



MARINE MICROPALEONTOLOGY

Marine Micropaleontology 59 (2006) 210-229

www.elsevier.com/locate/marmicro

Paleoenvironmental change at the Danian–Selandian transition in Tunisia: Foraminifera, organic-walled dinoflagellate cyst and calcareous nannofossil records

Elisa Guasti ^{a,*}, Robert P. Speijer ^b, Henk Brinkhuis ^c, Jan Smit ^d, Etienne Steurbaut ^{b,e}

^a Department of Geosciences (FB 5), Bremen University, P.O. Box 330440, 28334 Bremen, Germany

Received 8 July 2005; received in revised form 2 February 2006; accepted 20 February 2006

Abstract

In the present study, we document paleoenvironmental change across the Danian-Selandian transition (planktic foraminiferal interval P2-P3b; calcareous nannofossil Zone NP4, Subzones NTp6-NTp8A; 61-59Ma) in NW Tunisia, Diversifications of Paleogene planktic foraminifera with the evolution of the muricate and photosymbiotic lineages Morozovella, Acarinina and Igorina and of the biostratigraphically important nannofossils genus Fasciculithus are recorded within this interval. The present study aims to understand early Paleogene environmental changes in the southern Tethys, by analyzing the evolution of surfacewater and-to a lesser extent-seafloor conditions. Three localities were investigated: Ain Settara, Elles and El Kef, all representing outer neritic deposition in the same basin, the Tunisian Trough. Paleoenvironmental changes are explored by combining planktic foraminiferal, organic dinocyst and calcareous nannofossils assemblages and several proxy parameters (planktic/benthic ratio, numbers of planktic foraminifera per gram, peridinioid/gonyaulacoid ratio; terrestrial/marine palynomorph ratio). In addition, also some geochemical parameters (calcite content and stable isotopes) are examined. Our records indicate that the environment evolved from an initially oligotrophic, open marine, deep outer neritic setting in P2-P3a towards a shallower and nutrient-rich setting from the base of Subzone P3b. This change is seen in the foraminiferal assemblages, with the substitution of *Praemurica* by *Morozovella* among the planktic foraminifera and an upward decrease in deeper benthic taxa. Also the organic-dinocyst assemblages show a peak of peridinioid cysts (Cerodinium and Lejeunecysta). Associated to these dinocyst assemblages, the lowest occurrence of Apectodinium is recorded, which seem to have evolved in this region, possibly in response to enhanced nutrient levels on the shelf. Additionally, a distinct change in calcareous nannofossil assemblages is also described, marked by the lowest appearance of Chiasmolithus edentulus, the lowest consistent occurrence of Fasciculithus and a slight increase in near-shore taxa (essentially Pontosphaera).

This project provides an accurate understanding of paleoenvironmental change across the Danian-Selandian transition in Tunisia. Especially, integrating different proxies demonstrates a paleobathymetric shallowing from the Danian to the Selandian, associated to increase surface paleoproductivity. Furthermore, the results are compared with those from other localities along the

^b Department of Geography and Geology, K.U.Leuven, Celestijnenlaan 200E, 3001 Leuven, Belgium

^c Laboratory of Palaeobotany and Palynology, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, The Netherlands
^d Department of Sedimentology, Faculty of Earth and Life Sciences Vrije Universiteit, de Boelelaan 1085 1081HV Amsterdam, The Netherlands
^e Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 1000 Brussels, Belgium

^{*} Corresponding author. New address: Fugro Robertson Limited, stratigraphy group, Llandudno LL30 1SA, North Wales, UK. Tel.: +44 1492 581811; fax: +44 1492 583416.

E-mail addresses: elisa.guasti@fugro-robertson.com (E. Guasti), robert.speijer@geo.kuleuven.be (R.P. Speijer), H.Brinkhuis@bio.uu.nl (H. Brinkhuis), smit@geo.vu.nl (J. Smit), etienne.steurbaut@naturalsciences.be (E. Steurbaut).

Southern Tethyan margin (Egypt and Jordan) and a more regional paleoclimatic/paleoceanographic perturbation in the Southern Tethys is suggested.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Danian-Selandian transition; planktic foraminifera; organic-walled dinoflagellate cysts; Tunisia; calcareous nannofossils; paleoenvironment; Paleocene; stratigraphy

1. Introduction

The early Paleogene can be regarded as the warmest episode of the past ~100 million years (i.e. Zachos et al., 2001, 2003; Wing et al., 2003). Following the Cretaceous/Paleogene perturbation, the middle Paleocene (Selandian) is characterized by a first step of global warming. This warming culminated during the earliest Eocene in a brief, super-greenhouse period, known as Paleocene/Eocene thermal maximum (PETM; Zachos et al., 2003).

The lower-middle Paleocene, or Danian-Selandian (D-S) transition ($\sim 61-59$ Ma) is a poorly studied interval of the geological record, but interest is reviving. For example, recent studies indicate that the D-S transition was a time of marked global change, e.g. reflected in turnover of planktic foraminifera. Evolutionary novelties include evidence of increasing habitat stratification in the water column related to the acquisition of symbiotic partnerships as a trophic strategy (Quillévéré and Norris, 2003). Subbotinids and globanomalinids probably preferred living within or below the thermocline, whereas Acarinina, Morozovella and Igorina inhabited the upper mixed layer (Shackleton et al., 1985; Pearson et al., 1993; D'Hondt et al., 1994; Van Eijden, 1995; Kelly et al., 1996; Lu et al., 1998; Quillévéré and Norris, 2003). Probably most Morozovella, Acarinina and Igorina hosted photosymbionts, which may have facilitated these taxa to thrive in lownutrient water masses (D'Hondt et al., 1994; Norris, 1996; Berggren and Norris, 1997; Quillévéré and Norris, 2003).

In addition, the renewed interest for this time interval is also the result of studies defining the stage boundaries of the Paleocene (e.g., Berggren, 1994; Schmitz, 1994). Many of these studies were conducted in the Tethyan Realm, portraying biotic (Brinkhuis et al., 1994; Arenillas and Molina, 1995; Arenillas and Molina, 1996; Speijer, 2003) and geochemical changes (Schmitz et al., 1998) across this interval. Well-exposed, continuous, and now classic sections in Tunisia have played a central role in research on the Paleocene (e.g. Aubert and Berggren, 1976; Salaj et al., 1976; Peypouquet et al.,

1986; Saint-Marc and Berggren, 1988; Brinkhuis et al., 1994; Kouwenhoven et al., 1997; Steurbaut et al., 2000), but attention has been relatively limited when compared to the numerous studies on the Cretaceous/Paleogene boundary in various Tunisian sections (e.g. Brinkhuis and Zachariasse, 1988; Keller, 1988; Dupuis et al., 2001; Adatte et al., 2002; Galeotti and Coccioni, 2002; Gardin, 2002; Luciani, 2002; Peryt et al., 2002; Goolaerts et al., 2004).

The present study is part of a broader research effort, aiming to understand early Paleogene geo-biosphere changes as reflected on the continental margin of the southern Tethyan realm. During the early to middle Paleocene, several Tunisian successions (Elles, El Kef, Ain Settara) were deposited on the continental margin at outer neritic depths (i.e. Adatte et al., 2002). Guasti et al. (2005a) provided an overview of broad paleoenvironmental changes, involving mainly paleoproductivity and paleodepth, during the Paleocene (planktic foraminifera Zones P1b to P4) at El Kef, by combining organicwalled dinoflagellate cysts (dinocysts) and benthic foraminiferal data. It was concluded that the environment at El Kef evolved from an oligotrophic, open marine, outer neritic to upper bathyal setting during the early Paleocene towards a more eutrophic inner neritic setting, influenced by coastal upwelling during the late Paleocene. In particular, it was suggested that the main change in environmental setting took place across planktic foraminifera Subzones P3a-P3b, a stratigraphic interval we consider to comprise the D-S transition.

In this research, we aim to better understand the paleoenvironmental changes across the D–S transition, from planktic foraminifera Zone P2 to Subzone P3b, a time period of $\sim 2\,\mathrm{Ma}$.

A major emphasis is on paleodepth and the surface productivity, along an ancient Tethyan onshore—offshore transect at three different localities in NW Tunisia: Ain Settara, Elles and El Kef. In order to pursue this goal, mainly foraminifera, dinoflagellates cysts and calcareous nannofossil assemblages are evaluated, in order to integrate sea-surface (based on organic dinocysts, planktic foraminifera and calcareous nannofossil) with sea-floor (based on benthic foraminifera)

paleoenvironmental and paleoecological signals. Additionally, some geochemical parameters (calcite content and stable O, C isotopes) are included in order to enhance the stratigraphic framework and the paleoenvironment interpretation.

The current project provides and accurate stratigraphic framework for the D–S transition in NW Tunisia and sheds light on the paleoenvironmental changes during this poorly known interval. As part of a broader research, the results are also placed in a more global context and compared to those from Egypt and Jordan.

