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Late Paleocene–early Eocene dinoflagellate cyst records from the Tethys: Further observations on the global distribution of Apectodinium

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ABSTRACT

To further understand the distribution and abundance of *Apectodinium* through space and time, dinoflagellate cyst (dinocyst) records from two well-calibrated Paleogene sections in the Tethys (Tunisia and Uzbekistan) have been examined. *Apectodinium* was present in the southern Tethys (Tunisia) by the late Paleocene (planktonic foraminiferal Subzone P4a), confirming earlier findings that the genus evolved in lower latitudes. *Apectodinium* abundance was frequent to dominant from the upper Paleocene to lower Eocene in the Tethys. The initial Eocene thermal maximum (IETM) at lower latitudes appears to be characterized by high percentages of *Apectodinium,* although it may not always have dominated assemblages. Other dinocyst genera with thermophilic preferences may be abundant during the IETM. At mid to high latitudes, *Apectodinium* has been sporadically recognized during the upper Paleocene. Nevertheless, the IETM at mid to high latitudes was still characterized by *Apectodinium*-dominated assemblages. Additional *Apectodinium* acmes occurred in the lower Eocene, although as yet it is unclear if these are globally isochronous. Intervals of *Apectodinium*-dominated assemblages are indicative of environmental conditions that were apparently markedly different to "normal background settings" of the late Paleocene–early Eocene. Sea surface temperature (SST) was probably the main control in distribution since *Apectodinium* acmes at mid to high latitudes seem to have occurred during intervals of highest SSTs, such as the IETM. In addition, the probable heterotrophic *Apectodinium* "blooms" were intricately linked to enhanced runoff and increased delivery of nutrients in surface waters, probably as a result of intensification of the weathering cycle and other possible specific oceanic conditions.

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INTRODUCTION

The late Paleocene to early Eocene (~57.4–53.4 Ma) was characterized by globally warm climates, shallow latitudinal gradients and prevalent ice-free conditions (e.g., Stott et al., 1990; Zachos et al., 1994; Berggren et al., 1998). Superimposed on this equable climate was a short-lived, ~220 k.y. (Röhl et al., 2000), intense warming event currently referred to as the initial Eocene thermal maximum or IETM. This interval corresponds to a globally recognized negative 2‰–3‰ carbon isotope excursion (CIE) (Bralower et al., 1995; Koch et al., 1995) and a brief warming of deep ocean and high-latitude surface temperatures by 6–8 °C (Kennett and Stott, 1991; Thomas and Shackleton, 1996; Katz et al., 1999). The CIE is indicative of a massive injection of ^{12}C-rich carbon into the ocean-atmosphere system, most probably from methane released from seafloor gas hydrates (Dickens, 2000, 2001). Associated with the IETM are numerous changes in biota, including a prominent benthic foraminiferal extinction event (Thomas, 1998), turnovers in planktonic organisms (Kelly et al., 1996; Aubry, 1998), and a fundamental diversification of terrestrial mammal orders (Clyde and Gingerich, 1998). Although the IETM is best dated as beginning between 54.93 and 54.98 Ma (Norris and Röhl, 1999), this age is currently difficult to correlate with other stratigraphic events associated with the Paleocene-Eocene (P-E) transition. Hence, we use the age of 55.5 Ma for the onset of the IETM (Berggren and Aubry, 1998).

Marine dinoflagellates, surface dwelling plankton, also experienced significant changes during the upper Paleocene–lower Eocene. As part of their life cycle many dinoflagellates produce an organic-walled cyst (dinocyst) that can be preserved in the geological record. Ecologically, dinoflagellates appear to have either heterotrophic or autotrophic lifestyles (Fensome et al., 1993). The most profound change in dinocyst assemblages during the late Paleocene–early Eocene involved representatives of one particular genus, *Apectodinium.* Recently, an extraordinary event has been linked with the IETM: coeval with the beginning of the CIE, *Apectodinium* species suddenly dominate dinocyst assemblages at locations around the world (Bujak and Brinkhuis, 1998; Heilmann-Clausen and Egger, 2000; Bybell et al., 2001; Crouch et al., 2001).

Bujak and Brinkhuis (1998) compiled information regarding the distribution, abundance and ecological preference of *Apectodinium* through the upper Paleocene–lower Eocene from available global dinocyst data. Several important conclusions were established: (1) the oldest definite record of *Apectodinium* is from lower latitudes (Tethys) in the mid Paleocene, within calcareous nannoplankton Zone NP4 and planktonic foraminiferal Subzone P3a (2) *Apectodinium* may be abundant in lower latitudes during the upper Paleocene and lower Eocene (3) the motile stage of representatives of *Apectodinium* were probably thermophilic and heterotrophic, implying requirements of warm sea surface temperatures and a sufficient food source and (4) there is a lack of marine sections studied for dinocysts that contain well-calibrated ages and precise recognition of the IETM, particularly in equatorial regions and the Southern Hemisphere. Since this overview, dinocyst records have been documented from a lower-latitude sequence in the Northern Hemisphere (Austria; Fig. 1) and a mid to high latitude sequence in the Southern Hemisphere (New Zealand; Fig. 1). Both records are correlated with calcareous nannoplankton zones and the IETM (Egger et al., 2000; Heilmann-Clausen and Egger, 2000; Crouch et al., 2001).

Although these recent studies provide more information regarding *Apectodinium,* additional well-correlated dinocyst studies are needed to further document the spatial and temporal distribution of this genus, notably from equatorial regions. In this paper, dinocyst assemblages are examined from the lower-latitude setting of the Tethys. One section comes from the southern part of the basin (Elles section, Tunisia) and the other is from the northeast (Aktumsuk section, Uzbekistan) (Figs. 1 and 2). Both successions span the IETM and are correlated with carbon isotope records and calcareous nannoplankton and planktonic foraminiferal zonations.

The dinocyst record at Elles and Aktumsuk offer the possibility to increase our understanding of the distribution and relative abundance of *Apectodinium,* along with other significant dinocyst events, in the lower-latitude Tethys during the late Paleocene–early Eocene. Furthermore, by combining these results with other well-correlated dinocyst records from the Northern and Southern Hemispheres, a more up-to-date overview of the global pattern of *Apectodinium* during the upper Paleocene and lower Eocene can be provided.

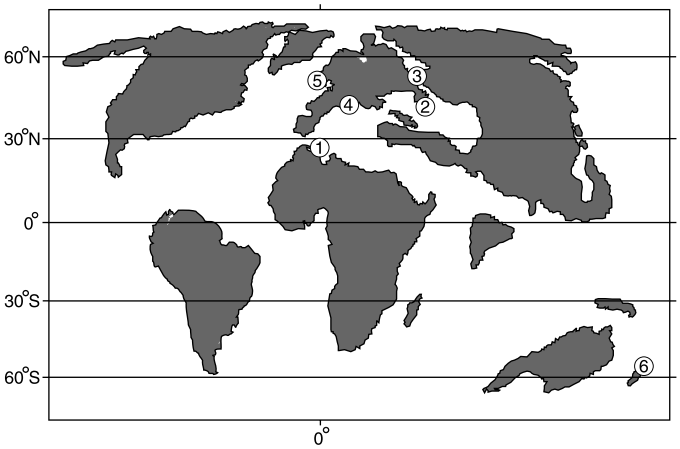


Figure 1. Global paleogeographic reconstruction during the late Paleocene (modified from Scotese and Golanka, 1992) with locations of all sections discussed. 1—Elles section, Tunisia; 2—Aktumsuk section, Uzbekistan; 3—Sokolovsky Quarry, northern Kazakhstan (Turgay Strait); 4—Anthering section, Austria; 5—North Sea Basin; 6—Tawanui section, New Zealand.

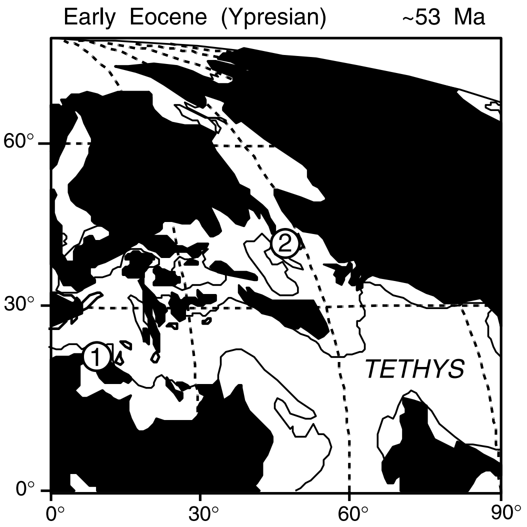


Figure 2. Paleogeographic reconstruction of the Tethys region during the early Eocene (ca. 53 Ma) with location of the Elles section, Tunisia (1) and Aktumsuk section, Uzbekistan (2). Map modified from Smith et al. (1994).

SETTING OF LOCATIONS

Elles section, Tunisia

The Elles section is located in the El Kef Basin, Tunisia (Figs. 1 and 2). During the Paleocene-Eocene, the El Kef Basin was situated in the northern tropical zone (~ paleolatitude 20°N) and in an open marine environment connected to the Tethys (Bolle et al., 1999, 2000b). The studied section at Elles is ~45 m thick and encompasses calcareous nannoplankton Zones NP7 to NP10 and planktonic foraminiferal Subzones P4a to P6a (Figs. 3 and 4). The IETM is thought to be associated with a ~2.7 m clay layer, within Subzone NP9b and Zone P5 (Bolle et al., 1999). The clay layer is characterized by a $\delta^{13}C$ shift of –1.3‰, decline in carbonate sedimentation, increased detrital input and high kaolinite/smectite ratio (Bolle et al., 1999). The negative shift in bulk rock carbon isotopic analyses, recognized in the clay layer, is less pronounced than the “typical” 2‰–3‰ excursion recorded at other marine locations during the IETM (e.g., Kennett and Stott, 1991). The most prominent negative shift in

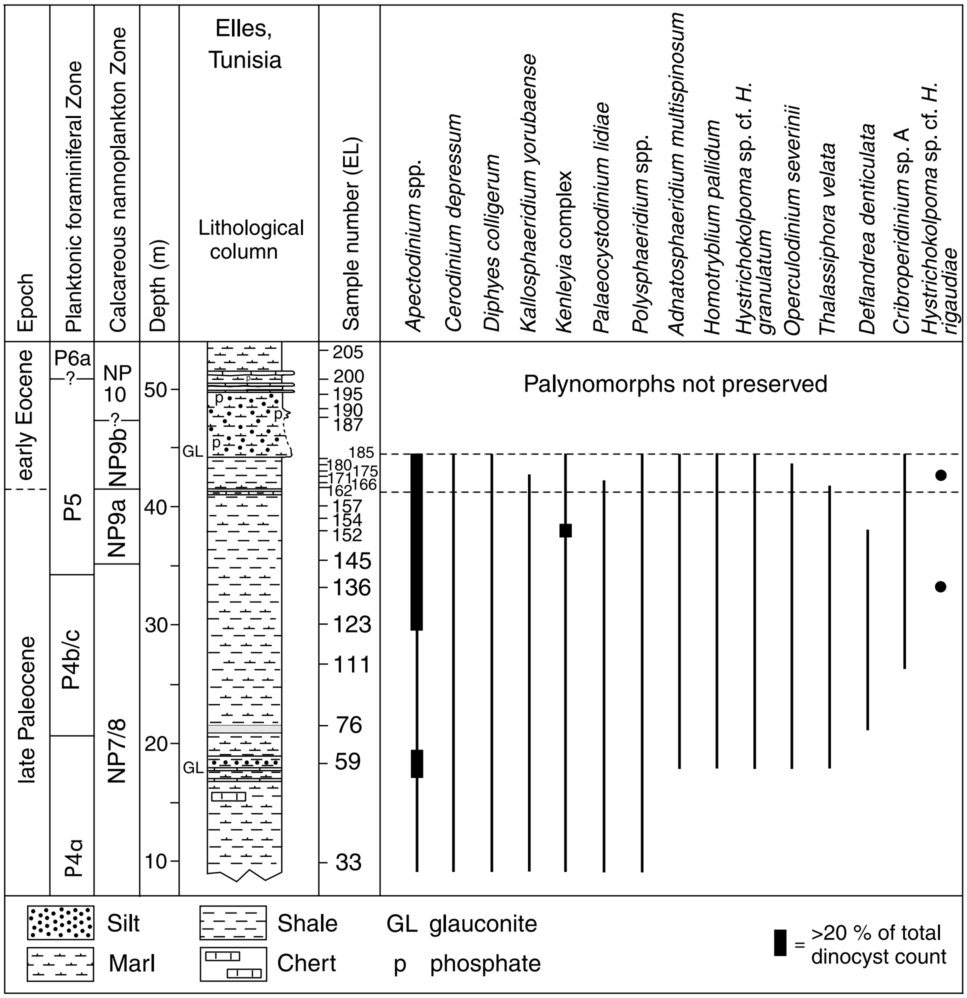


Figure 3. Stratigraphical distribution of selected dinocysts at Elles section, Tunisia. A summary lithological column and sample points are shown. Dashed line shows the proposed position of the initial Eocene thermal maximum (after Bolle et al., 1999). Calcareous nannoplankton and planktonic foraminiferal zonation scheme from Bolle et al. (1999).

