



Paleocene sea-level and productivity changes at the southern Tethyan margin (El Kef, Tunisia)

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Received 24 August 2004; received in revised form 22 December 2004; accepted 3 January 2005

Abstract

Integrated analysis of quantitative distribution patterns of organic-walled dinoflagellate cysts (dinocysts) and benthic foraminifera from the Paleocene El Kef section (NW Tunisia) allows the reconstruction of sea-level and productivity fluctuations. Our records indicate that the environment evolved from an initially oligotrophic, open marine, outer neritic to upper bathyal setting towards a more eutrophic inner neritic setting, influenced by coastal upwelling by the end of the Paleocene. An overall second order change in paleodepth is reflected by both microfossil groups. From the base of planktic foraminifera Zone P4 onwards, the main phase of shallowing is evidenced by an increase of inner neritic dinocysts of the *Areoligera* group, disappearance of deeper-water benthic foraminifera and increasing dominance of shallow-marine taxa (several buliminids, *Haplophragmoides* spp., *Trochammina* spp.). The total magnitude of this shallowing is obscured by interaction with a signal of eutrophication, but estimated to be around 150 m (from ~200 to ~50 m). Superimposed on the overall trend, third order sea-level fluctuations have been identified and correlated to sequences in other regions. Paleoproductivity indicators (notably protoperidinioid dinocysts and buliminids) show a trend from an oligotrophic to a eutrophic setting.

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Keywords: Organic-walled dinoflagellate cysts; Benthic foraminifera; Paleocene; Paleoenvironment; Sea-level; Tethys

1. Introduction

The Paleogene has become appreciated as a climatically highly dynamic period, involving the transition from the near ice-free world of the Cretaceous to the glacially dominated world of the Neogene (Zachos et al., 2001). In this context,

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the global warming trend recorded during the Paleocene and culminating in the early Eocene represents an important phase of biotic and environmental change (Zachos et al., 2001, 2003; Wing et al., 2003; Billups et al., 2004). Yet, relative to studies focusing on the Paleocene/Eocene thermal maximum (PETM) comparatively little is known of the preceding, longer-term paleoceanographic changes and climate dynamics. In addition, while ocean drilling is providing new insights in Paleocene oceanography, ancient continental margins remain poorly studied.

Here, we report on the succession at El Kef, NW Tunisia, a site located at the southern margin of the Tethys. Compressive tectonics resulting from convergence of the African and Eurasian plates prevailed in this area during the Cenozoic (Zaier et al., 1998). Shallow seas fringing the Tethys covered Tunisia in the late Mesozoic and early Cenozoic, and by the end of the Cretaceous the Jeffara and Kasserine Islands and other small areas emerged in southern and central Tunisia (Fig. 1). Kasserine Island separated a basin in the north from a narrow basin in the south. The El Kef area (Fig. 1) was part

of the northern basin (Zaier et al., 1998), also known as the Tunisian Trough (Burolet, 1956, 1991; Salaj, 1980; Bobier et al., 1991). Hemipelagic marl-shale sedimentation occurred in open marine conditions, but with significant terrigenous input from Kasserine Island, and intermittent influx from emerged land located to the west of El Kef (Adatte et al., 2002). Paleocene sediments in the Tunisian Trough are up to 500 m thick due to a high subsidence rate and sediment input. Paleocene sediment thickness reduces towards Kasserine Island (Zaier et al., 1998).

The El Kef section (Figs. 1 and 2) exposes the El Haria Formation, spanning the upper Maastrichtian to Eocene and consists mainly of brown-grey homogeneous marls and shales. It overlies the chalky limestones of the Campanian to lower Maastrichtian Abiod Formation and is overlain by limestones of the Ypresian Metlaoui Formation. Throughout the upper Maastrichtian and Paleocene, the sediments were deposited in a shelf to upper-slope setting (Brinkhuis and Zachariasse, 1988; Keller et al., 1995; Speijer and Van der Zwaan, 1996; Kouwenhoven et al., 1997; Galeotti and Coccioni, 2002). The

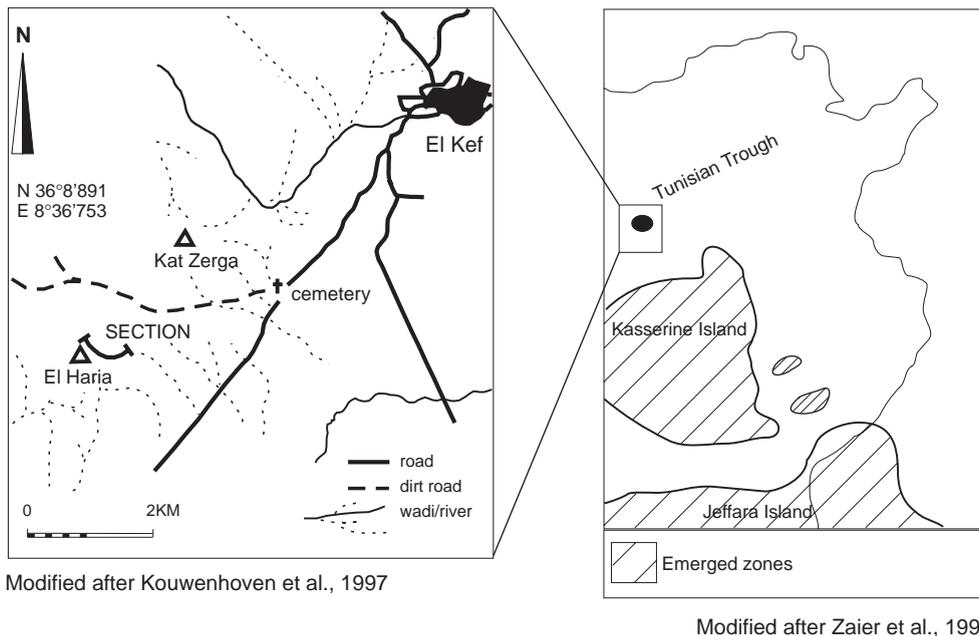


Fig. 1. Location map of the El Kef area with the sampled sections and paleogeographic reconstruction of the area during the Paleocene.