2. Danian and Selandian stages

In the type region, Denmark, the D/S boundary is marked by an unconformity, between the limestones of the Danskekalk Formation and the greensands and marls of the Lellinge Formation (Thomsen and Heilmann-Clausen, 1985) (Fig. 1). The time span included in this hiatus is poorly constrained (Thomsen, 1994), because the standard nannofossil markers of low and middle latitudes for delineating NP4 and NP5 (respectively, *Ellipsolithus macellus* and *Fasciculithus tympaniformis*) are missing (Thomsen and Heilmann-Clausen, 1985). Based on data from Gemmas Allé (Denmark), Stouge et al. (2000) assigned the uppermost Danian to the

Chiasmolithus bidens Subzone D10 sensu Perch-Nielsen (1979), comparable to part of Zone NP4 (Martini, 1971). The Selandian was assigned to the *Toweius selandianus* Subzone S2 sensu Perch-Nielsen (1979), equivalent to Zones NP4/NP5 (Martini, 1971) and which include the presence of *Neochiastozygus perfectus*. Moreover, Stouge et al. (2000) assume that, based on planktic foraminifera, the D/S hiatus corresponds approximately to Zone P2 sensu Berggren et al. (1995). In the same area, Clemmensen and Thomsen (2005) position the Danian/Selandian boundary at the lithological transition, corresponding to the boundary between calcareous nannofossil Zones NP4 and NP5, within planktic foraminifera Zone P3 at 60 Ma.

The Danian and Selandian stages are chronostratigraphically equivalent to the lower Paleocene and the lower upper ("middle") Paleocene, respectively. The boundary between these stages is delineated in different ways, using various criteria. Berggren (1994) and Berggren et al. (1995, 2000) proposed to correlate the D/S boundary with the P2/P3 zonal boundary, with an estimated age of 60.9 Ma, whereas Hardenbol et al. (1998) estimated the age for sequence boundary Sel 1 in Western Europe at 60.7 Ma (within lower Subzone P3a). Schmitz et al. (1998) studied the Zumaya section in northern Spain and suggested to define the base of the Selandian at a level close to the lowest occurrence (LO)

Denmark							Zumaya				Middle East				
Stage	Formation	Lithology	PF Zone (Berggren et al.1995)	CNP Zone (Perch- Nielsen,1979)	CNP Zone (Martini, 1971)		Lithology	PF Zone (see Schmitz et al., 1998)	CNP Zone (see Schmitz et al., 1998)		Formation	Lithology	PF Zone (Berggren et al., 1995)	CNP Zone (Martini, 1971)	
Selandian	Lellinge	Calcareous greensand	P3	S2	NP4-NP5		Red marls	ngulata	NP5		Dakhla or Muwaqqar	Marls	P3b	1 in NP5 I LO F. tympanifornis LO Fascichulithus spp.	
Regional unconformity							8	ella ai			or M	Shale	Neo- eve	Duwi Lascich	
Danian	Danskekalk	Limestone	P2	D10	NP4		Red marl- limestone couplets	Morozovella angulata	NP4		Dakhla	Marls	P2-P3a	Uppermost NP4	

Fig. 1. Lithostratigraphy and biostratigraphy of the Danian-Selandian transition in the type region (Denmark), in Zumaya and in the Middle East (Egypt and Jordan).

of *F. tympaniformis* thus just below the zonal boundary between calcareous nannofossil Zones NP4 and NP5. In Egypt and Jordan, Guasti et al. (2005b) reported on a brief biotic and sedimentary event, termed the "*Neoduwi* event", within the D/S transition. This event is located within basal Zone P3b, near the top of Zone NP4, between the respective LOs of *Fasciculithus* spp. (59.9 Ma based on Berggren et al., 1995) and *F. tympaniformis* (59.7 Ma based on Berggren et al., 1995).

Waiting for formal decision, we refer to the interval studied (planktic foraminiferal Zones P2-P3b) as the Danian-Selandian transition.

3. Geological setting and lithology, NW Tunisia

The successions at Ain Settara, Elles and El Kef (NW Tunisia) were located at the southern margin of the Tethys. During the late Mesozoic and early Cenozoic, Tunisia was bathed by shallow seas and by the end of the Cretaceous, the Jeffara and Kasserine Islands emerged in southern and central Tunisia. Kasserine Island separated a basin in the north from a narrow basin in the south. The studied localities (Fig. 2) were part of the northern basin known as the Tunisian Trough (Burollet, 1956, 1991; Salaj, 1980; Bobier et al., 1991). The successions are dominated by hemipelagic marlshale sedimentation, but with significant terrigenous input from Kasserine Island, and intermittent influx from emerged land located to the west (Adatte et al., 2002). Due to the high subsidence rate and sediment input, the Paleocene sequence in the Tunisian Through reaches up to 500m thickness, decreasing towards Kasserine Island (Zaier et al., 1998).

The three studied localities expose the El Haria Formation, spanning the Maastrichtian to lower Ypresian, and mainly consisting of brown-grey homogeneous marls and shales (Burollet, 1956). It overlies the chalky limestones of the Campanian/lower Maastrichtian Abiod Formation, and is overlain by the limestones of the Ypresian Metlaoui Formation (Burollet, 1956). The Danian-Selandian transition at Ain Settara and at Elles is marked by a distinct glauconitic marl bed (up to 70 cm thick at Ain Settara and about 20 cm at Elles), separating underlying grey marls from overlying essential dark brown shaley marls. At Ain Settara, these dark beds present a cyclic pattern, being intercalated with thin slightly glauconitic marl beds (see Steurbaut et al., 2000). At Elles, the shales are more monotonous.

Monotonous marls also characterize the studied interval at El Kef, becoming more shaley in Subzone P3b. At El Kef, a 9-m-thick interval within the D-S

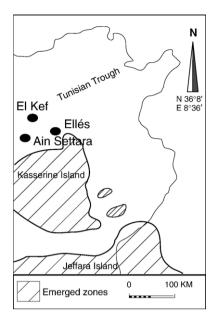


Fig. 2. Paleogeographic reconstruction of the study area (after Zaier et al., 1998) and position of the investigated localities.

transition (Subzone P3b) was not exposed (Kouwenhoven et al., 1997).

4. Material and methods

Samples from Ain Settara and Elles were collected in November 2002 from trenches and holes at 20-30cm depth below the weathered surface. Samples were collected every ~2m at Ain Settara and ~1m at Elles. Only the lower-middle Paleocene parts of these sections are evaluated here. Samples for foraminiferal studies were processed at Bremen University following standard micropaleontological procedures. They were dried in a stove at 60 °C for at least 24h. About 50g of dry rock was soaked in soda (60 g/l Na₂SO₄). When soda was not sufficient to break down the samples, Rewoquat (CH₃OSO₃₋) was used. After disintegration, the samples were washed and dried, and then sieved over three sieves of 630, 125 and 63 µm mesh size, respectively. The fraction >125 µm was used for our studies. Samples from El Kef were previously collected (Kouwenhoven et al., 1997) and prepared at Utrecht University, following similar procedures.

Qualitative distributions of benthic and planktic foraminifera have been determined. Planktic foraminifera were studied, counting at least 200 specimens classified at genus level, based mainly on Berggren and Norris (1997) and Olsson et al. (1999). The census counts were used to determine the percentage of planktics in the foraminiferal association (P/B ratio,

expressed as 100×P/(P+B), cf. Van der Zwaan et al. (1990) in order to gain paleobathymetric information. The number of planktic foraminifera per gram of dry sediment is expressed as the planktic foraminiferal number (PFN). Rock samples from El Kef were prepared at Utrecht University and not weighed prior to processing, thus the calculation of planktic foraminiferal numbers was not possible.

Biostratigraphic interpretations are based on planktic foraminifera and on calcareous nannofossils. Qualitative and quantitative calcareous nannofossil investigation was carried out using standard procedures as described in Steurbaut and King (1994). About 2cm² of glass-slide have been examined for each sample, using a light microscope at 1000× or 1250× magnification. Nannofossil taxonomy is essentially from Perch-Nielsen (1985), taking into account subsequent modifications by Varol (1992).

Benthic foraminifera of Ain Settara and Elles have been studied qualitatively, while at El Kef these were quantitatively studied before (Kouwenhoven et al., 1997; Guasti et al., 2005a).

The samples used for organic dinocyst studies were processed according to standard palynological techniques (cf. Brinkhuis et al., 2003). The residues were sieved using a 10-µm mesh-sieve, and prepared on slides using glycerin jelly. Palynomorphs were subdivided in seven categories (i.e. bisaccate pollen, other pollen and spores, acritarchs, determinable dinocysts, Pterospermella spp., indeterminable dinocysts, and inner walls of foraminifera, if more than 3 chambers are encountered). Non-saccate pollen and spores are identified and grouped together as terrestrial palynomorphs. Dinocysts were counted up to 200 determinable cysts where possible. Frequencies of dinocysts are calculated relative to the total numbers of identifiable cysts. Dinocyst taxonomy is in accordance with Williams et al. (2004). 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 (see e.g., Guasti et al., 2005a; Sluijs et al., 2005). The upper part of Ain Settara (samples ASP 19-21, and ASP12) did not yield any palynomorphs. Several ratios that are often used as paleoenvironmental proxies were calculated. Eukaryotic sea-surface productivity (SSP) has been estimated using the peridinioid/gonyaulacoid ratio (P/G), which includes all peridinioid cysts (P cysts) and is calculated as P/ G=nP/(nP+nG). 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).

Total calcite contents (CaCO₃ %) were measured on homogenized samples using the Scheibler method in the laboratory of sedimentary analysis of the Free University of Amsterdam. Stable isotopes (δ^{13} C and δ^{18} O) on whole-rock calcite on Elles were performed in the Department of Paleoecology and Paleoclimatology, Free University of Amsterdam, and on Ain Settara in the Department of Geosciences, Bremen University.

