tritaxia midwayensis* (Cushman). Faris: p. 203, pl. 2, Fig. 9
1985 *Tritaxia midwayensis* (Cushman). Luger: p. 77, pl. 3, figs. 7-8

1990 *Pseudoclavulina farafraensis* LeRoy. Shahin: p. 500, pl. 2, fig. 11
Remarks: this species has a fairly large test with a relatively long uniserial part. The outer test surface is rough.

Textulariacea
Eggerellidae
***Dorothia* sp. 1**
(Pl. II, Fig. 4)

cf. 1956 *Dorothia pontoni* Cushman. Said and Kenawy: p. 128, pl. 1, fig. 51
Remarks: a rather indistinct species, that resembles the figured specimen of *D. pontoni* in Said and Kenawy (1956), but differs from the type species in the more regular size increase and less smooth surface.

Miliolacea
Spiroloculinidae
***Spiroloculina* sp. 1**
(Pl. V, Fig. 2)

Remarks: well preserved specimens are rare in Egyptian material; often only the central part of the outer test surface is preserved; the remainder of the test consists of a calcitic mold.

Nodosariacea
Nodosariidae
Frondicularia phosphatica Russo
(Pl. IX, Fig. 2)

1934 *Frondicularia phosphatica* Russo: p. 358, pl. 16, figs. 6-8, 12
1950 *Frondicularia wanneri* Nakkady: p. 685, pl. 89, fig. 23
1976 *Frondicularia phosphatica* Russo. Aubert and Berggren: p. 414, pl. 2, fig. 12
1985 *Frondicularia wanneri* Nakkady. Luger: p. 80, pl. 4, fig. 2
Remarks: the elevated central ridge(s) on both sides of the test and occasional oblique costae lead to easy identification of this large species. *Frondicularia wanneri* Nakkady is considered to be a junior synonym.

Vaginulinidae
***Lenticulina* sp. 1**
(Pl. IX, Fig. 4)

Remarks: the (moderately) compressed test with the sharp sutural costae, the spiral structure, and the marginal carina are very characteristic for this species. It does not seem to have been described earlier from Egypt.

Bolivinacea
Bolivinidae
Loxostomoides applinae (Plummer)
(Pl. VIII, Figs. 1, 2)

1926 *Bolivina applini* Plummer: p. 69, pl. 4, fig. 1
1953 *Loxostomum applinae* (Plummer). LeRoy: p. 37, pl. 8, fig. 1
1956 *Loxostomum clavatum* (Cushman). Said and Kenawy: p. 144, pl. 4, fig. 21
1959 *Loxostomum applinae* (Plummer). Nakkady: p. 459, pl. 2, fig. 1
1976 *Loxostomoides applinae* (Plummer). Aubert and Berggren: p. 420, pl. 4, fig. 11
1982 *Loxostomoides applinae* (Plummer). Faris: p. 211, pl. 5, fig. 2
1985 *Loxostomoides applinae* (Plummer). Luger: p. 106, pl. 7, fig. 1
Remarks: this species is characterized by the crenulated base of the biserially arranged chambers and the longitudinal striae, that may fuse

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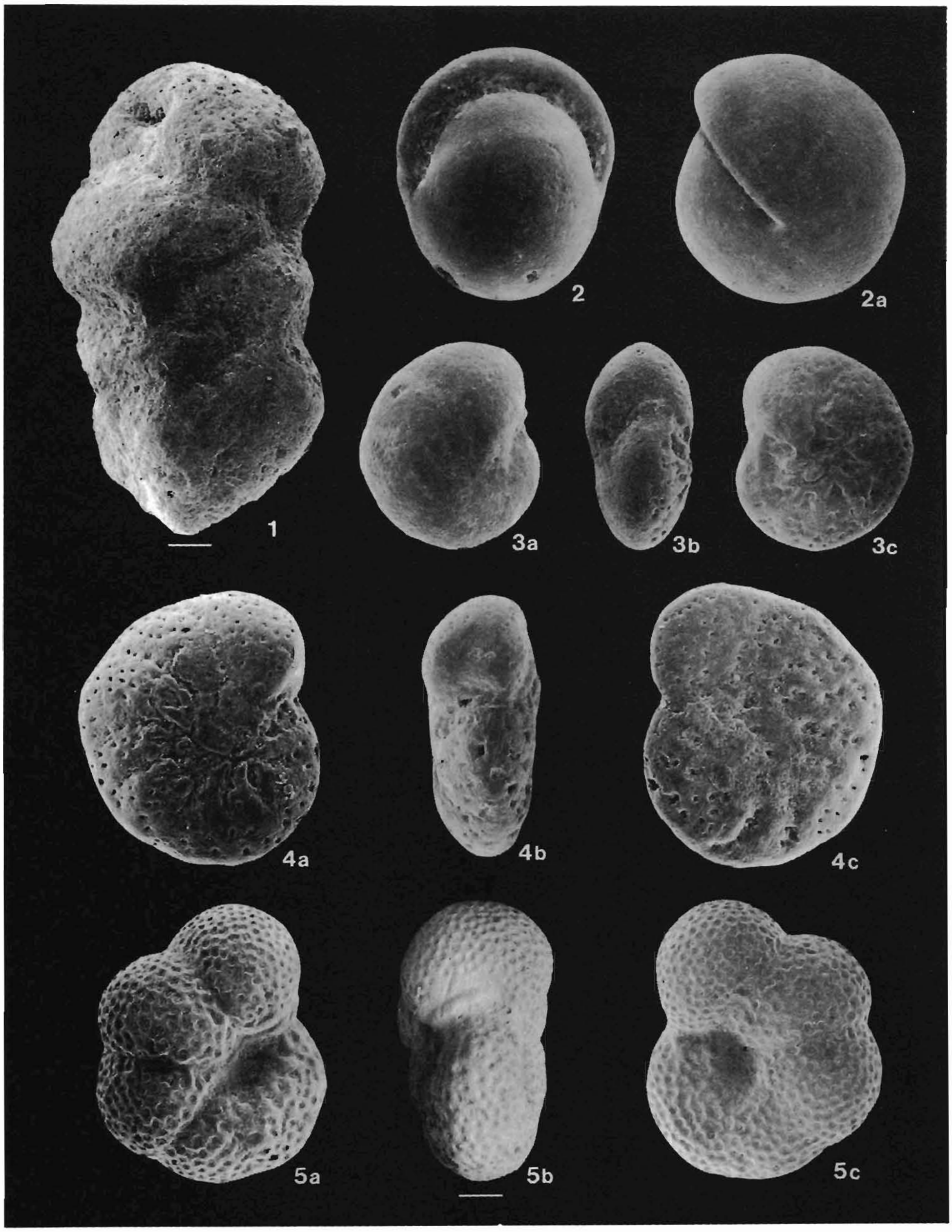
Plate I. Upper bathyal taxa of PA 1.

Fig. 1 *Gaudryina nekhlensis* Said and Kenawy, sample S 736, Wadi Nukhl (X 60)
Fig. 2 *Pullenia coryelli* White, sample S 736, Wadi Nukhl
Fig. 3 *Cibicidoides hyphalus* (Fisher), sample S 735, Wadi Nukhl
Fig. 4 *Gavelinella beccariiformis* (White), sample S 736, Wadi Nukhl
Fig. 5 *Anomalinoides rubiginosus* (Cushman), sample S 737, Wadi Nukhl (X 60)
All magnifications X 120 unless indicated otherwise (bar = 100 μm).

PLATE I



into low costae at the initial part of the test.

Cassidulinacea

Cassidulinidae

Globocassidulina subglobosa Brady

(Pl. III, Fig. 5)

1881 *Cassidulina subglobosa* Brady: p. 60 (not figured)
1884 *Cassidulina subglobosa* Brady: p. 430, pl. 54, fig. 17
1953 *Cassidulina globosa* Hantken. LeRoy: p. 17, pl. 6, figs. 4-5
1976 *Cassidulina globosa* Hantken. Aubert and Berggren: p. 427, pl. 7, fig. 10
Remarks: a rather small, tightly coiled species, that has also been referred to as the much more spherical *Cassidulina globosa*.

Turrilinacea

Stainforthiidae

Stainforthia farafraensis (LeRoy)

(Pl. VIII, Figs. 3, 4)

1953 *Neobulimina farafraensis* LeRoy: p. 39, pl. 8, figs. 3-4
Remarks: this smooth species has a very short triserial part and rather straight horizontal sutures. Specimens are often compressed due to sediment compaction.

Stainforthia sp. 1

(Pl. VIII, Fig. 5)

Remarks: this species has a very delicately ornamented earlier part and a smooth later part of the test.

Turrilinidae

Turrilina brevispira ten Dam

(Pl. III, Fig. 4)

1944 *Turrilina brevispira* ten Dam: p. 110, pl. 3, fig. 14
? 1953 *Bulimina esnaensis* LeRoy: p. 20, pl. 6, figs. 11-12
1983 *Turrilina robertsi* (Howe and Ellis). Tjalsma and Lohmann: p. 37, pl. 14, fig. 5
1986 *Turrilina brevispira* ten Dam. Van Morkhoven: p. 305, pl. 100
1987 *Turrilina brevispira* ten Dam. Revets: p. 325, pl. 5, figs. 1-5, pl. 6, figs. 1-4
1991 *Turrilina robertsi* (Howe and Ellis). Katz and Miller: pl. 3, fig. 4
1991 *Turrilina brevispira* ten Dam. Nomura: p. 23, pl. 1, fig. 15
Remarks: the slit-like aperture with a short perpendicular extension up the infolded apertural face and its glossy appearance, distinguish this species from all *Bulimina* in the Egyptian material. Possibly *Buliminella browni* (Finlay, 1940) is a senior synonym; a comparative study of the holotypes is required.

Buliminacea

Siphogenerinoididae

Siphogenerinoides eleganta (Plummer)

(Pl. V, Fig. 5)

1926 *Siphogenerina eleganta* Plummer: p. 126, pl. 8, fig. 1
1953 *Siphogenerinoides eleganta* (Plummer). LeRoy: p. 49, pl. 2, figs. 20-21
1976 *Siphogenerinoides eleganta* (Plummer). Aubert and Berggren: p. 421, pl. 5, fig. 3
Remarks: in large specimens the biserial arrangement is followed by a uniserial part. Surface ornamentation in the specimens from

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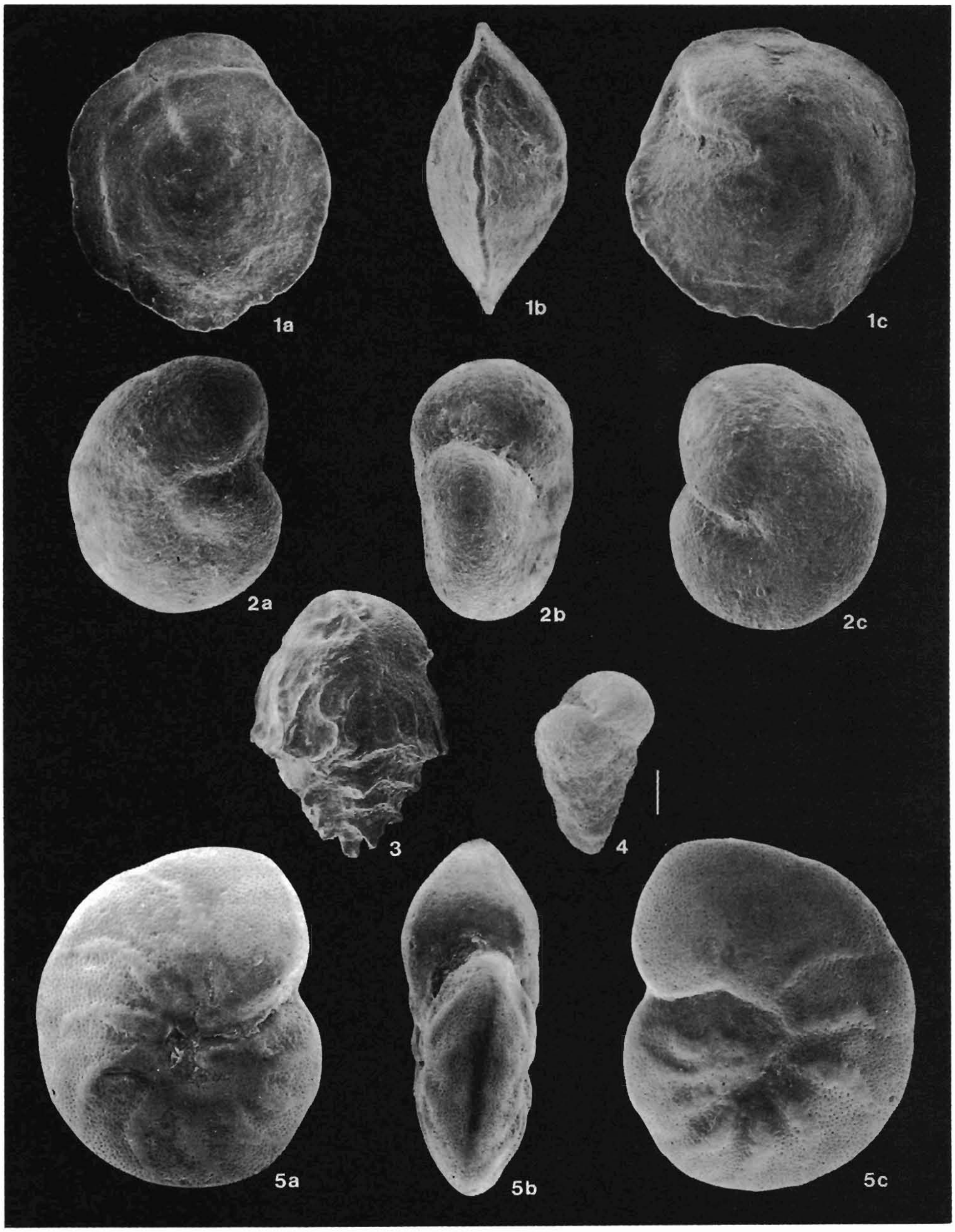
Plate II. Figs. 1-3 Upper bathyal taxa of PA 1; Figs. 4, 5 outer neritic taxa of PA 4

