

Calcareous nannofossil assemblage changes from early to middle Eocene in the Levant margin of the Tethys, central Israel

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ABSTRACT – Patterns of change in calcareous nannofossil assemblages during nannozones NP11 to NP16 on the southern Levant margin of the Tethys were observed from sections of early and middle Eocene age sediments of the Avedat Plateau, central Israel. A cooling process following the Early Eocene Climate Optimum (EECO) is supported by several events of biotic change over a 4 Ma interval. The rate of pelagic sedimentation varied from 7.5 at the EECO to 23.6 m Ma⁻¹ at the cooling transition phase. Reduced numbers of discoasters mark the end of the oligotrophic regime within the NP13 nannozone, followed by an increase in nannofossil richness especially marked by *Blackites* and *Chiasmolithus* spp. In the middle part of the cooling process a prominent peak of reworked Paleocene taxa, up to 7% of total taxa, suggests that enhanced current activity caused re-sedimentation on the Levant margin slopes. When stability resumed in the upper part of the NP15–16 interval, *Coccolithus*-type placoliths became rare and *Reticulofenestra*-type forms became dominant. Calcareous nannoplankton response to this gradual cooling became irreversible in the late Palaeogene, but the change was, however, diachronous across the Tethys. *J. Micropalaeontol.* 30(2): 129–139, September 2011.

KEYWORDS: *Eocene, calcareous nannofossils, Levant, EECO, Tethys*

INTRODUCTION

The early Eocene was marked by conditions of extreme Cenozoic warmth including the Early Eocene Climate Optimum (EECO) (Zachos *et al.*, 2008), with a lack of polar-ice, warm tropical climates (Pearson *et al.*, 2009) and low latitudinal temperature gradients (Bijl *et al.*, 2009). Some have suggested that stagnant warm saline waters formed in low latitudes, particularly in the Tethyan realm (Kennett & Stott, 1990). These early Eocene conditions of extreme warmth ended prior to the Ypresian/Lutetian (early/middle Eocene) boundary with the initiation of cooling, especially at high latitudes (Bijl *et al.*, 2009). The early to late Eocene cooling trend is one of the most distinct climatic changes in the Cenozoic and appears to strongly influence the evolution of many microplankton groups (Bown, 2005; Ezard *et al.*, 2011), forming the background for the evolution of many modern life forms, and is particularly well expressed in micropalaeontological studies.

Recent studies have stressed the sensitivity of coccolithophores to environmental change. Many researchers noted their biotic response to the dramatic changes of the early Cenozoic (e.g. Gibbs *et al.*, 2006), hence the growing use of calcareous nannofossils as palaeoclimatic proxies. Agnini *et al.* (2006) tracked the early/middle Eocene transition at Possagno, Italy, and emphasized the rise of clade Noellrhabdaceae as marking the development of a major part of the modern oceanic phytoplankton community during this interval. Agnini *et al.* (2006) also considered the Discoasteraceae acme event, coincident with the EECO, to represent a peak of oligotrophic opportunists during these conditions of extreme warmth. Tremolada & Bralower (2004) showed that the genus *Chiasmolithus* represents cooler and more nutrient-rich water.

Many studies have been carried out at the northern edges of the Tethyan realm (Fig. 1). Payros *et al.* (2006, 2007) established a biomagnetostratigraphical scheme for the Gorrondatxe section in the Pyrenees. Molina *et al.* (2000) and Ortiz *et al.* (2008) have

reviewed the Ypresian/Lutetian boundary in Agost, Spain, noting that the occurrence of *Blackites inflatus* is the most suitable marker event for this interval. These studies and others detail the response of calcareous nannofossils to early Cenozoic palaeoceanography, climatic change and rates of sedimentation. No similar studies have yet been carried out in the eastern Mediterranean Levant region. The current study is aimed at exploring oceanic change in this part of the Tethys, based on significant events in the calcareous nannofossil record, and correlating them to oceanic change elsewhere in the Tethys and beyond.

The Eocene strata of Israel were deposited off-shelf on the slope of the southern part of the Tethyan Ocean (Fig. 1). The typical lithology, divided into four formations, was described by Bendor & Vroman (1963, 1964), and Braun (1967) (Figs 2, 3): the Mor Formation, chalk with chert nodules; the Nizzana Formation of chalk and limestone intercalations; the Horsha Formation, primarily of massive, friable chalk; and the Matred Formation of more indurated chalk intercalated with limestone. Benjamini (1979, 1980) studied field and microfacies relationships among these units as well as the zonal biostratigraphy using planktonic foraminifera, stressing that the pelagic section at Avedat was remarkably continuous and somewhat expanded. Benjamini (1979, 1980) showed that the intercalated limestones within the Nizzana and Horsha formations, rich in larger benthic foraminifera, are often mass-transported. A more detailed investigation of these phenomena in the central region of Israel was carried out by Buchbinder *et al.* (1988) and is under further study at present. Most transport phenomena found in the Avedat plateau are currently interpreted as muddy debris flows.

Paleocene and early Eocene calcareous nannofossils from the Avedat Plateau were studied by Romein (1979), who concentrated on the Paleocene and compared this section with similar ones from Spain and Scandinavia. Ehrlich & Moshkovitz (1982)