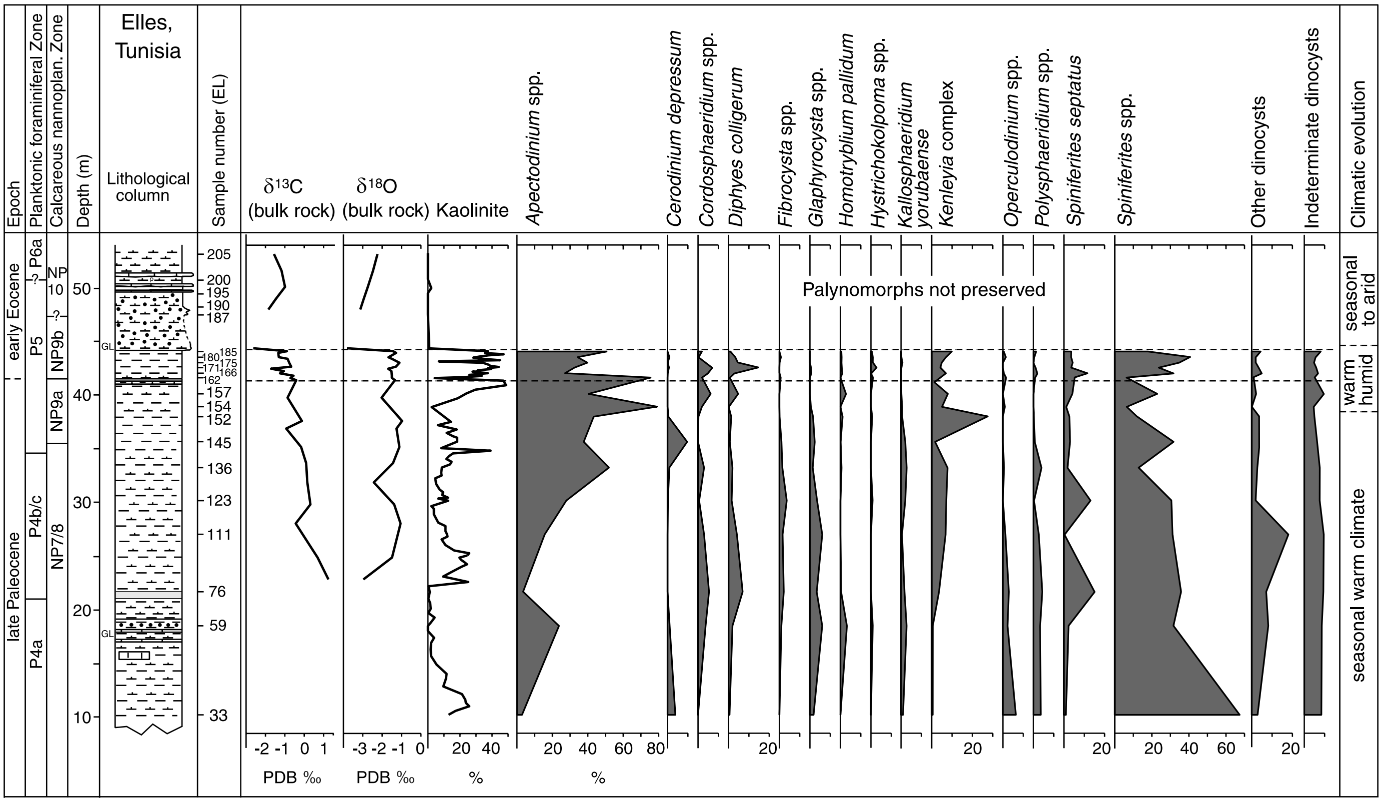


Figure 4. Relative abundance of dinocysts from the upper Paleocene to lowermost Eocene at Elles section, Tunisia. A summary lithological column and sample points are shown. Dashed line shows the proposed position of the initial Eocene thermal maximum (after Bolle et al., 1999). Calcareous nannoplankton and planktonic foraminiferal zonation scheme, and climatic evolution information from Bolle et al. (1999).

$\delta^{13}C$ (~1.7‰) is noted at the base of a ~6 m unit that overlies the clay layer (Fig. 4). This unit consists primarily of a glauconitic siltstone with phosphatic particles and francolite, which may have altered or overprinted the original marine isotopic signal (Bolle et al., 1999).

The section consists mainly of marls, shales, shaley marls and thin calcareous beds (Figs. 3 and 4). Two glauconitic siltstone layers are present that are considered to represent sequence boundaries associated with relative sea-level fall and possible increased tectonic activity (Bolle et al., 1999). The major components of the bulk rock sediment are phyllosilicates, with calcite becoming more abundant in the upper 9 m of section (Bolle et al., 1999). Although smectite is the major clay mineral component, kaolinite becomes increasingly more abundant in Zone NP9 (Fig. 4). Variations in clay minerals of the sediments indicate changing climatic conditions during the upper Paleocene–lower Eocene (Bolle et al., 1999). A low kaolinite content and abundant smectite suggest a seasonal warm climate during the upper Paleocene, while a very high kaolinite/smectite ratio across the P-E transition (Fig. 4) implies a warm and humid climate with enhanced terrestrial runoff. The disappearance of kaolinite and an increase in smectite and mica suggests development of arid to seasonal climatic conditions during the lowermost Eocene (Bolle et al., 1999).

Aktumsuk section, Uzbekistan

The Aktumsuk section is located southwest of the Aral Sea, Uzbekistan (Figs. 1 and 2), with a succession of ~32 m that spans calcareous nannoplankton Zone CC19 to NP14 (Bolle et al., 2000a). In this paper we focus on a ~3 m interval spanning the IETM, from calcareous nannoplankton Zones NP9 to NP11 (Figs. 5 and 6). The base of the succession is marked by a hiatus, with latest Paleocene sediments unconformably overlying Campanian white chalks (Bolle et al., 2000a). During the late Paleocene, Aktumsuk was located close to an emerged continental area that was subsequently flooded by a marine transgression at the end of the Paleocene (Gavrilov et al., 1997; Bolle et al., 2000a). During the lower Eocene, the marginal northeastern Tethys was marked by a period of high sea level and increasing water circulation, resulting in enhanced levels of oxygenation (Haq et al., 1988; Bolle et al., 2000a).

The IETM at Aktumsuk occurs within the lower part of a ~1 m organic-rich interval of grey to dark grey chalk, with cross

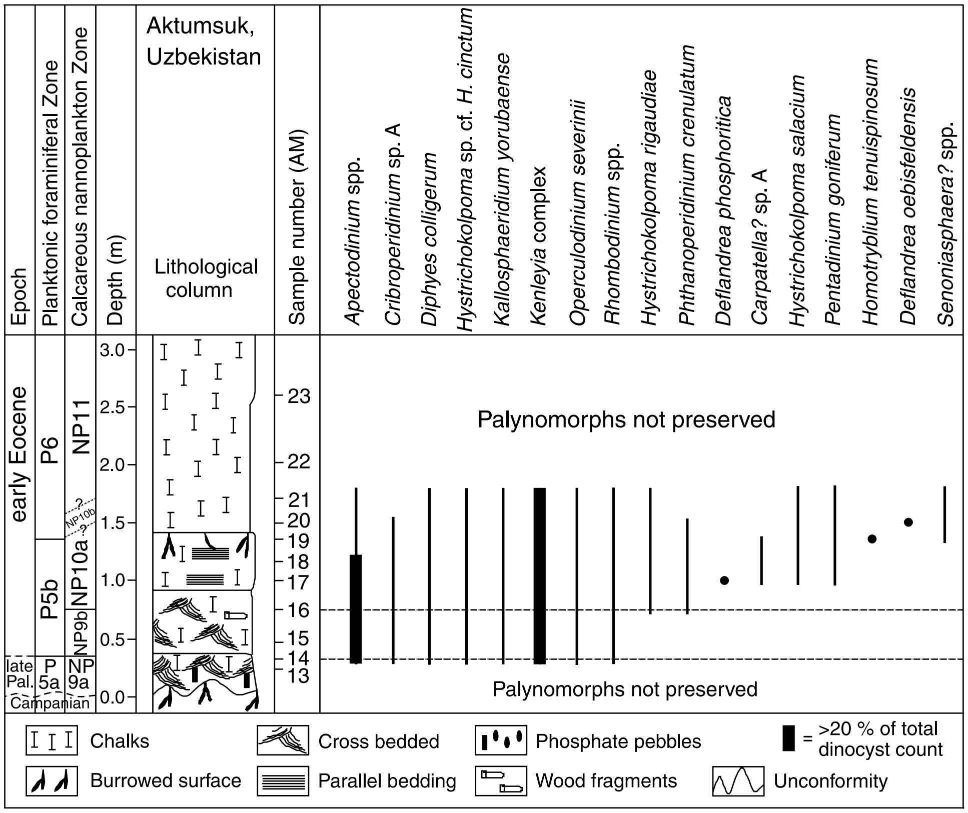


Figure 5. Stratigraphical distribution of selected dinocysts at Aktumsuk section, Uzbekistan. A summary lithological column and sample points are shown. Dashed line shows the proposed position of the initial Eocene thermal maximum (after Bolle et al., 2000a). Calcareous nannoplankton and planktonic foraminiferal zonation scheme from Bolle et al. (2000a).

bedding and wood fragments in the lower 0.5 m and parallel bedding in the upper 0.5 m (Figs. 5 and 6). The IETM is marked by a decrease of between ~1.8‰ and 5.9‰ in $\delta^{13}C$ isotopes of the bulk fine fraction (<63 µm), mixed planktonic foraminifera assemblages and total organic carbon (Fig. 6; Bolle et al., 2000a, 2000b). In addition, the IETM corresponds to minimum $\delta^{18}O$ values, high organic carbon content (maximum 8.44%) and an incursion of a transient subtropical planktonic foraminiferal fauna (Bolle et al., 2000a).

Distribution of clay minerals suggest that a temperate warm climate, with wet and arid seasons, was dominant during the upper Paleocene, and that a warm and humid climate was present during the IETM and lower Eocene (Bolle et al., 2000a). The presence of organic-rich sediments in the uppermost Paleocene can be correlated over a significant area of central and south Asia, the Caspian region and Caucasus (e.g., Gavrilov and Muzylöv, 1991; Gavrilov et al., 1997).

MATERIAL AND METHODS

Twenty-one rock samples were collected from across ~45 m of section at Elles (Figs. 3 and 4). The lowest sample was collected at ~10.2 m and a further nine samples were taken in the overlying ~30 m upper Paleocene interval. Six samples were taken from the ~2.7 m clay layer that is thought to represent the IETM and five samples from the overlying ~10 m of section. At Aktumsuk, 18 rock samples were collected from across ~5 m of section (Figs. 5 and 6). One sample was collected from below the organic-rich layer, six samples from within the ~1 m organic-rich layer and 11 samples from the overlying ~4 m of chalk.

All samples were prepared for palynological examination at the Laboratory of Palaeobotany and Palynology (LPP), Utrecht University, using standard techniques (e.g., Van Steenbergen, 1997). Between 1.5 and 10 g of sediment was crushed, and the carbonate and siliceous components removed by adding 30% HCl and 38% HF, respectively. Samples were then sieved over a 10 µm–mesh sieve and well-mixed representative fractions of the >10 µm residue were mounted on glass slides using a glycerine jelly medium.

Several samples from both sections contain no palynomorphs and these sediments have most likely experienced oxidation, either syn- or postdepositional. At Elles, the five samples (EL187 to EL205) collected above the ~2.7 m clay layer contain no palynomorphs. At Aktumsuk, one sample (AM13) below the organic-rich layer and the uppermost nine samples (AM22 to AM30) from the chalk are either barren or contain very sparse palynomorphs. When samples do contain palynomorphs they are generally well preserved and abundant. Quantitative analysis of dinocyst assemblages was completed on 16 samples from Elles and eight samples from Aktumsuk.

For all samples quantitatively examined, a minimum of 200 dinocysts were counted and the entire slide was scanned for the

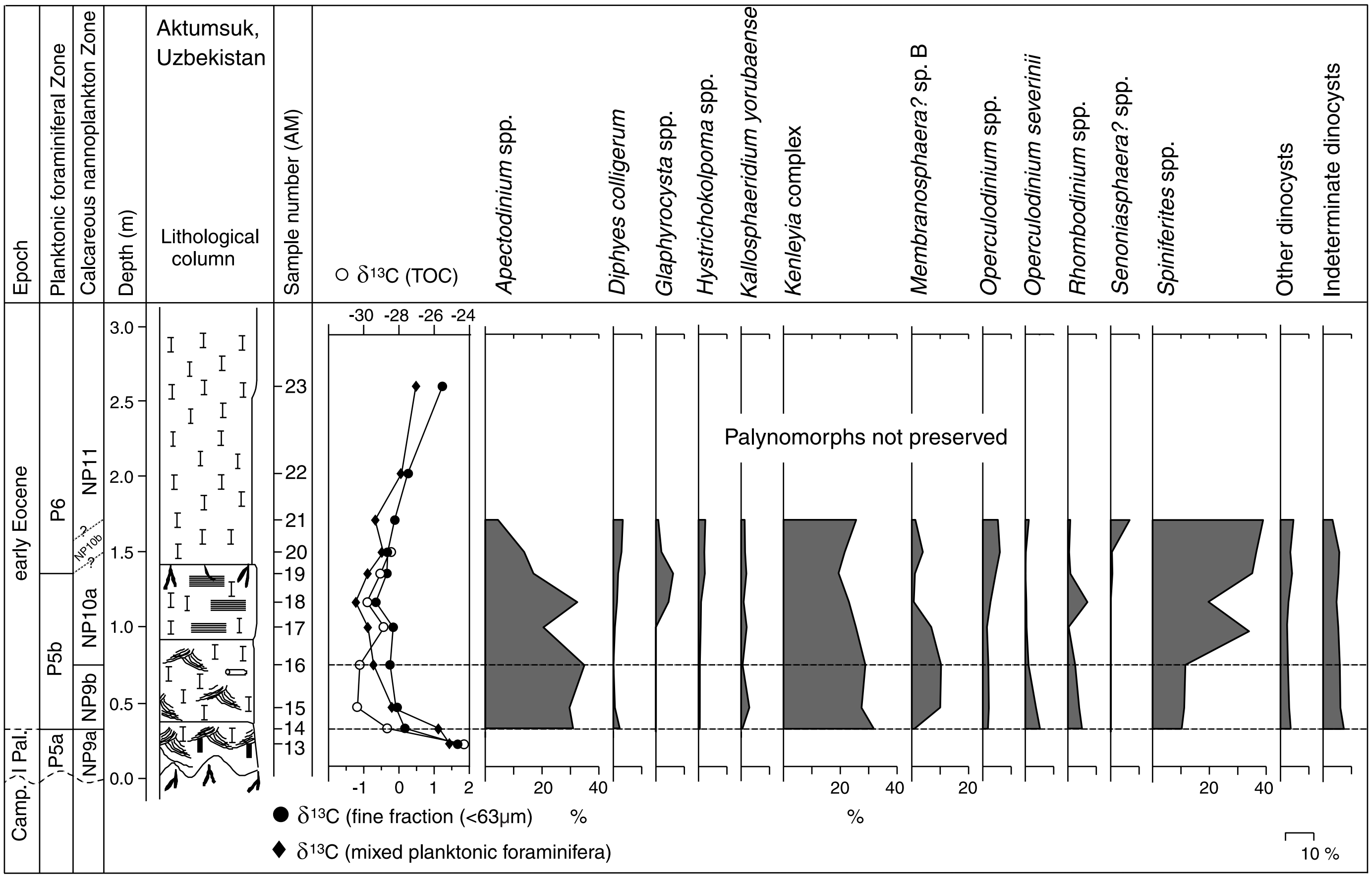


Figure 6. Relative abundance of dinocysts from the initial Eocene thermal maximum (IETM) and lower Eocene at Aktumsuk section, Uzbekistan. A summary lithological column and sample points are shown. Dashed line shows the proposed position of the initial Eocene thermal maximum (after Bolle et al., 2000a). Calcareous nannoplankton and planktonic foraminiferal zonation scheme from Bolle et al. (2000a).

presence of additional taxa. In this paper, most attention is given to stratigraphically significant dinocyst taxa, whose approximate ranges have been ascertained from previous research in lower-latitude regions (e.g., Jan du Chêne and Adediran, 1984; Brinkhuis and Zachariasse, 1988; Köthe, 1988; Brinkhuis et al., 1994; Iakovleva et al., 2001). A list of recorded species and brief taxonomic notes are provided in the Appendix. Light-photomicrographs were taken from permanent strew mounts. For photographed specimens England Finder coordinates are provided. All material is filed in the LPP collection of Utrecht University.