Fig. 1 *Nuttallides truempyi* (Nuttall), sample S 734, Wadi Nukhl
Fig. 2 *Gyroidinoides* sp. 1, sample S 734, Wadi Nukhl
Fig. 3 *Bulimina trinitatensis* Cushman and Jarvis, S 734, Wadi Nukhl
Fig. 4 *Dorothia* sp. 1, sample K/P + 65 m, Gebel Oweina (X 60)
Fig. 5 *Anomalinoides* cf.? *midwayensis* (Plummer), sample K/P + 68 m, Gebel Oweina
All magnifications X 120 unless indicated otherwise (bar = 100 µm).

PLATE II



Bir Inglisi I is coarsely punctate and slightly rugose. This ornamentation might be more pronounced than in the type species. This species is very rare in deeper sites

Siphogenerinoides cf. eleganta (Plummer)
(Pl. V, Fig. 6)

cf. 1926 *Siphogenerina eleganta* Plummer: p. 126, pl. 8, fig. 1
Remarks: This taxon is much smoother and more slender than *S. eleganta* from Bir Inglisi I, but it does resemble Plummer's species. Very low costae are present on the initial part of the test. Only observed in the Eocene of deeper sites

Buliminidae
Bulimina callahani Galloway and Morrey
(Pl. III, Fig. 3)

1931 *Bulimina callahani* Galloway and Morrey: p. 350, pl. 40, fig. 6
1953 *Bulimina rugifera* Glaessner. LeRoy: p. 21, pl. 6, figs. 13-14
1976 *Bulimina* cf. *farafraensis* LeRoy. Aubert and Berggren: p. 422, pl. 5, fig. 5
1983 *Bulimina callahani* Galloway and Morrey. Tjalsma and Lohmann: p. 24, pl. 11, figs. 6, 7
1986 *Bulimina callahani* Galloway and Morrey. Van Morkhoven et al.: p. 322, pl. 105
Remarks: very characterisitic are the closely spaced thin, irregular and branching costae extending from the initial part up to the last whorl. The lower part of the chambers in the last whorl are punctate, whereas the upper part is smooth and almost without pores. Judging from the type description of the species, it seems that the Egyptian specimens are more similar to the Mexican holotype than figured specimens from deep-sea deposits. The latter specimens have a strong reticulate development with a minor degree of development of costae. Possibly, these types are different eco-phenotypes of one species, with the costate variety common in shallower continental margin deposits.

Bulimina farafraensis LeRoy
(Pl. V, Fig. 4)

1953 *Bulimina farafraensis* LeRoy: p. 21, pl. 7, figs. 26-27
1982 *Bulimina* cf. *instabilis* Cushman and Parker. Faris (partim): p. 212, pl. 5, fig. 6 (not fig. 7)
Remarks: very distinct rounded triangular species with large branching costae over the entire test and with distinct pores except in the upper part of the chambers of the last whorl.

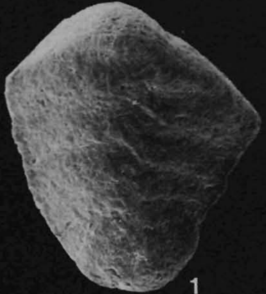
Bulimina midwayensis Cushman and Parker
(Pl. V, Fig. 3)

1926 *Bulimina aculeata* d'Orbigny. Plummer: p. 73, pl. 4, fig. 3
1936b *Bulimina arkadelphiana* Cushman and Parker var. *midwayensis* Cushman and Parker: p. 42, pl. 7, figs. 9-10
1953 *Bulimina inflata* Seguenza. LeRoy: p. 21, pl. 8, fig. 25
1956 *Bulimina arkadelphiana midwayensis* Cushman and Parker. Said and Kenawy: p. 142, pl. 4, fig. 11
1959 *Bulimina arkadelphiana* Cushman and Parker var. *midwayensis* Cushman and Parker. Nakkady: p. 458, pl. 1, fig. 9
1976 *Bulimina midwayensis* Cushman and Parker. Aubert and Berggren: p. 422, pl. 5, fig. 7
1982 *Bulimina midwayensis* Cushman and Parker. Faris: p. 213, pl. 5, figs. 3-5

Plate III. Outer neritic-upper bathyal taxa of PA 2.

Fig. 1 *Spiroplectinella esnaensis* (LeRoy), sample S 736, Wadi Nukhl
Fig. 2 *Tritaxia midwayensis* (Cushman), sample S 736, Wadi Nukhl (X 60)
Fig. 3 *Bulimina callahani* Galloway and Morrey, sample K/P + 92 m, Gebel Oweina
Fig. 4 *Turrilina brevispira* Ten Dam, sample K/P + 92 m, Gebel Oweina
Fig. 5 *Globocassidulina subglobosa* (Brady) sample K/P + 80 m, Gebel Oweina
Fig. 6 *Anomalinoides affinis* (Hantken), sample S 738, Wadi Nukhl
Fig. 7 *Angulogavelinella avnimelechi* (Reiss), sample S 736, Wadi Nukhl
All magnifications X 120 unless indicated otherwise (bar = 100 µm).

PLATE III



1

2

3

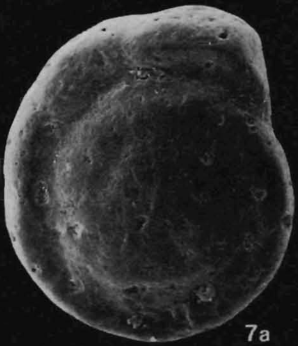
4

5

6a

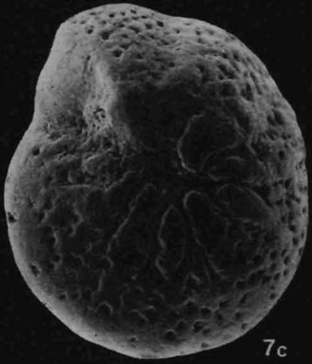
6b

6c



7a

7b



7c

1985 *Bulimina midwayensis* Cushman and Parker. Luger: p. 106, pl. 7, fig. 7

Remarks: the ornamentation of this species is subject to a considerable amount of variation; often only short spines at the base of the chambers are formed, whereas in other specimens they merge into short irregular costae on the chambers.

***Bulimina quadrata-ovata* plexus**
(Pl. VIII, figs. 6, 7)

1926 *Bulimina quadrata* Plummer: p. 72, pl. 4, figs. 4, 5
1953 *Bulimina pupoides* d'Orbigny. LeRoy: p. 22, pl. 8, fig. 21
1956 *Bulimina kickapooensis* Cole. Said and Kenawy: p. 142, pl. 4, fig. 12
1976 *Bulimina quadrata* Plummer. Aubert and Berggren: p. 422, pl. 5, fig. 9
1982 *Bulimina quadrata* Plummer. Faris: p. 214, pl. 5, fig. 8
1985 *Bulimina quadrata* Plummer. Luger: p. 107, pl. 7, fig. 6
1985 *Bulimina reussi* Morrow. Luger: p. 107, pl. 7, fig. 7

Remarks: this plexus comprises all smooth finely perforate species with a "globular" shape. It appeared to be rather difficult to assign all encountered specimens within this group to various species in a consistent way, since the specimens are often compressed and poorly preserved.

Bulimina trinitatensis Cushman and Jarvis
(Pl. II, Fig. 3)

1928 *Bulimina trinitatensis* Cushman and Jarvis: p. 102, pl. 14, fig. 12
1946 *Bulimina trinitatensis* Cushman and Jarvis. Cushman: p. 124, pl. 52, fig. 9
1956 *Bulimina stokesi* Cushman and Renz. Said and Kenawy: p. 143, pl. 4, fig. 14
1976 *Bulimina trinitatensis* Cushman and Jarvis. Aubert and Berggren: p. 423, pl. 5, fig. 12
1983 *Bulimina trinitatensis* Cushman and Jarvis. Tjalsma and Lohmann: p. 7, pl. 3, figs. 3-4, pl. 14, fig. 1
1986 *Bulimina trinitatensis* Cushman and Jarvis. Van Morkhoven: p. 299, pls. 98A, B
1990 *Bulimina trinitatensis* Cushman and Jarvis. Thomas: p. 589, pl. 2, fig. 7
1991 *Bulimina trinitatensis* Cushman and Jarvis. Nomura: p. 21, pl. 1, fig. 10

Remarks: superficially this large robust species somewhat resembles *B. midwayensis*, from which it is however easily distinguishable by the costae fusing into a rim at the base of the chambers and by the coarsely pitted surface between the costae.

Discorbacea
Bagginidae
Valvulineria scrobiculata (Schwager)
(Pl. VIII, Figs. 8)

1883 *Anomalina scrobiculata* Schwager: p. 129, pl. 29, fig. 18
1950 *Anomalina scrobiculata* Schwager var. *esnehensis* Nakkady: p. 691, pl. 90, figs. 33, 34
1953 *Valvulineria scrobiculata* (Schwager). LeRoy: p. 53, pl. 9, figs. 18-20
1959 *Valvulineria scrobiculata* (Schwager). Nakkady: p. 460, pl. 2, fig. 5
1985 *Gavelinella scrobiculata* (Schwager). Luger: p. 112, pl. 9, figs. 9, 10

Remarks: a very distinct, large species with large pores on both sides, except around the umibilicus, which is surrounded by nodes of clear shell material. The umbilical flaps do not entirely cover the umbilicus. In Tunisia two different species are recorded under the same name (Aubert and Berggren, 1976; Salaj et al., 1976). It is rather difficult to decide which species fits better with the type species. The