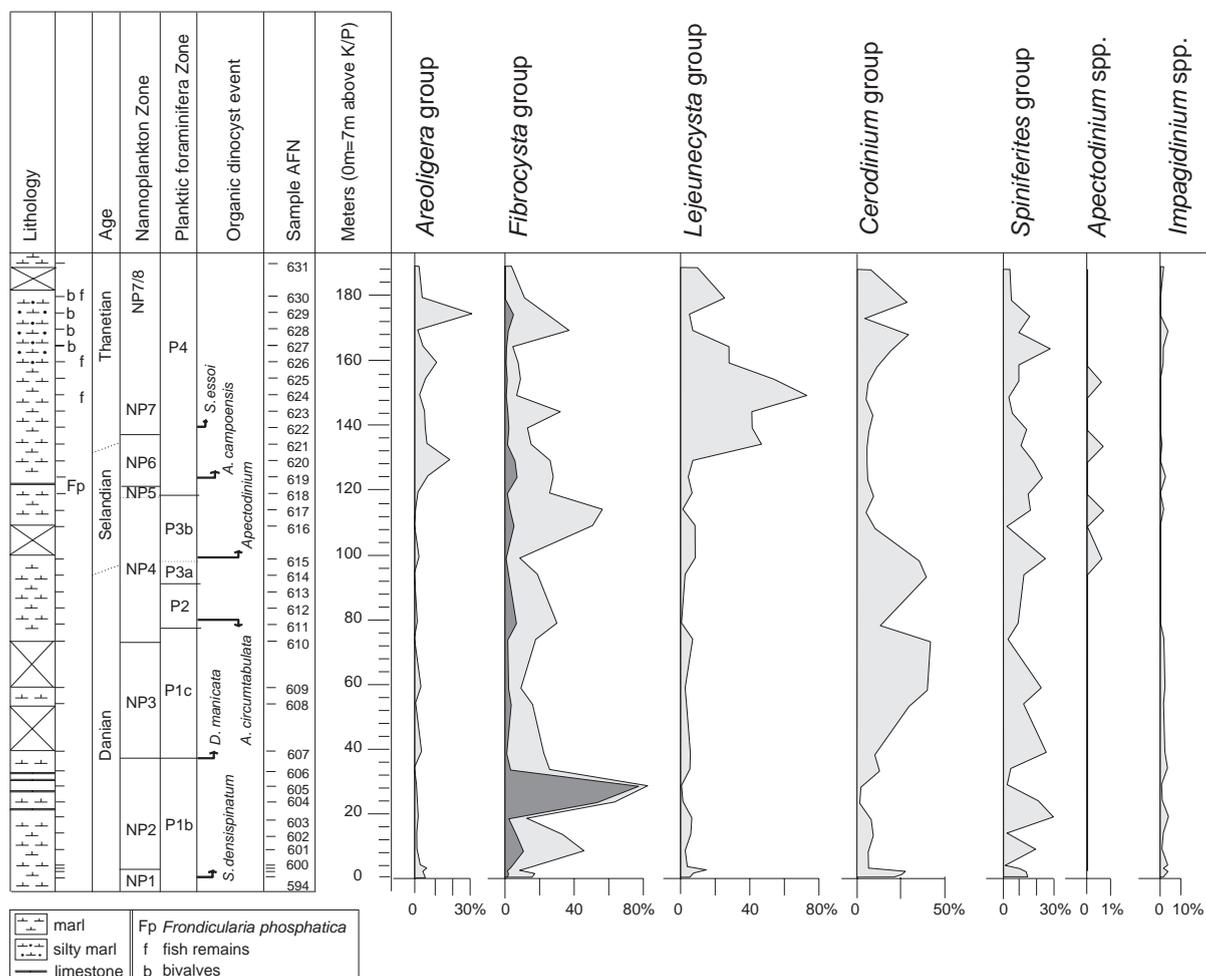


Fig. 2. The relative frequency of organic dinocysts is plotted against lithology, biostratigraphy (calcareous nannoplankton and planktic foraminifera), major organic dinocysts event and sample positions in the El Kef section. Personal observations on planktic foraminifera allow identification of *Globanomalina pseudomenardii* in sample AFN 618, and thus the base of planktic foraminifera Zone P4 has been repositioned to a stratigraphically lower level. The dinocysts taxa are grouped together as proposed in Appendix A. Within the *Fibrocysta* group, the relative abundance of *Kenleyia* spp. is plotted in a darker grey color. *Apectodinium* spp. is plotted with a different percentage scale than the other taxa.

section was chosen in view of its expanded and well-exposed nature, although four intervals (8 to 15 m thick) could not be sampled. A sample set covering the Paleocene, and including the Cretaceous–Paleogene (K/P) boundary (~65 Ma) was collected in 1982 by A.J.T. Romein and J. Smit near the village of El Kef (Fig. 1). The biostratigraphy is fairly well established (Salaj, 1980; Brinkhuis et al., 1994; Kouwenhoven et al., 1997).

Most previous studies concentrated on the Cretaceous/Paleogene boundary of the El Kef section, and

dinocysts, benthic and planktic foraminifera from the lowermost seven meters of the Paleocene, comprising the recovery after the K/P boundary were studied in great detail (Smit and Romein, 1985; Brinkhuis and Zachariasse, 1988; Keller, 1988a,b; Keller et al., 1995; Speijer and Van der Zwaan, 1996; Brinkhuis et al., 1998; Culver, 2003). Studies of the entire Paleocene interval were performed on ostracodes (Donze et al., 1982; Peypouquet et al., 1986), calcareous nannoplankton (Perch-Nielsen, 1981), and planktic and benthic foraminifera (Salaj, 1980;

Kouwenhoven et al., 1997). A preliminary report on the qualitative dinocyst distribution was published in Brinkhuis et al. (1994).

Whereas most previous studies were based on one microfossil group, this paper presents new quantitative palynological data, integrated with existing benthic foraminiferal data. We focus on the Danian to lower Thanetian interval (~64.8–56.7 Ma), corresponding to planktic foraminifera Zones P1b to P4 (Berggren et al., 1995) and calcareous nannoplankton Zones NP1 to NP7/8 of Martini (1971). By integrating sea-surface (dinocysts) with sea-floor (benthic foraminifera) groups, our study aims to reconstruct paleoenvironmental changes with emphasis on sea level and paleoproductivity. The main trends recorded in both groups can be considered more reliable than signals from each group individually. Hence, this procedure should reduce the potential of paleoenvironmental misinterpretations.

2. Methods

2.1. Palynological data

Thirty-six samples (AFN 594 to AFN 631) were studied, covering 190 m of the section. The samples were processed according to standard palynological techniques (Brinkhuis et al., 2003). The residues were sieved using a 10 µm mesh-sieve and prepared on slides using glycerin jelly. The slides are stored at the

Laboratory of Palaeobotany and Palynology, Utrecht University, The Netherlands.

Palynomorphs were subdivided in eight categories (i.e. bisaccate pollen, other pollen and spores, acritarchs, determinable dinocysts, *Leiosphaeridia* spp., *Pterospermella* spp., indeterminable dinocysts and inner walls of foraminifera, if more than three chambers were encountered). Non-saccate pollen and spores were identified and grouped together as terrestrial palynomorphs. A list of the palynomorphs is presented in Appendix B (Supplementary data).

Dinocysts were counted up to 100 determinable cysts where possible. Dinocyst taxonomy is in accordance with Williams et al. (1998). In order to obtain the main variations of the paleoecological signal along the succession, the taxa have been grouped based on their broad paleoecological characteristics (Appendix A).

Several ratios that are often used as paleoenvironmental proxies were calculated. Eukaryotic sea-surface productivity (SSP) has been estimated using the ‘classical’ P/G ratio (peridinioid/gonyaulacoid), which includes all peridinioid cysts (P cysts) and is calculated as $P/G = nP/(nP+nG)$. In addition, we generated the protoperidinioid/gonyaulacoid ratio (Pp/G), which only includes cysts of extant heterotrophic motile protoperidinioids (Pp) and is calculated as $Pp/G = nPp/(nPp+nG)$.

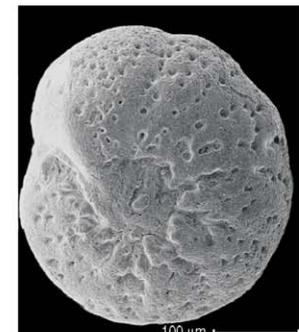
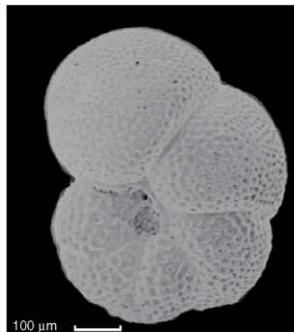
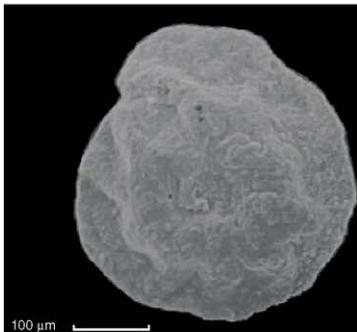
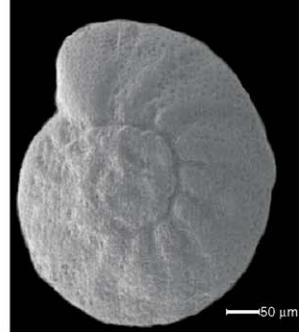
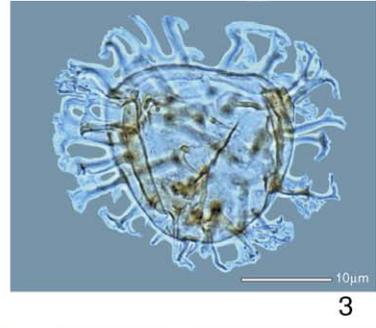
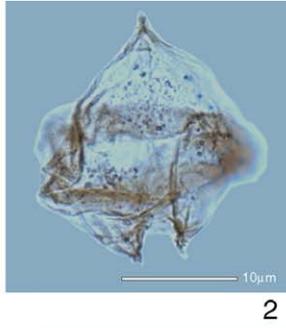
The ratio between inner neritic and outer neritic dinocysts (IN/ON) has been calculated applying the formula $IN/ON = nIN/(nIN+ON)$ (e.g., Versteegh, 1994).

Plate 1. Organic dinocysts.

1. *Paleocystodinium* sp., sample AFN 615 (K48/1);
2. *Lejeunecysta* sp., sample AFN 621 (L43/4);
3. *Areoligera* sp., sample AFN 629 (K42/4);
4. *Cerodinium* sp., sample AFN 615 (E41/3);
5. *Cerodinium* sp., sample AFN 615 (K44).

Benthic foraminifera.

6. *Bulimina* cf. *strobila* AFN 636;
7. *Bulimina* *midwayensis*, sample AFN 619;
8. *Cibicidoides pseudoacutus*, sample AFN 615;
9. *Haplophragmoides* sp., sample AFN 636;
10. *Anomalinoidea rubiginosus*, sample AFN 617;
11. *Gavelinella beccariiiformis*, sample AFN 599.



To estimate the relative contributions of terrestrial versus marine organic material, the S/D ratio was calculated, applying the formula $S/D = nS/(nD + nS)$, with S =number of sporomorphs (terrestrial) and D =number of dinocysts and marine acritarchs (Versteegh, 1994).