5. Biostratigraphy

The studied interval spans planktic foraminifera Zone P2, Subzone P3a and the lower part of Subzone P3b (Berggren et al., 1995), together corresponding to calcareous nannoplankton Zone NP4 (Martini, 1971) (Fig. 3).

5.1. Planktic foraminifera

Planktic foraminifera Zone P2, defined as the interval between the First Appearance Datum (FAD) of Praemurica uncinata and the FAD of Morozovella angulata (Berggren et al., 1995), spans ~12.5 m at Ain Settara and El Kef, and 5.5m in Elles. Zone P3 is defined as the biostratigraphic interval between the FAD of M. angulata and the FAD of Globanomalina pseudomenardii. Zone P3 is usually subdivided into Subzones P3a and P3b based on the FAD of *Igorina* albeari. The base of Zone P3a can be traced in every locality, but the top part is probably obscured by a hiatus (as clearly indicated by the calcareous nannofossil record, see below), which occurs at the P3a/b boundary at all localities. Subzone P3a spans ~3 m at Ain Settara and Elles, and ~7m at El Kef. Subzone P3b is more expanded: >20 m at Ain Settara, ~11 m at Elles, and \sim 15 m at El Kef.

Guasti et al. (2005b) discussed that in the Middle East, the identification of the P3a/P3b subzonal boundary on the basis of the LO of *I. albeari* can be problematic. Similar problems are also encountered in Tunisia. Typical specimens of *I. albeari* rarely occur only at higher stratigraphic levels. Therefore, we identify the base of Subzone P3b on the LO of slightly keeled *Igorina* in assemblages with abundant and well-diversified *Morozovella*, including *M. aequa*. The LO of the latter taxon in ocean deposits is described from Zone P4 upwards (Olsson et al., 1999), but in the Tethys it occurred near the base of Subzone P3b.

The base of Zone P4 was recognized at Elles and at El Kef, but not at the studied outcrop of Ain Settara,

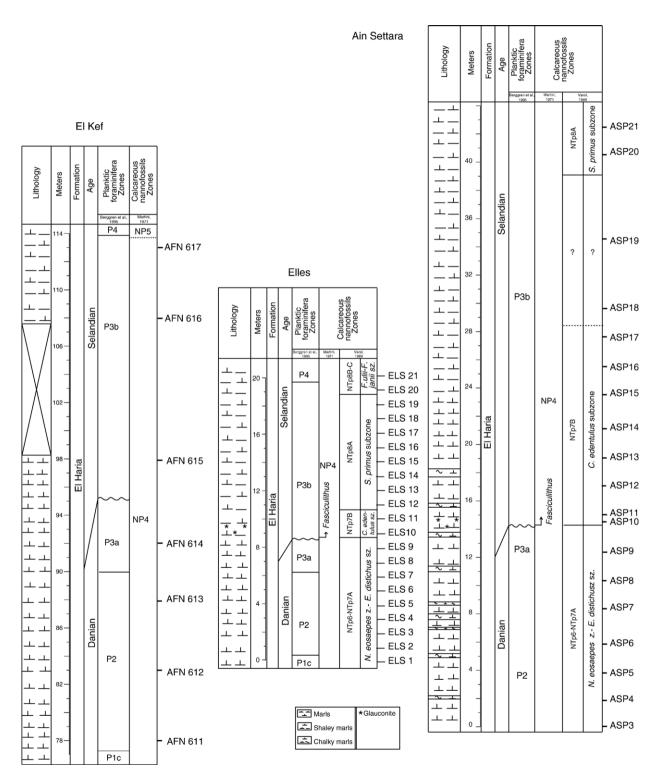


Fig. 3. Stratigraphy of the studied localities. Planktic foraminifera biostratigraphy is based on Berggren et al. (1995), calcareous nannofossil biostratigraphy on Martini (1971) and on Varol (1989). The base of the sections corresponds to the base of planktic foraminifera Zone P2.

where a fault contact separates the Ypresian limestones of the Metlaoui Formation from Subzone P3b.

5.2. Calcareous nannofossils

Calcareous nannofossil Zone NP4 (Martini, 1971) is defined by the First Appearance Datum (FAD) of E. macellus (base) and by the FAD of F. tympaniformis (top). The FAD of Chiasmolithus edentulus, which coincides with the FAD of Fasciculithus chowii, is used to subdivide Zone NP4 in low latitudes (Varol, 1989; Steurbaut et al., 2000). It occurs in the upper part of Zone NP4 Berggren et al. (1995), and marks the base of Varol's Subzone NTp7B, the top of which is defined by the FAD of Sphenolithus primus. A high-resolution study of the 05-NSC section at Ain Settara, a lateral equivalent of the section studied here (Van Itterbeeck et al., submitted for publication), has recently revealed that the lowest occurrence of F. chowii is preceded by an ephemeral occurrence of Fasciculithus magnus (very low numbers in a ~ 40 -cm-thick interval at the top of Zone NTp6). This short-ranged occurrence can easily be overlooked and has not been recorded in the present study. Hence, the lowest occurrence of F. chowii does not represent the first appearance of the genus, but corresponds to its lowest consistent occurrence (LCO).

In the Ain Settara section studied herein, the lowest consistent occurrence (LCO) of Fasciculithus is recorded at the glauconitic marker bed (ASP10). The LO of S. primus is difficult to pinpoint due to the rather poor quality of the upper samples (definitely present in sample ASP20, possibly overgrown specimens in sample ASP18). The base of NP5 is not present in this section, due to a fault (see Section 5.1). However, in a previous work, Steurbaut et al. (2000) located the base of NP5 at \sim 30 m above the LCO of Fasciculithus spp. in a section at Ain Settara, laterally equivalent of the one studied here. Considering that the glauconitic marker bed at ASP10 is equivalent to the glauconitic bed described by Steurbaut et al. (2000), we can assume a similar thickness of this Zone in this work.

At Elles the LCO of *Fasciculithus*, coinciding with the LO of *C. edentulus*, occurs in sample ELS10, the LO of *S. primus* in sample ELS12. The LO of *F. tympaniformis* is recorded in sample ELS26 (~16m above the LCO of *Fasciculithus* spp.).

In both localities, the LCO of *Fasciculithus* coincides with the lowest sample in Subzone P3b. Following Berggren et al. (1995), the FAD of *Fasciculithus* is recorded 0.1 Ma above the base of Subzone P3b, suggesting that the basal part of Zone P3b is missing in a hiatus in all sections. Such a hiatus between

Subzone P3a and P3b has been also suggested by Van Itterbeeck et al. (submitted for publication) in a parallel section at Ain Settara.

6. Results

6.1. Benthic foraminiferal assemblages

In planktic foraminifera Zones P2 and P3 at Ain Settara, diverse assemblages are recorded, composed of various Nodosarians, Textularians, Anomalinoides (A. midwayensis, A. praeacutus, A. rubiginosus), Alabamina, Osangularia, Bulimina, Neoflabellina, Gyroidinoides, and Cibicidoides pseudoacutus. Anomalinoides affinis and Anomalinoides susanaensis occur only in the lower part (P2–P3a) of the sections. Stainforthia spp. is frequent within Subzone P3b. At Elles within Zones P2 and P3a, the benthic assemblages are characterized by numerous neritic taxa as at Ain Settara, also include Gavelinella beccariiformis (a bathyal species) and Aragonia, Globocassidulina subglobosa, Cibicidoides spp., C. midwayensis. In lower Subzone P3b this assemblage persists, but G. beccariiformis disappears.

6.2. Planktic foraminifera

Within the interval P2–P3a, the assemblage is mainly composed of *Praemurica*, *Subbotina* and *Parasubbotina*, which together make up ~85% in all sections studied (Figs. 4–6). In particular, *Subbotina* and *Parasubbotina* are equally distributed between 30% and 40%. *Morozovella* and *Acarinina* already occur in Zone P2 in very low numbers (<1%) and slowly increase up to <10% in Subzone P3a, with highest numbers at Ain Settara. *Igorina* only occurs from the base of Subzone P3a in low numbers (<1%) and *Chiloguembelina* occurs only in the background (~1%) throughout P2–P3a.

From Subzone P3b onwards, above the unconformity, the planktic foraminiferal assemblages change. *Praemurica* disappears and, instead, *Morozovella* dominates the surface-dwelling taxa (~30%, ~50%, ~40% in Ain Settara, Elles and El Kef, respectively). *Parasubbotina* and *Subbotina* are still well represented, although *Parasubbotina* to a lesser extent. Only in a few samples, these taxa abruptly decrease (in ASP18 both decrease; in AFN616 *Parasubbotina* decreases to ~10%). Instead, at Elles, *Parasubbotina* generally decreases (to 10–20%). *Acarinina* and *Igorina* constitute a minor part of the surface dwellers (<10%). *Globanomalina* constantly ranges below 15%, and somewhat lower at Ain Settara (generally <10%).