RESULTS

Elles section, Tunisia

The dinocyst assemblages at Elles are primarily dominated by either *Apectodinium* or *Spiniferites* species (Figs. 3 and 4), and their overall composition is consistent with an open marine environmental setting, as suggested by Bolle et al. (1999). Dinocysts thought to be indicative of oceanic water masses, such as *Impagidinium,* are not recorded while many of the dinocysts, including *Operculodinium* and *Spiniferites,* are typically characteristic of open marine, neritic water masses (e.g., Wall et al., 1977; Brinkhuis, 1994; Powell et al., 1996; Stover et al., 1996; van Mourik et al., 2001).

Apectodinium is present in low percentages at the base of the succession (Fig. 3). The morphology of representatives of *Apectodinium* becomes more diverse up-section, although *Apectodinium augustum* (an extreme morphotype with well-developed lateral and antapical horns) is not recorded. Interestingly, several specimens, otherwise assignable to *Apectodinium,* show an archeopyle that involves two plates (2a and 4″ plates; Plate 1, Figures 1 and 2). This contrasts to the standard 2a quadra archeopyle that characterizes *Apectodinium* (Costa and Downie, 1976; Williams et al., 1998).

The first occurrence of *Homotryblium pallidum* (Plate 2, Figure 3) and *Hystrichokolpoma* sp. cf. *H. granulatum* (Plate 2, Figures 5 and 6), within calcareous nannoplankton Zone NP7/8 and the upper part of planktonic foraminiferal Subzone P4a, are noteworthy (Fig. 3). Another specimen of *Hystrichokolpoma,* tentatively assigned to *H.* sp. cf. *H. rigaudiae* (Plate 2, Figure 4), occurs in samples EL136 and EL171 (Fig. 3). At present, the oldest occurrence of *Homotryblium* is in sediments tentatively assigned to calcareous nannoplankton Zone NP6/7 from a section in Kazakhstan (Iakovleva et al., 2001), and our results confirm that *Homotryblium* was present in the southern Tethys in sediments assigned to calcareous nannoplankton Zone NP7/8. *Hystrichokolpoma* species are most commonly recorded from sediments of an early Eocene age or younger, although some species (e.g., *H. granulatum, H. salacium, H. unispinum*) have previously been recognized from lower-latitude upper Paleocene successions (Jan du Chêne and Adediran, 1984; Iakovleva et al., 2001).

The relative abundance of *Apectodinium* increases upsection and is a dominant component from the upper part of calcareous nannoplankton Zone NP7/8 and planktonic foraminifera Subzone P4b/c (Fig. 4). Prior to the ~2.7 m clay layer, three peaks in *Apectodinium* abundance are recorded, with values of ~24%, ~52% and ~79%, respectively. *Apectodinium*-dominated assemblages (~75%) mark the base of the ~2.7 m clay layer, although the relative abundance drops to between ~27% and 51% in the remaining interval. Notably, the pattern of *Apectodinium* abundance shows some covariance with the record of kaolinite content (Fig. 4).

The *Kenleyia* complex is a common element of the dinocyst assemblage, with the highest abundance (~28%) recorded in the lower part of calcareous nannoplankton Subzone NP9a (Fig. 4). Specimens assigned to this complex show a large variation in morphology (Plate 3, Figures 4–9), and are generally characterized by the presence of apical and antapical protrusions, and variable development of the periphragm (see Appendix).

Aktumsuk section, Uzbekistan

Similar to Elles, the dinocyst assemblages at Aktumsuk are dominated by either *Apectodinium* or *Spiniferites* species, and specimens assigned to the *Kenleyia* complex (Figs. 5 and 6). The overall dinocyst assemblage recorded at Aktumsuk is consistent with a neritic marine setting, as suggested by Bolle et al. (2000a).

Apectodinium is present throughout the succession and several morphological variations are recognized, although the extreme morphotype *Apectodinium augustum* is absent. As recorded at Elles, several *Apectodinium* specimens show an archeopyle that involves two plates (2a and 4″ plates). Specimens assigned to *Rhombodinium,* another member of the Wetzelielloideae subfamily, are common throughout (Fig. 5). Possible reworked dinocysts include specimens tentatively assigned to *Senoniasphaera?,* a genus primarily restricted to the Cretaceous. Reworked calcareous nannoplankton, mainly of Late Cretaceous age, have previously been noted in the same interval at Aktumsuk (Bolle et al., 2000a).

The highest *Apectodinium* percentages (up to ~35%) are recorded in calcareous nannoplankton Subzones NP9b and NP10a (Fig. 6). Although *Apectodinium* is relatively abundant during the IETM, the percentages associated with the onset of the CIE are not as high as those recorded from the presumed equivalent horizon (i.e., base of the ~2.7 m clay layer) at Elles (Figs. 4 and 6). Specimens assigned to the *Kenleyia* complex (Plate 3, Figures 10–12) constitute ~20%–32% of the assemblages and are consistently more abundant than at Elles, which may be related to the shallower depositional environment at Aktumsuk.

DISCUSSION

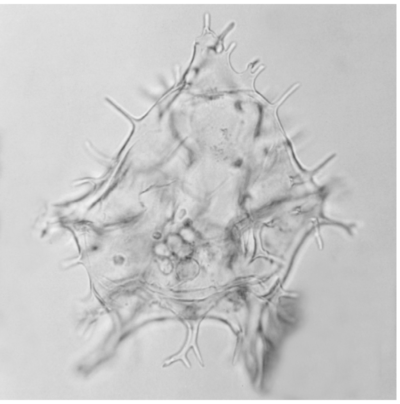
The combined dinocyst results at Elles and Aktumsuk provide a reasonably detailed record from the Tethys during the late Paleocene (calcareous nannoplankton Zone NP7/8 and planktonic foraminiferal Subzone P4a) to early Eocene (calcareous nannoplankton Zone NP10 and planktonic foraminiferal Zone P6).

Apectodinium

Apectodinium was present in the southern Tethys by the late Paleocene, becoming a notable component of dinocyst assemblages in upper calcareous nannoplankton Zone NP7/8, and continued to be a frequent to superabundant component (~20%–80%) during the remaining part of the late Paleocene and into the earliest Eocene (Figs. 4 and 6). A decrease in *Apectodinium* abundance is recorded within calcareous nannoplankton Zone NP10a (Fig. 6). At the Jebel Boudabous section in central Tunisia (Bujak and Brinkhuis, 1998), the relative abundance of *Apectodinium* also remained high during the early Eocene, although there it extends into calcareous nannoplankton Zone NP11 before the abundance declines.

At Elles, the interval of frequent to abundant *Apectodinium* corresponds to a phase of elevated kaolinite percentages (Fig. 4). In particular, kaolinite is a more significant component of clay mineral composition during planktonic foraminiferal Subzone P4b/c and Zone P5, with the highest percentages (up to ~49%) recorded just prior to the ~2.7 m clay layer and within the clay layer. Kaolinite is a mineral that typically develops on well-drained tropical soils characterized by a warm and humid climate with high precipitation (Robert and Kennett, 1994). The apparent link between elevated kaolinite and *Apectodinium* percentages is, therefore, consistent with the hypothesis that the motile representatives of *Apectodinium* required both warm temperatures and an availability of nutrients (in this case primarily supplied by terrestrial runoff) and/or tolerance of such conditions.

The timing of the two peaks in *Apectodinium* abundance (~24% and ~52%) within calcareous nannoplankton Zone NP7/8 at Elles (Fig. 4), appear to be approximately coeval with other late Paleocene occurrences of *Apectodinium* at higher latitudes in the Northern Hemisphere. In the North Sea Basin (Fig. 1), two short-lived excursions of *Apectodinium* have been recorded in the upper Paleocene; one within the lower part of calcareous nannoplankton Zone NP8 (sequence Tht-3 of Powell et al., 1996) and the other close to the NP8/NP9 zonal boundary (sequence Tht-4) (Bujak and Brinkhuis, 1998; Fig. 7). These ex-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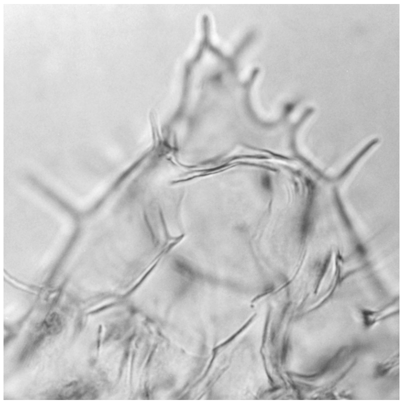
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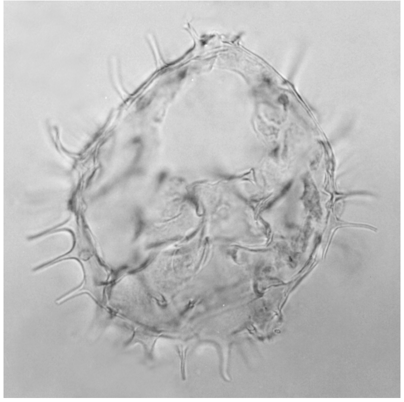
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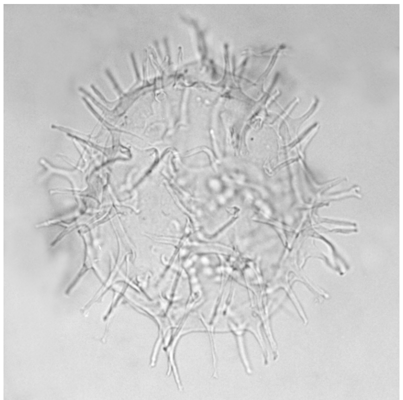
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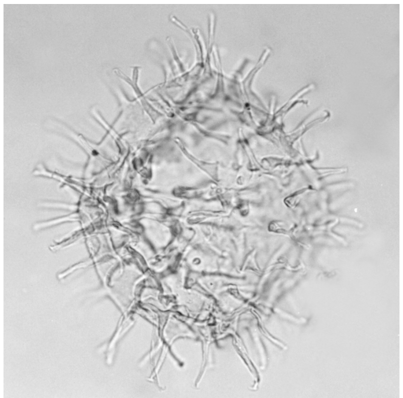
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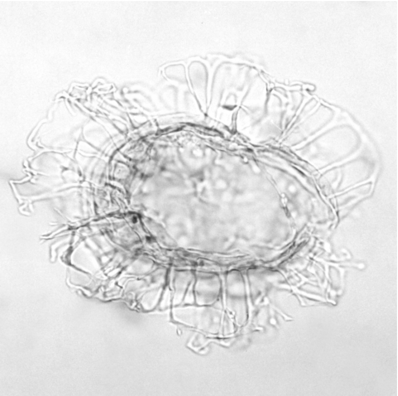
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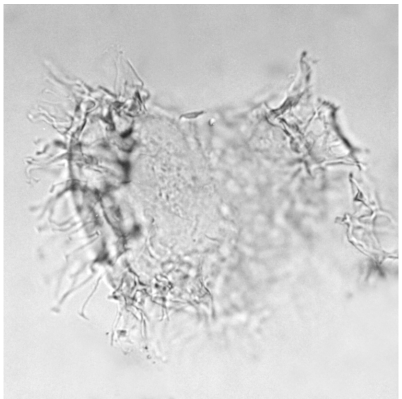
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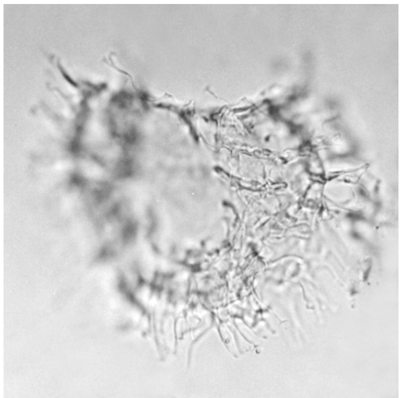
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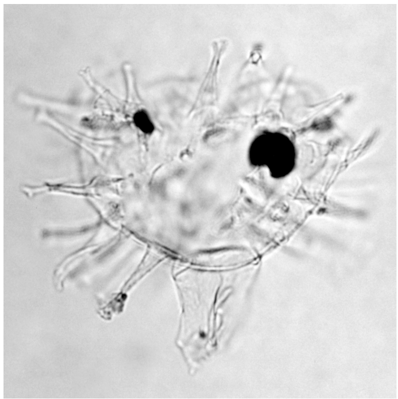
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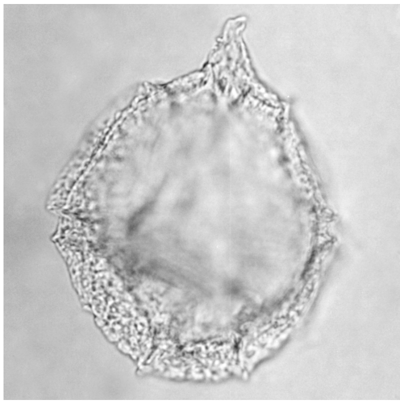
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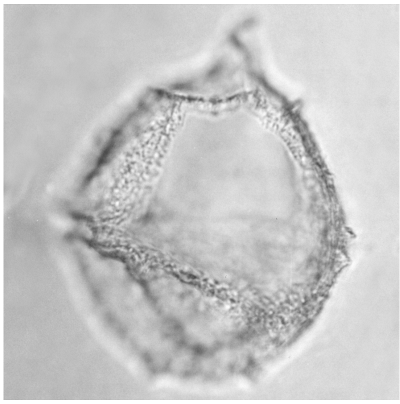
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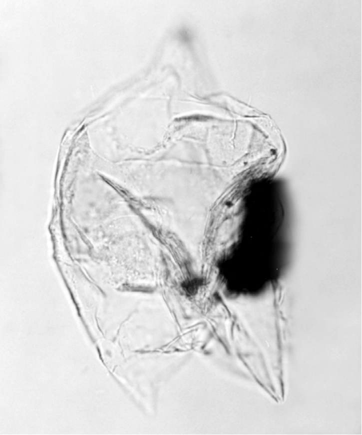