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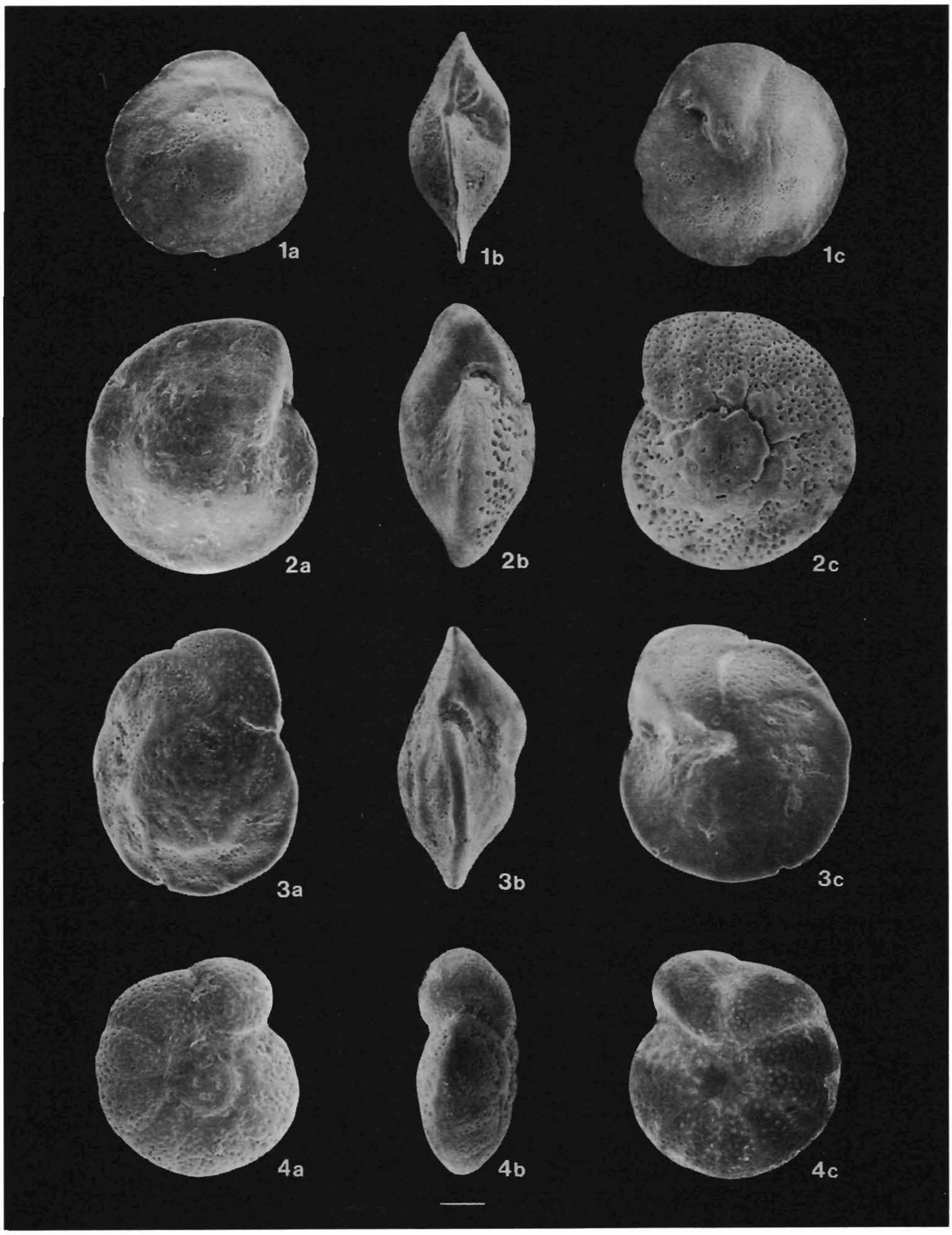
Plate IV. Outer neritic-upper bathyal taxa of PA 2

Fig. 1 *Osangularia plummerae* Brotzen, sample K/P +80 m, Gebel Oweina
Fig. 2 *Cibicidoides pseudoacutus* (Nakkady), sample K/P + 28 m, Gebel Oweina
Fig. 3 *Cibicidoides pharaonis* (LeRoy), sample K/P + 71 m, Gebel Oweina
Fig. 4 *Cibicidoides* cf. *hyphalus* (Fisher), sample S 734, Wadi Nukhl (X 60)
All magnifications X 120 unless indicated otherwise (bar = 100 μm).

PLATE IV



Tunesian specimens of Aubert and Berggren (1976; lower Paleocene) appear much more compressed, whereas the Egyptian specimens (upper Paleocene-lower Eocene) are more inflated than Schwager's holotype. The specimens referred to as this species in Salaj et al. (1976), are regarded in this paper as *Anomalinoides aegyptiacus* (LeRoy). Schwager described this species from the Eocene of the Libyan Desert

Discorbinellacea

Parrelloididae

Cibicidoides decoratus (LeRoy)
(Pl. X, Fig. 3)

1953 *Cibicides decoratus* LeRoy: p. 23, pl. 6, figs. 15-17
Remarks: a large strongly compressed species, with a thin marginal keel and large pores on both sides. The spiral side is almost entirely evolute and does not develop a spiral slit. Clear shell material thickens the center of both sides slightly.

Cibicidoides hyphalus (Fisher)
(Pl. I, Fig. 3)

1969 *Anomalinoides hyphalus* Fisher: p. 197, pl. 3
1983 *Gavelinella hyphalus* (Fisher). Tjalsma and Lohmann: p. 13, pl. 4, figs. 8, 9; pl. 7, fig. 11
1991 *Cibicidoides hyphalus* (Fisher). Katz and Miller: pl. 2, figs. 4, 5
1991 *Cibicidoides hyphalus* (Fisher). Nomura: p. 22, pl. 3, fig. 9
Remarks: the holotype figure of this species is somewhat confusing, since it suggests the presence of a slightly evolute spiral structure in the umbilical area. However, Fisher (1969) mentions an almost completely involute umbilical side with a "..deep umbilicus obscured by triangular flaplike extensions of later chambers, and by a sometimes imperfectly developed umbilical plug.". These features are clearly present in specimens figured by Tjalsma and Lohmann (1983). Specimens figured in Van Morkhoven et al., (1986) show a very distinct spiral structure and slit bordered by small umbilical flaps. Both morphologies have been observed in North African material. They do not show intergradation. A search for the holotype specimen in the Sedgwick Museum (Cambridge, England) revealed that it was never actually deposited in the museum's collection. We think that the specimens as depicted in Tjalsma and Lohmann (1983) fit best with the holotype. We refer to the specimens in Van Morkhoven et al. (1986) as *C.* cf. *hyphalus.*

Cibicidoides cf. hyphalus (Fisher)
(Pl. IV, Fig. 4)

cf. 1969 *Anomalinoides hyphalus* Fisher: p. 197, pl. 3
1986 *Cibicidoides hyphalus* (Fisher). Van Morkhoven et al.: p. 359, pl. 116
Remarks: see discussion of *C. hyphalus*

Cibicidoides pharaonis (LeRoy)
(Pl. IV, Fig. 3)

1953 *Cibicides pharaonis* LeRoy: p. 24, pl. 7, figs. 9-11
Remarks: the fairly large smooth test has an almost flat spiral side and a high convex umbilical side. The sutures on the spiral side are

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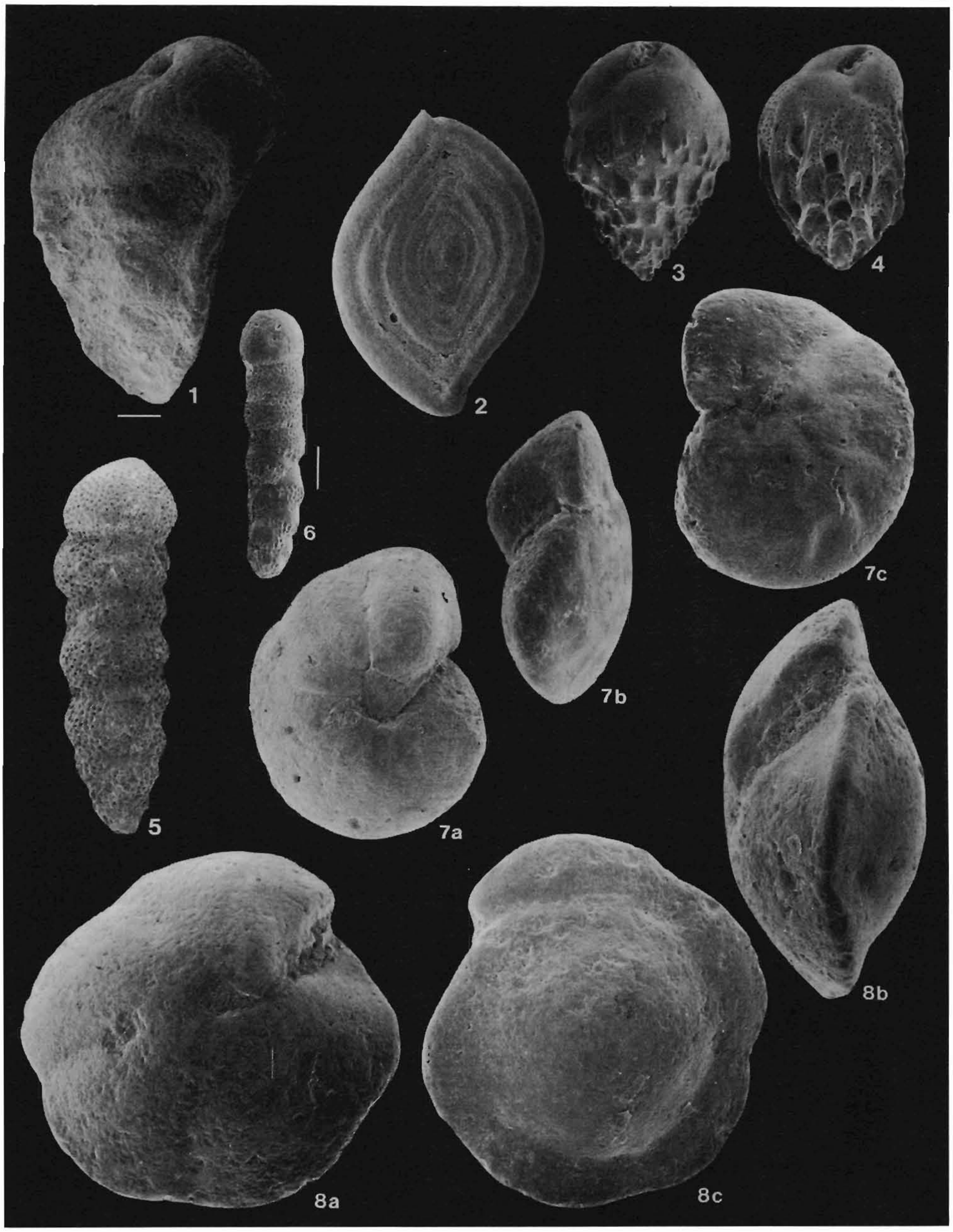
Plate V. Middle neritic-upper bathyal taxa of PA 3.

Fig. 1 *Gaudryina* cf. *ellisorae* Cushman, sample S 738, Wadi Nukhl (X 60)
Fig. 2 *Spiroloculina* sp. 1, sample K/P + 80 m, Gebel Oweina
Fig. 3 *Bulimina midwayensis* Cushman and Parker, K/P + 80 m, Gebel Oweina
Fig. 4 *Bulimina farafraensis* LeRoy, sample K/P + 80 m, Gebel Oweina
Fig. 5 *Siphogenerinoides eleganta* (Plummer), sample S 1025, Bir Inglisi I
Fig. 6 *Siphogenerinoides* cf. *eleganta* (Plummer), sample S 738, Wadi Nukhl (X 60)
Fig. 7 *Valvalabamina depressa* (Reuss), sample S 1016, Bir Inglisi I
Fig. 8 *Oridorsalis plummerae* (Cushman), sample S 737, Wadi Nukhl
All magnifications X 120 unless indicated otherwise (bar = 100 μm).

PLATE V



raised, oblique and slightly curved, whereas the sutures on the umbilical side are flushed and strongly curved. The spiral side is almost entirely evolute, but the aperture does not extend along earlier chambers to form a spiral slit as in *C. alleni*. Pores on the spiral side are larger and more abundant than on the umbilical side.

Cibicidoides pseudoacutus (Nakkady)
(Pl. IV, Fig. 2)

1950 *Anomalina pseudoacuta* Nakkady: p. 691, pl. 90, figs. 29-32
1976 *Cibicides commatus* Morozova. Salaj et al.: p. 158, pl. 11, figs. 1, 2
1982 *Cibicidoides alleni* (Plummer). Faris: p. 217, pl. 6, fig. 5
1985 *Cibicidoides constrictus* (Hagenow). Luger: p. 111, pl. 9, figs. 1, 2
Remarks: a large taxon with a very characteristic semi-involute spiral side, of which the center is extremely pronounced by secondary calcite. This spiral plug is surrounded by a deep slit and flap-like extensions from the chambers of the final whorl. These features may suggest a closer affinity to *Anomalinoides*; we get the impression, however, that this species is merely a more tightly coiled representative of *Cibicidoides*.

Cibicidoides* cf. *pseudoperlucidus (Bykova)
(Pl. VI, Fig. 1)

1983 *Cibicidoides* cf. *pseudoperlucidus* (Bykova). Tjalsma and Lohmann: p. 9, pl. 6 , fig. 9
Remarks: since most other *Cibicidoides* species are transparent and dull, this species is very characteristic due to its smooth, glossy, white appearance. The test is usually equally convex and perforate on both sides. The spiral side is almost entirely evolute and possesses a short spiral slit. Sutures on both sides are flush with the test surface. The test is also smaller than most other *Cibicidoides*.