2.2. Statistical analyses

The census counts of benthic foraminifera were re-evaluated for the present study. In order to group the benthic taxa, the relative frequency matrix was condensed by eliminating ill-defined groups and taxa occurring in frequencies below 6%. The resulting matrix (Appendix B, supplementary data) was introduced in R-mode hierarchical clustering (SPSS standard software, Pearson correlation).

With the purpose to establish biofacial units, we performed a Q-mode cluster analysis on the combined data sets (i.e., the relative frequencies of dinocyst and benthic foraminiferal taxa), in order to cluster the samples characterized by similar biofacies (SPSS standard software, Pearson correlation).

3. Results

3.1. Dinocyst assemblages

Nearly all samples contain palynological assemblages dominated by marine palynomorphs. Selected groups (cf. Appendix A) are plotted in Fig. 2. The *Fibrocysta* group, consisting of typical neritic cysts, is one of the main components of the assemblage. The peak occurrence in the lower Paleocene is due to the high abundance of the *Kenleyia* complex. High percentages of the *Fibrocysta* group (>40%) in planktic foraminifera Zones P3b and P4 are due to *Fibrocysta* spp. The *Cerodinium* group includes cavate peridinioid cysts. Maximum abundance is reached in Zones P1b and P3 (~40%). In the upper part of the studied interval (at 163 and 178 m), the abundance of the *Cerodinium* group increases again (Plate 1). The *Areoligera* group, which includes extinct taxa that were dominant in inner neritic and coastal environments, becomes more common from the base of planktic foraminifera Zone P4 and reaches a maximum abundance of 30% in the upper part of the

studied interval. The *Lejeunecysta* group (protoperidinioid cysts) shows maximum abundances from the base of Zone P4 onwards and dominates the assemblage (>80%) in sample AFN 624 within Zone P4. This group is commonly associated with inner neritic environments characterized by high eukaryotic productivity. *Spiniferites*, which is considered a cosmopolitan taxon often associated with open marine conditions, occurs throughout the section. The typical offshore taxon *Impagidinium* only occurs in the background.

Despite their low relative abundance, *Apectodinium* spp. are plotted because of their worldwide importance during the Paleocene–Eocene transition. The lowest occurrence of these representatives of the wetzeliellid lineage was found in sample AFN 615 at the base of planktic foraminifera Subzone P3b (Brinkhuis et al., 1994). Above this level, it reappears as single occurrences.

3.2. Benthic assemblages

R-mode clustering of the benthic foraminiferal assemblages resulted in two main clusters (Fig. 3, Table 1). Cluster I groups species that generally decrease upwards in numbers (e.g. *Osangularia plummerae*, *Pulsiphonina prima*). Within this cluster, sub-cluster IA (including *Gavelinella beccariiiformis*) is present in the lower part of the section and disappears altogether above 110 m. The assemblage in cluster IB dominates the benthic record from planktic foraminiferal Zones P1c to basis P4 and strongly decreases in the course of Zone P4.

Cluster II groups species that are more common in the upper part of the section (e.g. buliminids, *Haplophragmoides* spp.). Sub-cluster IIA groups the buliminids, increasingly abundant from upper Subzone P3b upwards and dominant in upper Zone P4. Sub-cluster IIB groups mainly *Lenticulina* spp. and the arenaceous taxa *Haplophragmoides* and *Trochammina* spp., which dominate the benthic record in the lower Zone P4 (Table 1).

Benthic diversity is relatively constant at moderately high levels until the lower part of Zone P4, where it decreases and it is significantly reduced at the basis of nannoplankton Zone NP7. Between 60 and 125 m, a decrease of the %P suggests a decrease of water depth. However, the percentage planktics (%P)

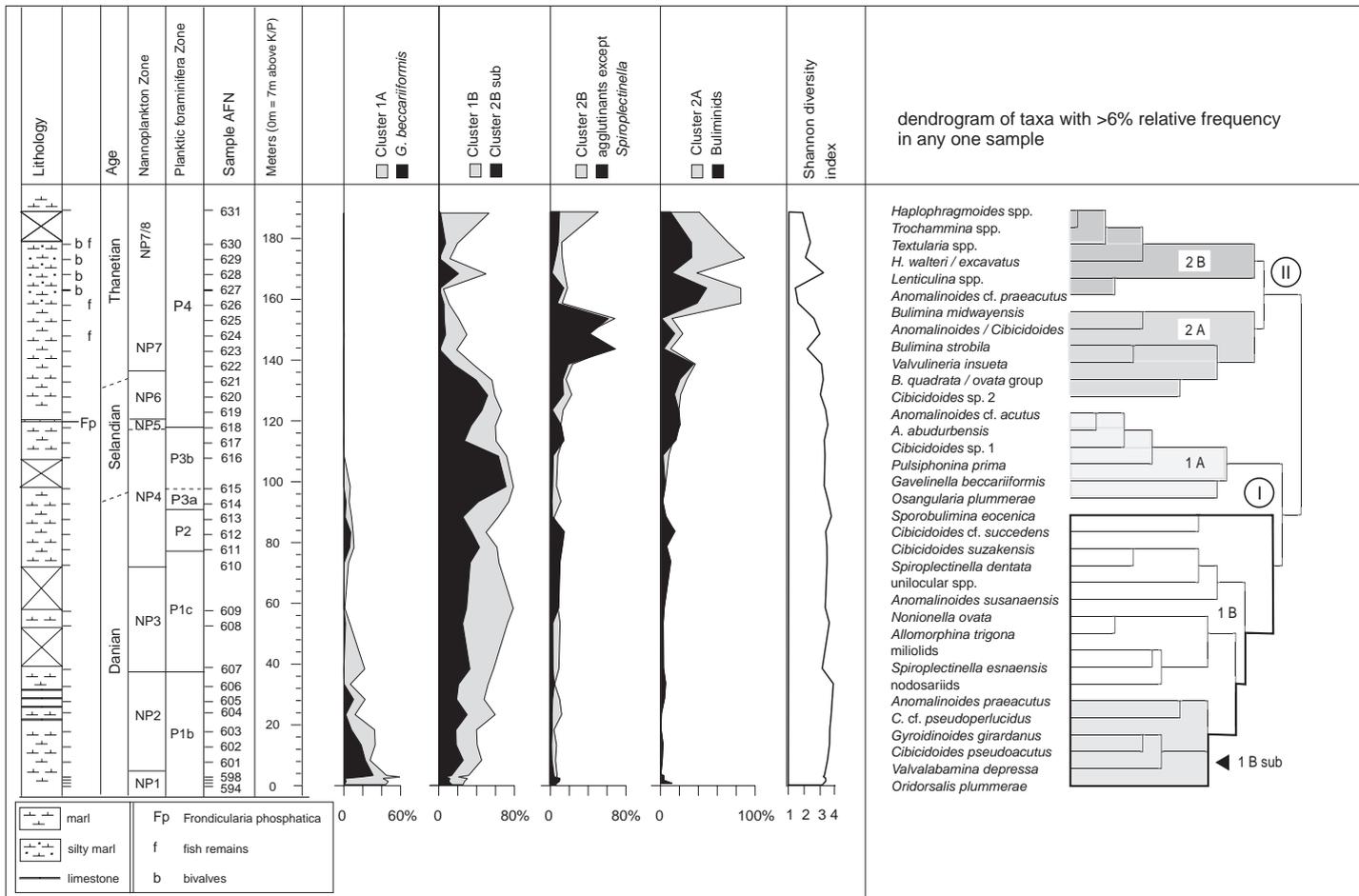


Fig. 3. Dendrogram clustering benthic foraminifera. Joint frequencies of the main clusters are plotted. Also represented are paleoenvironmentally significant sub-clusters, taxa and groups and Shannon diversity index of benthic foraminifera. See text for details.

