

Calcareous dinoflagellate turnover in relation to the Messinian salinity crisis in the eastern Mediterranean Pissouri Basin, Cyprus

KATARZYNA-MARIA BISON¹, GERARD J.M. VERSTEEGH², FRITS J. HILGEN³ & HELMUT WILLEMS¹

¹ Division of Palaeontology, University of Bremen, FB 5, Geowissenschaften, Postfach 330440, D-28334 Bremen, Germany
(e-mail: kbison@uni-bremen.de)

²Institut für Biogeochemie und Meereschemie, Universität Hamburg, Bundesstraße 55, D-20146 Hamburg, Germany

³University of Utrecht, Faculty of Earth Sciences, Budapestlaan 4, 3594 Utrecht, Netherlands

ABSTRACT – The extent to which the Messinian salinity crisis modified the initially Tethyan, eastern Mediterranean phytoplankton community has been investigated by monitoring the fate of calcareous dinoflagellate cyst assemblages prior to, during and after the salinity crisis in the Pissouri section (Cyprus). A rich, but low diversity open oceanic assemblage, dominated by *Calciodinellum albatrosianum*, is found in the upper Tortonian and lower Messinian. The upper Messinian (pre-evaporitic) sediments yield only few cysts but the assemblage is much more diverse and reflects unstable more neritic conditions (*Bicarinellum tricarinelloides*), fluvial influence (*Leonella granifera*) and varying, temporally increased salinities (*Pernambugia tuberosa*), probably related to the increasingly restricted environment. The basal Pliocene sediments reflect the return to normal marine conditions; the dinoflagellate assemblage is rich in cysts and again has a low diversity. However, in contrast to the *C. albatrosianum*-dominated upper Tortonian and pre-evaporitic Messinian sediments, *L. granifera* clearly dominates the basal Pliocene association just after the replenishment of the Mediterranean basin. Apart from this shift in dominance, the onset of the Pliocene is furthermore marked by the first appearance of *Calciodinellum elongatum*, which must have immigrated from the Atlantic Ocean. *Lebessphaera urania*, a postulated remnant of the Tethyan Ocean survived the salinity crisis, possibly in as yet unidentified marine refuges in the Mediterranean itself. Although the environmental changes caused by the Messinian salinity crisis did not lead to an extinction of calcareous dinoflagellate species of the Pissouri Basin, it resulted in a significant change in the assemblages and contributed to a more modern character of the Pliocene dinoflagellate association in the eastern Mediterranean. *J. Micropalaeontol.* 26(2): 103–116, October 2007.

KEYWORDS: Messinian, calcareous dinoflagellates, Mediterranean, Pliocene, Miocene

INTRODUCTION

The dramatic drop in sea-level of the Mediterranean Basin during the Messinian salinity crisis represents a major environmental breakdown within an oceanic basin. It led to extensive and widespread evaporite deposition underlying the modern Mediterranean Sea (e.g. Hsü *et al.*, 1973, 1977; Hsü, 1978; Butler *et al.*, 1999; Lofi *et al.*, 2005; Meijer & Krijgsman, 2005; Tay *et al.*, 2002). These evaporites reflect the progressive closure of the Mediterranean gateways, which resulted in the almost complete isolation of the Mediterranean from the Atlantic Ocean during the final stage of the Messinian salinity crisis (Hsü & Bernoulli, 1978; Krijgsman *et al.*, 1999; Bianchi & Morri, 2000; Seidenkrantz *et al.*, 2000; Blanc, 2002; Manzi *et al.*, 2005; Matano *et al.*, 2005).

Considering that the Mediterranean Sea is an old Tethys remnant, it is a natural heir to the Tethyan biodiversity (Bianchi & Morri, 2000; Bouillon *et al.*, 2004). Despite the connection between the Atlantic and the Mediterranean, one may expect that migration of Atlantic species into the Mediterranean must have been largely restricted to those niches not already occupied by the Tethys biota. The Messinian salinity crisis may have changed this. The drastic environmental changes during the salinity crisis caused by the significant fall in sea-level (e.g. Loget *et al.*, 2006) must have wiped out, or diminished, many taxa (Bouchet & Taviani, 1992; Bianchi & Morri, 2000; Seidenkrantz *et al.*, 2000; Logan *et al.*, 2004; Domingues *et al.*, 2005; Kouwenhoven *et al.*, 2006). In the Mediterranean, the relatively

stable open oceanic environment probably disappeared completely, in contrast to the neritic realms, which in part experienced a displacement only (Keogh & Butler, 1999; Bianchi & Morri, 2000). Therefore, oceanic extinction must have been most severe (Bianchi & Morri, 2000; Logan *et al.*, 2004); in particular, a remarkable decrease was recognized for deep-water representatives of most phyla (Seidenkrantz *et al.*, 2000; Emig & Geisdoerfer, 2004; Kouwenhoven *et al.*, 2006). After the crisis, the vacant niches will have been refilled by species migrating or re-migrating from the Atlantic into the Mediterranean (Bianchi & Morri, 2000; Logan *et al.*, 2004). An important biogeographical question is attached to this event: how and to what extent did the originally Tethyan marine biota survive this crisis and to what extent were they replaced by newcomers from the adjacent Atlantic?

Calcareous dinoflagellates could provide an important insight into the development of the Messinian environmental change and its biogeographical effects since they are sensitive to salinity, nutrient and temperature changes and they have representatives in the entire spectrum of marine environments, from open marine to estuarine (e.g. Dale, 1992; Höll *et al.*, 1998, 1999; Zonneveld *et al.*, 1999; Höll & Kemle-von Mücke, 2000; Wendler *et al.*, 2002a, b, c; Meier & Willems, 2003; Tanimura & Shimada, 2004; Vink, 2004; Kohring *et al.*, 2005).