cursions in the North Sea Basin are thought to represent periods of warmer surface waters during the late Paleocene (Bujak and Brinkhuis, 1998). From the Turgay Strait, Northern Kazakhstan (Fig. 1), a peak in the relative abundance of *Apectodinium* (~28%) has been recorded in upper Paleocene sediments thought to be equivalent to sequence Tht-4 in the North Sea Basin (Iakovleva et al., 2001; Fig. 7). This coincidence in the timing of late Paleocene *Apectodinium* bioevents suggests there may have been a link between high numbers of *Apectodinium* in lower latitudes, short-lived incursions of *Apectodinium* into mid to high latitudes, and the possibility of brief intervals of climatic warming or "hyperthermals" (Thomas et al., 2000; Thomas and Zachos, 2000). At present, the occurrence of short-lived migrations of *Apectodinium* into the Southern Hemisphere during the late Paleocene is not well established (Crouch, 2001).

At Elles, the base of the ~2.7 m clay layer (level recognized as the onset of the CIE) is characterized by *Apectodinium*-dominated assemblages (Fig. 4). At Aktumsuk it is difficult to obtain an overview of assemblage changes from the late Paleocene to the IETM, although *Apectodinium* percentages do not reach comparably high values during the interval of lowest $\delta^{13}C$ values (Fig. 6). Although it is difficult to establish a definitive record of *Apectodinium* abundance at lower latitudes during the IETM from these two sections, the differences in relative abundance suggest that *Apectodinium* may not always have dominated the IETM in lower-latitude regions. This is in contrast to current evidence from higher latitudes, where the IETM is consistently characterized by *Apectodinium*-dominated assemblages (Bujak and Brinkhuis, 1998; Heilmann-Clausen and Schmitz, 2000; Bybell et al., 2001; Crouch et al., 2001).

The morphology of representatives of *Apectodinium* varies considerably at both sections, although the extreme morphotype *Apectodinium augustum* was not recorded. At present, records of this species are restricted to the North Sea Basin, northern Kazakhstan and northern Tethys (Austria), and confined to a narrow time interval around the IETM (Powell et al., 1996; Bujak and Brinkhuis, 1998; Egger et al., 2000; Iakovleva et al., 2001).

Other dinocysts

The presence of specimens assignable to *Rhombodinium* (Plate 4, Figures 6–9), another member of the Wetzelielloideae subfamily, during the IETM at Aktumsuk is of note. It is generally accepted that the evolutionary lineage of Wetzelielloids begins in the mid Paleocene with the appearance of *Apectodinium* and that *Wetzeliella* and allied genera, including *Rhombodinium* and *Wilsonidium,* are considered to characterize the early Eocene (e.g., Bujak and Brinkhuis, 1998). Recently, taxa assignable to *Wilsonidium* have been recorded from uppermost Paleocene sediments in northern Kazakhstan (Iakovleva et al., 2001) and this is currently the oldest stratigraphic occurrence of representatives of the *Wetzeliella* group. Our data provide further evidence of taxa assignable to the *Wetzeliella* group prior to the characteristic taxa of the lower Eocene.

Deflandrea phosphoritica (Plate 1, Figure 12) was recorded at Aktumsuk within calcareous nannoplankton Subzone NP10a (Fig. 5). In the lower Eocene this species was common in dinocyst assemblages worldwide (e.g., Stover et al., 1996), although the origin of the species is less well documented. At present, the earliest occurrence of *D. phosphoritica* is from the IETM at an upper Paleocene–lower Eocene section in New Zealand (Crouch, 2001), suggesting this species may have evolved in a Southern Hemisphere region. The earliest records of *D. phosphoritica* in the Northern Hemisphere are similar to its first occurrence at Aktumsuk, in the lower part of calcareous nannoplankton Zone NP10 (Heilmann-Clausen, 1985; Bujak and Brinkhuis, 1998).

The common to abundant occurrence of the *Kenleyia* complex at both sections confirms evidence from earlier studies (e.g., Fechner and Mohr, 1986; Brinkhuis and Leereveld, 1988; Brinkhuis and Zachariasse, 1988; Brinkhuis et al., 1994) that taxa assignable to this complex had a preference for warm water conditions. The abundant presence of the *Kenleyia* complex at Aktumsuk, a succession thought to have been deposited in a marginal marine setting (Bolle et al., 2000a, 2000b), supports indications that taxa assignable to this complex may have also had a preference for shallow to brackish waters (H. Brinkhuis, 2002, personal commun.).

LATE PALEOCENE–EARLY EOCENE GLOBAL DISTRIBUTION OF *APECTODINIUM*

In order to develop a detailed temporal and spatial account of *Apectodinium* distribution, the dinocyst record at Elles and Aktumsuk is compared with several well-calibrated upper

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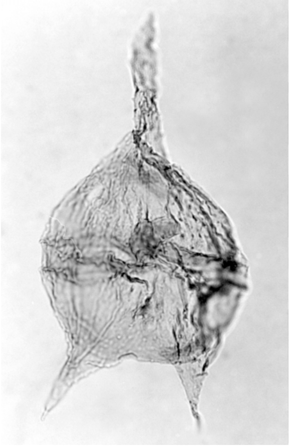
Plate 1. **1:** *Apectodinium* sp. Sample AM16, Slide 1 (E24/3). Aktumsuk section. Overall dimensions ~87 µm by 103 µm. Archeopyle that involves two plates; 2a and 4″ plates. **2:** *Apectodinium* sp. Sample AM16, Slide 1 (E24/3). Aktumsuk section. Vertical dimension ~60 µm; close up of archeopyle (2a and 4″ plates). **3:** *Apectodinium* sp. Sample EL145 (~35.75 m), Slide 1 (H24/0). Elles section. Overall dimensions ~80 µm by 85 µm. Archeopyle that involves two plates; 2a and 4″ plates. **4:** *Apectodinium* sp. Sample EL136 (~33.43 m), Slide 1 (R22/3). Elles section. Overall dimensions ~79 µm by 85 µm. **5:** *Apectodinium* sp. Sample EL162 (~41.8 m), Slide 1 (E20/0). Elles section. Overall dimensions ~90 µm by 100 µm. **6:** *Adnatosphaeridium multispinosum.* Sample EL59 (~18.4 m), Slide 1 (K20/3). Elles section. Overall dimensions ~78 µm by 98 µm. **7** and **8:** *Areoligera senonensis* group. Sample EL111 (~26.92 m), Slide 1 (U33/3). Elles section. Overall dimensions ~65 µm by 95 µm. **9:** *Diphyes colligerum.* Sample AM17, Slide 1 (P30/0). Aktumsuk section. Overall dimensions ~58 µm by 50 µm. **10** and **11:** *Cribroperidinium* sp. A. Sample AM19, Slide 1 (P35/0). Aktumsuk section. Overall dimensions ~50 µm by 61 µm. **12:** *Deflandrea phosphoritica.* Sample AM17, Slide 1 (R22/0). Aktumsuk section. Overall dimensions ~70 µm by 120 µm.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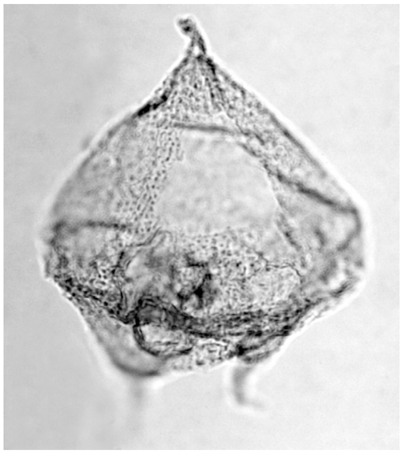
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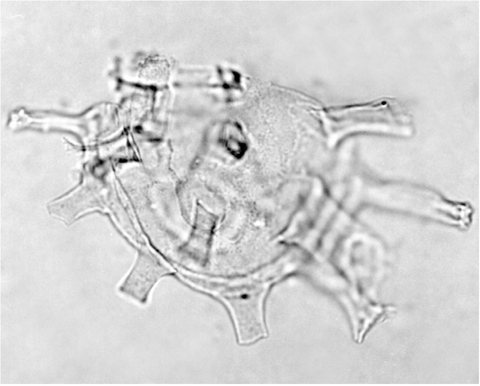
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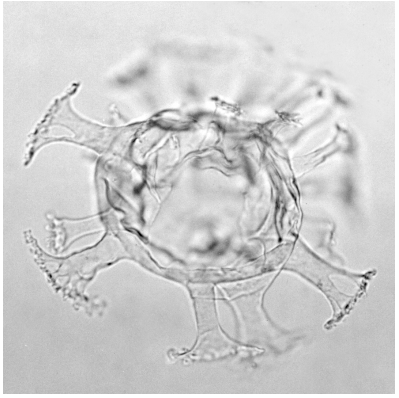
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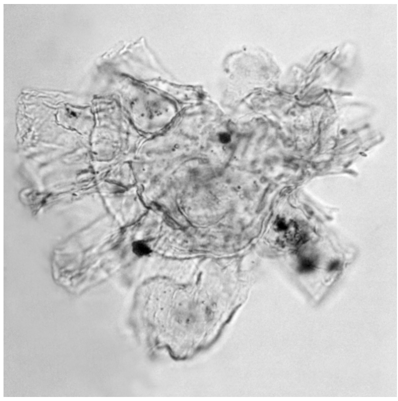
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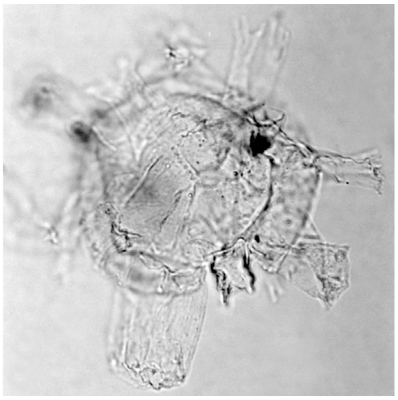
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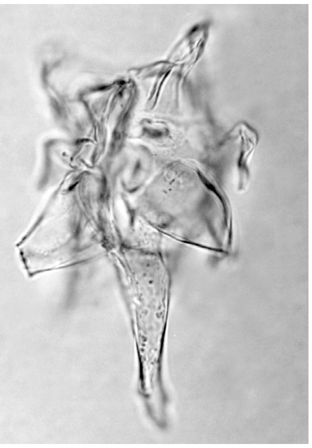
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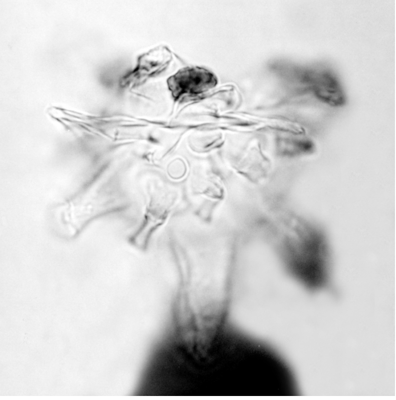
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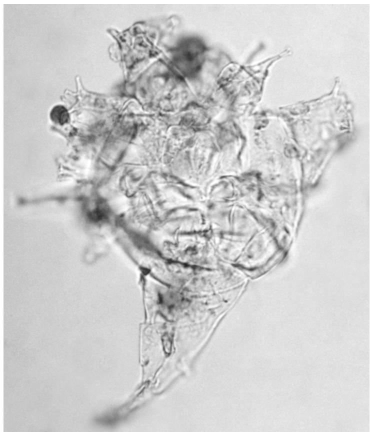
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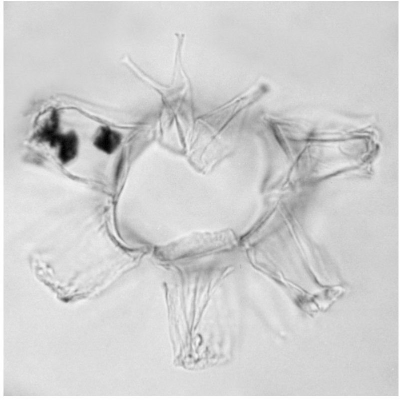
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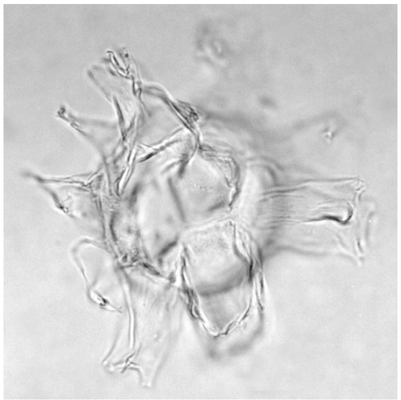
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Paleocene–lower Eocene records from other regions. A schematic overview of the *Apectodinium* record, along with other dinocyst bioevents of possible global significance, from selected locations in the Northern and Southern Hemispheres is shown in Figure 7.