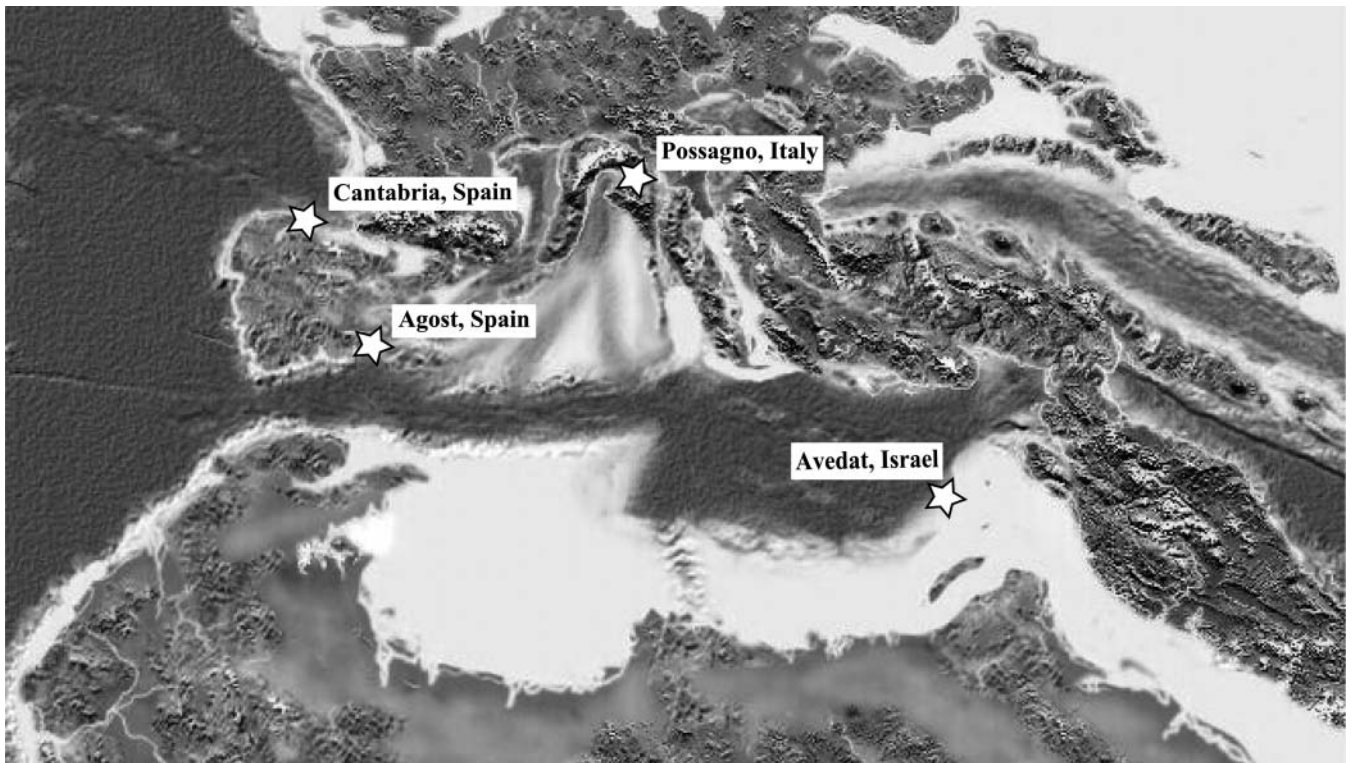


Fig. 1. Palaeogeographical map of southern Europe and the Mediterranean region in the Eocene. The locations of Agost and Cantabria, Spain together with Possagno in Italy are presented together with the location of the Avedat Plateau in the Levant region. (Source: http://www2.nau.edu/rcb7/paleogeographic_alps.html.)

matched the nannofossil-based biostratigraphical scheme of the southern part of Israel with the NP system of Martini (1971). However, they proposed that *Reticulofenestra umbilicus* be used as the marker species for the NP15/NP16 boundary rather than *Blackites* ('*Rhabdosphera*') *gladius* (Perch-Nielsen, 1985). A multiple biostratigraphical correlation of the northern Negev sections, using planktonic foraminifera, nummulites and calcareous nannofossils, was presented by Moshkovitz (1995) and by Schaub *et al.* (1995).

METHODS

A total of 207 m of chalk section from seven sub-sections were sampled in the Avedat Plateau, some 50 km south of Beer-Sheva, southern Israel: four sites at the Ein Avedat National Park (labelled EA1–4), two sub-sections in the Borot Ramallieh hill (some 2.5 km to the south, labelled BR1, 2) and one site at the Har Eldad roadcut (labelled EL). Locations of sections from the Avedat Plateau are shown in Figure 4. Outcrops were measured by Brunton and tape, and clean samples were taken at an average of 0.4–1.0 m interval. The continuity between sub-sections was made by measuring distances by theodolite, occasionally corrected by comparing the range-charts between sections.

In the laboratory, chalk samples were crushed to powder, then diluted in distilled water and ultrasonically disaggregated for five minutes. Without size segregation, a solids concentration of $70 \mu\text{g ml}^{-1}$ with about 10–20 individual nannoforms per field of view, evenly distributed on a slide, was examined under plain polarized light (PPL) and by scanning electron microscopy

(SEM). Slides for optical examination were prepared from 650 μl of suspension onto an 18×18 mm cover glass, while for SEM microscopy 230 μl of suspension was injected onto a 12 mm diameter round stub. Samples were dried at up to 60°C on a heating plate and glued by NOA61 optical adhesive. Samples were observed under Zeiss Photomicroscope II, PPL with CCD camera, in the sedimentology laboratory at Ben-Gurion University of the Negev, and under the JEOL JSM-840 SEM at the Geological Survey of Israel in Jerusalem. Data processing used PRIMER 6.0 software and plots were made by LogPlot7.0.

Biostratigraphy

Three hundred fields of view were inspected from each sample. Full range charts were prepared for each sub-section and then combined to make up a composite chart. The stratigraphic position for each sample was located according to the First/Last Occurrence (FO/LO) of the zonal markers, following Romein (1979), Ehrlich & Moshkovitz (1982), Perch-Nielsen (1985), Aubry (1986) and Moshkovitz (1995). The range charts were used as source data for the age model and for counting the number of species to obtain the richness indices of total nannofossils and *Chiasmolithus* spp. Sedimentation rates were calculated using the FOs/LOs of zonal marker species and nannofossil datum ages from the biostratigraphical scheme of IODP 320/321 report (Pälike *et al.*, 2008) including the FO of *R. umbilicus* (and see Backman, 1987; Cande & Kent, 1995). For the early–middle Eocene interval studied, this follows the time-scale of Cande & Kent (1995). Some parts of the Avedat