Unfortunately, information on Miocene and Pliocene calcareous dinoflagellate assemblages from this region is very sparse. Comparison of the associations from the few investigated

localities from the Mediterranean area (Keupp & Kohring, 1993, 1999; Kohring, 1993b, 1997; Keupp *et al.*, 1994) shows strong changes in cyst abundance but only little variability in species diversity and composition. On the basis hereof, an alternative scenario to that postulated above has been proposed: namely a permanent input of oceanic species from the Atlantic into the Mediterranean during the Miocene–Pliocene which kept the oceanic assemblages of the Atlantic and Mediterranean more or less identical (Keupp & Kohring, 1993, 1999; Kohring, 1993b). In this scenario, the Messinian salinity crisis is supposed to have affected the neritic species only. To shed more light on this controversy, the calcareous dinoflagellate assemblages from the eastern Mediterranean upper Miocene–lower Pliocene sedimentary succession from the Pissouri Basin of Cyprus were investigated.

Modern calcareous dinoflagellates

Calcareous dinoflagellates are primary producers and thus are restricted to the euphotic zone (e.g. Höll *et al.*, 1999; Wendler *et al.*, 2002b; Vink *et al.*, 2002; Vink, 2004). In modern oceans, they often dominate the total dinoflagellate flux to the sea floor (Dale, 1992; Zonneveld *et al.*, 1999; Vink *et al.*, 2000). In the Mediterranean, calcareous dinoflagellates are the second most important carbonate producers after coccolithophorids, with an average of 17% of the total biogenic carbonate flux (Ziveri *et al.*, 2000). Over the last decades, understanding of their phylogeny, biodiversity and ecology has increased greatly (e.g. Keupp & Versteegh, 1989; Höll *et al.*, 1998, 1999; Zonneveld *et al.*, 1999, 2000; Karwath *et al.*, 2000; Wendler *et al.*, 2002b, c; Friedrich & Meier, 2003; Gottschling & Plötner, 2004; Meier *et al.*, 2004; Tanimura & Shimada, 2004; Vink, 2004; Zonneveld, 2004). This knowledge has been applied successfully to reconstruct environmental parameters such as productivity and surface water stratification (Höll *et al.*, 1999; Höll & Kemle-von Mücke, 2000; Esper *et al.*, 2000; Wendler *et al.*, 2002c; Vink, 2004; Meier *et al.*, 2004).

Mediterranean assemblages

Mediterranean associations have been shown to differ from those of other marine environments. The apparent gradual west–east change in the Mediterranean dinoflagellate cyst assemblages is correlated strongly with the main environmental gradients in the surface waters (Meier & Willems, 2003; Meier *et al.*, 2004). Eastwards, salinity and temperature increase whereas nutrient concentrations decrease.

Today, *Thoracosphaera heimii* dominates the Mediterranean assemblages, with relative abundances >88% and its relative abundance in the eastern Basin is usually lower than in the Western Basin (Meier & Willems, 2003). *T. heimii* also dominates the Arabian Sea, Atlantic and Pacific oceans but, if one excludes *T. heimii*, the most abundant species are *Calciodinellum albatrosianum*, *Leonella granifera*, *C. levantinum* and *Pernambugia tuberosa* (e.g. Wendler *et al.*, 2002a; Hernández-Becerril & Bravo-Sierra, 2004; Tanimura & Shimada, 2004; Vink, 2004). From these taxa only *C. levantinum* reaches similar high relative abundances in the western Mediterranean Sea (Meier & Willems, 2003) which is considered to reflect an Atlantic influence through the Strait of Gibraltar (Meier & Willems, 2003). This species is closely similar to, and has been confused with

P. tuberosa, which is one of the main species in the tropical and South Atlantic Ocean (Höll *et al.*, 1999; Esper *et al.*, 2000).

Lebessphaera urania is known only from the eastern Mediterranean where it dominates the dinoflagellate associations (Meier *et al.*, 2002; Meier & Willems, 2003). *Scripsiella regalis* is a frequent component in the whole Mediterranean Sea. *C. albatrosianum* represents only <5% of the associations, whereas *Pernambugia tuberosa* (former name *Sphaerodina tuberosa*) is absent (Meier & Willems, 2003) but forms up to 75% in the South and equatorial Atlantic Ocean (Vink, 2004).

L. granifera is mostly rare to absent in Mediterranean sediments or traps (Meier & Willems, 2003) but it reaches high relative and absolute abundances in more shelfward regions of the Atlantic Ocean and Arabian Sea where river influence and/or continental nutrient supply (dust) play a major role (Vink *et al.*, 2000; Vink, 2004; Zonneveld *et al.*, 2001; Wendler *et al.*, 2002b, c; Meier *et al.*, 2004; Tanimura & Shimada, 2004). This species appears to be an excellent proxy for nutrient-enriched environments induced by terrigenous input (e.g. Wendler *et al.*, 2002b, c; Meier *et al.*, 2004; Vink, 2004).

This interpretation of *L. granifera* is applied to re-interpret environmental reconstructions of other Miocene and Pliocene assemblages, leading to a better understanding of past environmental settings. Until now, the fossil distribution pattern of *L. granifera* could not be related to any environmental parameter except as a general open marine species with no distinct ecological preferences (Fütterer, 1977; Keupp & Kohring, 1993; Kohring, 1993, 1997).