In the Northern Hemisphere, the best calibrated dinocyst records currently come from the North Sea Basin and the Tethys. From the North Sea Basin, information of dinocyst assemblages is taken from several upper Paleocene–lower Eocene studies (e.g., Heilmann-Clausen, 1985; Powell, 1992; Bujak and Mudge, 1994; Mudge and Bujak, 1996; Powell et al., 1996; Bujak and Brinkhuis, 1998). For the Tethys, the results from Elles and Aktumsuk are presented, along with information from an upper Paleocene–lower Eocene succession in Austria (Egger et al., 2000; Heilmann-Clausen and Egger, 2000; Crouch et al., 2001). In addition, dinocyst information is taken from a section in northern Kazakhstan (Iakovleva et al., 2001) that is located in the Turgay Strait (Fig. 1). During the Paleogene this seaway intermittently connected the Tethyan Basin and Boreal Arctic Sea-North Sea Basin (e.g., Benyamovsky et al., 1991). For the Southern Hemisphere, selected dinocyst information is taken from an upper Paleocene–lower Eocene succession in New Zealand (Crouch, 2001).

Lower latitudes

As established by Brinkhuis et al. (1994), and further documented in this paper and other recent studies (Bujak and Brinkhuis, 1998; Egger et al., 2000; Iakovleva et al., 2001), the earliest appearance of *Apectodinium* was in lower latitudes during the mid Paleocene. Well-correlated dinocyst records from these latitudes are currently restricted to the Tethys, although high percentages of *Apectodinium* have been recorded in upper Paleocene sections from other equatorial regions, including northern Africa (Jan du Chêne and Adediran, 1984), Pakistan (Köthe, 1988) and U.S. Gulf Coast (Harrington and Kemp, 2001).

At lower latitudes, the relative abundance of *Apectodinium* can be frequent to superabundant prior to and after the intense warming of the IETM (Fig. 7). At present it appears that the IETM at lower latitudes was characterized by high percentages of *Apectodinium,* although it may not always have dominated dinocyst assemblages. Moreover, other thermophilic genera, most likely dinoflagellates with autotrophic lifestyles (e.g., the *Kenleyia* complex), may have been a common component of assemblages during the IETM. Recent studies indicate that SSTs did not change markedly during the late Paleocene–early Eocene in equatorial regions (Lu et al., 1998; Thomas et al., 1999), which suggests that fluctuations in *Apectodinium* abundance in the Tethys may have been more intricately related to surface water conditions, including availability of nutrients, enhanced runoff and/or other specific oceanic conditions, rather than changes in SST.

Mid to high latitudes

Apectodinium has been recorded from upper Paleocene sediments at mid to high latitudes (North Sea Basin), although these occurrences appear to have been relatively short-lived and *Apectodinium* did not dominate dinocyst assemblages (Powell et al., 1996; Bujak and Brinkhuis, 1998). Further research is needed to ascertain whether the timing of *Apectodinium* incursions in the North Sea Basin during the late Paleocene (lower part of calcareous nannoplankton Zone NP8 and close to the NP8-NP9 zonal boundary; Fig. 7) can be recognized in other mid to high latitude regions. The relatively high percentage of *Apectodinium* (~28%) during the upper Paleocene at northern Kazakhstan (Fig. 7) suggests that the Turgay Strait was connected to the Tethyan Basin at this time (Iakovleva et al., 2001).

At present, the IETM is characterized at mid to high latitudes by the sudden appearance of *Apectodinium*-dominated assemblages. Subsequent to the IETM, the relative abundance of *Apectodinium* decreased at mid to high latitudes. However, additional *Apectodinium* acmes have been recorded during the lower Eocene in both Hemispheres (Fig. 7) and further research is needed to establish if these acmes were also synchronous on a global scale.

Correlation between lower latitude and mid to high latitudes

The frequent to superabundant presence of *Apectodinium* throughout the upper Paleocene and lower Eocene in equatorial regions makes it difficult to correlate *Apectodinium* acmes between lower latitudes and mid to high latitudes. However, cor-

Plate 2. **1:** *Deflandrea denticulaa.* Sample EL76 (~21.8 m), Slide 2 (W28/0). Elles section. Overall dimensions ~52 µm by 104 µm. **2:** *Cerodinium depressum.* Sample EL171 (~42.74 m), Slide 1 (O33/3). Elles section. Overall dimensions ~58 µm by 75 µm. **3:** *Homotryblium pallidum* Sample EL59 (~18.4 m), Slide 1 (P13/1). Elles section. Overall dimensions ~87 µm by 50 µm. **4:** *Hystrichokolpoma* sp. cf. *H. rigaudiae.* Sample EL136 (~33.43 m), Slide 1 (S19/0). Elles section. Overall dimensions ~100 µm by 88 µm. **5:** *Hystrichokolpoma* sp. cf. *H. granulatum.* Sample EL175 (~43.29 m), Slide 1 (P16/0). Elles section. Overall dimensions ~87 µm by 77 µm. **6:** *Hystrichokolpoma* sp. cf. *H. granulatum.* Sample EL152 (~37.38 m), Slide 1 (Q24/0). Elles section. Overall dimensions ~71 µm by 75 µm. **7:** *Hystrichokolpoma* sp. cf. *H. cinctum.* Sample AM20, Slide 1 (G34/0). Aktumsuk section. Overall dimensions ~50 µm by 80 µm. **8** and **9:** *Hystrichokolpoma* sp. cf. *H. cinctum.* Sample AM14, Slide 1a (T24/0). Aktumsuk section. Overall dimensions ~58 µm by 55 µm. **10:** *Hystrichokolpoma rigaudiae.* Sample AM16, Slide 1 (J30/2). Aktumsuk section. Overall dimensions ~75 µm by 92 µm. **11:** *Hystrichokolpoma* sp. cf. *H. salacium.* Sample AM17, Slide 2 (V26/3). Aktumsuk section. Overall dimensions ~73 µm by 65 µm. **12:** *Hystrichokolpoma* sp. cf. *H. salacium.* Sample AM19, Slide 1 (S30/2). Aktumsuk section. Overall dimensions ~60 µm by 60 µm.

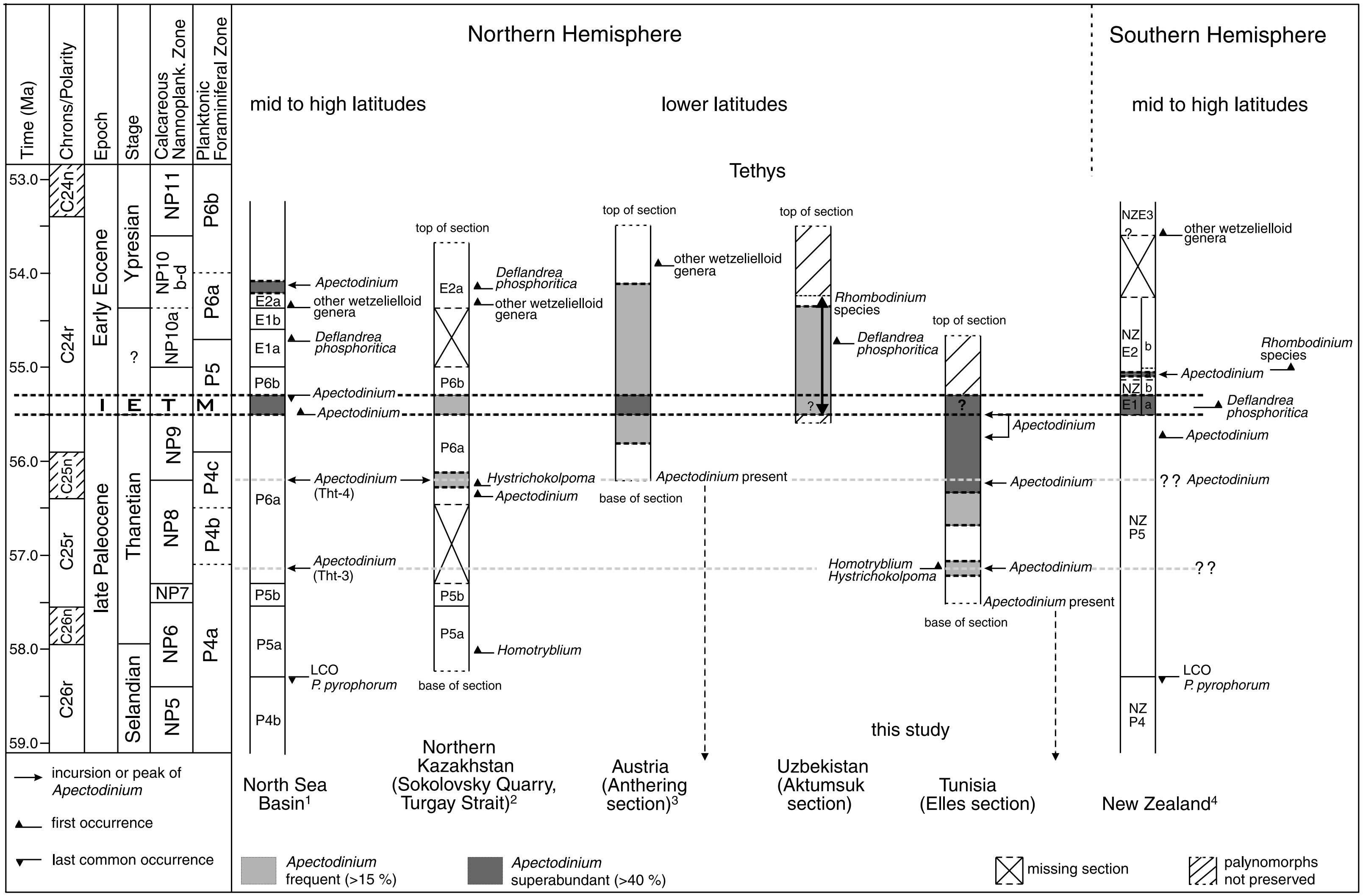

Figure 7. Global overview of the late Paleocene–early Eocene distribution and abundance of *Apectodinium,* and other selected dinocyst bioevents, from five Northern Hemisphere sites and one Southern Hemisphere site. Dashed line shows the position and duration of the initial Eocene thermal maximum (IETM). International chronology comes from Berggren et al. (1995), Berggren and Aubry (1998) and Aubry (2000). Dark grey color represents *Apectodinium* abundance >40% of dinocyst assemblage; light grey color represents *Apectodinium* abundance generally >15% of dinocyst assemblage. References: 1—Powell, 1992; Bujak and Mudge, 1994; Mudge and Bujak, 1996; Powell et al., 1996; Bujak and Brinkhuis, 1998. 2—Iakovleva et al., 2001. 3—Egger et al., 2000; Heilmann-Clausen and Egger, 2000; Crouch et al., 2001. 4—Crouch, 2000.

relation may be possible by further examination of intervals at lower latitudes where *Apectodinium* abundance increases relatively, and comparing this timing with incursions of *Apectodinium* into mid to high latitudes. One such example is the possible correlation between peaks in *Apectodinium* at the Elles section and incursions of *Apectodinium* into the North Sea Basin during the lower part of calcareous nannoplankton Zone NP8 and in close proximity to the NP8-NP9 zonal boundary (Fig. 7).

Correlation between mid to high latitudes in the Northern and Southern Hemispheres is potentially less complicated given that *Apectodinium*-dominated assemblages occur at specific horizons and are separated by intervals where *Apectodinium* may be absent or rare. The best example of this is the *Apectodinium* acme associated with the IETM, which at present is the most significant and globally synchronous dinocyst bioevent that occurred during the late Paleocene–early Eocene at mid to high latitudes. The presence of additional dinocyst taxa, which are confined to particular intervals within *Apectodinium*-dominated assemblages, offer the potential for further correlation between mid to high latitudes in both Hemispheres.

Environmental conditions

A special set of environmental conditions, notably different to the “normal background setting” of the upper Paleocene–lower Eocene, must have occurred at various times and locations to allow *Apectodinium* to dominate the dinocyst assemblages. Indeed, the character of the *Apectodinium* acme associated with the IETM suggests it acted as an opportunistic genus and was able to take advantage of the prevailing ecosystem better than other dinoflagellates. It is worth noting that the typical environment for *Apectodinium* was in lower latitudes, where it comprised a regular component of dinocyst assemblages. The genus was frequent to superabundant in these regions throughout the upper Paleocene–lower Eocene, implying that these “special” environmental conditions occurred more frequently in warmer water settings.

We suggest that *Apectodinium* was able to migrate into higher latitudes when SSTs were suitably warm, and that a marked increase in SST (such as at the IETM) was a crucial environmental factor controlling the occurrence of *Apectodinium* “blooms” in these regions. Moreover, it appears that intensification of biogeochemical feedbacks, such as chemical weathering, precipitation and runoff, during periods of intense warming may have resulted in enhanced delivery of nutrients to (marginal) ocean surface waters (Zachos and Dickens, 2000; Crouch et al., 2003; Ravizza et al., 2001). Intervals of abundant *Apectodinium* recognized at Tawanui, New Zealand (Crouch et al., 2003) and Elles, Tunisia (Fig. 4) appear to have occurred during phases of enhanced terrigenous input, increased runoff and elevated kaolinite percentages. This delivery of nutrients may have allowed primary productivity to increase and altered surface water conditions (e.g., freshwater lenses and stratified water masses).