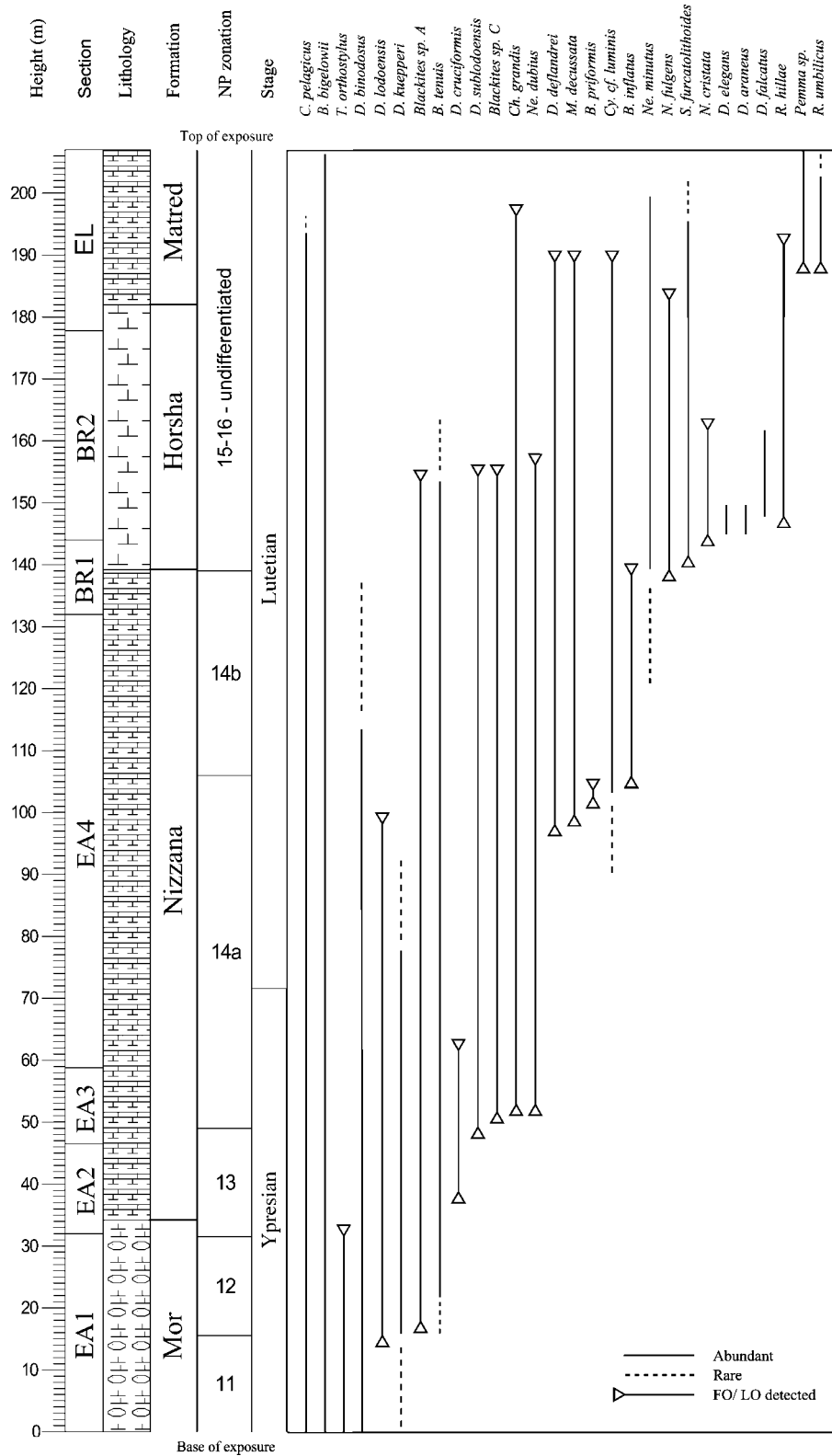


Fig. 2. Composite columnar section for the Avedat Plateau showing ranges of selected calcareous nannofossils.

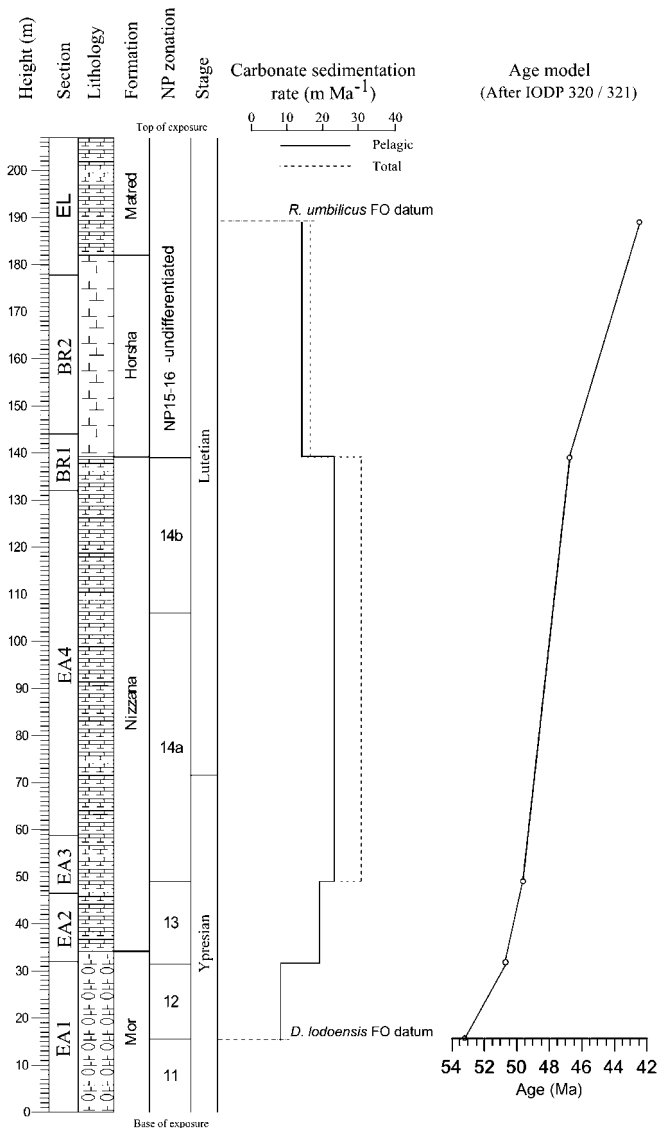


Fig. 3. Composite columnar section for the Avedat Plateau showing heights, lithology and NP zonation. Rates of sedimentation are correlated with heights. The regressions of height/age used for the age model are plotted. Time-scale from Pälike *et al.* (2008).

sections have mass-transport intercalations, averaging 25% of the measured sections. The rate of pelagic sedimentation was calculated by subtracting the thickness of these transported beds (Fig. 3). Sedimentation rates and ages of zonal markers were used to build the age model. EECO and the following cooling event were located using the digitized data of Zachos *et al.* (2001).

Assemblage counts

The current study aimed to test some known nannofossil forms for their usefulness as palaeoenvironmental indicators. For each slide, a total of 300 nannofossils was counted, from 10 slides with 3 repetitions. Error of counting was 5%. The counting emphasized a number of selected nannofossil groups.