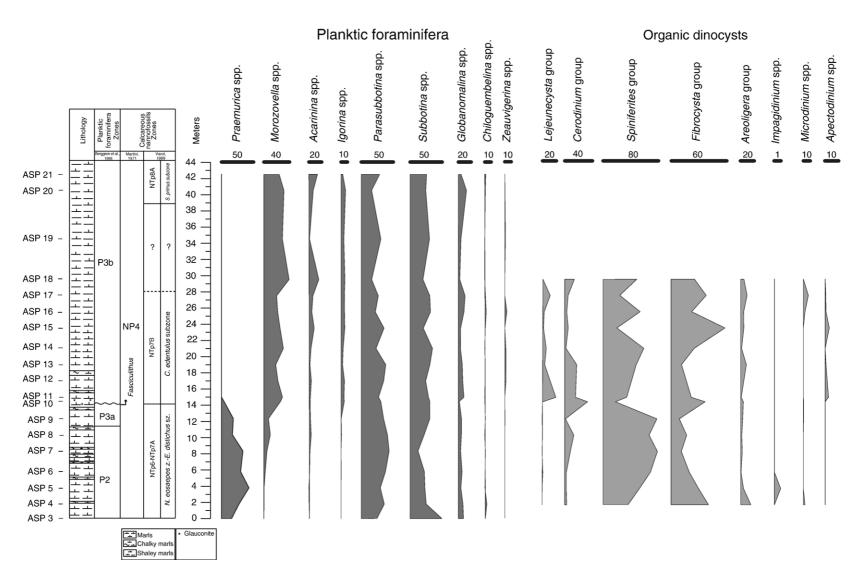


Fig. 4. The relative frequencies (expressed in %) of planktic foraminiferal (in dark grey) and organic dinocysts (in light grey) assemblages are plotted against lithology, biostratigraphy (planktic foraminifera and calcareous nannofossils) and sample position at Ain Settara.

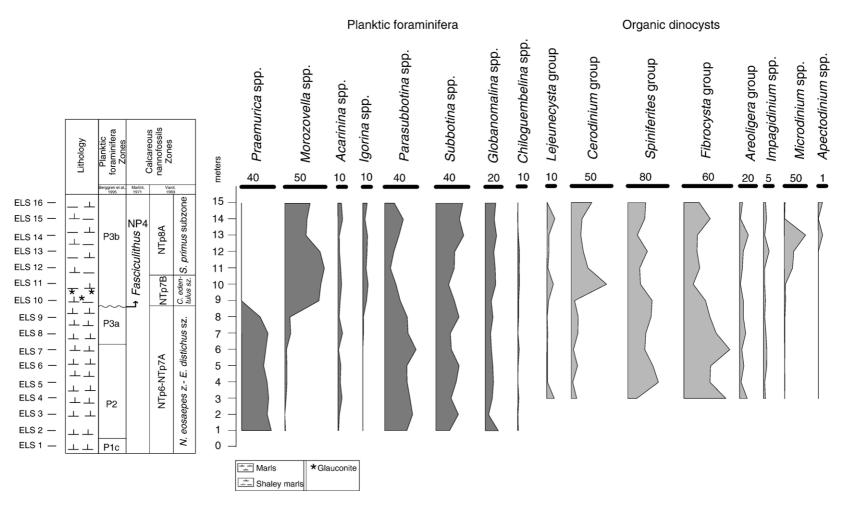


Fig. 5. The relative frequencies (expressed in %) of planktic foraminiferal (in dark grey) and organic dinocysts (in light grey) assemblages are plotted against lithology, biostratigraphy (planktic foraminifera and calcareous nannofossils) and sample position at Elles.

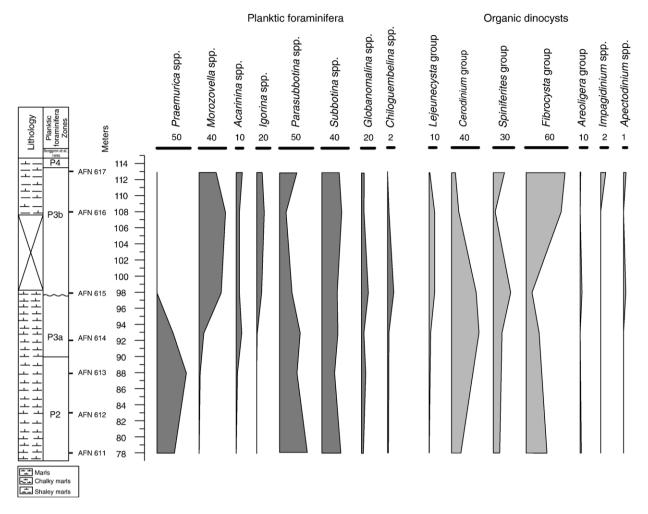


Fig. 6. The relative frequencies (expressed in %) of planktic foraminiferal (in dark grey) and organic dinocysts (in light grey) assemblages is plotted against lithology, biostratigraphy (planktic foraminifera and calcareous nannofossils) and sample position at El Kef.

Chiloguembelina is generally poorly represented, somewhat more abundant (\sim 2%) at Elles. Zeauvigerina occurs in several samples at Ain Settara, mainly in Subzone P3b (<3%), whereas this taxon is not found in the other localities.

6.3. Palynology

Nearly all samples contain palynological assemblages dominated by marine palynomorphs (Figs. 4–6). The dinocyst taxa are placed in ecogroups as established in Guasti et al. (2005a). Within the interval spanning P2–P3a, representatives of the *Spiniferites* group are the main component of the assemblage, comprising up to 80% at Ain Settara and Elles. The *Fibrocysta* group is also quite abundant, up to 40% at Ain Settara, and even higher at Elles (60%). Abundances of the *Cerodinium* and *Areoligera* groups are

<15%. Representatives of the *Lejeunecysta* group are generally rare (<1%), with the exception of a peak (9%) at Elles in the lowermost part. Representatives of the oceanic *Impagidinium* group are almost absent at Ain Settara and El Kef, whereas they occur consistently in low abundances (1–3%) at Elles.

From Subzone P3b onwards the assemblages start to diversify. At Ain Settara, at the distinct glauconitic bed, the assemblage is characterized by increasing *Fibrocysta* (\sim 35%), *Cerodinium* (\sim 35%, mainly *Isabelidium* spp.) and decreasing *Spiniferites* (<20%) groups.

Just above this bed, representatives of the *Cerodinium* group are still abundant (15%) and the *Lejeune-cysta* group abruptly increases (\sim 20%). From this level upwards, these taxa range through the entire Subzone P3b. The *Fibrocysta* group increases (<60%), while the *Spiniferites* group has generally lower abundances (<60%) than in P2–P3a.

At Elles, a major change is recorded ~ 1 m above the unconformity marking the base of Subzone P3b (ELS 11), indicated by a peak of the Cerodinium group (~45%,) and increased *Lejeunecysta* representatives (~10%), whereas the *Spiniferites* and *Fibrocysta* groups abruptly diminish (25% and 10%, respectively). Representatives of the Microdinium group usually occur in low numbers, except for a peak of 7% in sample ASP17, and in various peaks at Elles (up to 30% in sample ELS14). The Areoligera group does not vary considerably (usually <10%). Relative numbers of the *Impagi*dinium group remain low, except for a single peak of 3% (sample ELS13), with a concomitant peak of the Spiniferites group (35%). At Ain Settara (ASP11; NTp7B), the first occurrence of the Apectodinium group is recorded in this interval (2.4%). Up section, representatives of this group occur in several samples in low relative numbers, with the exception of a peak of 3% in sample ASP15. At Elles the LO of *Apectodinium* occurs at a higher stratigraphic level (ELS14; NTp8A), and is associated with a peak of the *Microdinium* (30%) and *Areoligera* groups (10%). At El Kef, members of the *Apectodinium* group occur immediately above the unconformity within an assemblage with a high number of representatives of the *Cerodinium* and *Spiniferites* groups; the numbers of the *Lejeunecysta* group also increase at this level.

6.4. Calcareous nannofossils

The nannofossil associations in the Tunisian sections are moderately preserved, quantitatively rich

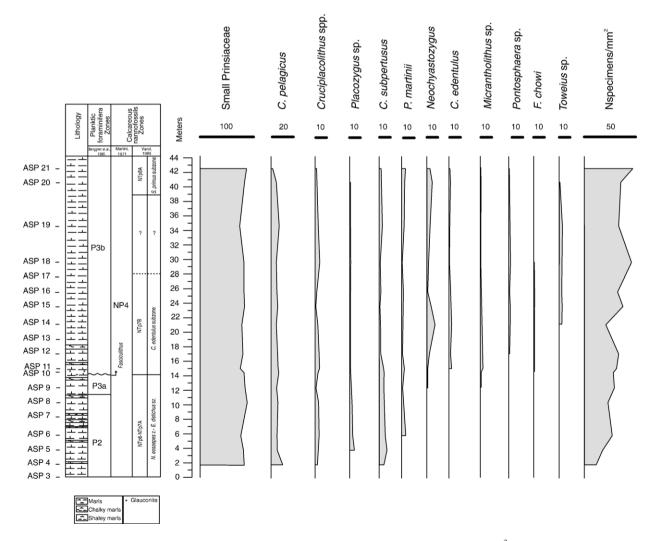


Fig. 7. The relative frequencies (expressed in %) of calcareous nannofossils and the number of specimens per mm² of surface of the smear slide is plotted against lithology, biostratigraphy (planktic foraminifera and calcareous nannofossils) and sample position at Ain Settara.