Palaeoenvironment of the Pissouri Basin

The Neogene sedimentary succession on Cyprus shows a gradual shallowing from Palaeogene deep-water pelagic carbonates (Lefkara Formation) through mixed detrital sediments, carbonates and reefal limestones, to the Messinian evaporites (Orszag-Sperber *et al.*, 1989; Robertson *et al.*, 1995; Krijgsman *et al.*, 2002). The Messinian evaporites on Cyprus were deposited in small sub-basins (e.g. Polemi, Psematismenos and Pissouri basins) (Orszag-Sperber *et al.*, 1989; Robertson *et al.*, 1995; Krijgsman *et al.*, 2002). With the beginning of the Pliocene, deeper-water conditions were re-established (Rouchy *et al.*, 2001; Krijgsman *et al.*, 2002). The Messinian sedimentary succession on Cyprus is characterized by pre-evaporitic deposits, overlain by two gypsum units followed by a lagoonal–lacustrine transitional facies (Lago Mare facies) leading to the marine marls of the basal Pliocene (Rouchy *et al.*, 2001; Krijgsman *et al.*, 2002). A small hiatus between 5.59 Ma and 5.52 Ma (Carnevale *et al.*, 2006), representing an erosive phase during the late Messinian lowstand, occurs between the upper gypsum deposits and the overlying lowermost Pliocene sediments (Orszag-Sperber *et al.*, 2000).

Palaeodepth estimations in the Pissouri section are based on foraminifera, bivalves and gastropods (Rouchy *et al.*, 2001; Krijgsman *et al.*, 2002; Kouwenhoven *et al.*, 2006). A progressive shallowing occurred from approximately 500 m during the Tortonian and early Messinian to very shallow-water conditions during the late Messinian. Sediments above Pissouri cycle 9 (Fig. 2) were probably deposited at depths of less than 100 m (Krijgsman *et al.*, 2002). Gypsum and its pseudomorphs already occur sporadically above cycle 22 (Fig. 2), with an increasing

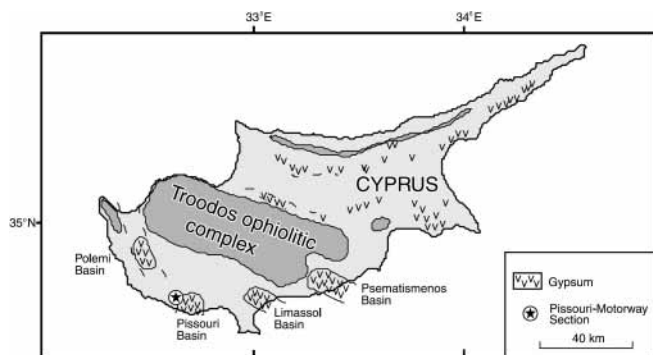


Fig. 1. Location of the Pissouri section on Cyprus (Krijgsman *et al.* 2002).

frequency and amount toward the evaporitic stage of the salinity crisis (Krijgsman *et al.*, 2002). For the earliest Pliocene of the Pissouri Basin a depth of at least 300 m has been estimated, with a deepening trend (Rouchy *et al.*, 2001).

Studies on Neogene and Pleistocene sediments from the Gulf of Suez and the Red Sea and on drilling sites of the Ocean Drilling Program (ODP sites 658–661) resulted in the assumption that northeastern Africa had a relatively humid climate during the late Messinian and was strongly influenced by high monsoonal activity (Griffin, 1999). This precipitation-rich period peaked into the late Messinian during the lowstand in the Mediterranean Basin and led to increased sedimentation rates caused by a higher clastic input by rivers (Griffin, 1999). The Tortonian was characterized by a relatively arid eastern Mediterranean (Griffin, 1999).

MATERIAL AND METHODS

Material

The upper Miocene marine succession of the Pissouri Basin in Cyprus consists of an alternation of indurated carbonate-rich and less indurated marlier beds and shows a distinct cyclicity (Krijgsman *et al.*, 2002; Kouwenhoven *et al.*, 2006). The softer marly beds of the Pissouri section can be correlated with contemporaneous sapropelic layers throughout the Mediterranean (Kouwenhoven *et al.*, 2006).

The record here from Cyprus comprises the complete marine succession of the Pissouri Basin before, during and after the Messinian salinity crisis. The calcareous dinoflagellate data of this paper are derived from two land sections in the Pissouri Basin (Fig. 1), the Pissouri motorway section (40 samples) (Krijgsman *et al.*, 2002) and the Pissouri village section (1 sample) (Orszag-Sperber *et al.*, 1989, 2000; Rouchy *et al.*, 2001). The Pissouri motorway section is located along the Limassol-Paphos motorway (Krijgsman *et al.*, 2002) about 100 m west of the Pissouri village section, which is exposed at the eastern entry of Pissouri (Rouchy *et al.*, 2001). The samples comprise the interval between the upper Tortonian at *c.* 7.6 Ma (cycle VII) up to the base of the massive lower gypsum deposits at 5.98 Ma (cycle 1) and the first centimetres of the basal Pliocene, belonging to the Miocene–Pliocene 1 Biozone of Cita (1975) (MPL1), deposited under deep-marine conditions (Rouchy *et al.*, 2001) (Fig. 2). The upper Messinian evaporitic and post-evaporitic

interval (5.96–5.32 Ma) was not considered due to its essentially non-marine character (e.g. Castradori, 1998; Rouchy *et al.*, 2001).

Except for the uppermost two cycles of the Tortonian, the upper Tortonian and lower Messinian cycles are thinner (around 2.6 cm ka^{-1}) than those from the upper Messinian (around 5 cm ka^{-1}) (Kouwenhoven *et al.*, 2006) (Fig. 2). Consequently, from cycle 18 upwards the sedimentation rates are on average twice as high as those in the cycles below. A detailed description of the Pissouri motorway section is given in Krijgsman *et al.* (2002) and Kouwenhoven *et al.* (2006).