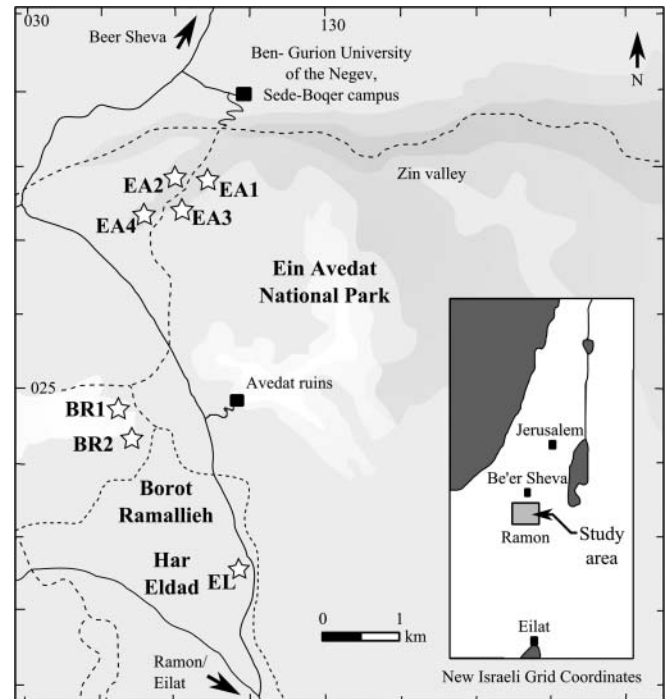


Fig. 4. Location of sub-sections in the Avedat Plateau, central Israel: EA1–EA4, Ein Avedat canyon sections; BR1–BR2, Borot Ramallieh hill sections; EL, Har Eldad road-cut section.

Genus *Chiasmolithus* Hay, Mohler & Wade, 1966 is expected to be a proxy for cool nutrient-rich conditions. For this purpose the current study used the simple species richness index of Hammer & Harper (2006, p. 187) of the number of species of *Chiasmolithus* within each sample.

Genus *Discoaster* Tan, 1927 represents warm saline oligotrophic conditions (Agnini *et al.*, 2006).

Reticulofenestra vs. *Coccolithus*-types – Bown *et al.* (2004) established the phylogeny of coccolithophores in the Cenozoic. Two of the dominant placolith-forming coccolithophore families, the Coccolithaceae (including *Coccolithus*) and Noelrhabdaceae (including *Reticulofenestra*) show distinct patterns of diversification through the Palaeogene, which may be related to environmental conditions (Bown, 2005) and have their split-point early in the Palaeogene. Within the latter group, Agnini *et al.* (2006) traced the transition from Prinsiaceae to Noelrhabdaceae in the early/middle Eocene transition. Here, we have grouped those heterococcoliths into two forms basically differentiated by their optical characteristics; these have common symplesiomorphic characters that follow the nomenclature of Young & Bown (1997) and Young *et al.* (1997). The *Reticulofenestra*-type have crystallographic units (V/R units, Young *et al.*, 1997) that show strong bright birefringence under crossed polarized light (XPL). The *Coccolithus*-type has *Coccolithus*-type rim-structure and a darkened outer distal shield when viewed under XPL. The two distinct forms were counted under XPL, and 50 SEM images from each sample verified the diagnostic features.

Genus *Blackites* Hay & Towe, 1962 emend. Stradner & Edwards, 1968 – the increased diversity of this genus around the early/middle Eocene boundary has been noted by many

authors (e.g. Bramlette & Sullivan, 1961; Perch-Nielsen, 1985). Weinbaum-Hefetz *et al.* (2000) showed the wealth of forms and variants in the NP14 zone, and remarked on the difficulties of grouping them using a simple species-concept. Some forms are rare and occur in just a few samples (e.g. *Blackites piriformis*), whereas others are highly abundant (e.g. *B. tenuis*). For these reasons the current study used the natural-log $H'(S)$ Shannon–Wiener index of diversity (Hammer & Harper, 2006, p. 192) that depends both on the number of species and on the number of counted individuals.

Reworked taxa – several nannofossil species found in the NP14 and NP15 zones are typical for the Paleocene (Romein, 1979; Perch-Nielsen, 1985). These species belong to *Ellipsolithus* (e.g. *E. macellus*, *Cruciplacolithus* (e.g. *Cr. cf. vanheckae*, *Cr. subrotundus*) and some discoasters (e.g. *D. araneus*, *D. elegans*). These species are interpreted as reworked taxa in the current study. The number of reworked taxa was standardized by the species richness index for each sample.

RESULTS

The calcareous nannofossils from the Avedat Plateau are normally well preserved, as mentioned by Romein (1979) and by Moshkovitz (1995). A few intervals display poor preservation, usually in proximity to thick chert horizons or dark chalks in the Mor Formation, or to the indurated chalks enclosing the mass-transported emplacement beds in the Nizzana and Matred formations. The most distinct transport events were in the EA4 section at 63 m, 110 m, at BR2 at 145 m, and EL at 185 m, interrupting the continuity of the project data, as can be seen in Figure 5.

Biostratigraphy

A total of 103 nannofossil taxa was determined and placed into Palaeogene calcareous nannofossil zones NP11–NP15/16 (Martini, 1971; Okada & Bukry, 1980). Species present are listed in Appendix A and some significant forms are shown in Figure 2. The rich calcareous nannoflora of the Avedat Plateau has already been illustrated by Moshkovitz (1995). A composite stratigraphy was constructed based on nannofossil and lithological correlations (Fig. 3), which spans Palaeogene calcareous nannofossil zones NP11–NP15/16 (Martini, 1971; Okada & Bukry, 1980). The lithostratigraphic formations are subdivided into NP zones.

NP11. The *Discoaster binodosus* Zone, 15 m thick, was found in the Mor Formation. The base of this zone is not exposed.

NP12. The *Tribrachiatulus orthostylus* Zone, 18 m thick in the Mor Formation. Its base is marked by the FO of *D. lodoensis*.

NP13. The *Discoaster lodoensis* Zone is 23 m thick and occurs in the lower part of the Nizzana Formation. Its base overlies the LO of *T. orthostylus*.

NP14. The *Discoaster sublodoensis* Zone is 85 m thick in the Nizzana Formation. The base of this zone is the FO of *Discoaster sublodoensis*. The top underlies the FO of *Nannotetrina fulgens*. The FO of *Blackites inflatus* marks the base of the NP14b subzone. Many inflated and curved-spine rhabdosphaerids occur within subzone NP14b, including *B. piriformis*. An increased variety of calcareous nannofossils was also found.