Table 1
Benthic taxa in the two groups resulting from R-mode hierarchical clustering

Cluster I	Cluster II
<i>Allomorphina trigona</i>	<i>Anomalinoides</i> cf. <i>praeacutus</i>
<i>Anomalinoides</i> cf. <i>acutus</i>	<i>Anomalinoides/Cibicidoides</i>
<i>Anomalinoides praeacutus</i>	<i>Bulimina midwayensis</i>
<i>Anomalinoides susanaensis</i>	<i>Bulimina quadrata-ovata</i> plexus
<i>Angulogavelinella abudurbensis</i>	<i>Bulimina strobila</i>
<i>Cibicidoides</i> cf. <i>succedens</i>	<i>Cibicidoides</i> sp. 2
<i>Cibicidoides pseudoacutus</i>	<i>Haplophragmoides</i> spp.
<i>Cibicidoides</i> cf. <i>pseudoperlucidus</i>	<i>H. walteri/excavatus</i> .
<i>Cibicidoides</i> sp. 1	<i>Lenticulina</i> spp.
<i>Cibicidoides suzakensis</i>	<i>Textularia</i> spp.
<i>Gavelinella beccariiiformis</i>	<i>Trochammina</i> spp.
<i>Gyroidinoides girardanus</i>	<i>Valvulineria(?) insueta</i>
Milioids	
<i>Nonionella ovata</i>	
Nosodariids	
<i>Oridorsalis plummerae</i>	
<i>Osangularia plummerae</i>	
<i>Pulsiphonina prima</i>	
<i>Spiroplectinella dentata</i>	
<i>Spiroplectinella esnaensis</i>	
<i>Sporobulimina eocenica</i>	
Unilocular spp.	
<i>Valvalabamina depressa</i>	

is less reliable as a paleodepth estimate in parts of planktic foraminiferal Zones P4 (NP7), due to poor preservation of foraminiferal faunas.

3.3. Proxies and Q-mode clustering: biofacial succession

The dinocyst and benthic assemblage data, biotic proxies and Q-mode clustering were used to define biofacial units (Figs. 4 and 5). These units serve as a tool to describe the paleoenvironmental history of the succession. Four main biofacies units can be recognized, each subdivided into two sub-facies.

Biofacies 1 is characterized by well-diversified assemblages. Although inner neritic taxa are slightly dominant in the dinocyst assemblage, the benthic assemblage is dominated by outer neritic taxa (cluster IA; 24% *Pulsiphonina prima*). Sub-facies 1a is present in the lower P1b Subzone (corresponding to NP1 and lowermost NP2) and shows relatively high *P/G* and *Pp/G* ratios. Sub-facies 1b is not confined to a certain period; it is present in a few Danian samples and in Subzone P3b (in sample AFN 615 at 98 m).

Biofacies 2 occurs in Subzone P1b, the interval that includes the limestone beds. The biofacies of some samples slightly deviate from the general biofacies in this interval. The *Fibrocysta* and *Spiniferites* dinocyst groups, and deeper-water benthic foraminifera of cluster IA are common. The *P/G* and *Pp/G* ratios are low and decrease upwards. Sub-facies 2a is also characterized by a maximum abundance of *Gavelinella beccariiiformis* (30%), by two maxima in terrestrial palynomorphs and by a maximum abundance of outer neritic dinocysts (low IN/ON ratio). Sub-facies 2b corresponds to the interval with the limestone beds, recording a peak occurrence of *Kenleyia* spp. (80%). Furthermore, the IN/ON ratio increases and the abundance of *G. beccariiiformis* strongly decreases.

Biofacies 3 is dominated by the *Fibrocysta* and *Cerodinium* dinocyst groups and by outer neritic benthic foraminifera of cluster IB. The assemblages are well diversified and the difference between the *P/G* and *Pp/G* ratios is at a maximum. At 73 m, an elevated *S/D* ratio corresponds with a maximum abundance of peridinioid cysts (*Paleocystodinium* spp.), a relatively high IN/ON ratio and a decrease of the %P. In Subzone P3b (sample AFN 615, 98 m), sub-facies 1b is found to separate sub-facies 3a and 3b. In this sample, the first occurrence of *Apectodinium* is observed, in association with a peak of the *Cerodinium* group. Sub-facies 3a is also present in Zone NP2 at 33 m and in the upper Zone NP7. Sub-facies 3b occurs briefly in lower Zone NP2, but is mainly found in Zones P3b and lower P4, where the main paleoenvironmental change becomes apparent. This change is characterized by a decrease in %P and a transition of the benthic assemblage. *Fronidularia phosphatica*, a relatively large benthic foraminiferal species not encountered in the 125–595 µm fraction of benthic foraminifera, is extremely abundant in a foraminiferal packstone, channel-like deposit in the lower Zone P4 (at the base of NP6).

Biofacies 4 records major changes in the assemblages and derived proxies. The IN/ON ratio is relatively high: inner neritic dinocysts dominate this interval. The *P/G* and *Pp/G* ratios show a strong similarity and abruptly increase to reach a maximum. The benthic diversity and the *P/B* ratio decrease and outer neritic benthic foraminifera virtually disappear.

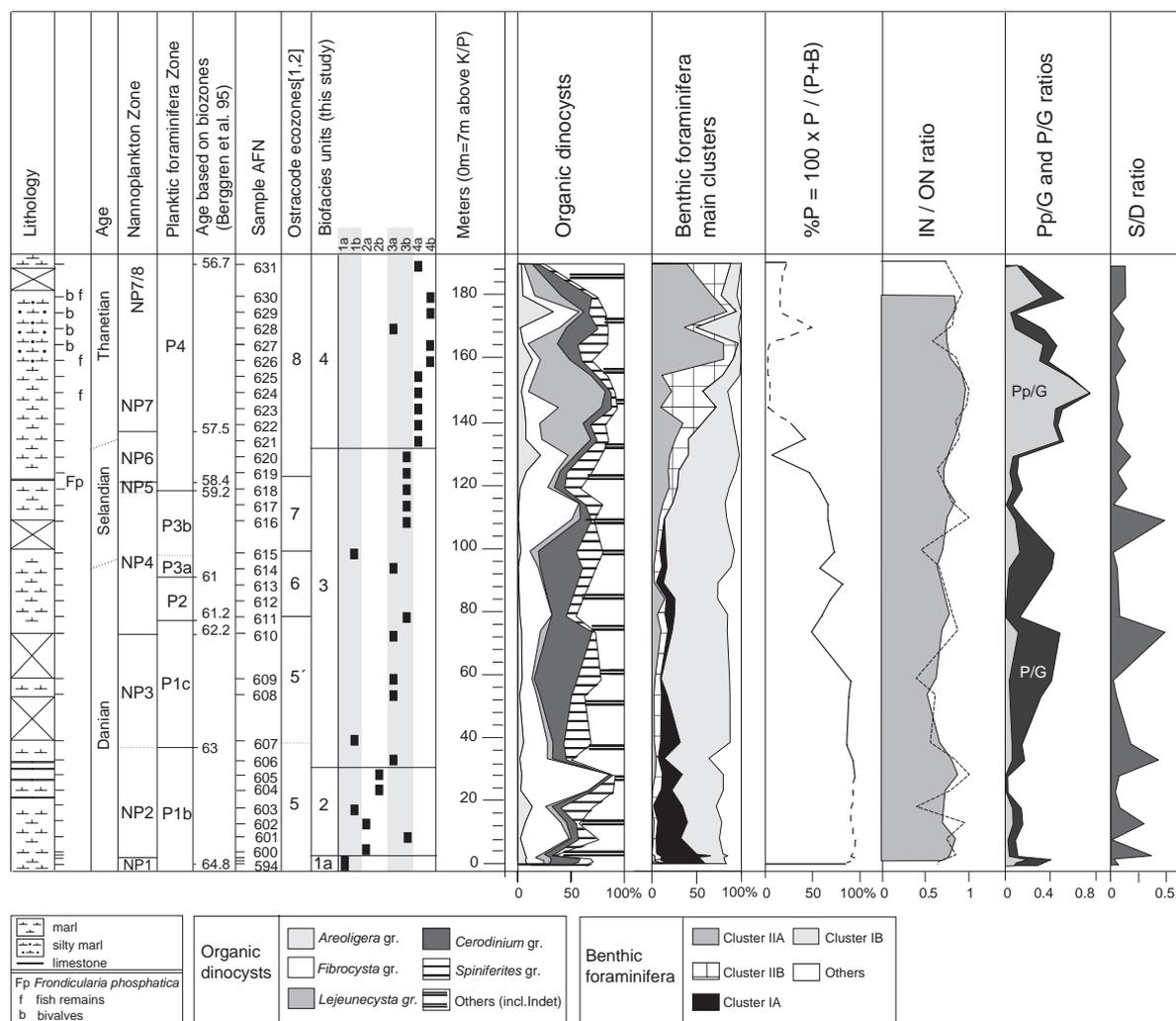


Fig. 4. Dinocysts distributions, benthic foraminiferal assemblages, planktic/benthic ratio, IN/ON ratio, Pp/G and P/G and S/D are represented. The dashed line indicates the actual values of the IN/ON, while the grey curve represents the three-point moving average. The biofacies proposed in this work are here represented next to the ecozones of Donze et al. (1982) and Peypouquet et al. (1986).

Sub-facies 4a is characterized by the high productivity *Lejeunecysta* group and by considerable changes in the benthic assemblages. In the silty interval between 160 and 180 m sub-facies 4b predominates, mainly characterized by shallow and high productivity dinocysts (*Lejeunecysta* and *Cerodinium* groups) and benthic foraminifera (buliminids). *Fronidularia phosphatica* occurs regularly in the coarse fractions (>595 μm) of the washed residues. Sub-facies 3a temporarily reappears at 170 m. Sub-facies 4a is recorded again in the uppermost part of the studied section.