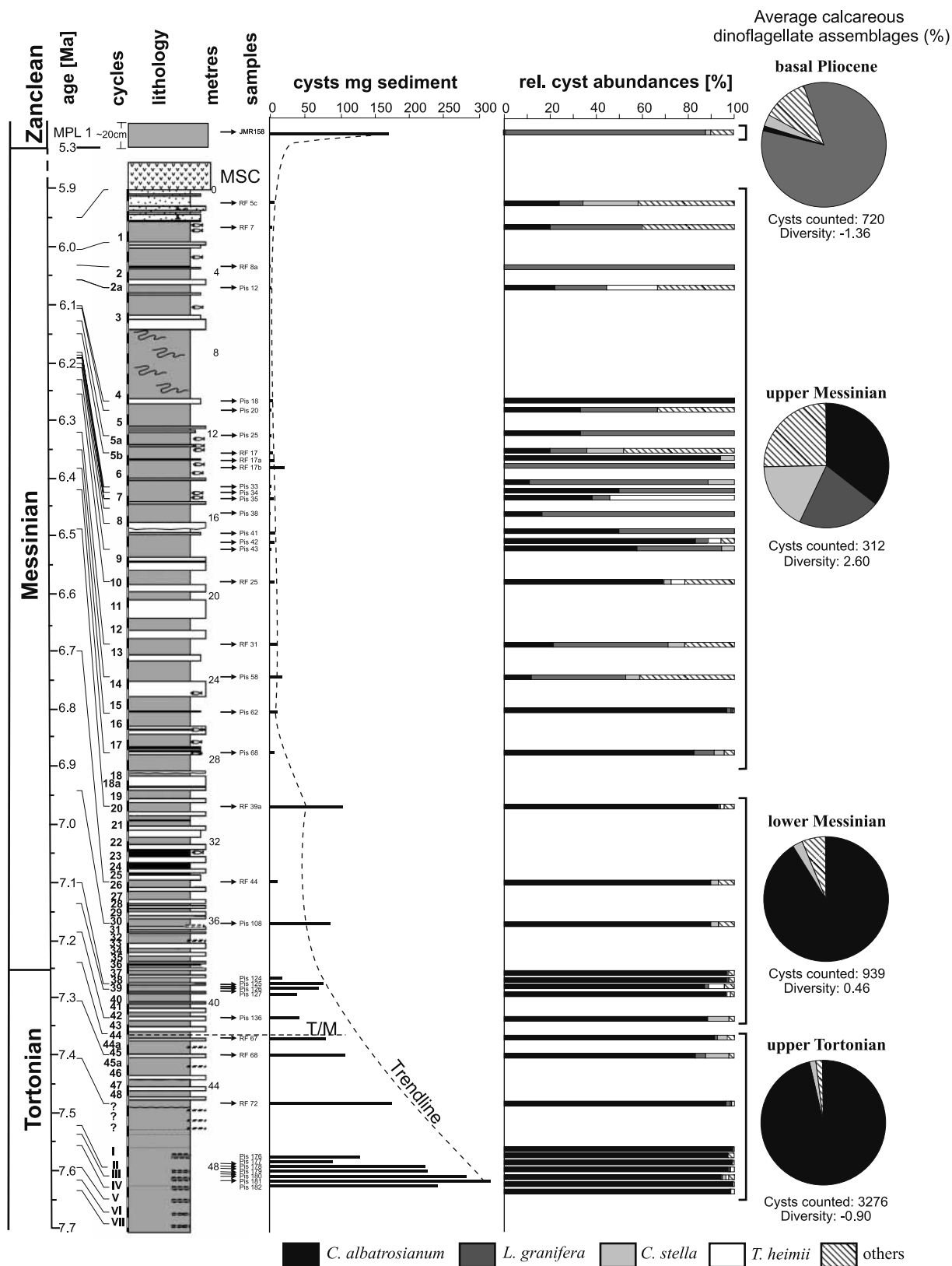
Methods

Samples consisting of 0.5 g dried sediment were disaggregated in 100 ml 0.6% Soda solution. For samples with elevated organic matter contents (e.g. from sapropels), disaggregating and organic matter oxidation were combined in a 10–15% H_2O_2 solution. To speed up the oxidation process samples were heated briefly to 50°C . Samples failing to disaggregate with these procedures were treated with repeated freezing and thawing in saturated sodium sulphate solution. After disaggregating, the suspensions were treated with ultrasound for less than 1 minute to further separate the particles. The 20–75 μm fraction was isolated from the sample by washing with tap water over 75 μm and 20 μm sieves. Randomly selected pilot samples of the <20 μm and >75 μm fractions appeared to contain no calcareous dinoflagellate cysts. To avoid carbonate dissolution, care was taken to perform all procedures in a slightly alkaline environment by adding a few drops of ammonia if necessary.

The 20–75 μm fraction was washed in a sealed 20 ml test tube with lid. To reduce the surface tension and avoid contamination by fungi a few drops of ammonia and ethanol were added (Vink *et al.*, 2000). After a few hours settling, the water was removed with a pipette to a sample volume of 12 ml or 15 ml, depending on the amount of material. For quantitative scanning electron microscopic (SEM) analyses, a round cover glass (13 mm \varnothing) was applied to the tab using a double-sided adhesive lead-tab. Subsequently, a 50 μl sub-sample was applied to the SEM stub. This sub-sample was taken at a depth of 1 cm below the surface of the thoroughly homogenized 12 ml or 15 ml sample using an Eppendorf micropipette. To get a better dispersion of the particles on the cover glass, surface tension was reduced by adding a small drop of ethanol. The solvents were evaporated by heating the stub to nearly 100°C . The stubs were sputtered with gold prior to SEM examination. SEM conditions were 15–20 kV, working distance 12–15 mm. Cysts were counted under the SEM, if necessary, multiple SEM stubs were analysed to reach a statistical relevant outcome. However, cyst concentrations were extremely low for the upper Messinian samples (see Appendix B). The number of cysts per milligram of dry sediment counted on the SEM stubs was calculated as:

$$\text{cysts/mg} = C \times S_t / (S_q \times N \times M), \quad (1)$$

where C is the number of counted cysts, S_t represents the total sample volume in ml (10–15), S_q represents the sub-sample volume applied to the stub in ml (0.05 or 0.10), N is the number of counted stubs and M represents the dry weight of the examined sediment. Diversity was calculated as follows:



$$H = -\sum_{i=1}^n (p_i \ln p_i), \quad (2)$$

Where H is the Shannon–Weaver Diversity Index, which increases with increasing heterogeneity of the sample. P_i is the relative abundance of individuals in the i th species, n is the total number of species in the community (richness), and \ln is the natural logarithm.

Additionally, selected samples were analysed by polarized light microscopy with a gypsum plate (Janofske, 1996) to study the crystallographic orientation of the wall crystals. Especially for species with strong morphological similarities, e.g. *C. levantinum* and *P. tuberosa*, or morphological variations due to diagenetic overprint such as for *L. granifera*, the light optical investigations were used for species differentiation. Within a precession cycle the carbonate beds and marly intervals represent opposite environmental conditions. To enable analysis of the longer-term environmental changes and to circumvent problems with the often unproductive carbonate beds and ensure sample intercomparability, samples were analysed from the marly beds only. For taxonomic information of the examined species see Appendix A.

Repository

The studied material is deposited in the collection of the Division of Historical Geology and Palaeontology, Department of Geosciences, University of Bremen, Germany.

RESULTS

Within the investigated interval 13, generally well-preserved calcareous dinoflagellate species have been identified with strongly varying relative and absolute abundances through time (Fig. 2; App. B). Cyst concentrations (cysts mg^{-1} of dry sediment) vary strongly (Fig. 2). Highest concentrations were recorded in the upper Tortonian samples (79–317 cysts mg^{-1}), while the lowest cyst concentrations are found in the upper Messinian samples (<21 cysts mg^{-1}).

The diversity of the recorded dinoflagellate assemblages fluctuates between very low diversities in the upper Tortonian interval (on average: $H = -0.90$) and moderate to low diversities in the lower Messinian (on average: $H = 0.46$) (Fig. 2; App. B). The dominating species of both time intervals is *C. albatrosianum* with relative abundances >83%, reaching maximum values of 100% in the upper Tortonian samples (Fig. 2). On average, *C. albatrosianum* distinctly dominates the upper Tortonian and lower Messinian assemblages, with 96% and 92% respectively (Fig. 2).

The upper Messinian is marked by strongly varying relative cyst abundances and very low cyst concentrations (0.2–21 cysts mg^{-1}). As a result of this high variability, the average assemblage of this interval is much more diverse ($H = 2.60$) and, depending on the sample, dominated by *C. albatrosianum*, *L.*

granifera or *Caracomia stella* (Fig. 2; App. B). Compared to the upper Tortonian/lower Messinian, *C. albatrosianum* loses its distinct supremacy and becomes rarer, with an average relative abundance of 34% in this interval (Fig. 2). *L. granifera* and *C. stella* clearly increase and temporally dominate the associations but with opposite trends (Fig. 2). *T. heimii*, *Pirumella parva*, *Calciodinellum operosum* and *Melodominula berlinensis* become more important (Fig. 2).

During the basal Pliocene the dominating species of the Tortonian/Messinian period are replaced by *L. granifera* with an 87% relative abundance (Fig. 2). This assemblage is marked by a relatively high cyst concentration (172 cysts mg^{-1}). The diversity is relatively low again ($H = -1.36$), even though the number of species (8) is comparatively high (Fig. 2). Species with slightly increased relative abundances are *Rhabdotherax* spp. (5%) and *C. stella* (3%). In addition *C. elongatum* occurs for the first time (2% of the assemblage) (Fig. 2).

Light microscopic observations of the sibling species *C. levantinum* and *P. tuberosa* showed that only the latter was present.

DISCUSSION

On the basis of calcareous dinoflagellates, the lithology and stratigraphy, four stratigraphic intervals were distinguished, reflecting environmental conditions caused by the Messinian salinity crisis: (1) upper Tortonian interval, (2) lower Messinian interval, (3) upper Messinian interval and (4) basal Pliocene (Fig. 2).

The upper Tortonian is more or less monospecific and strongly dominated by *C. albatrosianum*, similar to the open tropical to subtropical Atlantic Ocean today (Vink, 2004). *C. albatrosianum* has been suggested to be a typical thermocline-dwelling species with a clear connection to warm, oligotrophic waters (Janofske & Karwath, 2000; Wendler *et al.*, 2002a, b; Vink, 2004). It also occurs in the eutrophic upwelling regions of the Arabian Sea (Wendler *et al.*, 2002a, b) and the equatorial and Benguela upwelling areas (Vink, 2004) but always with lower abundances than in the open ocean (Wendler *et al.*, 2002a, b; Vink *et al.*, 2003; Vink, 2004).

One of the most striking features of the upper Tortonian interval is the extremely low diversity caused by the distinct dominance of *C. albatrosianum* (Fig. 2). Calcareous dinoflagellates which tolerate a wide range of environmental conditions have their highest diversity in coastal and more neritic regions (Karwath *et al.*, 2000; Vink *et al.*, 2003; Vink, 2004). Low diversities and dominance of a single species, such as during the Tortonian, indicates relatively stable oceanic conditions (Hildebrand-Habel & Willems, 1997; Kohring, 1997; Meier & Willems, 2003; Kohring *et al.*, 2005). This is in contrast to planktic foraminifera and coccolithophora, where low diversities are typical characteristics of unstable, restricted environmental conditions (Kouwenhoven, 2000; Wade & Bown, 2005; Kouwenhoven *et al.*, 2006).