Recent studies in different Hemispheres across the P-E transition suggest that nutrient availability in surface waters may have remained elevated subsequent to the IETM. In New Zealand, material derived from terrigenous sources remained elevated after the IETM (Crouch, 2001). Similarly, high concentrations of diatoms continued in the North Sea Basin above the IETM (Bujak and Brinkhuis, 1998). However, in both regions *Apectodinium*-dominated assemblages were replaced, near the end of the IETM, by a high abundance of other probable heterotrophic dinocysts, primarily taxa assignable to *Deflandrea* and *Cerodinium.* These dinocyst genera may be indicative of slightly less warm SSTs (Bujak and Brinkhuis, 1998; Crouch, 2001).

In summary, it appears that the principal environmental control on the presence and distribution of *Apectodinium* was warm SSTs. However, during intervals of *Apectodinium* “blooms” the crucial environmental parameters probably involved even higher SSTs and the interaction of this with the availability of nutrients, enhanced runoff and/or other “special” oceanic conditions (e.g., stratified water masses).

CONCLUSIONS

To further understand the distribution and abundance of *Apectodinium* through space and time, we have studied dinocyst records from two well-calibrated Paleogene successions in the Tethys. The combined records at Elles, Tunisia, and Aktumsuk, Uzbekistan, span the late Paleocene (calcareous nannoplankton Zone NP7/8 and planktonic foraminiferal Subzone P4a) to early Eocene (calcareous nannoplankton Zone NP10 and planktonic foraminiferal Zone P6). The main findings are:

1. *Apectodinium* was present in the southern Tethys by planktonic foraminiferal Subzone P4a, confirming earlier findings that this genus first evolved in lower latitudes.
2. *Apectodinium* abundance increased within planktonic foraminiferal Subzone P4b/c and remained a frequent to superabundant component of assemblages until the early Eocene (lower part of planktonic foraminiferal Zone P6).
3. At Elles, *Apectodinium*-dominated assemblages were present at the base of a ~2.7 m clay layer, which is thought to indicate the onset of the IETM. *Apectodinium* was abundant during the IETM at Aktumsuk, although percentages are generally lower than at Elles.
4. For the first time we recognize specimens assignable to *Apectodinium* that contain an archeopyle formation involving two plates (2a and 4″), rather than the standard 2a quadra archeopyle.

The Elles and Aktumsuk records have been compared to several well-correlated upper Paleocene–lower Eocene dinocyst records in other regions, to begin to develop a more detailed spatial and temporal overview of the distribution of *Apectodinium.* Our main observations are:

1. *Apectodinium* first appeared in lower latitudes and was frequent to superabundant during the late Paleocene and early Eocene. The IETM at lower latitudes was characterized by high percentages of *Apectodinium,* although it may not always have

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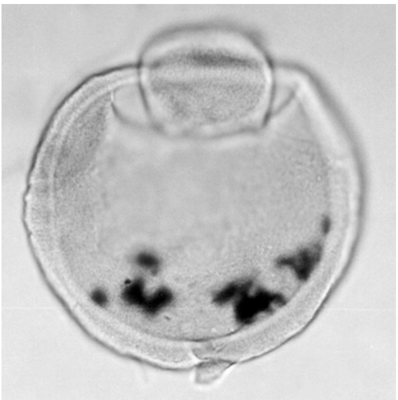

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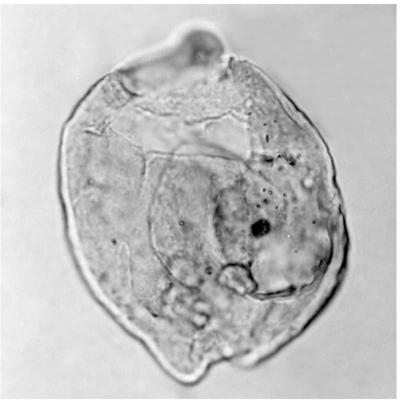

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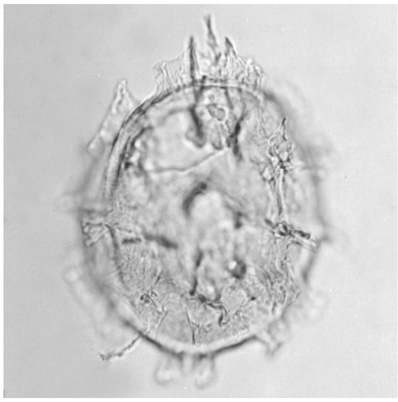

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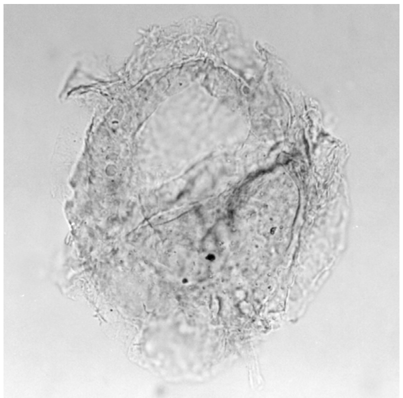

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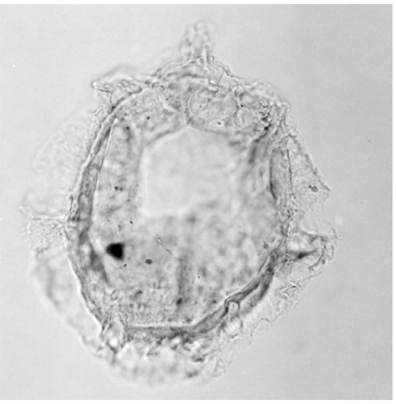

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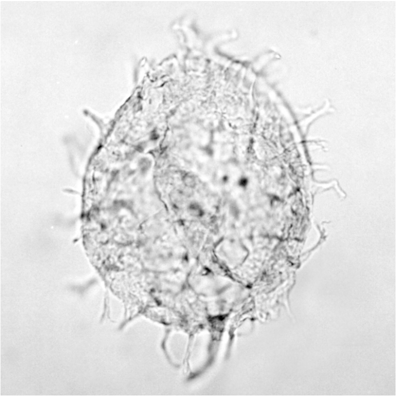

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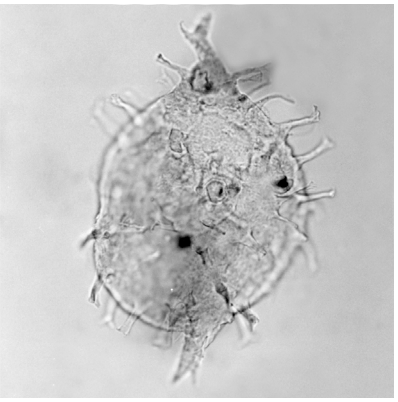

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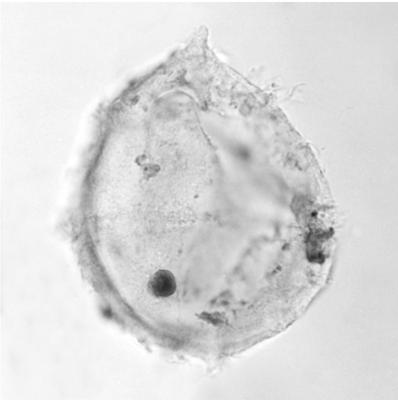

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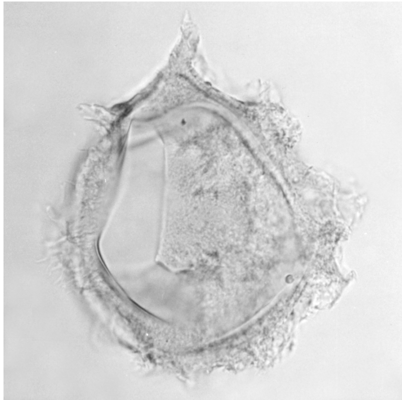

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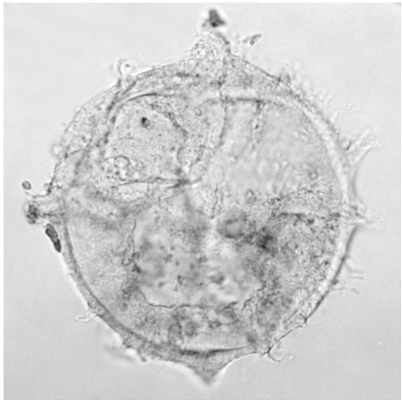

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dominated assemblages. Other dinocyst genera with thermophilic preferences may have also been abundant during the IETM.

2. *Apectodinium* sporadically occurred at mid to high latitudes during the late Paleocene, although incursions are geologically brief and *Apectodinium* was not dominant. The IETM at mid to high latitudes was characterized by *Apectodinium*-dominated assemblages. Additional *Apectodinium* acmes occurred during the early Eocene, however as yet it is unclear if these are globally isochronous.

3. Intervals of *Apectodinium*-dominated assemblages are indicative of environmental conditions that were markedly different to "normal background settings" of the late Paleocene–early Eocene. We suggest SST was the main control on their distribution since *Apectodinium* acmes at mid to high latitudes seem to have occurred during intervals of highest SSTs, such as the IETM. *Apectodinium* "blooms" were probably also intricately linked to enhanced runoff and increased delivery of nutrients to surface waters. This may have been a result of intensification of the weathering cycle, and other possible specific oceanic conditions such as stratified water masses.

ACKNOWLEDGMENTS

Natasja Welters is thanked for palynological processing of samples from the Elles and Aktumsuk sections. We thank Jamie Powell and Henrik Nøhr-Hansen for constructive and helpful comments on the manuscript. This is NSG publication number 20020404.

APPENDIX. DINOFLAGELLATE CYST SPECIES LIST AND TAXONOMIC NOTES

The generic allocation of taxa follows that cited in Williams et al. (1998) unless otherwise stated. Illustrated taxa are followed by plate and figure references in brackets. Some new taxa have been recorded and they are discussed briefly. These new taxa are not formally described. Notes on certain genera are also provided.

Adnatosphaeridium multispinosum (Plate 1, Figure 6)
Apectodinium spp. (Plate 1, Figures 1–5)

Remarks: A variety of *Apectodinium* morphotypes have been recognized and several typical specimens are illustrated. Species identified included *A. homomorphum, A. hypercanthum, A. parvum* and *A. quinquelatum. Apectodinium augustum* (an extreme morphotype with well-developed lateral and antapical horns) was not recorded. Several specimens, otherwise assignable to *Apectodinium,* show an archeopyle that involves two plates, the 2a and 4″ plates (Plate 1, Figures 1–3).

Areoligera senonensis group (Plate 1, Figures 7 and 8)
Carpatella? sp. A (Plate 3, Figure 3)

Remarks: The specimens encountered in this study broadly resemble *Carpatella cornuta.* The development of an apical horn is absent in some forms and, hence, they are tentatively assigned to *Carpatella. Carpatella cornuta* is typically known from lower Danian sediments (Damassa, 1988) and may have also had a preference for generally warm water settings (Brinkhuis and Zachariasse, 1988; Brinkhuis et al., 1998).

Cerodinium depressum (Plate 2, Figure 2)
Cordosphaeridium spp.
Cribroperidinium sp. A (Plate 1, Figures 10 and 11)

Remarks: Cysts assignable to *Cribroperidinium* sp. A are small, proximate and subspherical in shape. A small apical horn is present. The archeopyle is precingular and formed by the loss of 3″. The periphragm is strongly granulate, forming an almost microreticulum, and paratabulation is discernible by perforated septa.

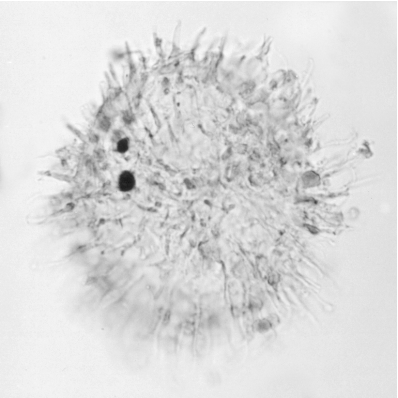
Deflandrea denticulata (Plate 2, Figure 1)
Deflandrea phosphoritica (Plate 1, Figure 12)
Deflandrea oebisfeldensis
Diphyes colligerum (Plate 1, Figure 9)
Fibrocysta spp.
Glaphyrocysta spp.
Homotryblium pallidum (Plate 2, Figure 3)
Homotryblium tenuispinosum
Hystrichokolpoma sp. cf. *H. cinctum* (Plate 2, Figures 7–9)

Remarks: Cysts assignable to *Hystrichokolpoma* sp. cf. *H. cinctum* differ from *Hystrichokolpoma cinctum* by being smaller and by having granules developed on the processes.