NP15–16 interval. The FO of *Nannotetrina fulgens* marks the base of NP15 and this species is present in an interval some 68 m

thick. *N. fulgens* first occurs near the top of the Nizzana Formation (at 139 m), continues through the Horsha Formation and terminates with the FO of *Reticulofenestra umbilicus* in the top 15 m of the composite section, within the Matred Formation. The FO of *R. umbilicus* falls within the NP16 zone. The criteria used for the definition of *R. umbilicus* followed Backman & Hermelin (1986) and Gallagher (1989). *Blackites gladius* marking the base of NP16 was not found within this interval, in agreement with Ehrlich & Moshkovitz (1982), so the NP15–16 interval was left undifferentiated (Fig. 2) with its top not exposed.

Rate of sedimentation

Figure 3 shows two calculations of sedimentation rates in the Avedat Plateau: the total and the pelagic carbonate sedimentation rate, calibrated against the Palaeogene time-scale of IODP 320/321 report (Pälike *et al.*, 2008). The position of the EECO, subsequent cooling and stable thermal trend of the middle Eocene, following Zachos *et al.* (2001), are shown in Figure 5. The highest rates of sedimentation measured in the Avedat Plateau were in NP14 at 31.5 m Ma⁻¹, including the thickness of the transported beds, but 23.6 m Ma⁻¹ for the autochthonous, undisturbed chalks in that section.

Initial rate of sedimentation in early Eocene Zone NP12 was 7.5 m Ma⁻¹. The total rate increases to 19.2 m Ma⁻¹ in zone NP13 with an equal pelagic rate. A further increase in pelagic rate occurred in NP14 to 23.6 m Ma⁻¹. In NP15, both total and pelagic rates fall to 14.0 and 13.0 m Ma⁻¹, respectively. All in all, carbonate flux to the sediment is, therefore, rather moderate in the early Eocene, and increases two-fold in the middle Eocene, before stabilizing in NP15.

Nannofossil assemblages

The changing trends in population can be correlated with the main events surrounding the early/middle Eocene transition (Fig. 5). A general trend of increase is observed with the species richness index: from a number of species average of 15 within the Mor Formation (EA1 and EA2 sections, NP11 and 12) to a peak of 69 within the Borot Ramallieh (BR1 section) at 137–140 m, correlated with ~46.9–46.6 Ma, species richness then declines to a minimum of 11. This time interval correlates with the cooling event of the early Lutetian. The pattern of *Chiasmolithus* species richness follows a similar trend: in NP11 and NP12 only *Chiasmolithus solitus* is found. The average number of species remains 2 until the NP14/NP15 boundary. At Borot Ramallieh (BR1 section) the number of species reaches a maximum of 8 at 142 m (~46.7 Ma), and other species of this genus appear, e.g. *Ch. medius*, *Ch. bidens* and *Ch. modestus*. In the upper part of the section, in the Matred Formation (NP16), the number of species falls to 11, with abundant *Ch. grandis*.

Blackites diversity. Species present include *B. tenuis*, *B. creber*, *B. scabrosus*, *B. inflatus*, *B. piriformis* and others. During most of the early Eocene, and later in the middle Eocene, mostly *B. tenuis* is present and the Shannon–Wiener index is 0.00–0.69. Across the early/middle Eocene (Ypresian/Lutetian) boundary, diversity of *Blackites* spp. increases sharply, levelling at 1.60 from 65–135 m (most of NP14) and decreases markedly during the early NP15 zone. A small peak might be present towards the