Fig. 2. Lithology (after Krijgsman *et al.*, 2002), age and cyst abundances (cysts mg^{-1} sediment) of the analysed samples and relative abundances of *C. albatrosianum*, *L. granifera*, *C. stella*, *T. heimii* and other cysts in the analysed samples against time. Lithology according to Krijgsman *et al.* (2002). White levels correspond to more indurated beds, black levels to organic-rich layers (sapropels) and grey levels to softer blue-greyish and laminated marls; dotted levels represent the transitional interval to the evaporites composed of stromatolitic limestones; the 'v'-signed levels symbolize gypsum. Additionally, average calcareous dinoflagellate assemblages in relative abundances and average diversity during the upper Tortonian, lower Messinian, upper Messinian and the basal Pliocene are shown.

The lower Messinian interval has much less cysts mg^{-1} of dry sediment than the upper Tortonian one (Fig. 2). The assemblages are almost similar with only a slight decrease of *C. albatrosianum* and conversely a slightly increased diversity within the lower Messinian samples. These changes are caused mainly by increased relative abundances of *L. granifera* and *C. stella*. In the case of *L. granifera* this indicates a progressively riverine influence (Vink *et al.*, 2000; Wendler *et al.*, 2002b, c; Vink, 2004) caused by the progressive separation of the Mediterranean Basin from the Atlantic Ocean. *C. stella* is, as yet, known only from warmer environments from low and middle latitudes of Miocene/Pliocene age (e.g. Fütterer, 1977; Kohring, 1993a, b, 1997; Keupp & Kohring, 1999; Streng *et al.*, 2002; Hildebrand-Habel & Streng, 2003) and from surface samples of the South Atlantic Ocean (Streng *et al.*, 2002). Higher relative abundances of *C. stella* are associated with more shelfward environments (Keupp & Kohring, 1999; this work) but with a distribution pattern opposite to *L. granifera* (Fig. 2). Furthermore, higher concentrations of *C. stella* in the Mediterranean upper Miocene/Pliocene (Keupp & Kohring, 1993, 1999; Kohring, 1993b, 1997; this work) occur together with *C. albatrosianum*, representatives of the *edgarii*-group and *P. tuberosa*, implying similar environmental preferences (Table 1, Fig. 2). Hence, higher abundances of *C. stella* are probably indicative of oligotrophic, coastal warm waters with normal or slightly increased salinities.

Thus, the modifications of the lower Messinian interval possibly already reflect the beginning of more unstable and restricted conditions caused by the Messinian salinity crisis. Importantly, this first notable shift in calcareous dinoflagellate assemblages already occurs shortly before the Tortonian–Messinian boundary at 7.3 Ma (Fig. 2; sample RF 66) and pre-dates the disappearance of a group of open-marine, deep-water benthic foraminifera taxa at 7.167 Ma in the Pissouri Basin (Kouwenhoven *et al.*, 2006).

The third, upper Messinian, interval is much more diverse ($H=0.58\text{--}4.61$) but possesses only few cysts. The dinoflagellate assemblages reveal striking variations in species abundances (Fig. 2) which are interpreted as reflecting fluctuating salinities, nutrients and temperatures towards the evaporitic stage. All samples show an inverse relationship between *L. granifera* on the one hand and *C. stella* and to an even larger extent *C. albatrosianum* on the other. Abundance peaks of *L. granifera*, together with a decrease in *C. albatrosianum* and *C. stella*, are likely the response to enhanced continental runoff, resulting in nutrient-enriched surface waters with reduced salinities. High abundances of *C. albatrosianum* can be interpreted as a temporary re-establishment of normal marine oligotrophic conditions. In contrast to this, the sporadic occurrence of the more neritic *Bicarinellum tricarinelloides*, *Melodromuncula berlinensis*, *Pirumella parva* and *Rhabdothorax* spp. indicate temporary shallowing of the basin. On average the upper Messinian assemblage is much more diverse ($H=2.6$) and reflects very unstable, more neritic conditions with varying fluvial input. Additionally, frequent occurrence of ascidian sclerites emphasizes the more neritic character of this interval (Fütterer, 1977).

The basal Pliocene assemblage reflects the restoration of normal marine conditions just after the replenishment of the Mediterranean Basin (Spezzaferri *et al.*, 1998; Rouchy *et al.*,

	Cyprus/Pissouri (upper Tortonian)	Cyprus/Pissouri (lower Messinian)	Crete/Episkopi I/II (upper Miocene/ Messinian)	Cyprus/Pissouri (upper Messinian)	Algeria/El Medhi (upper Miocene/ Messinian)	Sicily/Centruripe (lower Pliocene/ above Trubi)	Malta/Blue Clay (upper Miocene/ Serravalian)	Cyprus/Pissouri (basal Pliocene)
	Bison <i>et al.</i> (this work)	Bison <i>et al.</i> (this work)	NN 11 Keupp & Kohring (1999)	Bison <i>et al.</i> (this work)	NN 10–11 Keupp & Kohring (1993)	NN 12–15 Kohring (1993)	Kohring (1997)	MPL 1 Bison <i>et al.</i> (this work)
<i>C. albatrosianum</i>	96	92	45	34	13	16	7	1
<i>L. granifera</i>	1	2	—	22	15	22	80	87
<i>C. stella</i>	2	2	23	18	8	7	8	3
<i>P. edgarii</i> -group	—	—	21	1	45	33	2	—
<i>Rhabdothorax</i> spp.	—	1	4	—	8	8	1	5
<i>P. tuberosa</i>	—	—	3	5	—	10	—	—
Others	1	3	4	20	11	12	2	4

Table 1. Relative abundances (%) of calcareous dinoflagellate species from selected Neogene Mediterranean localities discussed in the text.