Cibicidoides succedens (Brotzen)
(Pl. VI, Fig. 2)

1948 *Cibicides succedens* Brotzen: p. 80,pl. 12, figs. 1, 2
1976 *Cibicidoides succedens* (Brotzen). Aubert and Berggren: p. 432, pl. 11, fig. 1
Remarks: a concavo-convex to plano-convex species with large pores on both sides. Sutures are thickened, oblique, and curved on the spiral side. Approximately semi-involute on the spiral side, although this character may vary. Variability in test shape might be due to an attached epibenthic mode of life. In view of this morphological variability, a rather wide taxonomical concept is employed.

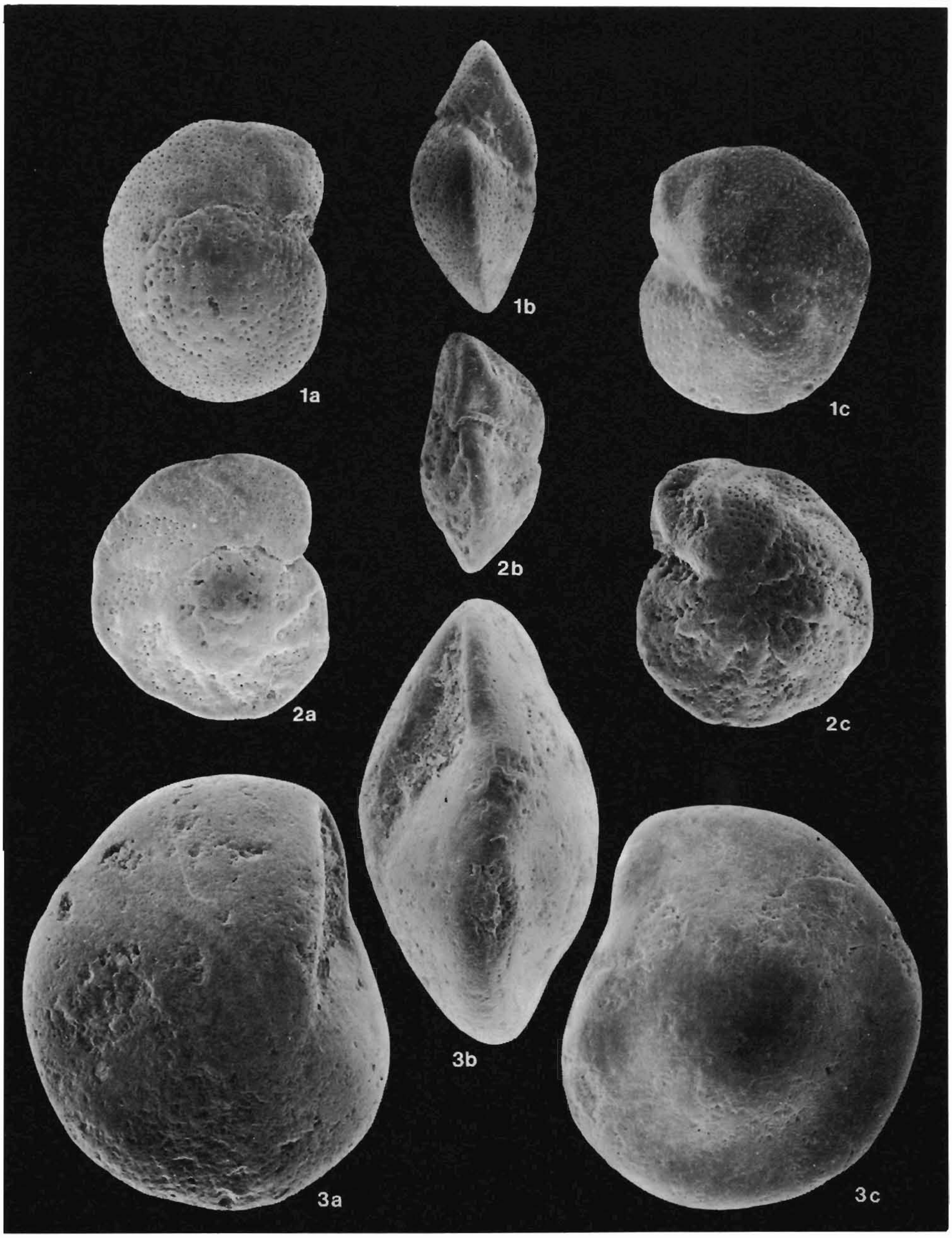
Asterigerinacea
Epistomariidae
Nuttallides truempyi (Nuttall)
(Pl. II, Fig. 1)

1930 *Eponides truempyi* Nuttall: p. 287, pl. 24, figs. 9, 13, 14
1976 *Nuttallides truempyi* (Nuttall). Aubert and Berggren: p. 425, pl. 6, fig. 5
1983 *Nuttallides truempyi* (Nuttall). Tjalsma and Lohmann: p. 17, pl. 6, fig. 4; pl. 17, figs. 4, 5; pl. 21, figs. 1-4
1986 *Nuttallides truempyi* (Nuttall). Van Morkhoven et al.: p. 288, pls. 96A-D
1990 *Nuttallides truempyi* (Nuttall). Thomas: p. 590, pl. 3, figs. 1, 2
1991 *Nuttallides truempyi* (Nuttall). Katz and Miller: pl. 4, figs. 7, 8
1991 *Nuttallides truempyi* (Nuttall). Nomura: p. 22, pl. 2, figs. 7, 9, 10
Remarks: a very distinct species with an almost planoconvex test and very narrow whorls. The umbilical-interiomarginal aperture is borderd by a slender lip at the base of the slightly curved apertural face. Many specimens have a well developed transparent umbilical boss.

Plate VI. Middle neritic-upper bathyal taxa of PA 3.

Fig. 1 *cibicidoides* cf. *pseudoperlucidus* (Bykova), sample S 1016, Bir Inglisi I
Fig. 2 *Cibicidoides succedens* (Brotzen), sample S 1016, Bir Inglisi I
Fig. 3 *Alabamina midwayensis* Brotzen, sample S 737, Wadi Nukhl
All magnifications X 120.

PLATE VI



Nonionacea

Nonionidae

Pullenia coryelli White

(Pl. I, Fig. 2)

1929 *Pullenia coryelli* White: p. 56, pl. 5, fig. 22
1946 *Pullenia coryelli* White. Cushman: p. 147, pl. 60, figs. 10, 11
1983 *Pullenia coryelli* White. Tjalsma and Lohmann: p. 18, pl. 5, fig. 5
1990 *Pullenia coryelli* White. Thomas: p. 590, pl. 3, fig. 6
1991 *Pullenia coryelli* White. Nomura: p. 22, pl. 4, fig. 9
Remarks: a very distinct almost sperical species with 5-6 chambers per whorl.

Chilostomellacea

Alabaminidae

Alabamina midwayensis Brotzen

(Pl. VI, Fig. 3)

1926 *Pulvinulina exigua* H.B. Brady. Plummer: p. 150, pl. 11, fig. 3
1948 *Alabamina midwayensis* Brotzen: p. 99, pl. 16, figs. 1, 2
1956 *Alabamina wilcoxensis* Toulmin. Said and Kenawy: p. 152, pl. 6, fig. 18
1959 *Alabamina midwayensis* Brotzen. Nakkady: p. 460, pl. 2, fig. 2
1976 *Alabamina midwayensis* Brotzen. Aubert and Berggren: p. 428, pl. 8, fig. 3
1985 *Alabamina midwayensis* Brotzen. Luger: p. 110, pl. 7, figs. 17, 18
Remarks: convexity of the spiral side is rather variable. In specimens with a clean aperture without sediment infill, an apertural lip as well as a rim erecting from the previous whorl below the aperture are visible.

Valvalabamina depressa (Alth)

(Pl. V, Fig. 7)

1850 *Rotalina depressa* Alth: p. 266, pl. 13, fig. 21
1946 Gyroidina depressa (Alth). Cushman: p. 139, pl. 58, figs. 1-4
1953 Gyroidina orbicularis d'Orbigny. LeRoy: p. 35, pl. 7, figs. 12-14
Remarks: we are uncertain whether Alth's species is the same as ours; the specimens depicted by Cushman (1946) bear great similarity. This species is characterized by its entirely evolute spiral side with slightly raised oblique, curved sutures; the umbilical sutures are almost straight and sometimes slightly incised around the umbilicus, which is covered by an umbilical flap in well preserved specimens. The apertural face is inflexed.

Valvalabamina planulata (Cushman and Renz)

(Pl. VII, Fig. 3)

1941 *Gyroidina planulata* Cushman and Renz: p. 23, pl. 4, fig. 1
1953 *Gyroidina planulata* Cushman and Renz. LeRoy: p. 35, pl. 11, figs. 1-3
1956 *Gyroidina planulata* Cushman and Renz. Said and Kenawy: p. 149, pl. 5, fig. 8
1959 *Valvulineria brotzeni* Nakkady and Talaat (in Nakkady, 1959): p. 460, pl. 7, fig. 2
Remarks: this species has a fairly large, flattened, and smooth test. Spiral and umbilical sutures are flush and only slightly curved; the apertural face is inflexed.

Osangulariidae

Osangularia plummerae Brotzen

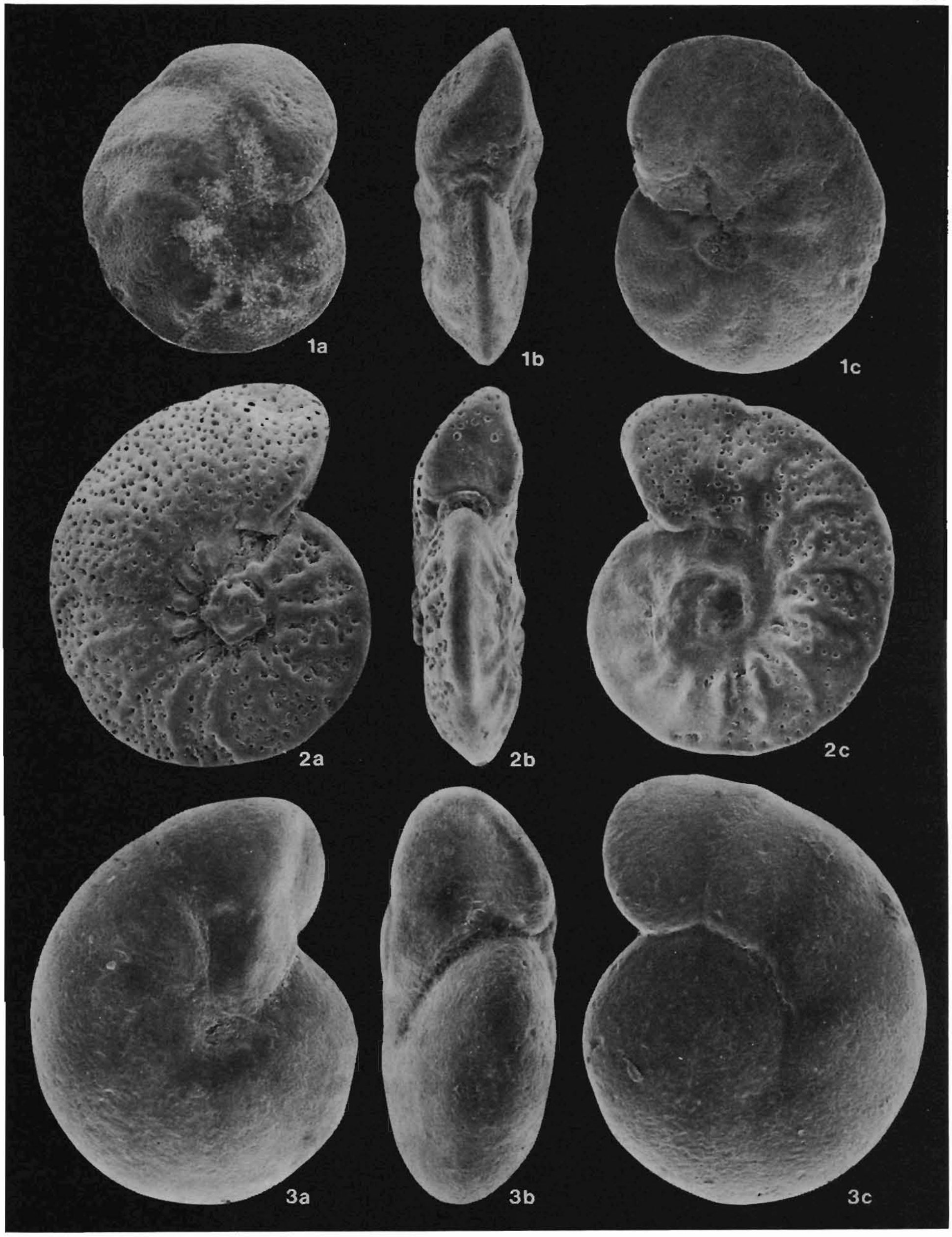
(Pl. IV, Fig. 1)

1926 *Truncatulina culter* (Parker and Jones). Plummer: p. 147, pl. 10, fig. 1; pl. 15, fig. 2
1940 *Osangularia plummerae* Brotzen: p. 30, text-fig. 8

Plate VII. Middle neritic-upper bathyal of taxa PA3.