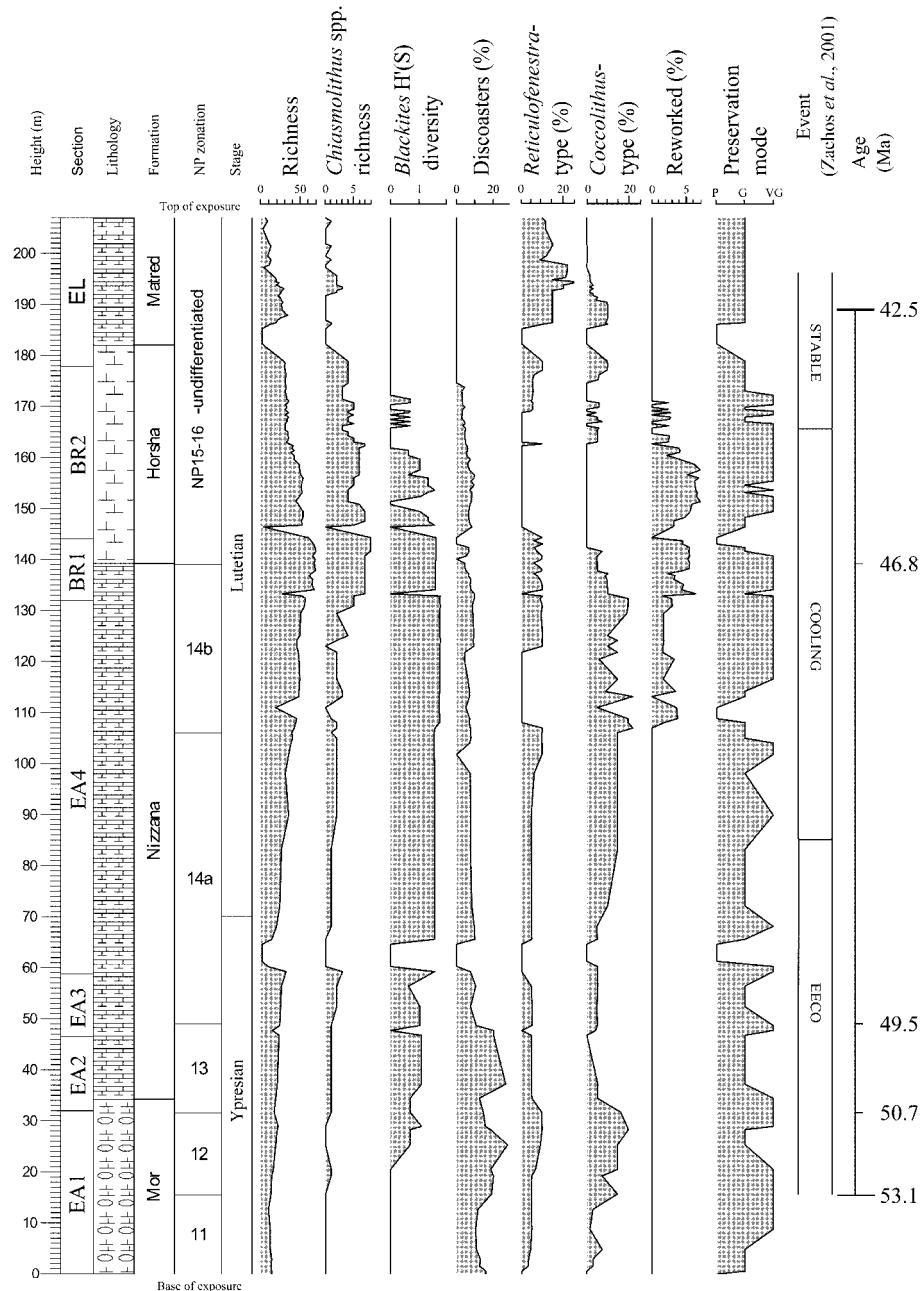


Fig. 5. Features of the calcareous nannofossil assemblages of the Avedat Plateau sections, calibrated against the Palaeogene time-scale (Pälike *et al.*, 2008). The position of the Early Eocene Climatic Optimum (EECO), subsequent cooling and stable thermal trend of the Middle Eocene are after Zachos *et al.* (2001). Preservation mode: P, Poor; G, Good; VG, Very Good. Reworked species are standardized by the species richness index.

end of NP14b that could be correlated to the NP14/15 boundary and the behaviour of *Blackites* spp. is remarkably stable during the long NP14 interval.

In contrast to both *Chiasmolithus* and *Blackites*, the discoasters are more dominant in the lower parts of Ein Avedat section, with an average of 25% of total counts in the lower parts of Ein Avedat section. The discoaster climax, when they form 46% of the total, is at 25 m, a position that correlates to 52.3 Ma, within the EECO interval. Thereafter, their abundance decreases gradually (allowing for horizons of poor preservation) through NP 14 and NP15/16 and shows no response to events at the

NP14/NP15 transition. No discoasters were found in the Matred Formation.

The dominant *Reticulofenestra*- and *Coccolithus*-type placoliths together have a baseline of an average ~20% of total counts in almost equal proportions. This baseline is found in the interval from NP11 to NP13, with a slight advantage of the *Coccolithus*-type, but the *Coccolithus*-type becomes distinctly more dominant during zone NP14. Across the NP14/NP15 transition there is a fall in abundance of both forms, but they were, however, the only affected placoliths, as other heterococcolith-forms, such as *Chiasmolithus*, were abundant.

The population of *Reticulofenestra*- and *Coccolithus*-types recovered in mid-NP15 (167 m, approximately 45 Ma) but significant turnover occurred around, and including, the first occurrence of *R. umbilicus* with the *Reticulofenestra*-type forms becoming abundant, while *Coccolithus*-type forms are sharply reduced. The upper part of the NP15–16 interval has mostly braarudosphaerids (e.g. *Pemma* sp.) and reticulofenestrids, but no *Coccolithus*-type placoliths.

Reworked taxa. Reworked taxa occur to some extent through most of the section, but counts are negligible (<1%). By the early Lutetian, at 108 m in the EA4 section (base of NP14b subzone), they increase to around 2% of the total and then increase sharply to 6.9% at 145–160 m at Borot Ramallieh (BR2), in the Horsha Formation. (This position correlates to 46.5–45.5 Ma). Reworked taxa disappear in the uppermost Horsha Formation and were not found in the Matred Formation (i.e. from the FO of *R. umbilicus* datum and upwards).

DISCUSSION

The clear FOs of *D. subloboensis*, *N. fulgens* and *R. umbilicus*, as well as the FO of inflated *Blackites* forms (*B. inflatus* and *B. piriformis*) highlights the similarity of the Avedat section to the Basque–Cantabrian sections (Bernaola *et al.*, 2006). The early/middle Eocene (Ypresian/Lutetian) boundary was located much higher by Benjamini (1980) and Schaub *et al.* (1995), at Borot Ramallieh at 175 m, within the Horsha Formation. At that point the first appearance of the planktic foraminifera *Hantkenina nutalli*, in the upper part of nannozone NP15 was observed. This remarkable difference of ~2.5 Ma between the early/middle Eocene boundaries as defined by calcareous nannofossils vs. planktic foraminifera was noted by Benjamini (1980) and by Moshkovitz (1995).

Sedimentation and reworking

Pelagic sedimentation rate changes at Avedat, after deletion of the thickness of the transported beds, range from 7.5–23.6 m Ma⁻¹. The rate of sedimentation during the EECO is at first (NP11) relatively low, but more than doubles in the latter part, in NP12 and NP13. The cooling trend terminating the EECO in NP14 is accompanied by a three-fold increase in sedimentation rate, and increased carbonate production continues to the NP14/NP15 boundary. Maximum sedimentation rates of 20–30 m Ma⁻¹ correspond to the highest rates reported for clean pelagic sediments (Berner, 1980). The friable, clay-free chalks at Avedat are composed of nearly 80% calcareous nannofossils, with the remainder mostly planktonic foraminifera; as the P/B ratios are extremely high (Fermont, 1982), benthic foraminifera, bioclasts and siliceous material are minor components. Therefore, the rate of sedimentation in the Avedat Plateau represents a significant pelagic carbonate flux during the transitional phase of NP14, until NP15. In the Horsha Formation (lower NP15–16) rates appear to stabilize. At the NP14/NP15 boundary the significant fall in carbonate production corresponds to the stabilization of the thermal regime, but to a rate that is still twice that of the later part of the early Eocene.

These sedimentation rates in nannozone NP 14 and NP15 are considerably higher than those of the more indurated deep marine marly limestones of Possagno (Agnini *et al.*, 2006) for

the same time intervals. Higher rates of 80–150 m Ma⁻¹, about four times that of the Avedat Plateau, were given for the Pamplona and Basque basins (Bernaola *et al.*, 2006). However, these uniquely high sedimentation rates are over an order of magnitude greater than typical deep-sea sections and can be attributed to the presence of a significant allochthonous contribution.

A brief interval in which reworked Paleocene nanofossils appear in Eocene nannozone was also reported by Schaub *et al.* (1995) and was considered to be of local origin. The source for reworked silt-size sediments including calcareous nannofossils could, in fact, be from anywhere in the adjacent Tethyan margins. Nevertheless, Eocene beds high on the Ramon structure some 25 km to the south locally overlie strata of various ages, some as early as Cenomanian, as summarized in Benjamini (1979). Easily eroded Paleocene hemipelagic marls in the vicinity of the Ramon structure are most likely the source. These marls are extremely uniform over the entire Levant region and the point source is difficult to identify (Speijer, 1995).