4. Discussion

4.1. Paleoenvironment, biofacies and ostracode ecozones

The K/P boundary interval and the following recovery of ecosystems are of such complex character that we refrained from incorporating them in our study. This much debated time slice was studied in great detail based on high-resolution records of, among others, dinocysts and benthic foraminifera (e.g., Brinkhuis and Zachariasse, 1988; Keller,

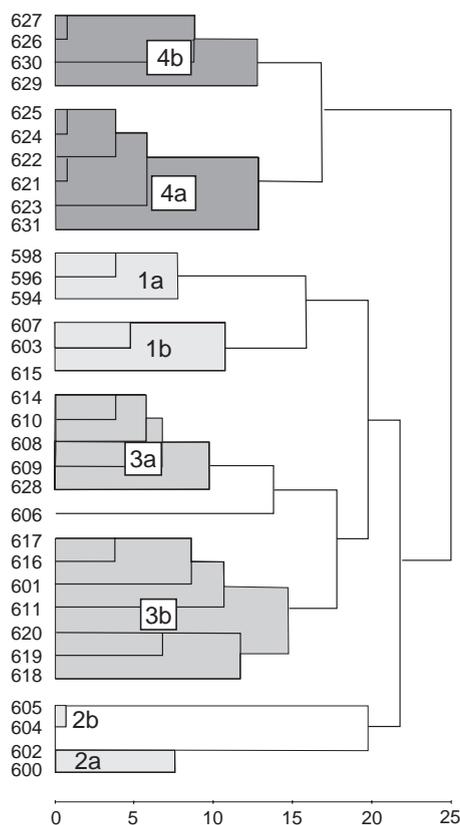


Fig. 5. Q-mode dendrogram of the complete dataset of organic dinocysts and benthic foraminifera. Clusters represent biofacies units.

1988a; Speijer and Van der Zwaan, 1996; Brinkhuis et al., 1998).

In our post-recovery record, we recognize two main intervals. The environment evolved from an open marine, oligotrophic setting in the lower Paleocene towards an inner neritic and more eutrophic setting in the upper Paleocene. Despite the monotonous marls and the scarcity of lithological changes, the palynological and foraminiferal assemblages and proxies indicate major paleoenvironmental changes that are reflected by the biofacies.

Biofacies 1 indicates a low to moderately productive outer neritic, open marine environment with diverse assemblages. Offshore oligotrophic dinocyst taxa (*Impagidinium* spp.) occur and the abundance of typical inner neritic taxa (*Lejeunecysta* group, *Areoligera* group) is low. The benthic taxa were described from relatively oligotrophic environments at outer

neritic to upper bathyal paleodepths in Egypt (e.g. *Gavelinella beccariiiformis*, *Pulsiphonina prima*; Speijer and Schmitz, 1998). Whereas sub-facies 1a characterizes the lowermost part of the section, sub-facies 1b indicates that similar open marine conditions recurred at several short-lived periods during the Danian.

Biofacies 2 is comparable to biofacies 1. Differences appear to be mainly related to movements in relative sea level. In sub-facies 2a, a short-lived maximum occurrence of *Gavelinella beccariiiformis* (>30%) together with a low IN/ON ratio may indicate a period of deepening. Sub-facies 2b may reflect a subsequent shallowing. The *S/D* ratios indicate low sediment supply from land, which is in line with limestone deposition. The *Fibrocysta* group dominates the middle Subzone P1b with a peak occurrence of *Kenleyia* spp. This group joins a number of autotrophic cysts, characterizing a variety of inner neritic environments. The *Kenleyia* complex is thought to have had a preference for shallow to brackish water and tropical conditions, as indicated by its high abundances concomitant with the bloom of *Apectodinium* during the PETM (Crouch et al., 2003). Its dominance may also be related to enhanced stratification of surface waters (compare Reichart et al., 2004), but this explanation is not supported by evidence in the other assemblage and proxy data. The occurrence of the *Kenleyia* peak might indicate a shallowing phase, as corroborated by the decreasing abundance of *G. beccariiiformis*.

In *biofacies 3*, the *P/G* and *Pp/G* ratios show maximum divergence. As none of the other proxies indicates elevated productivity levels, we tend to rely on the *Pp/G* ratio that reflects relatively low productivity in a fairly stable paleoenvironment. Sub-facies 3a is dominated by dinocysts of the *Cerodinium* group and the FO of *Apectodinium* is recorded in the top of this sub-facies. The subsequent dominance of *Fibrocysta* spp., together with increasing IN/ON ratios and decreasing *P/B* ratios indicates shallowing during deposition of sub-facies 3b, and marks the onset of environmental instability.

Biofacies 4 differs strongly from earlier biofacies types and reflects an important change in the paleoenvironment. A drastic increase of inner neritic dinocysts of the *Areoligera* and *Lejeunecysta* groups concurs with a turnover in the benthic assemblages.

The increase of *Areoligera* spp. precedes the main increase of *Lejeunecysta* spp., suggesting that shallowing preceded an increase of productivity. Benthic foraminifera indicate a similar change in paleoenvironmental conditions. Benthic sub-cluster IIB groups the arenaceous taxa *Trochammina* and *Haplophragmoides*, described from inner neritic and coastal (*Haplophragmoides* spp.) environments, respectively (LeRoy, 1953; Luger, 1985; Saint-Marc and Berggren, 1988; Speijer and Schmitz, 1998). These taxa show peak occurrences between 140 and 160 m. Calcareous benthic foraminifera appear to be suppressed in this interval, which may be an artefact related to dissolution of calcareous tests. Subsequently, the dominance of sub-cluster IIA, including common buliminids, indicates increasing productivity.

The occurrence of *Frondicularia phosphatica* and common fish remains in this interval suggests limited sea-floor oxygenation. However, the absence of laminations and the presence of epibenthic taxa (*Cibicides/Cibicidoides* and *Anomalinoidea* spp.) support a scenario of increased productivity and lowered oxygen levels rather than a prolonged and severe oxygen deficiency at the sea floor. The upper Paleocene benthic foraminiferal assemblage of El Kef is typical of highly productive inner to middle neritic environments in the southern Tethyan region, possibly as a result of trade wind induced upwelling (e.g., Speijer et al., 1996). Modelling studies confirm that the North African margin was probably affected by north-eastern winds during the early Paleogene. These were driven by strong tropical–subtropical temperature gradients and are held responsible for a southeast to west coastal current (Huber and Sloan, 2000) with significant upwelling along the North coast of Africa as a consequence (Huber and Sloan, 2000; Huber et al., 2003).

In general, there is a fairly good agreement between our data and ostracode records (Donze et al., 1982; Peypouquet et al., 1986) in the overall paleoenvironmental evolution and position of the main biotic transitions at El Kef. However, in more detail, our data do reveal some discrepancies with the interpretation based on the ostracodes (Donze et al., 1982; Peypouquet et al., 1986; Figs. 4 and 6). The paleodepth estimate based on the ostracode record is generally somewhat deeper than our estimate based on the combined dinocyst and benthic

foraminiferal records. Other discrepancies concern sea-floor oxygenation.

Ostracode ecozone 5 correlates with biofacies 1 and 2 of this study and is thought to be characterized by upwelling in an upper epibathyal, relatively well-oxygenated environment. Upwelling is, however, not evident in our data until much later in the Paleocene.

Ostracode ecozones 5' and 6 and sub-facies 3a agree on an open marine, oligotrophic environment. However, the benthic foraminifera assemblages do not support the slight decrease of oxygen at the sea floor suggested by Peypouquet et al. (1986).

Ostracode ecozone 7 mainly corresponds to sub-facies 3b. The ostracode assemblage records a shallowing trend from an upper bathyal to an outer neritic shelf environment starting at the transition from Subzones P3a to P3b (Peypouquet et al., 1986). During the same interval, a decrease of the bottom water oxygen is recognized (Donze et al., 1982). In our view, sub-facies 3b indeed indicates shallowing, but rather from outer to inner neritic depths. We do not find good evidence for decreasing oxygenation at the sea floor.

Ostracode ecozone 8, corresponding to biofacies 4, is characterized by a poorly diversified ostracode fauna, indicating increasing productivity and decreasing bottom water oxygenation, which is in agreement with our data. During middle Zone P4, a temporary return to previous, slightly deeper and more oligotrophic conditions is inferred at the re-occurrence of biofacies 3. Lower values of the *P/G* and *Pp/G* ratios coincide with a peak of *Areoligera* spp. and a lower abundance of the buliminids, which points to a weakening of the upwelling system. This brief return of more open marine conditions is not recorded in the ostracode assemblages and was possibly not sampled in the earlier studies.