(~ 34 to ~ 29 specimens/mm² glass-slide at Elles and Ain Settara, respectively) and well diversified (20 to 25 taxa). They are dominated by small Prinsiaceae ($<3\,\mu m$) (between 73% and 88% of the total number of specimens). The additional most frequent taxa, such as Coccolithus pelagicus s.l., Coccolithus subpertusus, Cruciplacolithus spp., Neochiastozygus spp. and Prinsius martinii (Figs. 7 and 8) occur throughout the sections, enhancing the uniformity of the assemblages. The most striking nannofossil change is recorded across the unconformity (at the planktic foraminiferal P3a/P3b boundary). It is marked by a major increase in species diversity including the LCO of Fasciculithus (F. chowii and 1 specimen of a not yet named species), the LO of C. edentulus, the LO of Toweius sp. (middle-sized elliptical form) and the consistent occurrence of Pontosphaera and Micrantholithus (at Ain Settara). This major change represents the first of a series of diversification events, marking

the upper part of Zone NP4 in Central Tunisia. The second diversification event, characterized by the radiation of *Fasciculithus* (first appearances of *F. ulii*, *F. billii*, *F. pileatus* and *F. janii*) has been identified at the top of the studied interval (in sample ELS 20; above uppermost sample ASP21). Between both events the nannofossil assemblages are very similar, and only differentiated by the occurrence of *S. primus* (LO in ELS 12).

6.5. Paleoenvironmental proxies

6.5.1. Foraminiferal parameters

In the interval spanning P2–P3a, at Ain Settara, the planktic/benthic ratio (P/B) fluctuates from 45% to 70% (Fig. 9), whereas at Elles, the P/B is constantly higher (80–90%). In Subzone P3b at Ain Settara a drop of the P/B (\sim 33%) coincides with the glauconitic bed; above this level, values are generally more constant around 50%.

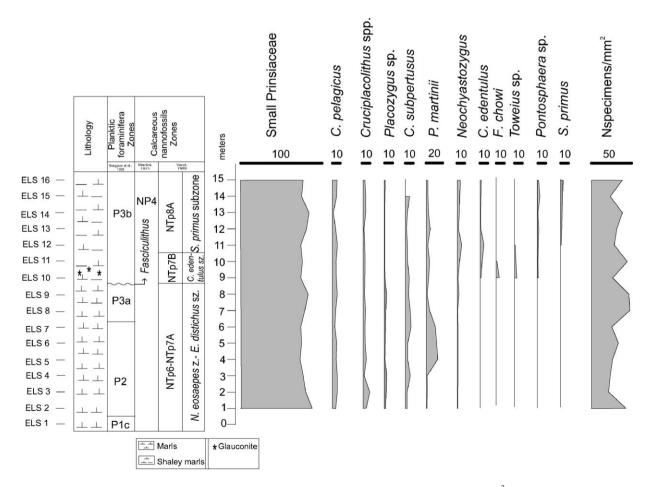


Fig. 8. The relative frequencies (expressed in %) of calcareous nannofossils and the number of specimens per mm² of surface of the smear slide is plotted against lithology, biostratigraphy (planktic foraminifera and calcareous nannofossils) and sample position at Elles.

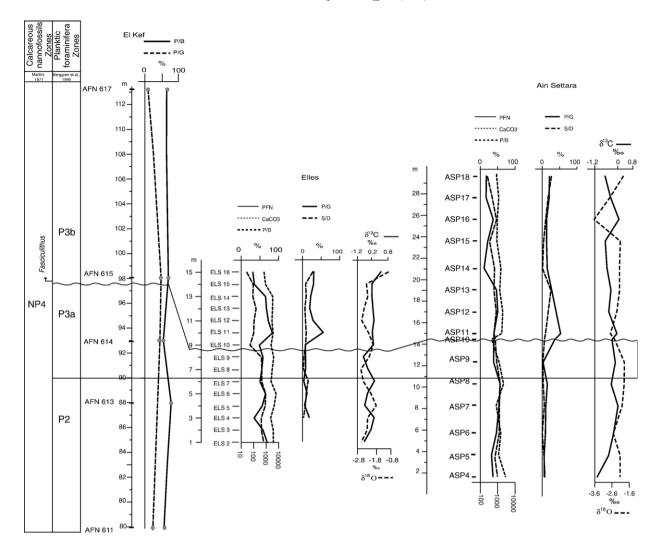


Fig. 9. The planktic/benthic ratio (P/B %), the number of planktic foraminifera/gram (PFN in logarithmic scale), the calcite content (CaCO₃ %), the peridinioid/gonyaulacoid cysts ratio (P/G ratio), the terrestrial/marine palynomorph ratio (S/D ratio), the oxygen and carbon stable isotopes are plotted for each studied locality. Planktic foraminifera and calcareous nannofossil biostratigraphy is shown on the left.

Little variation is recorded at Elles except for decreasing values (<65%) in the uppermost studied interval.

At Ain Settara, planktic foraminiferal numbers fluctuate between 200/g and 1300/g in upper Zone P2, and are generally lower in Subzone P3a ($<\sim500/g$). Similarly, at Elles, PFNs vary between 100 and 500/g within P2–P3a, with a minimum value in the lower part of Zone P2 ($\sim100/g$).

At Ain Settara, above the unconformity at the base of Subzone P3b, PFNs are lower than in P2–P3a (200-600/g), except a peak 1000/g in ASP 12. An opposite trend characterizes Elles, where increased values ($\sim 3000/g$) are recorded within Subzone P3b. In the uppermost part of Elles these numbers decrease (<100/g), similar to the P/B ratio trend.

6.5.2. Palynological parameters

At all localities, the relative numbers of peridinioid (P-) cysts (expressed in the P/G ratio) are generally very low in Zone P2 and Subzone P3a (Fig. 9). At Ain Settara, their numbers increase from the glauconitic bed upwards, where highest relative values occur. Further upwards, these values are lower, but still higher than those within P2–P3a. Similarly, at Elles, a peak of P/G ratio occurs in Subzone P3b, ~ 1 m above the occurrence of *Fasciculithus* and from this level upward, the values are generally higher than in lower samples. Also at El Kef, at the base of Subzone P3b a peak of P/G ratio is observed.

McCarthy and Mudie (1998) pointed out that the numbers of terrestrial palynomorphs in marine

sediments decreases exponentially with distance to shore, thus they are useful in sea-level reconstructions. In the studied localities, the relative contribution of continentally derived organic material (S/D ratio) is always low; therefore, they cannot support sea-level variation. As it was already pointed out for El Kef (Guasti et al., 2005a) these low S/D values might be related to the distance of the sedimentation area from the source of terrestrial input.

6.6. Geochemical parameters

6.6.1. Calcite content

The marls in P2–P3a contain up to 50% CaCO₃ at Ain Settara, and calcite content ranges between 20% and 40% in Subzone P3b. At Elles, the lower marls contain $\sim 60\%$ CaCO₃, decreasing to < 40% in Subzone P3b, where the marls are more shaley (Fig. 9).

6.6.2. Stable isotopes

In P2–P3a, δ^{13} C values are low at the base of Ain Settara (-1.2‰), and slowly increase up to a maximum 0‰ (ASP7), and they are slightly lower (-0.3‰) in Subzone P3a. At Elles, δ^{13} C values are generally higher than at Ain Settara (-0.7‰ and 0.2‰), and they exhibit more fluctuations. In Subzone P3b, values are similar to those at Ain Settara. At Ain Settara, a small positive peak occurs in sample ASP11 coinciding with increased peridinioid cysts and the lowest occurrence of *Apectodinium*, and another one in sample ASP16 coinciding with increased *Spiniferites* and increased PFN (Fig. 9). At Elles, from the lowest occurrence of *Fasciculithus* upward, δ^{13} C values are generally about 0.2‰.

The δ^{18} O values range between -2.6% and -1.6% in Zones P2–P3a at Ain Settara, with a minimum value (-2.6%) in ASP6. Similar values are recorded at Elles (-2.8% and -1.8%), but they exhibit wider fluctuations.

In Subzone P3b, the values are similar. At Ain Settara, negative wiggles are recorded together with higher δ^{13} C (ASP11 and ASP16: -2.6% and -3.6%, respectively).

7. Discussion

7.1. Paleoenvironmental conditions

7.1.1. Paleobathymetric change

At Ain Settara, P2–P3a, the benthic foraminiferal assemblage and P/B ratios are indicative of deep outer neritic (\sim 175 m) deposition shallowing upward to \sim 150 m (Fig. 10) as indicated by the successive

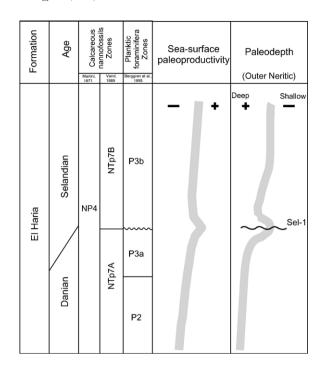


Fig. 10. Reconstruction of schematic sea-surface paleoproductivity and paleodepths is also proposed, including a sequence boundary of Hardenbol et al. (1998). Planktic foraminifera and calcareous nannofossil biostratigraphy is shown on the left.

disappearance of sporadically occurring deeper water taxa such as *Angulogavelinella avnimelechi*, *A. abudurbensis* and *A. affinis*. This is in agreement with the dinocysts being dominated by the shelf groups *Spiniferites* and *Fibrocysta*, and the absence (except in the deeper basal part) of the typical offshore taxa *Impagidinium* spp. (Brinkhuis and Zachariasse, 1988; Crouch et al., 2003). At Elles, higher P/B ratios and deeperwater benthic foraminiferal taxa (i.e. *G. beccariiformis*, *Aragonia* sp.) suggest a slightly deeper outer neritic setting (~200 m) in P2–P3a, which is in agreement with the more common and consistent presence of *Impagidinium*. Outer neritic paleodepths in P2–P3a were also inferred at El Kef (Guasti et al., 2005a).