Fig. 1 *Anomalinoides zitteli* (LeRoy), sample S 741, Wadi Nukhl
Fig. 2 *Anomalinoides praeacutus* (Vasilenko), sample K/P + 80 m, Gebel Oweina
Fig. 3 *Valvalabamina planulata* (Cushman and Renz), sample S 734, Wadi Nukhl
All magnifications X 120.

PLATE VII



1976 *Osangularia plummerae* Brotzen. Aubert and Berggren: p. 429, pl. 8, fig. 5
1985 *Osangularia plummerae* Brotzen. Luger: p. 110, pl. 8, fig. 6
Remarks: this species is usually equally convex. Oblique sutures on the spiral side are sometimes slightly raised; the straight to gently curved sutures on the umbilical side are flush. The apertural features of this genus are very distinct.

Oridorsalidae
Oridorsalis plummerae (Cushman)
(Pl. V, Fig. 8)

1926 *Truncatulina tenera* H. B. Brady. Plummer: 146, pl. 9, fig. 5
1948 *Eponides plummerae* Cushman: p. 44, pl. 8, fig. 9
1951 *Eponides plummerae* Cushman. Cushman: p. 52, pl. 14, figs. 20, 23
1953 *Eponides lunatus* (Brotzen). LeRoy: p. 30, pl. 9, figs. 24-26
1956 *Eponides lunatus* (Brotzen). Said and Kenawy: p. 148, pl. 5, fig. 3
1956 *Eponides mariei* Said and Kenawy: p. 148, pl. 5, fig. 2
1956 *Eponides sigali* Said and Kenawy: p. 148, pl. 5, fig. 6
1976 *Eponides plummerae* Cushman. Aubert and Berggren: p. 426, pl. 7, fig. 4
1985 *Alabamina obtusa* (Burrows and Holland). Luger: p. 110, pl. 8, figs. 4, 5
Remarks: we believe this species shows a high degree of morphological variability with respect to size, convexity of both sides, angularity of the margin, and the shape of the sutures. Apertural features (sometimes supplementary apertures visible on the spiral side) point to an assignment of this species to *Oridorsalis* and not to *Eponides* (see also Hauser and Grünig, 1993).

Heterolepidae
Anomalinoides aegyptiacus (LeRoy)
(Pl. X, Fig. 1)

1953 *Anomalina aegyptiaca* LeRoy: p. 17, pl. 7, figs. 21-23
1976 *Valvulineria scrobiculata* (Schwager). Salaj et al.: p. 156, pl. 8, figs. 1, 2
Remarks: a flattened bi-umbilicate species; both sides are partially involute, the umbilical side slightly more than the spiral side. In apertural view the periphery is rounded to bluntly acute. The suture between the last two chambers is depressed, the earlier sutures are usually flush, but may also be distinctly raised (see also discussion of *V. scrobiculata*).

Anomalinoides* cf. *aegyptiacus (LeRoy)
(Pl. X, Fig. 2)

cf. 1953 *Anomalina aegyptiaca* LeRoy: p. 17, pl. 7, figs. 21-23
Remarks: differs from *A. aegyptiacus* in its larger, more robust and less flattened test, and the higher degree of morphological variability; large plano-convex specimens are also included into this concept. It seems, however, to be intergrading with *A. aegyptiacus*.

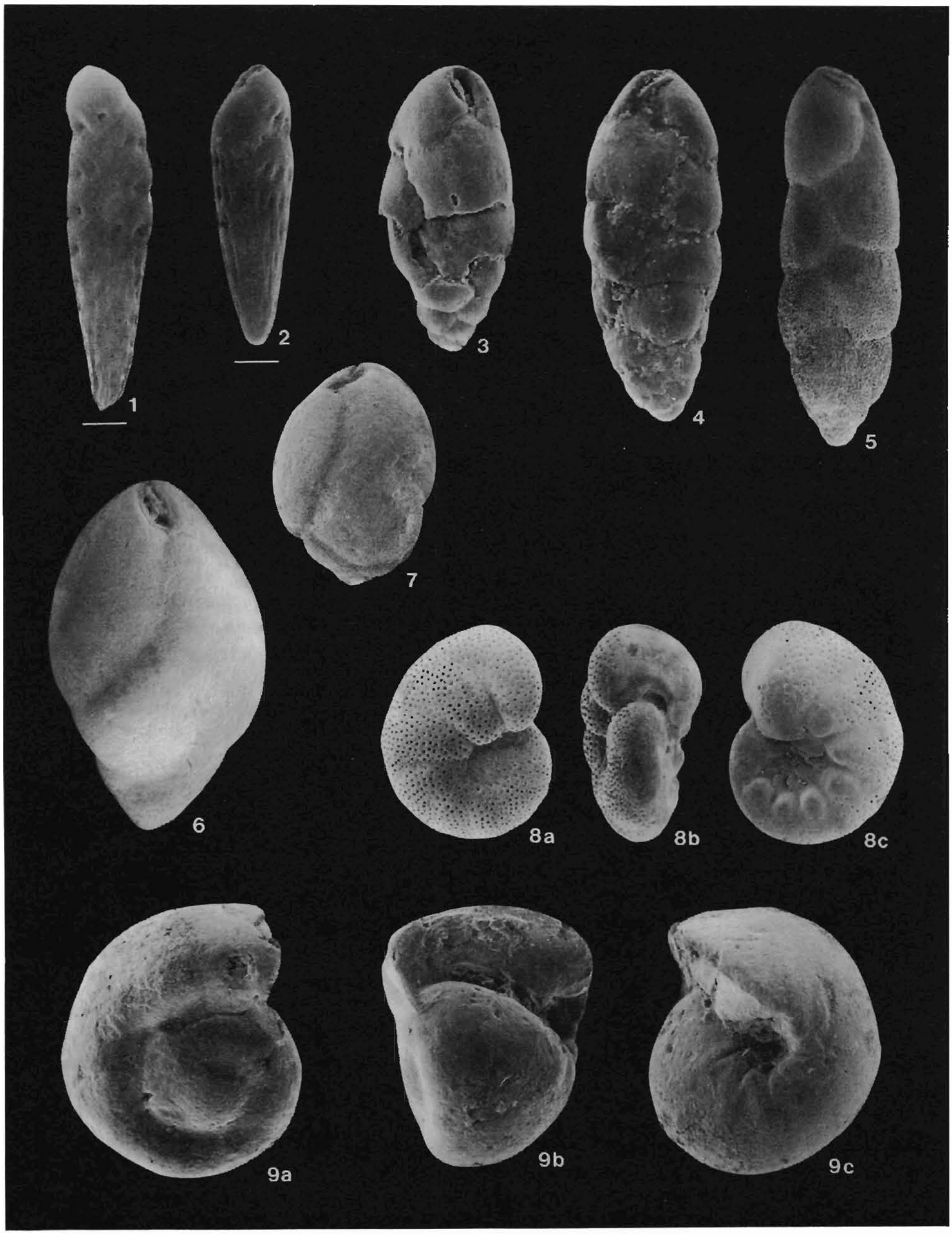
Anomalinoides affinis (Hantken)
(Pl. III, Fig. 6)

1875 *Pulvinulina affinis* Hantken: p. 78, pl. 10, fig. 6

Plate VIII. Middle-outer neritic taxa of PA 5.

Fig. 1 *Loxostomoides applinae* (Plummer), sample S 1025, Bir Inglisi I (X 60)
Fig. 2 *Loxostomoides applinae* (Plummer), sample K/P + 69 m, Gebel Oweina (X 60)
Fig. 3 *Stainforthia farafraensis* (LeRoy), sample S 1032, Bir Inglisi I
Fig. 4 *Stainforthia farafraensis* (LeRoy), sample S 1372, Wadi Nukhl
Fig. 5 *Stainforthia* Sp. 1, sample K/P + 80 m, Gebel Oweina
Fig. 6 *Bulimina quadrata-ovata* plexus, sample K/P + 69 m, Gebel Oweina
Fig. 7 *Bulimina quadrata-ovata*, plexus sample S 1025, Bir Inglisi I
Fig. 8 *Valvulineria scrobiculata* (Schwager), sample K/P + 80 m, Gebel Oweina
Fig. 9 *Gyroidinoides girardanus* (Reuss), sample S 1016, Bir Inglisi I
All magnifications X 120 unless indicated otherwise (bar = 100 μm).

PLATE VIII



1926 *Truncatulina welleri* Plummer: p. 143, pl. 9, fig. 6
1953 *Anomalina desertorum* LeRoy: p. 17, pl. 7, figs. 18-20
1976 *Anomalinoides welleri* (Plummer). Aubert and Berggren: p.430, pl. 9, fig. 5
1976 *Anomalinoides affinis* (Hantken). Salaj et al.: p. 162, pl. 9, figs. 1, 2
1982 *Gavelinella velascoensis* (Cushman). Faris: p. 218, pl. 6, fig. 12

Remarks: this species has a distinct flattened, biumbilicate, and biconvex test. The spiral side is semi-involute, the umbilical side is completely involute. The open umbilicus is surrounded by indistinct umbilical flaps. Near the periphery the large pores are aligned into elongate pore depressions. The limbate sutures are flush with the test surface. In the studied material this species can not be confused with another species. We follow Salaj et al. (1976) in regarding *A. welleri* as a junior synonym of *A. affinis*

Anomalinoides* (cf.?) *midwayensis (Plummer)
(Pl. II, Fig. 5)

(cf.?) 1926 *Truncatulina midwayensis* Plummer: p. 141, pl. 9, fig. 7; pl. 15, fig. 3

Remarks: a large *Anomalinoides* with strongly raised limbate, tapering sutures. The spiral side is semi-involute, whereas the umbilical side is completely involute. The aperture is extra-umbilical and does not reach the peripheral margin. Pores are relatively small. Although our specimens bear great similarity with the holotype, they appear rather different from the ones depicted in Berggren and Aubert (1975). Therefore, we are uncertain whether this species is conspecific with *A. midwayensis*.

Anomalinoides praeacutus (Vasilenko)
(Pl. VII, Fig. 2)

1950 *Anomalina praeacuta* Vasilenko: p. 208, pl. 5, figs. 2, 3
1976 *Anomalinoides praeacuta* (Vasilenko). Aubert and Berggren: p. 430, pl. 9, fig. 2; pl. 12, fig. 5

Remarks: a very distinct species with considerable morphological variability. The spiral side is always semi-involute and may develop a transparent plug which covers the earlier whorls. The sutures on this side are flush to strongly raised and large pores are confined to the the later half of the last whorl. The umbilical side has a distinct irregular plug surrounded by umbilical flaps. The sutures on this side are flush to slightly raised and large pores are evenly distributed over the entire surface. The aperture is extra-umbilical to peripheral and is covered by a distinct lip.