The ~7% reworked material has a minor effect on the rate of sedimentation, but the temporally limited nature of this reworking event suggests a connection to the cooling event of the early/middle Eocene transition. Localization of the peak (at 149–157 m in the composite section) to the end of the post-EECO cooling trend can be explained by concomitant increased current activity that enhanced redeposition of oceanic sediments in the Levant region.

Nannofossil assemblages

There appear to be four distinct periods of nannofossil assemblage change across the studied early to middle Eocene succession. First, in the early Eocene age Mor and lower Nizzana formations (NP11–13), assemblages are characterized by relatively high proportions of discoasters. A similar peak in discoaster abundance, broadly coincident with the EECO, has been observed in other Tethys sections (Agnini *et al.*, 2006). Based on the generally accepted preference of the discoasters for warm-oligotrophic conditions, this would indicate that more stratified and less productive waters were widespread in the Tethys during the EECO and declined when cooling introduced nutrients and mixing.

The next interval is marked by the rise in diversity of the genus *Blackites* across the early/middle Eocene boundary. They then reached a diversity climax by the end of the EECO that remained steady throughout the relatively long NP14 interval. The Shannon–Wiener index of diversity shows that this increase is not controlled by changes in other nannofossil groups. This peak in *Blackites* diversity in the middle Eocene, flourishing during a time of climatic change, may be driven by the evolutionary diversification of this group around the early/middle Eocene transition, but causes of this diversification are not well understood.

The third interval is characterized by the clear rise in the species diversity within the genus *Chiasmolithus*, a genus which is considered to favour cooler and probably more nutrient-rich water (Tremolada & Bralower, 2004). It thus appears that the increasing nannofossil diversity is linked to the pattern of gradual global cooling after the extreme warmth of the EECO.

The final interval begins with declines in the total nannofossil species diversity, *Chiasmolithus* diversity and *Blackites* diversity

within the NP15–16 interval in the Matred Formation. The diversity of *Chiasmolithus* spp. declines after the passage of the cooling event, reflecting the final stage of stabilized surface water conditions in the Levant region.

***Reticulofenestra*- vs. *Coccolithus*-type dominance**

The dramatic transition in dominance from the *Coccolithus*-type to the *Reticulofenestra*-type placoliths takes place close to the NP15/16 boundary in the basal Matred Formation (~44.5 Ma). This is also associated with the global first appearance of the large reticulofenestrid, *R. umbilicus* and appears to be an important moment in the establishment of ‘modern’ reticulofenestrid-dominated coccolithophore assemblages. This event is considerably later than the transition from *Toweius*- to *Reticulofenestra*-dominated assemblages at Possagno, which is associated with the discoaster acme and occurs between 50 Ma and 51 Ma, well within the early Eocene. The switch from *Coccolithus*-type to *Reticulofenestra*-type placoliths occurs some 4 Ma later at Avedat, close to the first appearance of the planktic foraminifera *Hantkenina nuttalli* Tourmarkine 1981. Agnini *et al.* (2006) suggested that the change to the successful Noelrhabdaceae reflects a permanent and irreversible transformation of the way calcareous nannofossils interacted with the ocean–atmosphere system. This change occurred at the EECO in the northern Tethys, and much later in lower latitudes. The data from Avedat show that this was a progressive transition that took place during the Eocene, including a number of key points at which the dominance of the Noelrhabdaceae increased markedly, through to the restructuring of nannofossil communities at the Eocene/Oligocene boundary (Dunkley Jones *et al.*, 2008).

CONCLUSIONS

The early Eocene of the Levant region was characterized by oligotrophic conditions, particularly during the EECO. Rates of sedimentation during the EECO were similar to those calculated in higher latitudes (Possagno, Italy). The dominant calcareous nannofossil taxa were low diversity *Coccolithus*-type placoliths and discoasters, both adapted to high temperatures, stable water stratification and, potentially, high pCO₂ levels (Henderiks & Rickaby, 2007).

Rates of sedimentation increased substantially just prior to the early/middle Eocene transition, and remained high during the post-EECO cooling trend. This interval was accompanied by an increase in the diversity of *Blackites* spp. as well as in the total number of nannoplankton species. These climatic changes reflect termination of the highly stratified super-greenhouse world of the early Eocene, replaced by a mixed water column structure with significant current activity that caused much re-sedimentation on Levant margin slopes.

From the EECO peak, decline of oligotrophy and enrichment of nutrients near the ocean surface was enhanced at the high latitudes of the northern edge of the Tethys, relative to the lower latitudes of the southern Tethyan margin. Towards the top of the studied section, in the Horsha and Matred formations, NP15 witnessed climatic stabilization. Under these conditions *Blackites* diversity decreased, as did the species richness of nannoplankton assemblages and the rise of *Reticulofenestra*-type placoliths was enhanced.

The transformation from *Coccolithus*-type dominance to *Reticulofenestra*-type placoliths took place at Avedat at the NP15/NP16 transition, around 4 Ma later than at Possagno, Italy. The temporal discrepancy of this changeover is significant, in contrast to the preceding NP12 discoaster acme and subsequent decline that were coeval in both locations. The Possagno palaeoposition was at the northern edge of the Tethys, whereas the Levant margin at that time was at least 15° south of its current latitude. This indicates the difference in palaeoceanographic conditions between the northern and the southern Tethys so that the turnover (expressed by cooling and nutrient enrichment) was highly diachronous and first occurred in the northern parts of the Tethys. This diachrony corroborates the observation of Pearson *et al.* (2009) that cooling begins primarily at the poles and influences the tropical belts only at later stages.

In fact, the middle Eocene cooling event has not particularly been considered by most workers on the Tertiary as a significant part of the mid-Tertiary global cooling trend, although global climate curves clearly show a consistent decline from the EECO to the Middle/Late Eocene transition, prior to the steep decline culminating at the onset of the Oligocene. We consider that the calcareous nannoplankton response to development of cooler water layers in the Tethys in the middle Eocene set the stage for their subsequent response at the late Eocene–early Oligocene global changeover. Had the later events not resulted in such extreme global cooling, the transition may not have been irreversible, and the middle Eocene placolith turnover may then have been a short-lived event.