At Ain Settara, at the conspicuous glauconitic bed, the benthic assemblage does not change, whereas the P/B decreases. In Subzone P3b, the disappearance of some further benthic taxa characteristic of the deeper shelf (A. susanaensis and Pulsiphonina prima) together with a decreasing P/B ratio suggest further shallowing. This is also observed in the dinocyst assemblages, where neritic taxa, in particular peridinioid cysts, are more abundant, and in the nannofossil assemblages, where slight, but distinct increases in the near-shore taxa (essentially Pontosphaera, but also Micrantholithus spp. at Ain Settara) point to a basinward shift of the coastline.

Because of its more proximal (onshore) position in the basin, this shallowing trend is much more expressed at Ain Settara than at Elles in terms of nannofossil evolution (e.g. absence of *Micrantholithus* spp. throughout the entire studied interval at Elles). We estimate that the paleodepth changed from $150-175\,\mathrm{m}$ in P2-P3a to $100-125\,\mathrm{m}$ in Subzone P3b. Similarly, at the base of Subzone P3b at Elles, we find the disappearance of the bathyal taxon *G. beccariiformis* and an increase of peridinioid cysts, suggesting a shallowing to outer neritic deposition at $\sim 150\,\mathrm{m}$ depth. A similar shallowing was also observed at El Kef from Subzone P3a to Subzone P3b (Guasti et al., 2005a).

7.1.2. Danian

The evolutionary trend of planktic foraminifera from spinose and praemuricate taxa towards assemblages dominated by muricate taxa (Norris, 1996; Kelly et al., 1996; Berggren and Norris, 1997; Olsson et al., 1999) is well observed in the studied area. In planktic foraminifera Zone P2, spinose genera (Subbotina and Parasubbotina) and Praemurica dominate the assemblage. Already in upper Zone P2, the earliest specimens of Morozovella (M. praeangulata) and Acarinina (A. praeaequa) are observed. Our data show that Praemurica survived up into Subzone P3a in the southern Tethys, as it was already described in Egypt and Jordan (Guasti et al., 2005b). The decrease of this taxon corresponds to a gradual increase of Morozovella. The well-diversified planktic assemblages present in P2-P3a suggest fairly oligotrophic conditions (Fig. 10). The benthic foraminiferal assemblages composed by numerous shelf taxa and by the scarcity of buliminids reflect similarly oligotrophic conditions on the seafloor. During the same interval, the dinocyst assemblages are dominated by oligotrophic taxa, such as Spiniferites and Fibrocysta and by low P/G ratio in accordance with the foraminiferal signal. A similar oligotrophic setting for this stratigraphic interval was also proposed at El Kef (Guasti et al., 2005a).

7.1.3. Danian-Selandian transition and Selandian

The transition between Subzones P3a and P3b is marked by an unconformity, observed in each locality. The foraminiferal, palynological and nannofossil assemblages and proxies indicate a distinct paleoenvironmental change across the D/S unconformity (Fig. 10), which is very similar to the biofacial shift observed at the same level at El Kef (Guasti et al., 2005a).

Whereas *Praemurica* dominated the mixed layer planktic foraminiferal assemblages during the late

Danian, *Morozovella* became the most common taxon during the early Selandian. At the base of Subzone P3b, the high numbers of *Morozovella* correspond to a slight decrease in the subsurface taxa, such as *Parasubbotina* and *Subbotina*. This is evidence for successful strategy of *Morozovella* for being dominant in the surface waters.

At these localities, above the base of Subzone P3b and the lowest consistent occurrence (LCO) of Fasciculithus, high numbers of peridinioid cysts (Cerodinium and Lejeunecysta) are recorded and are also associated with the LO of Apectodinium. Enhanced numbers of peridinioid is generally related to elevated primary productivity. In particular, as it was proposed by Guasti et al. (2005a), increase heterotrophic/autotrophic ratio (P/G) based on protoperidinioid cysts (Lejeunecysta) is more reliable in the studied area and suggested higher nutrient availability. Moreover, at Elles, this peak corresponds to increase planktic foraminiferal numbers, which may also be interpreted as a signal of increased productivity.

The abundance of asymbiontic thermocline dweller Globanomalina (Berggren and Norris, 1997) appears to co-vary with the P/G ratio, which is in agreement with increased productivity. On the other hand the simultaneous increase in Morozovella poses a problem. Considering that Morozovella is thought to bear symbionts (i.e. Berggren and Norris, 1997), suggesting a preference for oligotrophic conditions, their high abundance during time of higher productivity is unexpected. This pattern underlines the view that the ecology of Paleocene planktic foraminifera is still poorly known. The general high abundance of Morozovella (and Acarinina) in late Paleocene Tethyan marginal seas indicates that the relationship between, presumably, photosymbiotic planktic foraminifera and nutrient conditions in surface waters is far from straightforward (see discussion in Guasti and Speijer, 2005).

The environmental changes recorded across the D/S unconformity are also emphasized by the decrease of calcite content mainly at Elles. Considering that a decrease in the production of biogenic calcite is not suggested by the biotic proxies, a dilution due to the increase of sediment supply of land-derived sediment is probably most likely. This is supported by the higher rock-accumulation rate in Subzone P3b. In fact, we estimated rock-accumulation rate of $27.5\,\text{m/Ma}$ and $55\,\text{m/Ma}$ in Zone P2 (at Elles and at Ain Settara, respectively), which increases up to $70\,\text{m/Ma}$ and $\sim 150\,\text{m/Ma}$ between the lower occurrence of Fasciculithus spp. and F. tympaniformis (at Ain Settara this datum is based on Steurbaut et al., 2000).

At the base of Subzone P3b a glauconitic bed is present at Ain Settara (60-70 cm thick), and at Elles (10-20 cm). Although the genesis of glauconite is poorly known, it is generally associated with slow deposition, under reducing conditions on the continental margin (often between 30-700 m) and facilitated by presence of organic matter (Reading, 1986). Steurbaut et al. (2000) suggested that the glauconitic bed at Ain Settara could represent the transgressive phase of the sequence Sel-1. It was also suggested that the interval underneath this transgressive bed could represent a lowstand deposit with channel incision into Danian highstand deposits. Our faunal data (P/B ratios, benthic foraminifera and dinocysts) from this level however do not support a low-stand below the glauconitic bed. Depositional depth is gradually shallowing but similar to the interval immediately below. In our view the main unconformity is situated below the glauconitic bed and thus the Selandian transgressive deposits rest on top of Danian high-stand deposits. This lithological sequence within the D/S transition can be traced throughout the Tunisian Trough, albeit less distinct at greater paleodepths such as at Elles and El Kef (Guasti et al., 2005a and unpublished observations). Consequently, the sequence is to some extent reminiscent of the Danian/ Selandian transition in the type region in Denmark, where the base of the Selandian (basal Lellinge Formation) is also marked by transgressive glauconitic greensands and marls overlying Danian chalks (Thomsen and Heilmann-Clausen, 1985; Clemmensen and Thomsen, 2005). The main difference is of course that the Tunisian successions are altogether much more pelitic. The sequence boundary between the Danian and Selandian was referred to as Sel 1 by Hardenbol et al. (1998). As far as it is currently possible to constrain our stratigraphic framework and match it to the Danish successions, the same sequence boundary is observed in the Tunisian Trough.

During the Selandian, within Subzone P3b, a shallower environment, richer in nutrients succeeds the oligotrophic conditions of P2–P3a. Accordingly, peridinioid cysts are more abundant; in particular, representatives of the *Lejeunecysta* group increase, whereas *Spiniferites* and *Fibrocysta* groups decrease. Among the planktic foraminifera, *Chiloguembelina* slightly increases at Elles, and *Zeauvigerina* at Ain Settara. As both these taxa are thought to belong to the heterohelicids and to be more tolerant to low oxygen conditions (Boersma and Premoli Silva, 1989), such an increase is in agreement with increasing primary productivity and decreasing oxygen levels in the subsurface. Similarly, the increase of *Stainforthia* and

other buliminids in the benthic assemblage also indicates lower oxygen levels at the seafloor at Ain Settara. A shallower and more nutrient-enriched environment also characterizes Subzone P3b at El Kef, where eventually eutrophic inner neritic conditions settle during the late Paleocene (Kouwenhoven et al., 1997; Guasti et al., 2005a). Overall, in the study area, the Selandian is characterized by a more productive paleoenvironment, both in surface and bottom waters, compared to rather oligotrophic and well-ventilated conditions during the Danian. A similar paleoenvironmental change has been also documented by Van Itterbeeck et al. (submitted for publication) based on variation in the ostracod record.