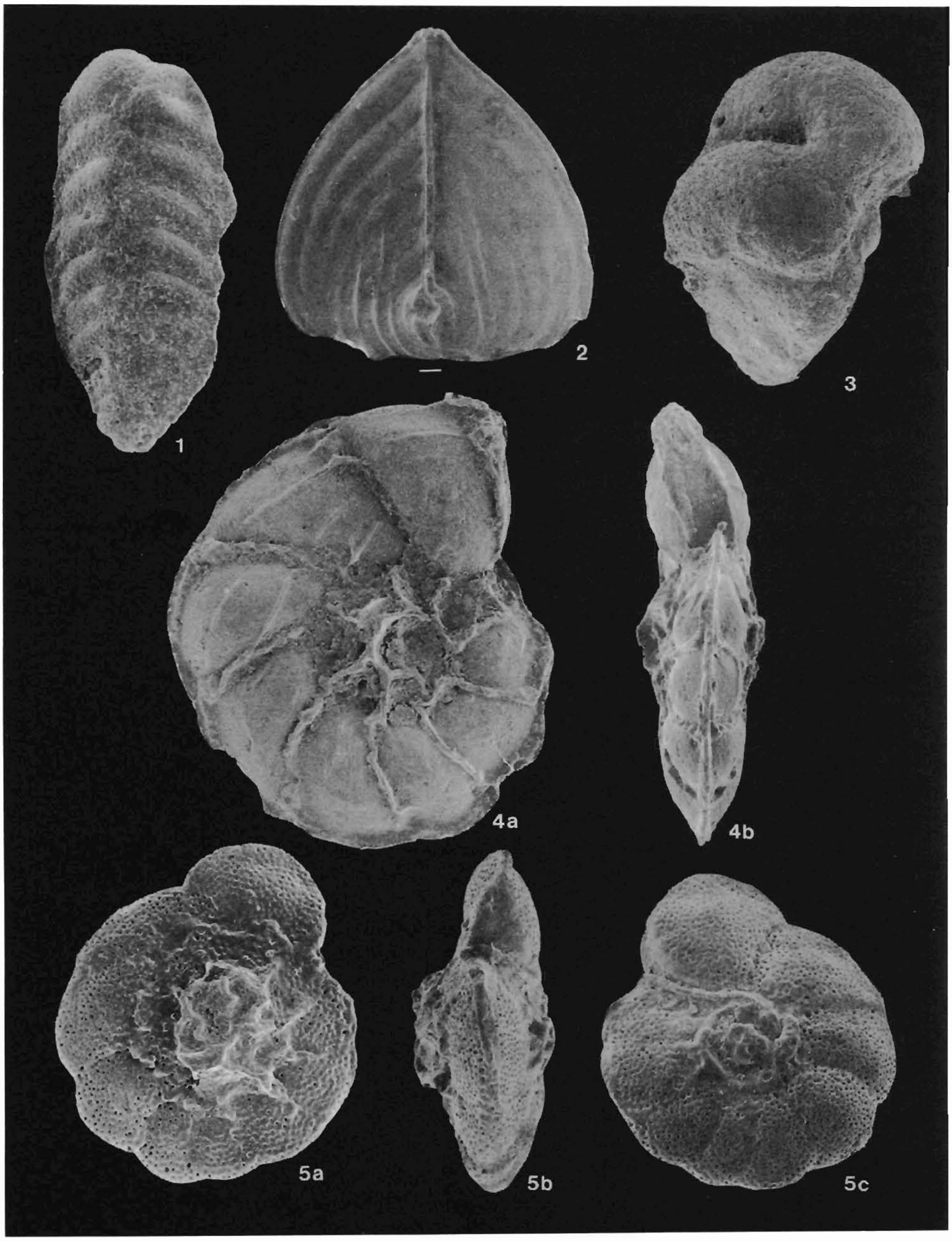
Anomalinoides rubiginosus (Cushman)
(Pl. I, Fig. 5)

1926 *Anomalina rubiginosa* Cushman: p. 607, pl. 21, fig. 6
1946 *Anomalina rubiginosa* Cushman. Cushman: p. 156, pl. 64, figs. 4-6
1948 *Anomalinoides danica* Brotzen: p. 87, pl. 14, fig. 1
1953 *Anomalina granosa* (Hantken). LeRoy: p. 17, pl. 6, figs. 1-3
1956 *Anomalina granosa* (Hantken). Said and Kenawy: p. 153, pl. 6, fig. 20
1959 *Anomalinoides danicus* (Brotzen). Nakkady: p. 463, pl. 5, fig. 2
1976 *Gavelinella danica* (Brotzen). Aubert and Berggren: p. 433, pl. 11, fig. 5; pl. 12, fig. 1
1976 *Gavelinella rubiginosa* (Cushman). Aubert and Berggren: p. 433, pl. 12, fig. 3

Plate IX. Middle neritic taxa of PA 6.

Fig. 1 *Spiroplectinella* cf. *plummerae* (Cushman), sample S 1024, Bir Inglisi I
Fig. 2 *Frondicularia phosphatica* Russo, sample S 1025, Bir Inglisi I (X 30)
Fig. 3 *Gaudryina africana* LeRoy, sample S 1016, Bir Inglisi I
Fig. 4 *Lenticulina* sp. 1, sample S 1025, Bir Inglisi I
Fig. 5 *Gavelinella? guineana* Petters and Adegoke, sample S 1028, Bir Inglisi I
All magnifications X 120 unless indicated otherwise (bar = 100 µm).

PLATE IX



1982 *Anomalina grosserugosa* Franke (non Gümbel). Faris: p. 215, pl. 6, fig. 11
1983 *Gavelinella danica* (Brotzen). Tjalsma and Lohmann: p. 13, pl. 5, fig. 7
1985 *Gavelinella rubiginosa* (Cushman). Luger: p. 112, pl. 9, fig. 6
1986 *Anomalinoides rubiginosus* (Cushman). Van Morkhoven et al.: p. 366, pl. 119
1991 *Anomalinoides danicus* (Brotzen). Katz and Miller: pl. 2, figs. 10, 11
1991 *Anomalinoides danicus* (Brotzen). Nomura: p. 21, pl. 2, fig. 4

Remarks: a distinct, very large, coarsely perforate, glossy-white species with 6 to 9 chambers in the last whorl. This species shows a large degree of variation in the amount of inflation of the chambers and the decoration with secondary calcite. The spiral side is only slightly evolute. We follow Van Morkhoven et al. (1986) in regarding *A. danicus* as a junior synonym of *A. rubiginosus.*

Anomalinoides zitteli (LeRoy)
(Pl. VII, Fig. 1)

1953 *Cibicides zitteli* LeRoy: p. 25, pl. 6, figs. 20-22

Remarks: this species has a compressed, biumbilicate test; both sides are slightly evolute. Sutures on both sides are limbate, raised and strongly curved. The periphery is (sub)acute and has a narrow imprforate keel.

Gavelinellidae

Gyroidinoides girardanus (Reuss)
(Pl. VIII, Fig. 9)

1851 *Rotalina girardana* Reuss: p. 73, pl. 5, fig. 34
1953 *Gyroidina girardana* (Reuss). LeRoy: p. 35, pl. 5, figs. 10-12
1956 *Gyroidina girardana* (Reuss). Said and Kenawy: p. 148, pl. 5, fig. 7
1959 *Gyroidina aegyptiaca* Nakkady and Talaat (in Nakkady, 1959): p. 459, pl. 6, fig. 7; pl. 7, fig. 1
1959 *Gyroidina girardana* (Reuss). Nakkady: p. 460, pl. 3, fig. 1
1976 *Gyroidinoides subangulata* (Plummer). Aubert and Berggren: p. 429, pl. 8, fig. 6
1982 *Gyroidinoides subangulata* (Plummer). Faris: p. 215, pl. 6, figs. 1, 2, 4
1982 *Anomalinoides acuta* (Plummer). Faris (partim): p. 216, pl. 6, fig. 7 (not figs. 8, 10)
1985 *Gyroidinoides girardanus* (Reuss). Luger: p. 110, pl. 8, figs. 2, 3

Remarks: a very distinct plano-convex species. The umbilical side is high conical and has a deep open umbilicus, which may be partly covered by umbilical flaps. The central part of the sutures on this side are slightly incised and bordered by an elevated tapering rim of clear shell material. The sutures on the spiral side are straight and flush to slightly depressed. The chambers on the spiral side are slightly concave and the spiral suture is depressed. The periphery is angular. The aperture may extend from the umbilicus to the periphery, but it may also terminate well before the peripheral margin.

***Gyroidinoides* sp. 1**
(Pl. II, Fig. 2)

Remarks: this species slightly resembles *G. globosus*, but is much more compressed and has about 10 chambers to a whorl. The earlier worls are slightly visible on the transparent spiral side. Sutures on both sides are flush.

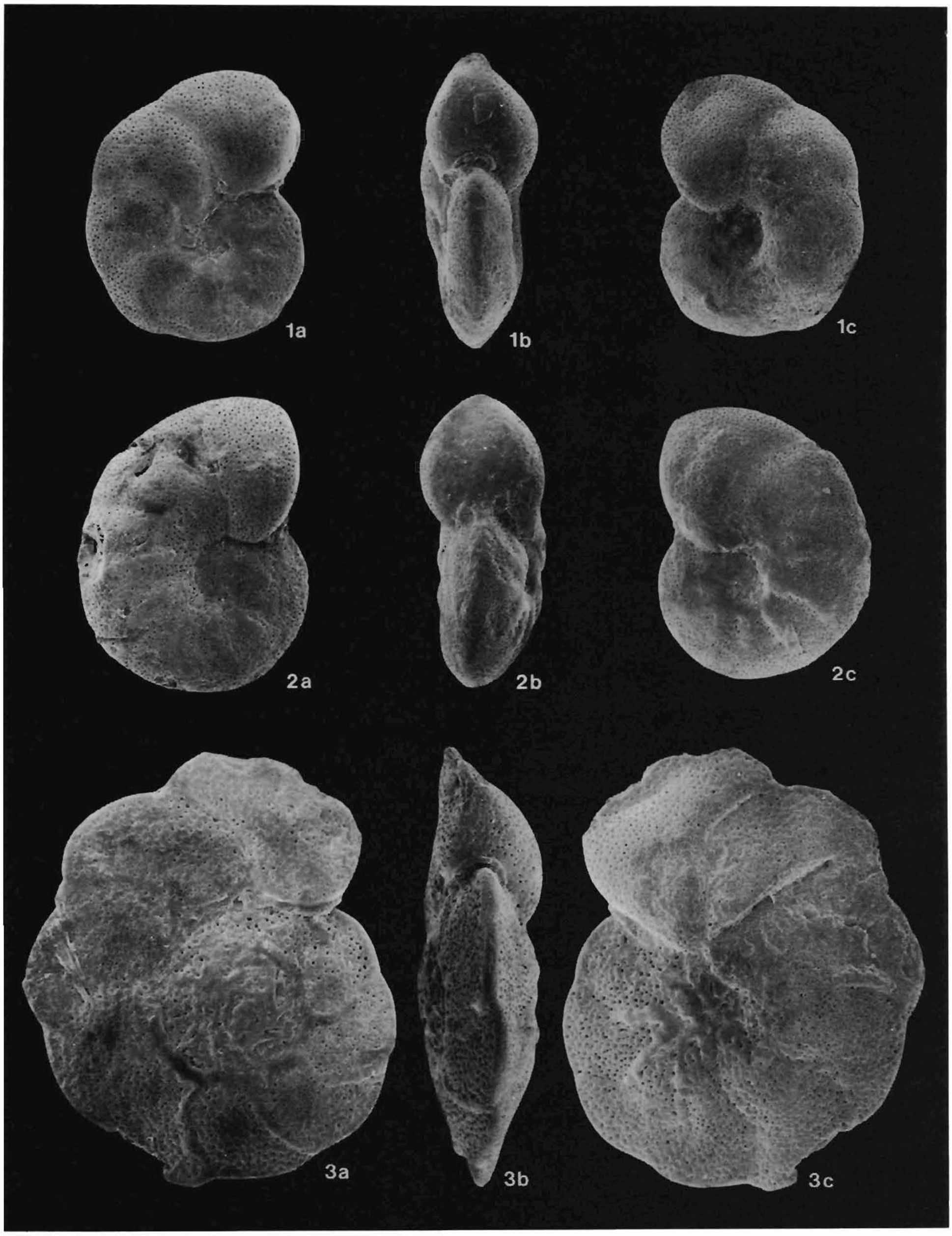
Angulogavelinella avnimelechi (Reiss)
(Pl. III, Fig. 7)

1952 *Pseudovalvulineria avnimelechi* Reiss: p. 269, pl. 2
1953 *Rotalia convexa* LeRoy: p. 48, pl. 9, figs. 13-15

Plate X. Middle neritic taxa of PA 6.

Fig. 1 *Anomalinoides aegyptiacus* (LeRoy), sample S 1020, Bir Inglisi I
Fig. 2 *Anomalinoides* cf. *aegyptiacus* (LeRoy), sample S 1006, Bir Inglisi I
Fig. 3 *Cibicidoides decoratus* (LeRoy), sample S 1026, Bir Inglisi I
All magnifications X 120.

PLATE X



1956 *Streblus convexus* (LeRoy). Said and Kenawy: p. 153, pl. 6, fig. 19
1976 *Angulogavelinella avnimelechi* (Reiss). Aubert and Berggren: p. 431, pl. 10, fig. 1
1985 *Angulogavelinella avnimelechi* (Reiss). Luger: p. 111, pl. 8, figs. 8, 9
1986 *Angulogavelinella avnimelechi* (Reiss). Van Morkhoven et al.: p. 344, pl. 112
Remarks: a very distinct species with a coarsely perforate umbilical side with ridges of secondary calcite in the central part. The smooth spiral side is entirely evolute and shows no pores. The sutures on the spiral side are limbate and slightly oblique, the spiral suture is somewhat depressed. The periphery is bordered by an imperforate keel.