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APPENDIX A: LIST OF SPECIES

- Birkelundia staurion* (Bramlette & Sullivan, 1961) Perch-Nielsen, 1971
- Blackites creber* Deflandre, 1954
- Blackites inflatus* Bramlette & Sullivan, 1961
- Blackites scabrosus* Deflandre, 1954
- Blackites* sp. A
- Blackites* sp. C
- Blackites piriformis* (Pavsic in Khan *et al.*, 1975) Aubry, 1999
- Blackites tenuis* Bramlette & Sullivan, 1961
- Braarudosphaera bigelowii* Deflandre, 1947
- Calcidiscus* sp. B
- Calcidiscus* sp. A
- Campylosphaera dela* (Bramlette & Sullivan, 1961) Hay & Mohler, 1967
- Chiasmolithus bidens* (Bramlette & Sullivan, 1961) Hay & Mohler, 1967
- Chiasmolithus consuetus* (Bramlette & Sullivan, 1961) Hay & Mohler, 1967
- Chiasmolithus expansus* (Bramlette & Sullivan, 1961) Gartner, 1970
- Chiasmolithus grandis* (Bramlette & Riedel, 1954) Radomski, 1968

- Chiasmolithus modestus* Perch-Nielsen, 1971
Chiasmolithus solitus (Bramlette & Sullivan, 1961) Locker, 1968 var. A
Chiasmolithus solitus (Bramlette & Sullivan, 1961) Locker, 1968 var. B
Chiasmolithus sp. cf. *Ch. medius* Perch-Nielsen, 1971
Coccolithus pelagicus (Wallich, 1877) Schiller, 1930
Cruciplacolithus cf. *Cr. edwardsii* Romein, 1979 var. A
Cruciplacolithus cf. *Cr. edwardsii* Romein, 1979 var. B
Cruciplacolithus sp. cf. *Cr. frequens* (Perch-Nielsen, 1971) Romein, 1979
Cruciplacolithus cruciformis (Hay & Towe, 1962) Roth, 1970
Cruciplacolithus sp. cf. *Coccolithus* sp. of Sullivan, 1964
Cruciplacolithus sp. cf. *Cr. vanheckae* Perch-Nielsen, 1986
Cruciplacolithus subrotundus Perch-Nielsen, 1969
Cyclicargolithus cf. *luminis* Sullivan, 1965
Cyclococcolithus sp.
Dictyococcites sp.
Discoaster araneus Bukry, 1971
Discoaster barbadiensis Tan, 1927 emend. Bramlette & Riedel, 1954
Discoaster binodosus Martini, 1958
Discoaster cruciformis Martini, 1958
Discoaster deflandrei Bramlette & Riedel, 1954
Discoaster distinctus Martini, 1958
Discoaster elegans Bramlette & Sullivan, 1961
Discoaster falcatus Bramlette & Sullivan, 1961
Discoaster gemmifer Stradner, 1961
Discoaster germanicus Martini, 1958
Discoaster incomptus Hay, 1967
Discoaster kuepperi Stradner, 1959
Discoaster lodoensis Bramlette & Riedel, 1954
Discoaster pacificus Haq, 1969
Discoaster sp.
Discoaster sp. cf. *D. trinus* Stradner, 1961
Discoaster sublodoensis Bramlette & Sullivan, 1961
Ellipsolithus lajollaensis Bukry & Percival, 1971
Ellipsolithus macellus (Bramlette & Sullivan, 1961) Sullivan, 1964
Ericsonia sp. A
Ericsonia sp. B
Helicosphaera lophota Bramlette & Sullivan, 1961
Helicosphaera seminulum Bramlette & Sullivan, 1961
Lophodolichus nascens Bramlette & Sullivan, 1961
Lophodolichus reniformis Bramlette & Sullivan, 1961
Lophodolichus rotundus Bukry & Percival, 1971
Micrantholithus crenulatus Bramlette & Sullivan, 1961
Micrantholithus flos Deflandre, 1950
Micrantholithus vesper Deflandre, 1950
Micula decussata Vekshina, 1959
Nannotetrina cristata (Martini, 1958) Perch-Nielsen, 1971
Nannotetrina fulgens (Stradner, 1960) Achuthan & Stradner, 1969
Neochiastozygus digitosus Perch-Nielsen, 1971
Neochiastozygus distentus (Bramlette & Sullivan, 1961) Perch-Nielsen, 1971
Neococcolithes dubius (Deflandre, 1954) Black, 1967
Neococcolithes minutus (Perch-Nielsen, 1967) Perch-Nielsen, 1971
Pemma sp.
Pontosphaera distincta (Bramlette & Sullivan, 1961) Roth & Thierstein, 1972 var. A
Pontosphaera distincta (Bramlette & Sullivan, 1961) Roth & Thierstein, 1972 var. B
Pontosphaera enormis (Locker, 1967) Perch-Nielsen, 1984
Pontosphaera sp. A
Pontosphaera versa (Bramlette & Sullivan, 1961) Sherwood, 1974 var. A
Pontosphaera versa (Bramlette & Sullivan, 1961) Sherwood, 1974 var. B
Pseudotriquetrorhabdulus inversus (Bukry & Bramlette, 1969) Wise & Constans, 1976
Reticulofenestra conuera (Reinhardt, 1966) Roth, 1970
Reticulofenestra dictyoda (Deflandre & Fert, 1954) Stradner, 1968
Reticulofenestra hillae Bukry & Percival, 1971
Reticulofenestra samodurovii (Hay, Mohler & Wade, 1966) Roth, 1970
Reticulofenestra scissura Hay, Mohler & Wade, 1966
Reticulofenestra scripasse (Bukry & Percival, 1971) Roth, 1973
Reticulofenestra umbilicus (Levin, 1965) Martini & Ritzkowski, 1968
Scapholithus sp.
Scyphosphaera sp. A
Scyphosphaera sp. B
Sphenolithus editus Perch-Nielsen, 1978
Sphenolithus furcatolithoides Locker, 1967
Sphenolithus radians Deflandre, 1952
Sphenolithus sp. A
Sphenolithus sp. B
Thoracosphaera heimii (Lohmann, 1919) Kamptner, 1941
Thoracosphaera prolata Bukry & Bramlette, 1969
Thoracosphaera saxea Stradner, 1961
Thoracosphaerae tuberosa Kamptner 1963
Transversopontis exilis (Bramlette & Sullivan, 1961) Perch-Nielsen, 1971
Transversopontis fimbriatus (Bramlette & Sullivan, 1961) Locker, 1968
Transversopontis latus Müller, 1970
Transversopontis obliquipons (Deflandre, 1952) Hay, Mohler & Wade, 1966
Transversopontis rectipons (Haq, 1968) Roth, 1970
Transversopontis sigmoidalis Locker, 1967
Tribrachiatum orthostylus Shamrai, 1963 var. A
Tribrachiatum orthostylus Shamrai, 1963 var. B
Zygrhablithus bijugatus Deflandre, 1959

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