4.2. Evaluation of palynological proxies

In modern oceans, productive regions such as coastal and upwelling areas are characterized by a high relative amount of protoperidinioid dinoflagellate cysts (Versteegh, 1994; Batten, 1996; Firth and Clark, 1998; Prauss, 2001). Changes in productivity are considered to influence the ratio between the heterotrophic protoperidinioid and the autotrophic gonyau-

settings (Powell et al., 1996; Brinkhuis et al., 1998; Zonneveld et al., 2001; Reichart and Brinkhuis, 2003; Roncaglia, 2004; Sprangers et al., 2004). Next to a P/G ratio, we generated a Pp/G ratio for this study, which only includes cysts of extant heterotrophic motile protoperidinioids (Pp), such as *Lejeunecysta* spp. (Brinkhuis et al., 1998; Pross and Schmiedl, 2002; Sangiorgi et al., 2002; Roncaglia, 2004). Eukaryotic sea-surface productivity (SSP) has thus been estimated using the ‘classic’ P/G ratio in addition to the Pp/G ratio.

From the middle Danian until the middle Selandian (upper Zone P3b), important differences distinguish the P/G and Pp/G ratios due to the scarcity of the extant *Lejeunecysta* group. Considering the P/G ratio, one would estimate two intervals of increased productivity. Instead, the Pp/G ratio indicates a relatively oligotrophic setting until the uppermost Zone NP6, which is in agreement with the other proxies.

From Zone NP7 to the top of the studied interval, the P/G and Pp/G ratios show a strong similarity due to the dominance of the *Lejeunecysta* group. Although it cannot be excluded that preferential preservation plays a role in the abundance of the peridinioid cysts (cf. Reichart and Brinkhuis, 2003), we consider this abrupt increase of protoperidinioid cysts to indicate an increase in paleoproductivity. Increasing productivity is also reflected by the benthic taxa: buliminids, *Anomalinoides* cf. *aegyptiacus* and *F. phosphatica* (Speijer et al., 1996; Kouwenhoven et al., 1997). Taking the ecology of modern dinoflagellates into account, we consider the Pp/G ratio more reliable than the P/G ratio in terms of paleoproductivity.

The entire record is strongly dominated by the inner neritic dinocyst assemblage: the IN/ON ratio rarely falls below 0.5. This ratio represents the proportion of taxa typical of an inner neritic environment (*Fibrocysta*, *Areoligera* and *Lejeunecysta* groups) (Brinkhuis and Zachariasse, 1988; Brinkhuis, 1994; Powell et al., 1996; Sluijs et al., 2005; Pross and Brinkhuis, 2005) as compared to the neritic to oceanic taxa (e.g., the *Spiniferites* and *Impagidinium* spp.) (Brinkhuis and Zachariasse, 1988; Zonneveld et al., 1997; Devillers and de Vernal, 2000; Sluijs et al., 2005). Consequently, the generally upward increasing IN/ON ratio can be

interpreted as an overall shallowing trend, interrupted by several temporary deepening phases. This is in agreement with depth estimates based on the benthic foraminiferal record, although some differences in paleodepth reconstructions occur in the lower Paleocene.

A large number of studies reveals the significance of the quantitative distribution of terrestrial palynomorphs in marine settings for sea-level reconstructions (e.g. Versteegh, 1994; McCarthy and Mudie, 1998; Santarelli et al., 1998; Prauss, 2001). According to McCarthy and Mudie (1998), the concentration of pollen and spores in marine sediments decreases exponentially with distance to shore. The S/D ratio, expressing the relative contribution of continentally derived organic material, is generally low, although single sample peaks occur in the lower part of the record. Only in a few cases the S/D peaks recorded in the Danian and lower Selandian correlate to increased P/G , Pp/G and IN/ON ratios, indicating a low correspondence between these proxies. In a regressive scenario, one would expect a general increase of terrestrial palynomorphs. The generally low S/D values recorded in the section might be related to the distance of the sedimentation area from the source of terrestrial input. Alternatively, since we only consider relative values, an increase in terrestrial palynomorphs may be overshadowed by the high abundance of dinocysts under the high-productivity regime of the late Paleocene.

4.3. Paleobathymetry: comparison with regional and global sea-level records

An overall second order change in paleodepth is recognized in the Paleocene of El Kef. The main phase of shallowing is recorded in the P3b and P4 Zones. Superimposed on the second-order trend, third-order cycles are recognized, and compared with regional sea level cycles reported from Egypt (Lüning et al., 1998; Speijer, 2003) and the global record. During the Danian the faunal assemblages restrict the paleodepth estimation to an outer neritic environment; the abundance of *Gavelinella beccariiiformis* may indicate deposition at upper bathyal depths in the lower Subzone P1b. Within Subzone P1b (NP2), we suspect a temporary shallowing,

based on the peak occurrence of inner neritic *Kenleyia* spp. and the decrease of deeper-water benthic taxa. However, the *S/D* ratio does not reflect a shallowing and, as there is only an approximate correlation to the sequence boundary Da3 (Hardenbol et al., 1998), this shallowing might represent a local phenomenon or not a real shallowing.

During the middle Paleocene, at the Subzones P3a–P3b transition, a sea-level fall can be identified in our data. The reduced thickness of Subzone P3a suggests that a stratigraphic gap marks the boundary between Subzones P3a and P3b. This gap can be correlated to sequence boundary Sel1. A sea-level lowering was previously inferred on the basis of the ostracode record (Donze et al., 1982) and was observed elsewhere in Tunisia (Donze et al., 1982; Saint-Marc and Berggren, 1988). A similar sea-level fluctuation has been described in Subzone P3a at different locations in Egypt (Lüning et al., 1998; Speijer, 2003) and in western Europe by Hardenbol et al. (1998).

From Subzone P3b onwards, all evidence is in favour of a regressive trend. The total magnitude of the shallowing is obscured by the interaction with the eutrophication signal, but is estimated to be some 150 m (from ~200 to ~50 m depth). The *Fronicularia phosphatica* bed at the base of Zone NP6 can be correlated with the Sel2 sequence boundary of Hardenbol et al. (1998) and with unconformities in eastern Egypt (Lüning et al., 1998; Speijer and Schmitz, 1998). A correlation with the Thanetian sequence boundaries of Zones P4 and NP7/8 (Hardenbol et al., 1998) cannot be confirmed, although the level where the benthic assemblages are dominated by agglutinated taxa (i.e. *Haplophragmoides* spp.) can be tentatively correlated to Th2.

Higher resolution studies are needed to better constrain the timing of sea-level fluctuations and to improve the correlation with sequences elsewhere in North Africa and Europe.

5. Conclusions

The integrated paleoecological analysis of quantitative distribution patterns of Paleocene organic-

walled dinocysts and benthic foraminifera from the El Kef section (NW Tunisia) allows a better understanding of the evolution of the Paleocene paleo-environment. Our records indicate that from an initially oligotrophic, open marine, outer neritic to upper bathyal setting the environment evolved towards a more eutrophic inner neritic setting, influenced by coastal upwelling by the end of the Paleocene.

Lower and middle Paleocene sediments were deposited in an outer neritic to uppermost bathyal environment at ~200 m depth. A long-term shallowing toward an inner neritic environment set in at the base of planktic foraminifera Subzone P3b and continued in Zone P4. The total magnitude of the shallowing is obscured by the interaction with the eutrophication signal, but is estimated to be some 150 m (from ~200 to ~50 m) and occurred in discrete cycles of which several can be correlated throughout the southern Tethyan margin and to the eustatic curve of Hardenbol et al. (1998). During the late Paleocene, intensified upwelling is inferred to explain increased productivity, leading to eutrophication of the water column and oxygen deficiency at the sea floor.

Acknowledgments

We thank A. Sluijs for fruitful discussions on the paleoecological signal and taxonomy of organic dinocysts. G. Versteegh and E. Susek are thanked for helping in taking pictures of dinocysts. The manuscript benefited from thoughtful and constructive reviews by G. Keller and J. Pross. This project was supported by the DFG within the European Graduate College “Proxies in Earth History”. This is NSG contribution no. 20041104.

Appendix A

The taxonomy of dinocysts is in accordance with Williams et al. (1998). The establishment of dinocysts groups implying similar paleoecological conditions is mainly due to the occurrence of certain genera related to certain environmental conditions, based on literature data

(see Sluijs et al., 2005; Pross and Brinkhuis, 2005).

A.1. *Areoligera* group

This group includes inner neritic and coastal skolochorate dorsally–ventrally compressed Gonyaulacoid taxa, such as *Areoligera* spp. and *Glaphyrocysta* spp. (Brinkhuis and Zachariasse, 1988; Brinkhuis, 1994).