2001). However, a strong change in the association, compared with the Miocene assemblages, took place: *L. granifera* clearly dominates the assemblage and obviously replaced *C. albatrosianum*. It is hypothesized that a low salinity, high nutrient layer of fresh water must have spread out over the dense, saline waters. Rouchy *et al.* (2001) and Iaccarino *et al.* (1999) also observed a continued and significant fresh-water input in the Mediterranean Basin, which probably affected particularly proximal land areas such as the Pissouri Basin in the eastern Mediterranean (Iaccarino *et al.*, 1999; Rouchy *et al.*, 2001). These observations support the hypothesis that simultaneous to the salinity crisis, the Mediterranean climate changed from a more arid Tortonian to a humid late Messinian and basal Pliocene one (Diester-Haass *et al.*, 1998; Fauquette *et al.*, 1998), marked by high monsoonal activity (Griffin, 1999). Such intensified monsoonal precipitation also occurs during orbital precession minima which are, in turn, associated with strong Northern Hemisphere (NH) summer insolation, resulting in increased discharge from the Nile (e.g. Rossignol-Strick, 1985; Hilgen, 1991; Diester-Haass *et al.*, 1998). Although Mediterranean sapropels have been formed during precession minima (Wehausen & Brumsack, 1998; Lange *et al.*, 1999; Meier *et al.*, 2004), precession minima at the basal Pliocene (Rossignol-Strick, 1985; Hilgen, 1991; Castradori, 1998; Steenbrink *et al.*, 2006; Van der Laan *et al.*, 2006) did not lead to sapropel formation in the Pissouri Basin.

Comparison with other Neogene Mediterranean assemblages

The species spectrum of calcareous dinoflagellates from the Pissouri section agrees well with that reported by most other Neogene studies from the Mediterranean so far (Keupp & Kohring, 1993, 1999; Kohring, 1993, 1997; Table 1). Only some rare species, such as *Cervisiella saxea* and *Calcipterellum colomi*, could not be found in the Pissouri samples. One exception is *Orthopithonella sicelis*, which is known only from a poorly preserved lower Pliocene section on Sicily, where it dominates (26%) the calcareous dinoflagellate assemblage (Kohring, 1993; Table 1, included in the *edgarii*-group). In the authors' opinion this basal Pliocene assemblage from Sicily reflects a more neritic environment, with *O. sicelis* as the dominating species and abundant *P. parva*. In the material *O. sicelis* could not be found, whereas *P. parva* is scarce (Fig. 2). An obvious explanation is that the basal Pliocene of the Pissouri Basin represents a deeper-marine environment (Rouchy *et al.*, 2001) unsuitable for these taxa.

However, a comparison of the Pliocene dinoflagellate assemblage from Sicily (Kohring, 1993) and Messinian assemblages from Algeria (Keupp & Kohring, 1993) with this upper Messinian assemblage shows more agreement in relative abundances and the species spectrum (Table 1). All three assemblages are relatively highly diverse and share most major members (*L. granifera*, *C. albatrosianum*, *C. stella*); however, there are deviations in relative abundances and lower contributions of *C. albatrosianum* and *C. stella* in the Algerian and Sicilian assemblages (Table 1). The striking difference between the upper Miocene assemblage of the Pissouri section and those of the Algerian and Sicilian ones is the high abundance of representatives of the *edgarii*-group in the latter sections (Table 1), which gives them a stronger neritic character. Furthermore, the Sicilian

assemblage is characterized by a slightly higher amount (10%) of *O. tuberosa* (now *Pirumella tuberosa*), reflecting elevated salinity and more oligotrophic conditions (Vink, 2004). Therefore, the dilution and eutrophication via fluvial input might have been less significant.

A relatively shallow warm-water environment is proposed, with mesotrophic and mesohaline conditions for the late Miocene Algerian and basal Pliocene Sicilian sedimentation areas. Although Kohring (1993) and Keupp & Kohring (1993) also assumed warm-water conditions and revealed the nearshore character of the *edgarii*-group, a concluding interpretation of the environment is missing. Abundance variations of *C. albatrosianum* and *L. granifera* (formerly *Sphaerodina albatrosiana* and *Orthopithonella granifera*, respectively) are seen merely as fluctuating Atlantic influences. These variations are interpreted as fluctuating terrigenous runoff and associated salinity and nutrient variations.

Regardless of the different stratigraphical and palaeogeographical positions, the basal Pliocene assemblage and the upper Miocene (Serravallian) assemblage of Kohring (1997) from Malta (Blue Clay Formation) agree well (Table 1). Both assemblages are more or less monospecific, with a clear dominance of *L. granifera* (87% and 80% respectively), reflecting a strong fluvial influence.