Hystrichokolpoma sp. cf. *H. granulatum* (Plate 2, Figures 5 and 6)

Remarks: Cysts assignable to *Hystrichokolpoma* sp. cf. *H. granulatum* closely resemble *Hystrichokolpoma granulatum,*

Plate 3. **1:** *Kallosphaeridium yorubaense.* Sample EL123 (~30.04 m), Slide 1 (R18/0). Elles section. Overall dimensions ~54 µm by 53 µm. **2:** *Kallosphaeridium yorubaense.* Sample AM19, Slide 1 (U34/1). Aktumsuk section. Overall dimensions ~60 µm by 65 µm. **3.** *Carpatella?* sp. A. Sample AM17, Slide 1 (F23/2). Aktumsuk section. Overall dimensions ~80 µm by 80 µm. **4:** *Kenleyia* complex. Sample EL111 (~26.92 m), Slide 1 (N32/0). Elles section. Overall dimensions ~55 µm by 70 µm. **5:** *Kenleyia* complex. Sample EL166 (~42.21 m), Slide 1 (W19/2). Elles section. Overall dimensions ~75 µm by 93 µm. **6:** *Kenleyia* complex. Sample EL145 (~35.75 m), Slide 1 (X26/0). Elles section. Overall dimensions ~80 µm by 95 µm. **7:** *Kenleyia* complex. Sample EL145 (~35.75 m), Slide 1 (F28/0). Elles section. Overall dimensions ~82 µm by 95 µm. **8:** *Kenleyia* complex. Sample EL123 (~30.04 m), Slide 1 (J16/4). Elles section. Overall dimensions ~65 µm by 85 µm. **9:** *Kenleyia* complex. Sample EL162 (~41.8 m), Slide 1 (R21/0). Elles section. Overall dimensions ~72 µm by 112 µm. **10:** *Kenleyia* complex. Sample AM15, Slide 1 (O28/4). Aktumsuk section. Overall dimensions ~75 µm by 90 µm. **11:** *Kenleyia* complex. Sample AM15, Slide 1 (Q22/3). Aktumsuk section. Overall dimensions ~85 µm by 100 µm. **12:** *Kenleyia* complex. Sample AM16, Slide 1a (T18/0). Aktumsuk section. Overall dimensions ~86 µm by 92 µm.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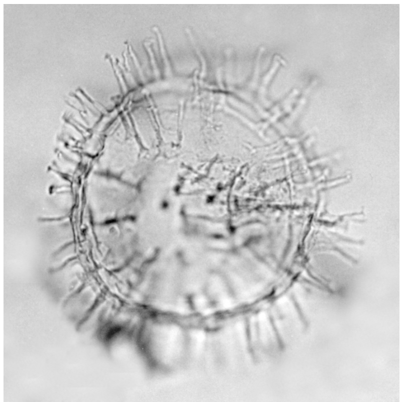
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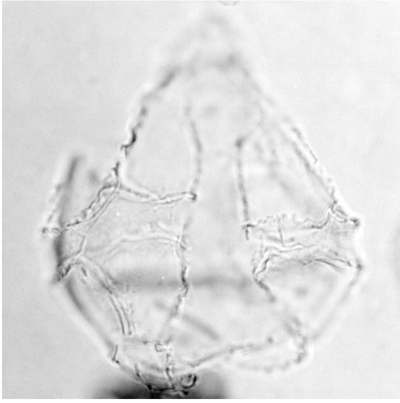
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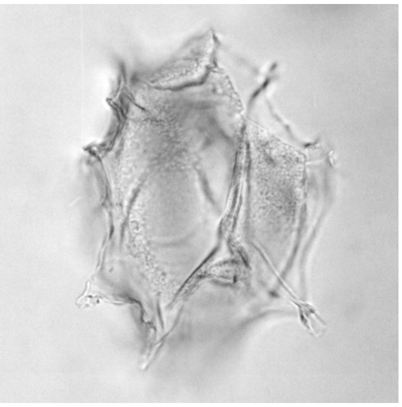
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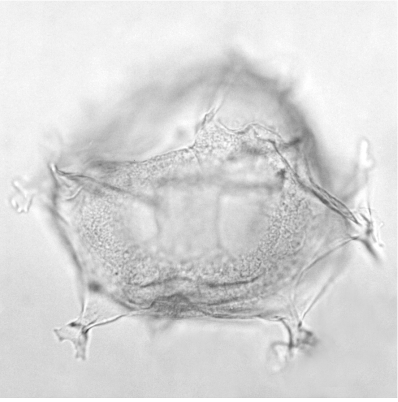
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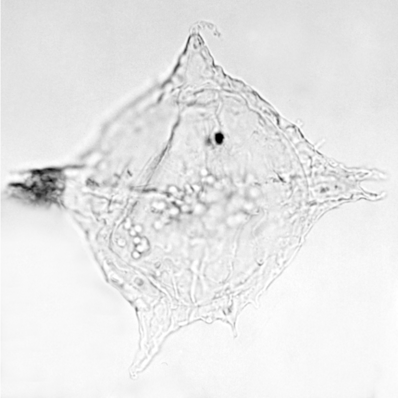
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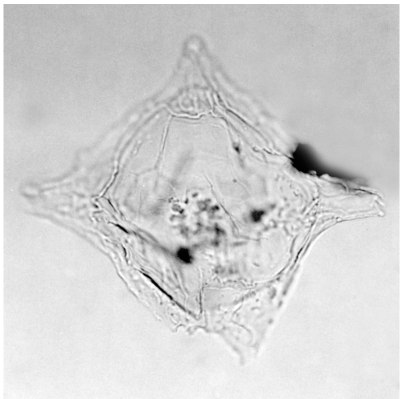
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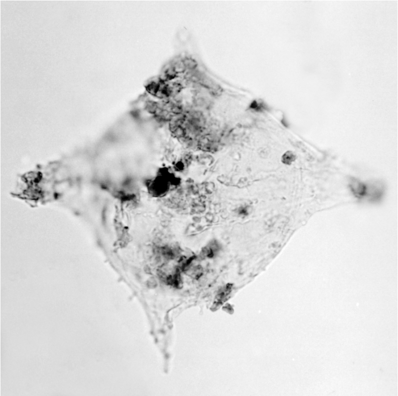
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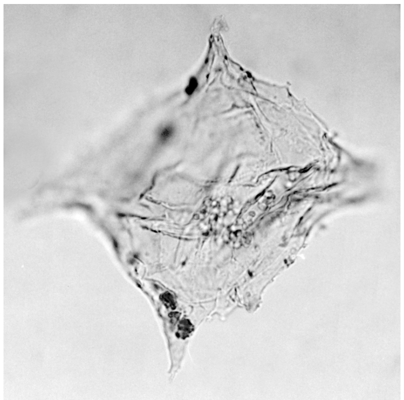
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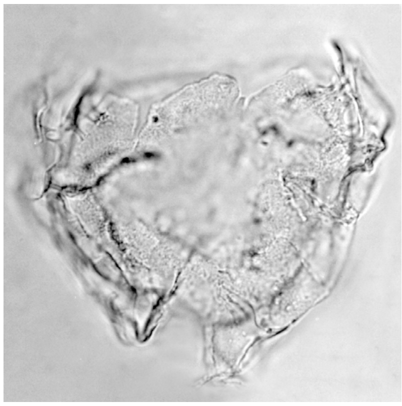
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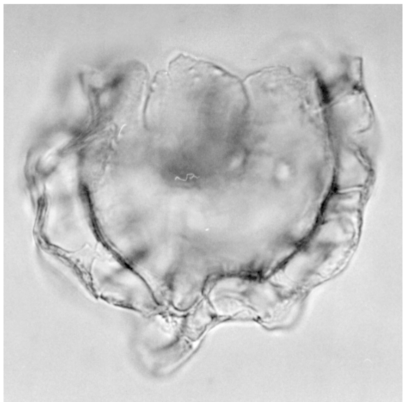
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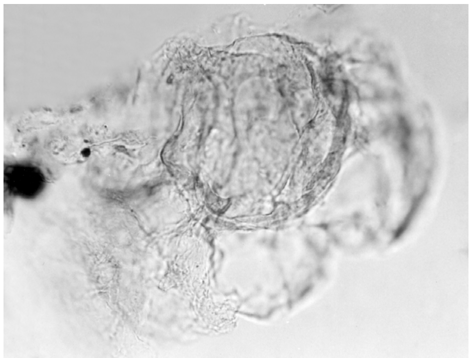
12

although they appear to be thinner walled and are generally poorly preserved making confident assignment to *Hystrichokolpoma granulatum* difficult.

Hystrichokolpoma rigaudiae (Plate 2, Figure 10)
Hystrichokolpoma sp. cf. *H. rigaudiae* (Plate 2, Figure 4)

Remarks: Cysts assignable to *Hystrichokolpoma* sp. cf. *H. rigaudiae* broadly resemble *Hystrichokolpoma rigaudiae,* but differ in having distinctly different process terminations. In addition, the antapical process is not as well developed.

Hystrichokolpoma salacium (Plate 2, Figures 11 and 12)
Hystrichokolpoma spp. (pars.)

Remarks: This includes all other taxa assignable to *Hystrichokolpoma.*

Kallosphaeridium yorubaense (Plate 3, Figures 1 and 2)
Kenleyia complex (Plate 3, Figures 4–12)

Remarks: Cysts assignable to the *Kenleyia* complex exhibit a wide morphological variation and some of the main forms are illustrated. The cysts are characterized by having apical and antapical protrusions and a precingular (3″) archeopyle. There is substantial variation in the development of the periphragm, ranging from nearly smooth to the development of processes, spines and membranes. Some of the more extreme forms appear to cross generic boundaries, such as *Cordosphaeridium, Fibrocysta,* and *Muratodinium.* For the purpose of this study all of these morphological variations are placed in the *Kenleyia* complex.

Membranosphaera? sp. B De Coninck, 1975
Operculodinium severinii (Plate 4, Figure 1)
Operculodinium spp. (pars.)

Remarks: This includes all other taxa assignable to *Operculodinium.*

Palaeocystodinium lidiae
Pentadinium sp. cf. *P. goniferum* (Plate 4, Figures 4 and 5)
Phelodinium spp.
Phthanoperidinium crenulatum (Plate 4, Figure 3)
Polysphaeridium spp. (Plate 4, Figure 2)
Rhombodinium spp. (Plate 4, Figures 6–9)
Senegalinium spp.
Senoniasphaera? spp. (Plate 4, Figures 10 and 11)

Remarks: Specimens assigned here to *Senoniasphaera?* spp. closely compare with Upper Cretaceous morphotypes of *Senoniasphaera rotundata* and are possibly reworked in to Eocene sediments at Aktumsuk. Alternatively, they may represent a previously undescribed Eocene species of *Senoniasphaera.*

Spinidinium spp.
Spiniferites cornutus
Spiniferites septatus
Spiniferites spp. (pars.)

Remarks: This includes all other taxa assignable to *Spiniferites.*
Thalassiphora velata (Plate 4, Figure 12)

REFERENCES CITED

Aubry, M.-P., 1998, Early Paleogene calcareous nannoplankton evolution: A tale of climatic amelioration, *in* Aubry, M.-P., et al., eds., Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records: New York, Columbia University Press, p. 158–203.

Aubry, M.-P., 2000, Where should the Global Stratotype Section and Point (GSSP) for the Paleocene-Eocene boundary be located?: Bulletin de la Société Géologique de France, v. 171, p. 461–476.

Benyamovsky, V.N., Levina, A.P., and Pronin, V.G., 1991, Lower Eocene sediments of the Turgay Passage: Izvestiya Vysshikh Uchebnykh Zavedeniy, Geologia i Razvedka, v. 7, p. 3–15.

Berggren, W.A., and Aubry, M.-P., 1998, The Paleocene–Eocene Epoch/Series boundary: Chronostratigraphic framework and estimated geochronology, *in* Aubry, M.-P., et al., eds., Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records: New York, Columbia University Press, p. 18–36.

Berggren, W.A., Kent, D.V., Swisher, C.C., and Aubry, M.-P., 1995, A revised Cenozoic chronology and chronostratigraphy, *in* Berggren, W.A., et al., eds., Geochronology, time scales, and global stratigraphic correlation: SEPM (Society for Sedimentary Geology) Special Publication 54, p. 129–212.

Berggren, W.A., Lucas, S., and Aubry, M.-P., 1998, Late Paleocene–early Eocene climatic and biotic evolution: An overview, *in* Aubry, M.-P., et al., eds., Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records: New York, Columbia University Press, p. 1–17.

Bolle, M.-P., Adatte, T., Keller, G., Von Salis, K., and Burns, S., 1999, The Paleocene–Eocene transition in the southern Tethys (Tunisia): Climatic and environmental fluctuations: Bulletin de la Société Géologique de France, v. 170, p. 661–680.

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Plate 4. **1:** *Operculodinium severinii.* Sample AM15, Slide 1 (P23/1). Aktumsuk section. Overall dimensions ~80 µm by 85 µm. **2:** *Polysphaeridium* sp. Sample EL59 (~18.4 m), Slide 1 (J24/0). Elles section. Overall dimensions ~70 µm by 72 µm. **3:** *Phthanoperidinium crenulatum.* Sample AM16, Slide 1 (R27/2). Aktumsuk section. Overall dimensions ~54 µm by 63 µm. **4:** *Pentadinium* sp. cf. *P. goniferum.* Sample AM17, Slide 1 (R28/4). Aktumsuk section. Overall dimensions ~65 µm by 83 µm. **5:** *Pentadinium* sp. cf. *P. goniferum.* Sample AM17, Slide 2 (L28/0). Aktumsuk section. Overall dimensions ~100 µm by 90 µm. **6:** *Rhombodinium* sp. Sample AM17, Slide 2 (R37/0). Aktumsuk section. Overall dimensions ~93 µm by 88 µm. **7:** *Rhombodinium* sp. Sample AM18, Slide 1 (W18/2). Aktumsuk section. Overall dimensions ~95 µm by 86 µm. **8:** *Rhombodinium* sp. Sample AM15, Slide 1 (M26/0). Aktumsuk section. Overall dimensions ~98 µm by 92 µm. **9:** *Rhombodinium* sp. Sample AM16, Slide 1 (K26/2). Aktumsuk section. Overall dimensions ~96 µm by 95 µm. **10:** *Senoniasphaera?* sp. Sample AM19, Slide 1 (X20/2). Aktumsuk section. Overall dimensions ~72 µm by 66 µm. **11:** *Senoniasphaera?* sp. Sample AM21, Slide 1 (P20/0). Aktumsuk section. Overall dimensions ~65 µm by 60 µm. **12:** *Thalassiphora velata.* Sample EL111 (~26.92 m), Slide 1 (U34/4). Elles section. Overall dimensions ~125 µm by 100 µm.

Bolle, M.-P., Pardo, A., Hinrichs, K.-U., Adatte, T., Von Salis, K., Burns, S., Keller, G., and Muzylöv, N., 2000a, The Paleocene–Eocene transition in the marginal northeastern Tethys (Kazakhstan and Uzbekistan): International Journal of Earth Sciences, v. 89, p. 390–414.

Bolle, M.-P., Pardo, A., Adatte, T., Tantawy, A.A., Hinrichs, K., Von Salis, K., and Burns, S., 2000b, Climatic evolution on the southern and northern margins of the Tethys from the Paleocene to early Eocene: GFF, v. 122, p. 31–32.

Bralower, T.J., Zachos, J.C., Thomas, E., Parrow, M., Paull, C.K., Kelly, D.C., Premoli Silva, I., Sliter, W.V., and Lohmann, K.C., 1995, Late Paleocene to Eocene paleoceanography of the equatorial Pacific Ocean: Stable isotopes recorded at Ocean Drilling Program Site 865, Allison Guyot: Paleoceanography, v. 10, p. 841–865.