A.2. *Cerodinium* spp.

This group includes cavate Peridinioid cysts, such as *Cerodinium* spp., *Paleocystodinium* spp., *Spinidinium* spp. and *Senegalium* spp. *Cerodinium* is morphologically extremely similar to *Deflandrea*, which are neritic to ocean heterotrophic cysts (Sluijs et al., 2005). High abundance of *Senegalium* is associated with elevated nutrients (Brinkhuis and Zachariasse, 1988).

A.3. *Fibrocysta* group

This group includes fibrous proximate to chorate gonyaulacoid cysts such as *Fibrocysta* spp. and *Kenleyia* spp., which are the most abundant taxa in this record, together with *Cordospheridium* spp., *Operculodinium* spp., *Carpatella* spp., *Damassadinium californicum* and *Cribroperidinium* spp., which show very low abundances.

These taxa generally characterized inner neritic environment (Brinkhuis, 1994; Brinkhuis et al., 1994; Powell et al., 1996; Sluijs et al., 2005; Pross and Brinkhuis, 2005).

A.4. *Impagidinium* spp.

Proximochorate Gonyaulacoid cysts. In recent environments, *Impagidinium* is characteristic of open marine oligotrophic settings (Brinkhuis and Zachariasse, 1988; Dale, 1996; Crouch et al., 2003; Piasecki, 2003).

A.5. *Lejeunecysta* group

This group includes proximate acavate (or weakly cornucavate) protoperidinioid cysts. This group is

typical of high productivity areas (Brinkhuis et al., 1998; Pross and Schmiedl, 2002; Sangiorgi et al., 2002; Roncaglia, 2004).

A.6. *Spiniferites* group

This group includes *Spiniferites* spp. and *Achomosphaera* spp., cosmopolitan proximochorate Gonyaulacoid cysts (Brinkhuis, 1994; Brinkhuis et al., 1994; Pross, 2001; Sluijs et al., 2003).

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.marmicro.2005.01.001](https://doi.org/10.1016/j.marmicro.2005.01.001).

References

- Adatte, T., Keller, G., Stinnesbeck, W., 2002. Late Cretaceous to early Paleocene climate and sea-level fluctuations: the Tunisian record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 178, 165–196.
- Batten, D.J., 1996. Palynofacies and paleoenvironmental interpretation. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, pp. 1011–1064.
- Berggren, W.A., Kent, D.V., Swisher, C.C., Aubry, M.P., 1995. A revised Cenozoic geochronology and chronostratigraphy. In: Berggren, W.A., Kent, D.V., Aubry, M.P., Hardenbol, J. (Eds.), *Geochronology, Time Scales and Global Stratigraphic Correlation*, pp. 129–212.
- Billups, K., Rickaby, R.E.M., Schrag, D.P., 2004. Cenozoic pelagic Sr/Ca records: exploring a link to paleoproductivity. *Paleoceanography* 19, A3005. [doi:10.1029/2004PA001011](https://doi.org/10.1029/2004PA001011).
- Bobier, C., Viguié, C., Chaari, A., Chine, A., 1991. The post-Triassic sedimentary cover of Tunisia: seismic sequences and structure. In: Freeman, R., Huch, M., Mueller, S. (Eds.), *The European Geotraverse. Tectonophysics*, pp. 371–410.
- Brinkhuis, H., 1994. Late Eocene to early Oligocene dinoflagellate cysts from the Priabonian type-area (northeast Italy): biostratigraphy and paleoenvironmental interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107, 121–163.
- Brinkhuis, H., Zachariasse, W.J., 1988. Dinoflagellate cysts, sea level changes and planktonic foraminifera across the Cretaceous–Tertiary boundary at El Haria, northwest Tunisia. *Marine Micropaleontology* 13, 153–191.
- Brinkhuis, H., Romein, A.J.T., Smit, J., Zachariasse, W.J., 1994. Danian–Selandian dinoflagellate cysts from lower latitudes with special reference to El Kef section, NW Tunisia. GFF, “Stratigraphy of the Paleocene” 116, 46–48.

- Brinkhuis, H., Bujak, J.P., Versteegh, G.J.M., Visscher, H., 1998. Dinoflagellate-based sea surface temperature reconstructions across the Cretaceous–Tertiary boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 141, 67–83.
- Brinkhuis, H., Munsterman, D.K., Sengers, S., Sluijs, A., Warnaar, J., Williams, G.L., 2003. Late Eocene–Quaternary dinoflagellate cysts from ODP Site 1168, off Western Tasmania. In: N.F. Exon, J.P. Kennet, M.J. Malone (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results, volume 189*, pp. Available from World Wide Web: http://www-odp.tamu.edu/publications/189_SR/106/106.htm.
- Burollet, P.F., 1956. Contribution à l'étude stratigraphique de la Tunisie Centrale. *Annales des Mines et de la Geologie (Tunisia)*, 350.
- Burollet, P.F., 1991. Structures and tectonics of Tunisia. In: Freeman, R., Huch, M., Mueller, S. (Eds.), *The European Geotransverse. Tectonophysics*, pp. 359–369.
- Crouch, E.M., Brinkhuis, H., Visscher, H., Adatte, T., Bolle, M.P., 2003. Late Paleocene–early Eocene dinoflagellate cyst records from the Tethys: further observations on the global distributions of *Apectodinium*. In: Wing, S., Gingerich, P.D., Schmitz, B., Thomas, E. (Eds.), *Causes and Consequences of Globally Warm Climates in the Early Paleogene. Special Paper-Geological Society of America*, vol. 369, pp. 113–131. Boulder, Colorado.
- Culver, S.J., 2003. Benthic foraminifera across the Cretaceous–Tertiary (K–T) boundary: a review. *Marine Micropaleontology* 47, 177–226.
- Dale, B., 1996. Dinoflagellate cyst ecology: modeling and geological applications. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications. American Association of Stratigraphic Palynologists Foundation, Dallas*, pp. 1249–1276.
- Dale, B., Fjellså, A., 1994. Dinoflagellate cysts as paleoproductivity indicators: state of art, potential, and limits. In: Zahn, R., Pedersen, T.F., Kaminski, M.A., Labeyrie, L. (Eds.), *Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change*. Springer, Berlin, pp. 521–537.
- Devillers, R., de Vernal, A., 2000. Distribution of dinoflagellate cysts in surface sediments of the northern Atlantic in relation to nutrient content and productivity in surface water. *Marine Geology* 166, 103–124.
- Donze, P., Colin, J.P., Damotte, R., Oertli, H.J., Peypouquet, J.P., Said, R., 1982. Le ostracodes du Campanien terminal à l'Eocène inférieur de la coupe du Kef, Tunisie Nord-Occidentale. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* 6, 273–307.
- Firth, J.V., Clark, D.L., 1998. An early Maastrichtian organic-walled phytoplankton cyst assemblage from an organic-rich black mud Core F1-533, Alpha Ridge: evidence for upwelling conditions in the Cretaceous Arctic Ocean. *Marine Micropaleontology* 34, 1–27.
- Galeotti, S., Coccioni, R., 2002. Changes in coiling direction of *Cibicidoides pseudoacutus* (Nakkady) across the Cretaceous–Tertiary boundary of Tunisia: palaeoecological and biostratigraphic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 178, 197–210.
- Hardenbol, J., Thierry, J., Farley, M.B., Jacquin, T., de Graciansky, P.-C., Vail, P.R., 1998. Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins. *SEPM special publication* 60, 3–13.
- Huber, M., Sloan, L.C., 2000. Climatic responses to tropical sea surface temperature changes on a “greenhouse” earth. *Paleoceanography* 15 (4), 443–450.
- Huber, M., Sloan, L.C., Shellito, C.J., 2003. Early Paleogene oceans and climate: a fully coupled modelling approach using the NCAR CCSM. In: Wing, S.L., Gingerich, P.D., Schmitz, B., Thomas, E. (Eds.), *Causes and Consequences of Globally Warm Climates in the Early Paleogene. Special Paper-Geological Society of America*, vol. 369, pp. 25–47. Boulder, Colorado.
- Keller, G., 1988a. Biotic turnover in benthic foraminifera across the Cretaceous/Tertiary boundary at El Kef, Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 66, 153–171.
- Keller, G., 1988b. Extinction, survivorship and evolution of planktic foraminifera across the Cretaceous/Tertiary boundary at El Kef, Tunisia. *Marine Micropaleontology* 13, 239–263.
- Keller, G., Li, L., MacLeod, N., 1995. The Cretaceous/Tertiary boundary stratotype section at El Kef, Tunisia: how catastrophic was the mass extinction? *Palaeogeography, Palaeoclimatology, Palaeoecology* 119, 221–254.
- Kouwenhoven, T.J., Speijer, R.P., van Oosterhout, C., van der Zwaan, G.J., 1997. Benthic foraminiferal assemblages between two major extinction events: the Paleocene El Kef section, Tunisia. *Marine Micropaleontology* 29, 105–127.
- LeRoy, L.W., 1953. Biostratigraphy of the Maqfi section, Egypt. *GSA, Mem.*, 54, 73 pp.
- Luger, P., 1985. Stratigraphie der marinen Oberkreide und des Alttertiärs im südwestlichen Obermil-Becken (SW Ägypten) unter besonderer Berücksichtigung der Mikropaläontologie, Paläökologie und Paläogeographie. *Berliner Geowissenschaftliche Abhandlungen. Reihe A, Geologie und Paläontologie* 63, 151.
- Lünig, S., Marzouk, A.M., Kuss, J., 1998. The paleocene of central east Sinai, Egypt: “sequence stratigraphy” in monotonous hemipelagites. *Journal of Foraminiferal Research* 28 (1), 19–39.
- Martini, E., 1971. Standard Tertiary and Quaternary calcareous nannoplankton zonation. *Proceeding of the II Planktonic Conference, Roma*, pp. 739–785.
- McCarthy, F.M.G., Mudie, P.J., 1998. Oceanic pollen transport and pollen: dinocyst ratios as markers of late Cenozoic sea level change and sediment transport. *Palaeogeography, Palaeoclimatology, Palaeoecology* 138, 187–206.
- Perch-Nielsen, K., 1981. Les coccolithes du Paleocene pres de El Kef, Tunisie, et leurs ancetres. *Cahiers de Micropaleontologie* 3, 7–23.
- Peypouquet, J.P., Grousset, F., Mourguiart, P., 1986. Paleogeography of the Mesogean sea based on ostracods on the northern Tunisian continental shelf between the late Cretaceous and early Paleogene. *Geologische Rundschau* 75 (1), 159–174.
- Piasecki, S., 2003. Neogene dinoflagellate cysts from Davis strait, offshore West Greenland. *Marine and Petroleum Geology* 20, 1075–1088.