Gavelinella beccariiformis (White)
(Pl. I, Fig. 4)

1928 *Rotalia beccariiformis* White: p. 287, pl. 39, figs. 2-4
1976 *Gavelinella beccariiformis* (White). Aubert and Berggren: p. 433, pl. 11, fig. 4
1983 *Gavelinella beccariiformis* (White). Tjalsma and Lohmann: p. 12, pl. 6, figs. 1-3
1986 *Stensioina beccariiformis* (White). Van Morkhoven et al.: p. 346, pls. 113A-D
1990 *Gavelinella beccariiformis* (White). Thomas: p. 590, pl. 3, fig. 5
1991 *Stensioina beccariiformis* (White). Katz and Miller: pl. 2, figs. 8, 9
1991 *Stensioina beccariiformis* (White). Nomura: p. 21, pl. 1, figs. 8, 9
Remarks: a very distinct species with large umbilical flaps completely covering the umbilicus. Both sides can be coarsely perforate, but the spiral side may be almost poreless. Secondary calcite forms ridges on the umbilical side. The spiral side is usually completely evolute, but may be semi-involute. Umbilical features suggest a relationship with *Stensioina*, but the spiral side lacks the sutural ridges so characteristic for this genus (Loeblich and Tappan, 1988).

Gavelinella? guineana Petters and Adegoke
(Pl. IX, Fig. 5)

1982 *Gavelinella guineana* Petters and Adegoke. Petters: p. 83, pl. 15, figs. 1, 2
Remarks: a very distinct species, referred to as *Eponides elevatus* by Luger (1985), with which it may be related; therefore the tentative generic assignment. The umbilical side is slightly evolute and develops an irregular central plug. The umbilical sutures are depressed to raised near the central plug. The spiral side is entirely evolute and the earlier whorls are decorated by a reticulate pattern which develops from short costae on the inner part of the sutures. Both sides, as well as the sharp margin (in adult specimens) are coarsely perforate.

- CHAPTER VII -

Synthesis

Introduction

In the previous chapters we discussed various aspects of extinction and recovery patterns of southern Tethyan benthic foraminiferal assemblages across the K/P and P/E boundaries. In this final chapter we compare these faunal patterns and highlight similarities and discrepancies. Next we try to fit the patterns within a framework of global change. But first we describe the general global and Tethyan paleoenvironmental background for the Late Cretaceous to Early Paleogene.

General paleogeographic and paleoclimatic background

The plate-tectonic configuration for 60 Ma ago (Barron et al., 1981) is considered to be roughly representative for the position of the African continent during the entire studied time-slice (Late Maastrichtian-early Ypresian, 66-54 Ma). There is however, still considerable uncertainty with respect to the exact paleogeography, in particular concerning the position of the Indian plate, that was in rapid northward transit at that time (e.g. Besse and Courtillot, 1988). The Tethys separated North from South America and Eurasia from Africa and India. Haq (1984) argued that during the Paleocene the Tethys may have encompassed an E-W running ("circum-equatorial") surface current as suggested for the Cretaceous (Gordon, 1973), but GCM studies do not confirm this view (Barron and Peterson, 1991). Marginal basins of the southern Tethys were situated between 15° N (Egypt) and 25° N (Tunisia). In general, Late Cretaceous to Early Paleogene sea-level was high, although short-term sea-level falls may have occurred (Haq et al., 1987). Consequently, marine incursions reached far south across the African craton; apart from locally uplifted blocks, Egypt and Tunisia were largely flooded (Salaj, 1980; Said, 1990; Chapter VI). In vast, tectonically fairly stable and slowly subsiding, areas considerable amounts of marine marls and shales accumulated (Burollet, 1956; Said, 1960). Within the short intervals we studied (around the K/P boundary less than 1 Ma; P/E boundary less than 2 Ma), we could not discern major sea-level variations, although these were previously suggested for the K/P boundary interval (Brinkhuis and Zachariasse, 1988; Keller, 1988b; see Chapter II).

The Earth experienced a warm equable climate, but undergoing a long-term cooling trend up to the middle Paleocene: at that time the cooling trend reversed (Frakes et al., 1992), leading to the Early Eocene thermal maximum (Zachos et al., 1994). In particular during the warmest periods, excessive evaporation in the subtropics (Tethys) and precipitation in the tropics (African continent) may have invoked strong atmospheric contrasts between these regions (Barron, 1986); intensified NE tradewinds invoked NW Ekman transport and widespread upwelling along the southern Tethyan rim. Likely consequences of such conditions are preserved in the rock record: widespread organic-rich and phosphatic deposits mark the Late Cretaceous to Early Paleogene (e.g. Bock, 1987; Notholt et al., 1989).

At times of high evaporation in Tethyan marginal basins, dense warm and saline water may have been formed, driving halotherm circulation (Brass et al., 1982). At the same time deep and/or intermediate water may have been formed at high southern and northern latitudes (Barrera and Huber, 1990; Barron and Peterson, 1991), driving thermohaline circulation as in the recent situation. However, since these high latitude areas were largely ice-free (Frakes et al., 1992), dense cool water formation was probably much more seasonal and restricted. Therefore, the balance between the warm and cold watermasses may have been a very delicate one. Eventual disturbances in this balance, driven by changes in the thermal balance of the Earth, could have had important bearing on evolutionary and distributional patterns in benthic foraminifera.

Benthic foraminiferal paleobathymetry

The interplay between nutrient and oxygen availability, salinity, substratum, temperature, Ph, and stability of these parameters, largely determine the composition, and relative and absolute proportions of benthic foraminiferal assemblages. All these parameters generally vary with depth, resulting in an arrangement of benthic foraminiferal assemblages along a bathymetric gradient. Relatively stable, well oxygenated, oligotrophic bathyal environments usually yield highly diverse communities, containing many specialistic taxa; in general, diversity decreases from bathyal depths to coastal waters, due to larger environmental instability and nutrient supply, favouring taxa with more opportunistic strategies.

Late Cretaceous-early Paleogene benthic foraminiferal assemblages also display this diversity trend: southern Tethyan bathyal paleocommunities are highly diverse; shallow neritic assemblages are oligotaxic, dominated by a few abundant taxa, whereas deeper neritic ones are moderately diverse. We inferred (Chapters II and VI) that gradients in nutrient availability (dereasing with depth), oxygenation (increasing with depth) and temporal variations therein (decreasing with depth), determined the major differences between neritic and bathyal paleocommunities. Due to these distinct paleoenvironmental gradients, upper bathyal and middle neritic assemblages bear very little resemblance, having few species in common. In contrast, transitional outer neritic assemblages yield a mixture of shallow and deep water components; very few species occur exclusively within this depth zone. These distributional patterns suggest that the neritic and bathyal domain were, environmentally, not sharply separated: apparently, environmental conditions rather gradually changed with depth.

Our study reveals major reorganisations (partially temporal) of paleobathymetric distribution patterns across the K/P and P/E boundaries. At first glance, faunal data from our deepest localities (El Kef and Wadi Nukhl) could suggest sudden and very rapid major sea-level falls (in the order of 150-400 m), followed after some time by a slightly more gradual sea-level rise with the same order of magnitude. Even in the deep-sea locality of Maud Rise (1500-2000 m paleodepth, Southern Ocean) a very similar pattern across the P/E boundary was observed (Thomas, 1990b): supposedly neritic species dominated temporarily, followed by the re-appearance of a normal deep-sea assemblage. The P/E boundary sequence of our shallowest locality (50-100 m paleodepth) clearly indicates that a major sea-level fluctuation across the boundary can be excluded. For the K/P boundary, we unfortunately lack a detailed shallow water sequence to test the hypothesis of rapid sea-level variations, but at least sedimentary aspects in the El Kef section do not support a major sea-level fall across the K/P boundary. In our opinion the sequences of El Kef, Wadi Nukhl, and Maud Rise show a typical faunal response, i.e. a downward bathymetric shift, to suddenly deteriorating conditions (in particular, oxygen deficiency, see below) in deeper waters. Our data indicate that opportunistic shallow water species were the first ones to repopulate the deep water ecological vacuum, because of their better adaption to oxygen deficiency. Interestingly, one particular species (*Tappanina selmensis*) proliferates during both extinctions, i.e. during the earliest Paleocene in El Kef, as well as during the earliest Eocene of Maud Rise.

Another important, and probably generally occurring biotic response of the environmental changes occurring during the boundary intervals is the permanent paleobathymetric shift of certain species while remaining within the studied bioprovince: some species appear to have acquired broader depth ranges, whereas others became more restricted (Chapters II and VI).

The cosmopolitan deep-sea marker *Gavelinella beccariiformis* provides a highly interesting example of an upward bathymetric expansion across the K/P boundary. During the Late Maastrichtian this species occupied only the deeper bathyal domains of the Tethys. During the early Paleocene, however, it becomes one of the most abundant species in Tethyan upper bathyal assemblages. In our view, the appearance of *G. beccariiformis* in shallower waters indicates a significantly altered paleoceanographic regime (see discussion below).

These (temporal) modifications in paleobathymetric ranges once more indicate, that depth itself can not be considered as an independant, environmental parameter, determining foraminiferal distribution patterns.

Extinction patterns

Basically, we follow Jablonski (1986) in considering duration (the amount of time involved), magnitude (the number of taxa becoming extinct), and breadth (the variety of taxonomic groups affected) as the basic ingredients of a major extinction. Since we focus on benthic foraminiferal extinctions we do not consider breadth; instead we discuss ecological selectivity and differential effects in (bathymetric) domain. Table 1 displays a summary of these features for the K/P and P/E boundary studies in the southern Tethys; we incorporate in our discussion the basic results from deep-sea research.

Table 1. The most important features of benthic foraminiferal extinction patterns within the various bathymetric domains.

EXTINCTION	Domain	Tempo	Magnitude	Selectivity
P/E	M. neritic	gradual	minor	
	O. neritic	rapid	moderate	predominantly
	U. bathyal	rapid	mod.-maj.	"epibenthic"
	Deep-sea	rapid	major	
K/P	M. neritic	?	major	
	O. neritic	?	moderate	predominantly
	U. bathyal	rap.(grad.)	major	"endobenthic"
	Deep-sea	rap.(grad.)	minor	

Both events, K/P and P/E boundary, clearly affected all studied paleobathymetric domains, although the magnitude strongly varied between the compartmens. Essentially, the K/P event had a more pronounced effect on continental margin paleocommunities (at least in the southern Tethys; see Chapter II), whereas the impact of the P/E event increased with depth (Chapter VI). Consequently, the driving forces behind these extinctions strongly differ, although the local expressions, in particular in the upper bathyal domain, may appear similar.

In our view the pronounced long-term fertility crisis, leading to reduced nutrient heterogeneity and supply to benthic ecosystems, primarily caused the K/P extinctions, although regional oxygen deficiency had a profound effect on local faunal patterns (Chapter II). Paleoecological model studies suggest that the effect of such a perturbation would be most pronounced in shallow ecosystems and have little effect on deep-sea ecosystems (Sjoerdsma and Van der Zwaan, 1992). Our study combined with deep-sea results indeed confirms this prediction. The relationship with the fertility crisis is further exemplified by the selective extinction of taxa with presumed higher nutrient demands, in particular taxa with elongate "endobenthic" test shapes (e.g. *Sitella*, *Eouvigerina*, *Orthokarstenia*, and *Bolivinoides*). These taxa were abundant in the southern Tethyan paleocommunities, but rare or even absent in deep-sea faunas.

From the data available, it appears that oxygen deficiency was the overall governing parameter invoking the extinctions at the P/E boundary (Chapter VI). In all known detailed records, the extinction of the cosmopolitan deep-sea *Gavelinella beccariiformis* assemblage coincides with a level suggestive of oxygen deficiency, indicated by dark, or even sapropelitic, clays and/or low diversity foraminiferal assemblages. As mentioned earlier, deep-sea ecosystems were adjusted to relatively stable and well-oxygenated conditions. Not surprisingly, a large group of epibenthic taxa (presumably living on the sediment surface (e.g. *Gavelinella*, *Cibicidoides*, *Gyroidinoides*, and *Neoeponides*), that are generally considered to be least resistant to lowered oxygen levels, was most severely affected during the event.

During the P/E boundary interval, at least in the sections studied, shallow water ecosystems were generally subjected to oxygen deficiency, as evidenced by the preservation of lamination and the sometimes high organic carbon contents (Chapters V and VI). Consequently, shallow water taxa probably adopted effective strategies to cope with (temporal) oxygen deficiency. The most common taxa in these shallow water paleocommunities (e.g. *Bulimina*, *Valvulineria*, and *Anomalinoides*) are also commonly present in modern eutrophic, oxygen poor, environments (Sen Gupta and Machain-Castillo, 1993). This explains why the dysoxic-anoxic event at the P/E boundary had relatively little effect on these shallow systems.