7.2. First appearance of Apectodinium

The Paleocene-Eocene thermal maximum is amongst other things characterized by a global bloom of Apectodinium along the continental margins (Crouch et al., 2001). It has been suggested that this taxon preferred warm eutrophic neritic waters (Crouch et al., 2003). Brinkhuis et al. (1994) reported the lowest occurrence (LO) of representatives of the genus from El Kef. We record the LO of Apectodinium at Ain Settara and El Kef immediately above the unconformity at the base of Subzone P3b. At Ain Settara, this level corresponds to the C. edentulus Subzone (Zone NTp7B). In both localities, it is associated with increased peridinioid cysts and a small positive shift of δ^{13} C. It is striking that in both localities, the LO of Apectodinium is associated with peak values of representatives of the Cerodinium group, suggesting relatively shallow marine conditions and increased nutrient supply (e.g. Sluijs et al., 2005). The apparent delayed appearance of Apectodinium at Elles (S. primus Subzone, NTp8A) probably results from the rare occurrence of this taxon in its lower range as also indicated by just one specimen at the base of Subzone P3b at El Kef. The overall pattern indicates that Apectodinium evolved in the early Selandian at low latitudes in an inner to shallow outer neritic setting, where it favored a high nutrient availability.

7.3. Comparison with the Middle East

In Egypt and Jordan, shaley marls dominate in most Paleocene successions in the region and the Danian–Selandian transition is not marked by an overall lithological change. However, this transition is marked by organic-rich dark bed characterized by anomalous faunal assemblages, named as event "*Neo-duwi* event"

(Speijer, 2003; Guasti et al., 2005b). Whereas planktic foraminiferal biostratigraphy is poorly constrained due to the problematic identification of *I. albeari*, the P3a/b zonal marker, calcareous nannofossils enable a precise limitation of this event. In fact, this transient episode occurred near the top of Zone NP4 between the respective LOs of Fasciculithus spp. and F. tympaniformis, which corresponds to the base of Subzone P3b. Following Berggren et al. (1995), these bio-events occurred at 59.9 Ma and at 59.7 Ma, respectively, suggesting that the "Neo-duwi event" lasted for less than 200 ky. Although in Tunisia, such a distinct marker bed and associated anomalous faunal assemblages are not present, some similarities can still be traced. A longterm environmental change from open marine oligotrophic conditions toward eutrophic neritic settings in the upper Paleocene started at the base of Subzone P3b. about 1 m above the lowest occurrence of Fasciculithus spp., and coincided with the lowest occurrence of Apectodinium.

Differences between Tunisia and the Middle East are mainly evidenced in the high sediments thickness between the LOs of *Fasciculithus* spp. and of *F. tympaniformis* in Tunisia, indicating much higher rock-accumulation rate in Tunisia as compared to the Middle East. A rock-accumulation rate varying between 70 m/Ma and ~150 m/Ma in Tunisia (at Elles and at Ain Settara, respectively) and between ~27 m/Ma and 35 m/Ma in the Middle East (at Shaubak and at Awaina, respectively) is estimated (Guasti, 2005). The high rock-accumulation rate in the Tunisian localities suggests high subsidence rates accommodating for the high clay input from land filling the basin (Tunisian Trough). The studied parts of the basins in Egypt and Jordan received less input and experienced much lower subsidence rates.

Considering the differences in basic basin dynamics between these areas, it is striking that the environmental changes observed occurred at the same stratigraphic level, suggesting that these local perturbations were probably part of a more regional environmental reorganization, and we suggest that they represent the local expression of a more general, paleoclimatic/paleoceanographic perturbation.

8. Conclusions

The Danian–Selandian transition (61–59Ma) has been documented in three localities in NW Tunisia (Ain Settara, Elles and El Kef) by integrating foraminifera (planktic and benthic), organic dinocysts and calcareous nannofossil assemblages. Hence, the paleoenvironmental evolution across planktic foraminifera Zones P2–P3

(calcareous nannofossil Zone NP4, Subzones NTp6-NTp8A) has been investigated.

During the Danian (P2–P3a), the studied localities are located in an outer neritic setting, where Ain Settara was located in a slightly shallower position ($\sim 150-175 \, \text{m}$) than Elles and El Kef ($\sim 200 \, \text{m}$). An oligotrophic setting characterizes the area.

At the transition between planktic foraminifera Subzones P3a and P3b, an overall sea-level fall is observed and an unconformity is identified, which is correlated to the sequence boundary Sel 1 of Hardenbol et al. (1998). Within Subzone P3b and above the lowest occurrence of *Fasciculithus* spp. (Zone NP4, Subzone NTp7B), the biotic record indicates an increase in surface productivity and a reduction of subsurface and seafloor ventilation.

It appears that the early evolution of *Apectodinium*— an important genus during the Paleocene–Eocene thermal maximum, occurred in shallow Tethyan environments with a high nutrient availability.

Generally, our records show an increase in productivity during an overall regressive phase of the late Danian and early Selandian in the Tunisian Trough.

This project provides an accurate understanding of paleoenvironmental change across the Danian–Selandian transition in Tunisia. As part of a broader research, the results are also placed in a more global context and compared with the results from other localities along the Southern Tethyan margin (Egypt and Jordan), suggesting that a more regional paleoclimatic/paleoceanographic perturbation occurred in the Southern Tethys.

Acknowledgments

We would like to thank Christian Scheibner for stimulating discussions, Jochen Kuss for discussions and logistic support and David Fischer for sampling preparation for micropaleontological analysis. Natasja Welters and Jan van Tongeren are thanked for helping in the preparation of samples for palynological studies in the laboratory of Palaeobotany and Palynology at Utrecht University. Dick Kroon is thanked for enabling isotopic measurements at the Free University of Amsterdam. Abdel Aziz Tantawy and an anonymous reviewer are thanked for their constructive suggestions, which greatly helped improving this manuscript. EG thanks Simon Cole for improving English spelling and grammar.

This project was supported by Europrox "Proxies in Earth History" funded by the DFG (Germany) and by grants from the FWO (Belgium) and the Research Fund of the K.U.Leuven to RPS.

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.
- Arenillas, I., Molina, E., 1995. Análisis cuantitativo de los foraminíferos planctónicos del Paleoceno en Zumaya: implicaciones paleoambientales y eventos paleoceanográficos. Geogaceta 17, 23–26.
- Arenillas, I., Molina, E., 1996. Bioestratigrafia con foraminiferos planctonicos y eventos paleoceanograficos del transito Daniense/Selandiense en el corte de Zumaya (Guipúzcoa). Tomo extraordinario 125, 272–276 (Aniversario de la RSEHN).
- Aubert, J., Berggren, W.A., 1976. Paleocene benthic foraminiferal biostratigraphy and paleoecology of Tunisia. Bulletin Centre de Recherches Routieres 10, 379–469 (Pau-SNPA).
- Berggren, W.A., 1994. In defense of the Selandian. GFF 116, 44–46. Berggren, W.A., Norris, R.D., 1997. Biostratigraphy, phylogeny and systematics of Paleocene trochospiral planktic foraminifera. Micropaleontology 43 (supplement 1), 1–116.
- 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.
- Berggren, W.A., Aubry, M.P., van Fossen, M., Kent, D.V., Norris, R. D., Quillévéré, F., 2000. Integrated Paleocene calcareous plankton magnetobiochrology and stable isotope stratigraphy: DSDP Site 384 (NW Atlantic Ocean). Palaeogeography, Palaeoclimatology, Palaeoecology 159, 1–51.
- Bobier, C., Viguier, 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.
- Boersma, A., Premoli Silva, I., 1989. Atlantic Paleogene biserial heterohelicid foraminifera and oxygen minima. Paleoceanography 4 (3), 271–286.
- 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., Sengers, S., Sluijs, A., Warnaar, J., Williams, G.L., 2003. Latest Cretaceous—earliest Oligocene and Quaternary dinoflagellate cysts, ODP Site 1172, East Tasman Plateau. In: Exon, N.F., Kennet, J.P., Malone, M.J. (Eds.), Proceedings of the Ocean Drilling Program. Scientific Results, vol. 189. Available from World Wide Web: http://www-odp.tamu.edu/publications/189_SR/105/105.htm.
- Burollet, P.F., 1956. Contribution á l'etude stratigraphique de la Tunisie Centrale. Annals Mineral Geology (Tunis) 350.
- Burollet, P.F., 1991. Structures and tectonics of Tunisia. In: Freeman, R., Huch, M., Mueller, S. (Eds.), The European Geotraverse. Tectonophysics, pp. 359–369.
- Clemmensen, A., Thomsen, E., 2005. Palaeoenvironmental changes across the Danian–Selandian boundary in the North Sea Basin. Palaeogeography, Palaeoclimatology, Palaeoecology 219, 351–394.