- Powell, A.J., Brinkhuis, H., Bujak, J.P., 1996. Upper Paleocene–lower Eocene dinoflagellate cyst sequence biostratigraphy of southeast England. Special Publication–Geological Society of London 101, 145–183.
- Prauss, M., 2001. Sea-level changes and organic-walled phytoplankton response in a late Albian epicontinental setting, Lower Saxony basin, NW Germany. *Palaeogeography, Palaeoclimatology, Palaeoecology* 174, 221–249.
- Pross, J., 2001. Paleo-oxygenation in Tertiary epeiric seas: evidence from dinoflagellate cysts. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166, 369–381.
- Pross, J., Schmiedl, G., 2002. Early Oligocene dinoflagellate cysts from the Upper Rhine Graben (SW Germany): paleoenvironmental and paleoclimatic implications. *Marine Micropaleontology* 45, 1–24.
- Pross, J., Brinkhuis, H., 2005. Organic-walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene; a synopsis of concepts. *Paläontologische Zeitschrift* 79, 53–59.
- Reichart, G.J., Brinkhuis, H., 2003. Late quaternary *protoperidinium* cysts as indicators of paleoproductivity in the northern Arabian Sea. *Marine Micropaleontology* 49, 303–315.
- Reichart, G.J., Brinkhuis, H., Huiskamp, F., Zachariasse, W.J., 2004. Hyper-stratification following glacial overturning events in the northern Arabian Sea. *Paleoceanography* 19, A2013. doi:10.1029/2003PA000900.
- Roncaglia, L., 2004. Palynofacies analysis and organic-walled dinoflagellate cysts as indicators of paleo-hydrographic changes: an example from Holocene sediments in Skálafjörður, Faroe Islands. *Marine Micropaleontology* 50, 21–42.
- Saint-Marc, P., Berggren, W.A., 1988. A quantitative analysis of paleocene benthic foraminiferal assemblages in central Tunisia. *Journal of Foraminiferal Research* 18 (2), 97–113.
- Salaj, J., 1980. Microbiostratigraphie du Crétacé et du Paléogène de la Tunisie Septentrionale et Orientale (Hypostratotypes Tunisiens). Bratislava, Slovakia, 238 pp.
- Sangiorgi, F., Capotondi, L., Brinkhuis, H., 2002. A centennial scale organic-walled dinoflagellate cyst record of the last deglaciation in the South Adriatic Sea (Central Mediterranean). *Palaeogeography, Palaeoclimatology, Palaeoecology* 186, 199–216.
- Santarelli, A., Brinkhuis, H., Hilgen, F.J., Lourens, L.J., Versteegh, G.J.M., Visscher, H., 1998. Orbital signatures in a late Miocene dinoflagellate from Crete (Greece). *Marine Micropaleontology* 33, 273–297.
- Sluijs, A., Brinkhuis, H., Stickley, C.E., Warnaar, J., Williams, G.L., Fuller, M., 2003. Dinoflagellate cysts from Eocene–Oligocene transition in the southern ocean: results from ODP Leg 189. *Proceedings of the Ocean Drilling Program. Scientific Results* 189, 1–42.
- Sluijs, A., Pross, J., Brinkhuis, H., 2005. From greenhouse to icehouse; organic-walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene. *Earth-Science Reviews* 68, 281–315.
- Smit, J., Romein, A.J.T., 1985. A sequence of events across the Cretaceous–Tertiary boundary. *Earth and Planetary Science Letters* 74, 155–170.
- Speijer, R.P., 2003. Danian–Selandian sea-level change and biotic excursion on the southern Tethyan margin (Egypt). In: Wing, S.L., Gingerich, P.D., Schmitz, B., Thomas, E. (Eds.), *Causes and consequences of globally warm climates in the early Paleogene*, Special Paper–Geological Society of America, pp. 275–290. Boulder, Colorado.
- Speijer, R.P., Schmitz, B., 1998. A benthic foraminiferal record of Paleocene sea-level and trophic/redox conditions at Gebel Aweina, Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology* 137, 79–101.
- Speijer, R.P., Van der Zwaan, G.J., 1996. Extinction and survivorship of southern Tethyan benthic foraminifera across the Cretaceous/Paleogene boundary. *Geological Society Special Publication* 102, 343–371.
- Speijer, R.P., Van der Zwaan, G.J., Schmitz, B., 1996. The impact of Paleocene/Eocene boundary events on middle neritic benthic foraminiferal assemblages from Egypt. *Marine Micropaleontology* 28, 99–132.
- Sprangers, M., Dammers, N., Brinkhuis, H., van Weering, T.C.E., Lotter, A.F., 2004. Modern organic-walled dinoflagellate cyst distribution offshore NW Iberia; tracing the upwelling system. *Review of Palaeobotany and Palynology* 128, 97–106.
- Versteegh, G.J.M., 1994. Recognition of cyclic and non-cyclic environmental changes in the Mediterranean Pliocene: a palynological approach. *Marine Micropaleontology* 23, 147–183.
- Williams, G.L., Lentin, J.K., Fensome, R.A., 1998. The Lentin and Williams index of fossils dinoflagellates. *AASP Contributions Series Number* 34, 817.
- Wing, S.L., Gingerich, P.D., Schmitz, B., Thomas, E. (Eds.), 2003. *Causes and Consequences of Globally Warm Climates in the early Paleogene*, Special Paper vol. 369. The Geological Society of America, Boulder, Colorado, 614 pp.
- Zachos, J.C., Pagani, M., Sloan, L., Thomas, D.J., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.
- Zachos, J.C., Wara, M.W., Bohaty, S., Delaney, M.L., Petrizzo, M.R., Brill, A., Bralower, T.J., Premoli Silva, I., 2003. A transient rise in tropical sea surface temperature during the Paleocene–Eocene thermal maximum. *Science* 302, 1551–1554.
- Zaier, A., Beji-Sassi, A., Sassi, S., Moody, R.T.J., 1998. Basin evolution and deposition during the early Paleogene in Tunisia. In: MacGregor, D.S., Moody, R.T.J., Clark-Lowes, D.D. (Eds.), *Petroleum Geology of North Africa*. Geological Society, Special Publication, London, pp. 375–393.
- Zonneveld, K.A.F., Versteegh, G.J.M., de Lange, G.J., 1997. Preservation of organic-walled dinoflagellate cysts in different oxygen regimes: a 10,000 year natural experiment. *Marine Micropaleontology* 29, 393–405.
- Zonneveld, K.A.F., Hoek, R.P., Brinkhuis, H., Willems, H., 2001. Geographical distribution of organic-walled dinoflagellate cysts in surficial sediments of the Benguela upwelling region and their relationship to upper ocean conditions. *Progress in Oceanography* 48, 25–72.