Both extinction events appear to have initiated very suddenly at the epoch boundaries. Except for the shallow water P/E sequence (due to local enhanced productivity, Chapter V), the studied Late Maastrichtian and late Paleocene paleocommunities were fairly stable up to the boundary (Chapters II, IV, and VI). For the K/P boundary sequence of El Kef, it is clear that the extinction was very sharp, coinciding with the boundary. On a regional and global scale, however, the extinctions were clearly diachronous: although it is often difficult to distinguish in situ specimens from reworked ones (cf. discussions on "Cretaceous" planktonic survivors in the early Paleocene), in particular in relatively condensed deep-sea records, we are certain that at least a few species became extinct later during the early Paleocene. Additional research is required to establish to what extent this might apply to the other species. In our view, this diachronism is probably related to the local variability in an altered paleoceanographic setting, long-term food restrictions and biotic interactions.

It seems likely that the extinction of tropical planktonic foraminifera was more severe and progressed more rapidly than the extinction of benthic foraminifera. This differential effect is determined by the different niches the organisms occupy in the foodweb. Most planktonic foraminifera depend on fresh phyto- and zooplankton. In contrast, many benthic foraminifera are deposit- and detritus feeders and are able to live on dead organic matter and bacteria. A major drop in pelagic productivity will therefore have almost instantaneous repercussions on planktonic foraminifera, whereas the extinction of mud-dwelling benthic foraminifera is buffered by the possibility of sustaining on more degraded matter.

The P/E boundary oxygen deficiency event seems to have progressed very rapidly through the various bathymetric compartments. As noted above, the extinctions appear to have been synchronous with the onset of the event; only in our shallowest site we noted sequential pre-boundary (local and/or temporal) disappearances, due to locally increasing environmental stress. Yet, also this locality was minimally ventilated at the P/E boundary (Chapter V).

Recovery patterns

The main elements of faunal recovery after extinction are diversification by migrationary shifts and by evolution of new taxa. The recovery phase after (or perhaps better, during) extinction events is often marked by the short-term settlement of a low diversity paleocommunity, consisting of highly opportunistic pioneer taxa, the so-called disaster fauna. This initial phase is followed by decline and disappearance of the disaster fauna and concomitant re-migration of Lazarus taxa (taxa that disappeared during an earlier phase of the extinction event), leading to a more diverse paleocommunity. The next step in the succession is the advent of new immigrants, and eventually new taxa evolve, occupying vacated niches. Table 2 lists in which domains such features were observed in our and other records.

Table 2. The most important features of benthic foraminiferal recovery patterns within the various bathymetric domains.

RECOVERY	Domain	Disaster	Lazarus	Immigrants
P/E	M. neritic	impoverished	yes	yes
	O. neritic	?	?	yes
	U. bathyal	yes	yes	yes
	Deep-sea	yes	yes	yes
K/P	M. neritic	?	?	yes
	O. neritic	?	?	yes
	U. bathyal	yes	yes	yes
	Deep-sea	no	no	yes

Disaster assemblages are encountered in the bathyal records of El Kef (K/P), Wadi Nukhl (P/E), and Maud Rise (P/E). As noted in a previous section, a suite of predominantly opportunistic shallow water taxa invaded deeper environments at or after a time of more or less severe oxygen deficiency. As conditions ameliorated, these taxa were in turn replaced by normal (but impoverished) bathyal assemblages. The latter consist of ubiquitous taxa (often taken together as lump categories, because of their infrequent occurrence, poor preservation, or problematic taxonomic status), Lazarus taxa and taxa that immigrated from other bathymetric compartments or bioprovinces. In the shallow P/E boundary sequence of Bir Inglisi I the earliest Eocene fauna is strongly impoverished compared with the normal shallow water assemblage and bears great resemblance with the contemporaneous disaster fauna of the bathyal site of Wadi Nukhl.

All our detailed records show Lazarus effects for various taxa. Since our data set is rather limited, we can not positively identify refugium areas, but we guess that for the earliest Paleocene these were situated in the deep-sea. This domain did apparently not experience such widespread oxygen deficiency as in the shallower parts of the Tethys, and many Lazarus taxa are indeed well known from Late Cretaceous and early Paleocene deep-sea deposits. In contrast, the deep-sea does not appear to have provided protected habitats at the P/E boundary; some of the Lazarus taxa had wide paleobathymetric ranges and possibly survived at very shallow depths, presumably protected from oxygen deficiency. Others, such as the surviving deep-sea taxon *Nuttallides truempyi* probably had wider tolerance limits to lowered oxygen levels.

Duration estimates of faunal recovery strongly depend on the accuracy of calculated sedimentation rates, that may be flawed by unrecognized hiatusses, variations in sedimentation rates, or inaccurate time scales. Though realizing this, we estimate the duration of most recovery intervals (i.e. diversification by immigration) at 100-400 kyr. Such estimates match fairly well with recovery in other marine paleocommunities e.g. of shallow marine invertabrates at the K/P boundary (e.g. Hansen et al., 1993).

Evolutionary consequences

The two extinction events resulted in a stepwise reduction of Cretaceous lineages. First, the K/P boundary event eliminated several characteristic Cretaceous lineages that dominated the shallower domains. Subsequently, during the P/E event many of the surviving deep-sea taxa became extinct. Thus, the major break for neritic paleocommunities was at the K/P boundary, giving rise to the Paleocene to Early Eocene Midway- type fauna (Berggren and Aubert, 1975); the major break for deep-sea paleocommunities occurred at the P/E boundary, terminating the existence of the Late Cretaceous-Paleocene Velasco-type fauna (Berggren and Aubert, 1975; Thomas, 1992). Localities that were continuously in an intermediate (upper bathyal) position such as Wadi Nukhl and Nahal Avdat (El Kef shallowed during the Paleocene, see Chapter II) clearly recorded both events, since upper bathyal paleocommunities were composed of a mixture of shallow and deep water elements.

Few taxa (e.g. *Cibicidoides alleni*, *N. truempyi* and *Bulimina trinitatensis*) survived both events, others had evolved into new species (e.g. *Bulimina farafraensis* from *B. strobila*). The extinct lineages were eventually replaced by new Cenozoic lineages. In particular, various opportunistic groups appear to have diversified during the Paleocene, possibly as a result of the gradual return to more fertile environments. For instance, various taxa, considered to have adopted opportunistic strategies, such as *Anomalinoides aegyptiacus*, *Valvulineria scrobiculata*, *B. farafraensis*, *B. callahani*, and *Stainforthia farafraensis*, all first appeared during the middle Paleocene (unpublished data). It seems likely that the rapidly radiating *Bulimina* occupied the niches vacated by characteristic Cretaceous endobenthic taxa as *Sitella*, *Eouvigerina*, and *Orthokarstenia*. Other modern opportunistic endobenthic taxa as *Uvigerina* and *Turrilina* first appeared in the late Paleocene and experienced the first major radiations in the Eocene. Future research will hopefully shed more light on this aspect of biotic recovery after mass extinction.

Late Cretaceous to Early Paleogene paleoceanographic and paleoclimatic evolution of the southern Tethys

The combination of our data with literature results, clearly indicates that both boundaries are marked by temporal, but widespread, sea-floor oxygen deficiency: during the earliest Paleocene most notably at intermediate depths in low-middle latitude regions, and during the earliest Eocene in deep and intermediate waters of all oceans, and even in shallow waters of the Tethys. Bottom oxygenation depends on the balance between oxygen supply, by ventilation through fresh bottom water formation or mixing, and oxygen consumption, by degradation of organic matter and respiration. Since at the boundaries the organic flux to the sea-floor remained virtually constant or even dropped dramatically (particularly at the K/P boundary), we can only conclude that ventilation was severely reduced during both events. This implies that some external forcing inhibited deep and/or intermediate water formation.

During the Late Cretaceous relatively cool deep water was formed at high latitudes, at least near Antarctica (e.g. Barrera and Huber, 1990). Simultaneously, relatively warm but highly saline dense water (due to excessive evaporation) may have been formed within the Tethys (Brass et al., 1982). Depending on the relative density and flux, this watermass possibly spread out at intermediate depths at low-middle latitudes (cf. Thomas, 1992). The differential response at the K/P boundary between the deep and intermediate bathymetric compartments is indeed compatible with the presence of two main watermasses originating in distinctly different source areas. Several lines of evidence (faunal, floral, and stable isotope records, see Chapter II) suggest that an abrupt cooling event, superimposed on a long-term cooling trend, occurred at the K/P boundary. We infer that this sudden cooling led to weakened atmospheric contrasts between the tropics and the subtropics (Barron, 1986), and resulted in strongly reduced evaporation and upwelling at the Tethyan margin. In this way, the formation of intermediate water was blocked, resulting in widespread oxygen deficiency in intermediate waters. After some time, this intermediate Tethyan watermass was gradually replaced by an upward expanding deep and cooler watermass, as suggested by the upward expansion of the *G. beccariiformis* assemblage. Eventually, relatively cool watermasses originating at high southern latitudes, and perhaps in the North Pacific as well (Barron and Peterson, 1991), dominated the deep and intermediate domains of the Paleocene ocean. This situation persisted to the end of the Paleocene, a period during which no major reorganizations in benthic foraminiferal distribution patterns occurred: the Paleocene was primarily a time of increased speciation (Tappan and Loeblich, 1988), in particular in shallow marine southern Tethyan paleocommunities.

During the middle Paleocene, the gradual cooling trend reversed into a warming trend that culminated in the early Eocene thermal maximum (Zachos et al., 1994). At the P/E boundary, almost the reverse of the K/P event took place: peak warming in polar regions led to the cessation of cool deep and intermediate water formation, and consequently to widespread oceanic oxygen deficiency. At the same time, enhanced atmospheric contrasts between the tropics and subtropics led to intensified upwelling in the Tethys, and enhanced evaporation led to the re-establishment of deep and intermediate water formation in low latitudes. The widespread dominance of the *N. truempyi* assemblage indeed suggests that during the early Eocene deep ocean circulation reversed. Now the Tethys was the major source of intermediate and deep water, driving halothermal circulation. This situation lasted some time in the Eocene, until gradually high latitude sources cooled again and deep water, produced in the Southern Ocean replaced Tethyan watermasses.

As indicated, we relate the K/P turnover to sudden cooling, whereas the P/E turnover seems to be linked to sudden warming. Modelling experiments have shown the climatic sensitivity for CO_2 during the Cretaceous (see overview in Crowley and North, 1991). Since Early Paleogene geography (plate-configuration, low relief, and high sea-level) was similar to the Late Cretaceous situation, climatic sensitivity for CO_2 was probably alike. In our view, both the long-term climatic trends as well as the short-term perturbations may have been tightly coupled to variations in atmospheric CO_2 contents (cf. Berner, 1989, 1994). The sudden K/P boundary cooling was probably triggered by the impact of an extraterrestrial object (Alvarez et al., 1980). The injection of enormous amounts of dust and aerosols into the upper atmosphere caused the initial cooling, which was further amplified by positive feed-back mechanisms (e.g. CO_2 drawdown by the reduction in carbonate production, Caldeira et al., 1990), required to invoke sufficient long-term cooling.

The reversal of the cooling trend during the middle Paleocene, may have been caused by enhanced metamorphic CO_2 degassing, resulting from the India-Asia collision (Kerrick and Caldeira, 1994). Superimposed on this trend, was the massive eruption of North Atlantic flood basalts, supplying large amounts of CO_2 to the atmosphere. This event may have been responsible for the sudden warming and subsequent events at the P/E boundary (Eldholm and Thomas, 1993), marking the initiation of the Eocene thermal maximum.

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Curriculum Vitae

Robert Pieter Speijer was born on 13 September 1963 in Veldhoven, the Netherlands. He attended secondary school in Eindhoven from 1975 to 1981. In September 1981 he started at Utrecht University, where he obtained his B.Sc. degree in Geology in January 1986, followed by a M.Sc. degree in August 1988. His principal subject was Stratigraphy/Micropaleontology and subsidiary subjects were Climatology and Economical Geology. Between September 1988 and October 1989 he had several temporary appointments as research assistant at the Department of Geology, Utrecht University. Between October 1989 and October 1993 he was employed as a Ph.D. candidate and subsequently, until October 1994, as research associate and associate lecturer, respectively, at the same institution. From January 1995 onward he will continue his research on a post-doc grant at the Department of Marine Geology at the University of Göteborg, Sweden.