- Crouch, E.M., Heilmann-Clausen, C., Brinkhuis, H., Morgans, H.E. G., Rogers, K.M., Egger, H., Schmitz, B., 2001. Global dinoflagellate event associated with the late Paleocene thermal maximum. Geology 29 (4), 315–318.
- 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. Geological Society of America Special Paper, vol. 369, pp. 113–131. Boulder, Colorado.
- D'Hondt, S., Zachos, J.C., Schultz, G., 1994. Stable isotopic signal and photosymbiosis in late Paleocene planktic foraminifera. Paleobiology 30 (3), 391–406.
- Dupuis, C., Steurbaut, E., Molina, E., Rauscher, R., Tribovillard, N., Arenillas, I., Arz, J.A., Robaszynski, F., Caron, M., Robin, E., Rocchia, r., Lefeve, I., 2001. The Cretaceous–Paleogene (K/P) boundary in the Ain Settara section (Kalaat Senan, central Tunisia): lithological, micropaleontological and geochemical evidence. Bulletin de L'institut royal des sciences naturelles de Belgique 71, 169–190.
- 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, Palaeoelimatology, Palaeoecology 178, 197–210.
- Gardin, S., 2002. Late Maastrichtian to early Danian calcareous nannofossils at Elles (Northwest Tunisia). A tale of one million years across the K-T boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 178, 131–211.
- Goolaerts, S., Kennedy, W.J., Dupuis, C., Steurbaut, E., 2004. Terminal Maastrichtian ammonites from the Cretaceous-Paleo-gene global stratotype section and point, El Kef, Tunisia. Cretaceous Research 25, 313–328.
- Guasti, 2005. Early Paleogene environmental turnover in the Southern Tethys as recorded by foraminiferal and organic-walled dinoflagellate cysts assemblages. PhD thesis, Berichte aus dem Fachbereich Geowissenschaften der Universität Bremen, p. 203.
- Guasti and Speijer, 2005. The Paleocene–Eocene thermal maximum in Egypt and Jordan: an overview of the planktic foraminiferal record. Chapter V of PhD E. Guasti, Early Paleogene environmental turnover in the Southern Tethys as recorded by foraminiferal and organic-walled dinoflagellate cysts assemblages. Berichte aus dem Fachbereich Geowissenschaften der Universität Bremen, pp. 111–145.
- Guasti, E., Kouwenhoven, T.J., Brinkhuis, H., Speijer, R.P., 2005a. Paleocene sea-level and productivity changes at the southern Tethyan margin (El Kef, Tunisia). Marine Micropaleontology 55, 1–17.
- Guasti, E., Speijer, R.P., Fornaciari, E., Schmitz, B., Kroon, D., Gharaibeh, A., 2005b. Transient biotic change within the Danian– Selandian transition in Egypt and Jordan. Chapter IV of PhD E. Guasti, Early Paleogene environmental turnover in the Southern Tethys as recorded by foraminiferal and organic-walled dinoflagellate cysts assemblages. Berichte aus dem Fachbereich Geowissenschaften der Universität Bremen, pp. 75–110.
- 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.
- Keller, G., 1988. Biotic turnover in benthic foraminifera across the Cretaceous/Tertiary boundary at El Kef, Tunisia. Paleogeography, Paleoclimatology, Paleoecology 66, 153–171.

- Kelly, C.D., Arnold, A.J., Parker, W.C., 1996. Paedomorphosis and the origin of the Paleogene planktonic foraminiferal genus *Morozo-vella*. Paleobiology 22 (2), 266–281.
- 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.
- Lu, G., Keller, G., Pardo, A., 1998. Stability and change in Tethyan planktic foraminifera across the Paleocene–Eocene transition. Marine Micropaleontology 35, 203–233.
- Luciani, V., 2002. High-resolution planktonic foraminiferal analysis from the Cretaceous-Tertiary boundary at Ain Settara (Tunisia): evidence of an extended mass extinction. Paleogeography, Paleoclimatology, Paleoecology 178, 299–319.
- 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.
- Norris, R.D., 1996. Symbiosis as an Evolutionary Innovation in the radiation of Paleocene planktic foraminifera. Paleobiology 22 (4), 461–480.
- Olsson, R.K., Hemleben, C., Berggren, W.A., Huber, B.T. (Eds.), 1999. Atlas of Paleocene planktonic foraminifera. Smithsonian Contributions to Paleobiology, 85 (254 pp.).
- Pearson, P.N., Shackleton, N.J., Hall, M.A., 1993. Stable isotope paleoecology of middle Eocene planktonic foraminifera and multispecies isotope stratigraphy, DSDP Site 523, South Atlantic. Journal of Foraminiferal Research 23 (2), 123–140.
- Perch-Nielsen, K., 1979. Calcareous nannofossil zonation at the Cretaceous/Tertiary boundary in Denmark. In: Bromley, R.G. (Ed.), Cretaceous-Tertiary Boundary Events. Symposium I: The Maastrichtian and Danian of Denmark, Copenhagen, pp. 115–135.
- Perch-Nielsen, K., 1985. Cenozoic calcareous nannofossils. In: Bolli, H.M., Saunders, J.B., Perch-Nielsen, K. (Eds.), Plankton Stratigraphy. Cambridge Earth Science Series, 1 (11). Cambridge University Press, pp. 427–554.
- Peryt, D., Alegret, L., Molina, E., 2002. The Cretaceous/Paleogene (K/P) boundary at Ain Settara, Tunisia: restructuring of benthic foraminiferal assemblages. Terra Nova 14 (2), 101–107.
- Peypouquet, J.P., Grousset, F., Mourguiart, P., 1986. Paleoceanography 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.
- Reading, H.G. (Ed.), 1986. Sedimentary Environments and Facies. Blackwell scientific publications, Oxford. 615 pp.
- Quillévéré, F., Norris, R.D., 2003. Ecological development of acarininids (planktonic foraminifera) and hydrographic evolution of Paleocene surface waters. In: Wing, S.L., Gingerich, P.D., Schmitz, B., Thomas, E. (Eds.), Causes and Consequences of Globally Warm Climates in the Early Paleogene. Geological Society of America Special Paper, vol. 369, pp. 223–238. Boulder, Colorado.
- 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 Paléogéne de la Tunisie Septentrionale et Orientale (Hypostratotypes Tunisiens), Bratislava, Slovakia. 238 pp.

- Salaj, J., Pozaryska, K., Szczechura, J., 1976. Foraminiferida, zonation and subzonation of the Paleocene of Tunisia. Acta Palaeontologica Polonica 21, 127–190.
- Schmitz, B., 1994. The Paleocene Epoch stratigraphy, global change and events. GFF 116, 39–41.
- Schmitz, B., Molina, E., von Salis, K., 1998. The Zumaya section in Spain: a possible global stratotype section for the Selandian and Thanetian Stages. Newsletters on Stratigraphy 36 (1), 35–42
- Shackleton, N.J., Corfield, R.M., Hall, M.A., 1985. Stable isotope data and the ontogeny of Paleocene planktonic foraminifera. Journal of Foraminiferal Research 15 (4), 321–336.
- 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.
- 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. Geological Society of America Special Paper, vol. 369, pp. 275–290. Boulder, Colorado.
- Steurbaut, E., King, C., 1994. Integrated stratigraphy of the Mont-Panisel borehole section (151E340), Ypresian (Early Eocene) of the Mons Basin, SW Belgium. Bulletin de la Société belge de Géologie 102, 175–202.
- Steurbaut, E., Dupuis, C., Arenillas, I., Molina, E., Matmati, M.F., 2000. The Kalaat Senan section in central Tunisia: a potential reference section for the Danian/Selandian boundary. GFF "Early Paleogene Warm Climates and Biosphere Dynamics" 122, 158–160.
- Stouge, S., Ferré Hjortkjaer, B., Rasmussen, J.A., Roncaglia, L., Sheldon, E., 2000. Micro- and nannofossil biostratigraphy across the Danian/Selandian boundary. GFF 122, 161–162.
- Thomsen, E., 1994. Calcareous nannofossil stratigraphy across the Danian–Selandian boundary in Denmark. GFF 116, 65–67.
- Thomsen, E., Heilmann-Clausen, C., 1985. The Danian-Selandian boundary at Svejstrup with remarks on the biostratigraphy of the boundary in western Denmark. Bulletin of Geology and Society of Denmark 33, 341–362.
- Van der Zwaan, G.J., Jorissen, F.J., de Stigter, H.C., 1990. The depth dependency of planktonic/benthic foraminiferal ratios: constraints and applications. Marine Geology 95, 1–16.
- Van Eijden, A.J.M., 1995. Morphology and relative frequency of planktic foraminiferal species in relation to oxygen isotopically inferred depth habitats. Palaeogeography, Palaeoclimatology, Palaeoecology 113, 267–301.
- Van Itterbeeck, J., Spronge, J., Dupuis, C., Speijer, R.P., Steurbaut, E., submitted for publication. Danian/Selandian boundary stratigraphy and ostracod records from Sidi Nasseur, Tunisia. Marine Micropaleontology (Special publication ISO, Berlin).
- Varol, O., 1989. Palaeocene calcareous nannofossil biostratigraphy. In: Crux, J.A., van Heck, S.E. (Eds.), Nannofossils and their Applications. British Micropalaeontological Society, vol. 12, pp. 267–310.
- Varol, O., 1992. Sullivania a new genus of Palaeogene coccoliths. Journal of Micropalaeontology 11 (2), 141–149.
- 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., Brinkhuis, H., Pearce, M.A., Fensorne, R.A., Weegink, J.W., 2004. Southern Ocean and global dinoflagellate cyst events compared: index events for the Late Cretaceous—

- Neogene. In: Exon, N.F., Kennett, J.P., Malone, M.J. (Eds.), Proceeding of the Ocean Drilling Program, Scientific Results, pp. 1–98.
- 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.