Brinkhuis, H., 1994, Late Eocene to early Oligocene dinoflagellate cysts from the Priabonian type-area (Northeast Italy): Biostratigraphy and paleoenvironmental interpretation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 107, p. 121–163.

Brinkhuis, H., and Leereveld, H., 1988, Dinoflagellate cysts from the Cretaceous–Tertiary boundary sequence of El Kef, northwest Tunisia: Review of Palaeobotany and Palynology, v. 56, p. 5–19.

Brinkhuis, H., and Zachariasse, W.J., 1988, Dinoflagellate cysts, sea-level changes, and planktonic foraminifera across the Cretaceous–Tertiary boundary at El Haria, northwest Tunisia: Marine Micropaleontology, v. 13, p. 153–191.

Brinkhuis, H., Romein, A.J.T., Smit, J., and Zachariasse, W.J., 1994, Danian–Selandian dinoflagellate cysts from lower latitudes with special reference to the El Kef section, northwest Tunisia: GFF, v. 116, p. 46–48.

Brinkhuis, H., Bujak, J.P., Smit, J., Versteegh, G.J.M., and Visscher, H., 1998, Dinoflagellate-based sea surface temperature reconstructions across the Cretaceous–Tertiary boundary: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 141, p. 67–83.

Bujak, J., and Mudge, D., 1994, A high-resolution North Sea dinocyst zonation: Journal of the Geological Society of London, v. 151, p. 449–462.

Bujak, J., and Brinkhuis, H., 1998, Global warming and dinocyst changes across the Paleocene–Eocene epoch boundary, *in* Aubry, M.-P., et al., eds., Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records: New York, Columbia University Press, p. 277–295.

Bybell, L.M., Gibson, T.G., Heilmann-Clausen, C., and Zachos, J.C., 2001, Events associated with the late Paleocene thermal maximum in the northeastern U.S., *in* Ash, A.W., and Wing, S.L., eds., Climate and biota of the early Paleogene: International Meeting July 3–8, 2001, Northwest College, Powell, Wyoming, USA, Abstract volume, p. 18.

Clyde, W.C., and Gingerich, P.D., 1998, Mammalian community response to the latest Paleocene thermal maximum: An isotaphonomic study in the northern Bighorn basin, Wyoming: Geology, v. 26, p. 1011–1014.

Costa, L.I., and Downie, C., 1976, The distribution of the dinoflagellate *Wetzeliella* in the Paleogene of northwestern Europe: Palaeontology, v. 19, p. 591–614.

Crouch, E.M., 2001, Environmental Change at the time of the Paleocene–Eocene biotic turnover [Ph.D. thesis]: Utrecht, Netherlands, Utrecht University, Laboratory of Palaeobotany and Palynology Contributions Series, v. 14, 216 p.

Crouch, E.M., Dickens, G.R., Brinkhuis, H., Aubry, M.-P., Hollis, C.J., Rogers, K.M., and Visscher, H., The *Apectodinium* acme and terrestrial discharge during the Paleocene-Eocene thermal maximum: New palynological, geochemical and calcareous nannoplankton observations at Tawanui, New Zealand: Palaeogeography, Palaeoclimatalogy, Palaeoecology, in press.

Crouch, E.M., Heilmann-Clausen, C., Brinkhuis, H., Morgans, H.E.G., Rogers, K.M., Egger, H., and Schmitz, B., 2001, Global dinoflagellate event associated with the late Paleocene thermal maximum: Geology, v. 29, p. 315–318.

Damassa, S.P., 1988, *Carpatella cornuta* Grigornovich 1969 (Dinophyceae): A member of the Aptiana-Vetriosum complex: Palynology, v. 12, p. 167–177.

De Coninck, J., 1975, Microfossiles à paroi organique de l'Ypresian de Bassin Belge: Professional Paper, Service Géologique de Belgique, v. 12, 165 p.

Dickens, G.R., 2000, Methane oxidation during the late Paleocene thermal maximum: Bulletin de la Société Géologique de France, v. 171, p. 37–49.

Dickens, G.R., 2001, Carbon addition and removal during the late Paleocene thermal maximum: Basic theory with a preliminary treatment of the isotope record at Ocean Drilling Program Site 1051, Blake Nose, *in* Kroon, D., et al., eds., Western North Atlantic Paleogene and Cretaceous palaeoceanography: Geological Society [London] Special Publication 183, p. 293–305.

Egger, H., Heilmann-Clausen, C., and Schmitz, B., 2000, The Paleocene–Eocene boundary interval of a Tethyan deep-sea section and its correlation with the North Sea basin: Bulletin de la Société Géologique de France, v. 171, p. 207–216.

Fechner, G.G., and Mohr, B., 1986, Zur tertiören Dinoflagellaten-Gattung *Carpatella* Grigorovich 1969 (Gonyaulacystaceae): Paläontologische Zeitschrift, v. 60, p. 181–188.

Fensome, R.A., Taylor, F.J.R., Norris, G., Sarjeant, W.A.S., Wharton, D.I., and Williams, G.L., 1993, A classification of fossil and living dinoflagellates: Micropaleontology, Special Publication, v. 7, p. 1–351.

Gavrilov, Y.O., and Muzylöv, N.G., 1991, The geochemistry of sapropelic interbeds in the Paleogene of the Central Caucasus: Lithology and Mineral Resources, v. 26, p. 485–590.

Gavrilov, Y.O., Kodina, L.A., Lubchenko, I.Y., and Muzylöv, N.G., 1997, The late Paleocene anoxic event in epicontinental seas of Peri-Tethys and formation of the Sapropelite Unit: Sedimentology and geochemistry: Lithology and Mineral Resources, v. 32, p. 427–450.

Haq, B.U., Hardenbol, J., and Vail, P.R., 1988, Mesozoic and Cenozoic chronostratigraphy and cycles of relative sea-level change, *in* Wilgus, C.K., et al., eds., Sea-level changes: An integrated approach: Society of Economic Paleontologists and Mineralogists Special Publication 42, p. 71–108.

Harrington, G.J., and Kemp, S.J., 2001, U.S. Gulf Coast vegetation dynamics during the latest Paleocene: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 167, p. 1–21.

Heilmann-Clausen, C., 1985, Dinoflagellate stratigraphy of the uppermost Danian to Ypresian in the Viborg 1 borehole, central Jylland, Denmark: Danmarks Geologiske Undersøgelse, series A, v. 7, p. 1–69.

Heilmann-Clausen, C., and Egger, H., 2000, The Anthering outcrop (Austria): A key-section for correlation between Tethys and northwestern Europe near the Paleocene–Eocene boundary: GFF, v. 122, p. 69.

Heilmann-Clausen, C., and Schmitz, B., 2000, The late Paleocene thermal maximum δ^{13}C in Denmark?: GFF, v. 122, p. 70.

Iakovleva, A.I., Brinkhuis, H., and Cavagnetto, C., 2001, Late Paleocene–early Eocene dinoflagellate cysts from the Turgay Strait, Kazakhstan: Correlations across ancient seaways: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 172, p. 243–268.

Jan du Chêne, R.E., and Adediran, S.A., 1984, Late Paleocene to early Eocene dinoflagellates from Nigeria: Cahiers de Micropaléontologie, Centre National de la Recherche Scientifique, v. 3, p. 5–38.

Katz, M.E., Pak, D.K., Dickens, G.R., and Miller, K.G., 1999, The source and fate of massive carbon input during the latest Paleocene thermal maximum: Science, v. 286, p. 1531–1533.

Kelly, D.C., Bralower, T.J., Zachos, J.C., Premoli Silva, I., and Thomas, E., 1996, Rapid diversification of planktonic foraminifera in the tropical Pacific (ODP Site 865) during the late Paleocene thermal maximum: Geology, v. 24, p. 423–426.

Kennett, J.P., and Stott, L.D., 1991, Abrupt deep sea warming, paleoceanographic changes and benthic extinctions at the end of the Paleocene: Nature, v. 353, p. 225–229.

Koch, P.L., Zachos, J.C., and Dettmann, D.L., 1995, Stable isotope stratigraphy and paleoclimatology of the Paleogene Bighorn basin (Wyoming, USA): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 115, p. 61–89.

Köthe, A., 1988, Biostratigraphy of the Surghar Range, Salt Range, Sulaiman Range and the Kohat area, Pakistan, according to Jurassic through Paleogene calcareous nannofossils and Paleogene dinoflagellates: Geologisches Jahrbuch, v. B71, p. 3–87.

Lu, G., Adatte, T., Keller, G., and Ortiz, N., 1998, Abrupt climatic, oceanographic, and ecologic changes near the Paleocene–Eocene transition in the deep Tethys basin: The Alademilla section, southern Spain: Eclogae Geologicae Helvetiae, v. 91, p. 293–306.

Mudge, D.C., and Bujak, J.P., 1996, Paleocene biostratigraphy and sequence stratigraphy of the UK central North Sea: Marine and Petroleum Geology, v. 13, p. 295–312.

Norris, R.D., and Röhl, U., 1999, Carbon cycling and chronology of climate warming during the Paleocene–Eocene transition: Nature, v. 401, p. 775–778.

Powell, A.J., 1992, Dinoflagellate cysts of the Tertiary System, *in* Powell, A.J., ed., A stratigraphic index of dinoflagellate cysts: British Micropaleontological Society series, London, Chapman and Hall, p. 155–251.

Powell, A.J., Brinkhuis, H., and Bujak, J.P., 1996, Upper Paleocene–lower Eocene dinoflagellate cyst sequence biostratigraphy of southeast England, *in* Knox, R.W.O'B., et al., eds., Correlation of the early Paleogene in northwest Europe: Geological Society [London] Special Publication 101, p. 145–183.

Ravizza, G., Norris, R.N., and Blusztajn, J., 2001, An osmium isotope excursion associated with the late Paleocene thermal maximum: Evidence of intensified chemical weathering: Paleoceanography, v. 16, p. 155–163.

Robert, C., and Kennett, J.P., 1994, Antarctic subtropical humid episode at the Paleocene–Eocene boundary: Clay-mineral evidence: Geology, v. 22, p. 211–214.

Röhl, U., Bralower, T.J., Norris, R.D., and Wefer, G., 2000, New chronology for the late Paleocene thermal maximum and its environmental implications: Geology, v. 28, p. 927–930.

Scotese, C.P., and Golanka, J., 1992, Paleogeographic Atlas: PALEOMAP progress report 20–0692, Arlington, University of Texas, 34 p.

Smith, A., Smith, D., and Funnel, B., 1994, Atlas of Mesozoic and Cenozoic coastlines: Cambridge, UK, Cambridge University Press, 99 p.

Stott, L.D., Kennett, J.P., Shackleton, N.J., and Corfield, R.M., 1990, The evolution of Antarctic surface waters during the Paleogene: Inferences from stable isotopic composition of planktonic foraminifera, ODP Leg 113, *in* Barker, P.F., et al., eds., Proceedings of the Ocean Drilling Program, Scientific Results: Texas A & M University, College Station, Texas, USA, v. 113, p. 849–864.

Stover, L.E., Brinkhuis, H., Damassa, S.P., de Verteuil, L., Helby, R.J., Monteil, E., Partridge, A.D., Powell, A.J., Riding, J.B., Smelror, M., and Williams, G.L., 1996, Mesozoic–Tertiary dinoflagellates, acritarchs, and prasinophytes, *in* Jansonius, J., and McGregor, D.C., eds., Palynology: Principles and applications: American Association of Stratigraphic Palynologists Foundation, p. 641–750.

Thomas, D.J., Bralower, T.J., and Zachos, J.C., 1999, New evidence for subtropical warming during the late Paleocene thermal maximum: Stable isotope evidence from DSDP Site 527, Walvis Ridge: Paleoceanography, v. 14, p. 561–570.

Thomas, E., 1998, Biogeography of the late Paleocene benthic foraminiferal extinction, *in* Aubry, M.-P., et al., eds., Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records: New York, Columbia University Press, p. 214–243.

Thomas, E., and Shackleton, N.J., 1996, The Paleocene–Eocene benthic foraminiferal extinction and stable isotope anomalies, *in* Knox, R.W.O'B., et al., eds., Correlation of the early Paleogene in northwest Europe: Geological Society [London] Special Publication 101, p. 401–444.

Thomas, E., and Zachos, J.C., 2000, Was the late Paleocene thermal maximum a unique event?: GFF, v. 122, p. 169–170.

Thomas, E., Zachos, J.C., and Bralower, T.J., 2000, Deep-sea environments on a warm Earth: Latest Paleocene–early Eocene, *in* Huber, B.T., et al., eds., Warm climates in Earth history: Cambridge, UK, Cambridge University Press, p. 132–160.

van Mourik, C.A., Brinkhuis, H., and Williams, G.L., 2001, Mid to late Eocene organic-walled dinoflagellate cysts from ODP Leg 171B, offshore Florida, *in* Kroon, D., et al., eds., Western North Atlantic Paleogene and Cretaceous palaeoceanography: Geological Society [London] Special Publication 183, p. 225–251.

Van Steenbergen, A., 1997, Palynological techniques for rock sampling: Utrecht, Netherlands, Laboratory of Palaeobotany and Palynology internal report, 25 p.

Wall, D., Dale, B., Lohmann, G.P., and Smith, W.K., 1977, The environmental and climatic distribution of dinoflagellate cysts in modern marine sediments from regions in the North and South Atlantic Oceans and adjacent seas: Marine Micropaleontology, v. 2, p. 121–200.

Williams, G.L., Lentin, J.K., and Fensome, R.A., 1998, The Lentin and Williams index of fossil dinoflagellates: American Association of Stratigraphic Palynologists Foundation, Dallas, 817 p.

Zachos, J.C., and Dickens, G.R., 2000, An assessment of the biogeochemical feedback response to the climatic and chemical perturbations of the LPTM: GFF, v. 122, p. 188–189.

Zachos, J.C., Stott, L.D., and Lohmann, K.C., 1994, Evolution of early Cenozoic marine temperatures: Paleoceanography, v. 9, p. 353–387.

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