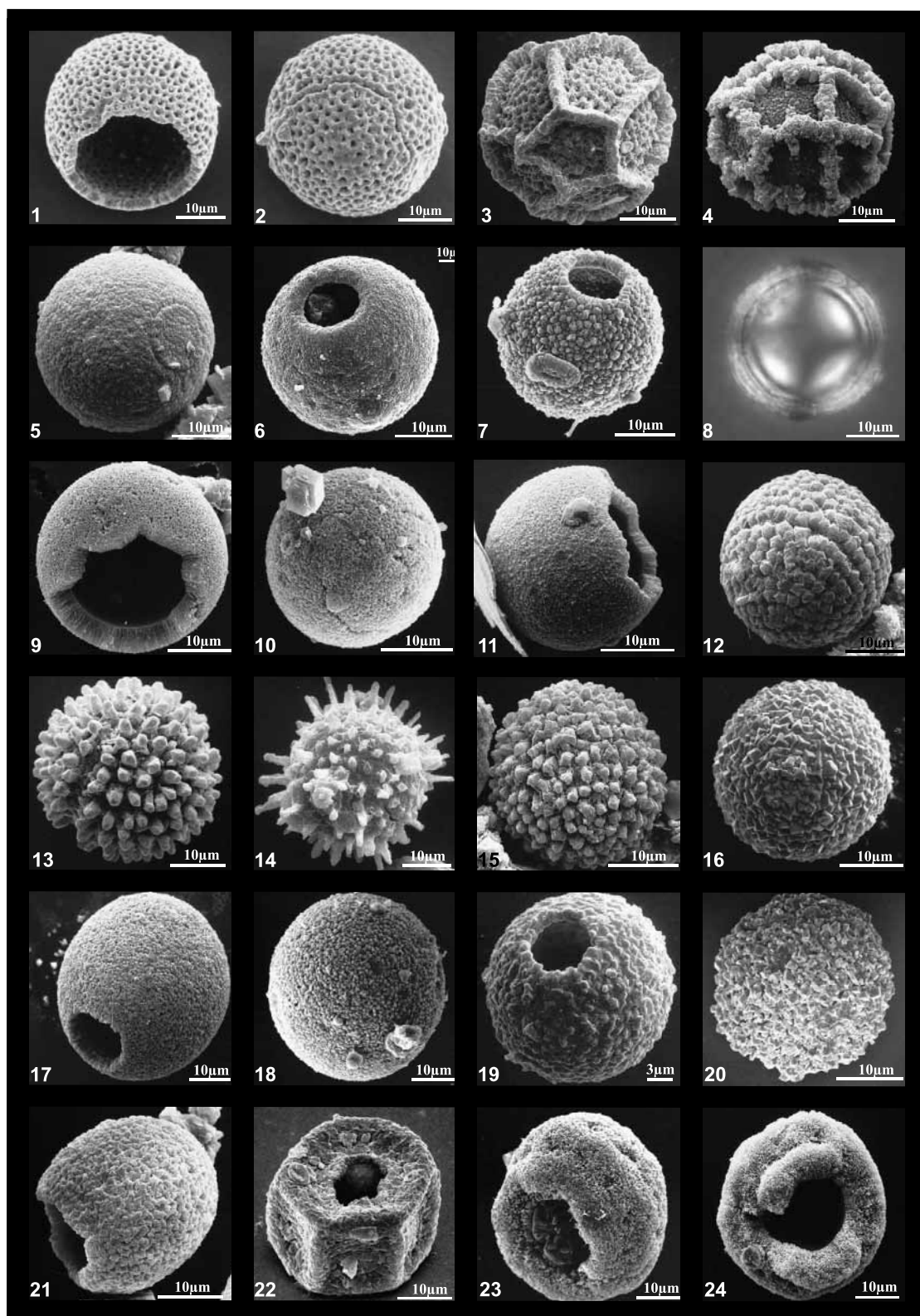
Keupp & Kohring (1999) described a calcareous dinoflagellate assemblage from the upper Miocene of Crete (Episkopi) (Table 1) which differs from the aforementioned associations by the absence of *L. granifera* and elevated amounts of *C. albatrosianum*. Again, due to its interpretation as a typical pelagic open marine species (Kohring, 1993, 1997), Keupp & Kohring (1999) interpreted the absence of *L. granifera* as a decreasing Atlantic influence. The absence of *L. granifera* is further attributed to missing fluvial influence.

These results agree well with other microfossil studies of the Pissouri Basin (Rouchy *et al.*, 2001; Krijgsman *et al.*, 2002; Kouwenhoven *et al.*, 2006). Only the calcareous dinoflagellates reported by Kouwenhoven *et al.* (2006) differ significantly from the current data; this relates to the use of different methodologies and taxonomic concepts.

The interpretation of a warm, oligotrophic environment for the upper Tortonian interval correlates well with the distribution pattern of coccoliths and planktic foraminifera (Kouwenhoven *et al.*, 2006). These authors infer a transition from a cool-water, high-productivity environment (abundance maximum of *Coccolithus pelagicus*) to higher sea surface temperatures (SST) and oligotrophic conditions just below the lowermost sample at 7.5 Ma. This shift is also apparent from the decrease in the cold-water-indicating planktic foraminifera (Neoglobobulimina and *Globobulimina* spp.) and an increase in the subtropical and oligotrophic *Globigerinoides* spp. (Kouwenhoven *et al.*, 2006).

Pissouri Basin associations versus recent Mediterranean assemblages

The calcareous dinoflagellate assemblages from the Pissouri Basin are very unlike those of the recent Mediterranean Sea. Although most of the main upper Miocene to lower Pliocene calcareous dinoflagellate species are extant, some species of the modern Mediterranean are missing in the record from this study



and vice versa. The most relevant species in this context are *C. levantinum* and *P. parva*. *C. levantinum* today dominates the western Mediterranean associations but distinctly decreases eastwards (Meier & Willems, 2003). Currently it is unknown when *C. levantinum* started its extension into the eastern Mediterranean Basin. *P. parva*, a representative of the *edgarii*-group, is lacking in the modern Mediterranean. This species disappeared possibly somewhere during the late Pliocene, possibly in relation to the onset of the Northern Hemisphere glaciations (Streng *et al.*, 2004). *P. parva* has been suggested to prefer nearshore environments and warm waters (Hildebrand-Habel & Willems, 2000; Hildebrand-Habel & Streng, 2003).

The dominance of *C. albatrosianum* in the upper Tortonian to lower Messinian assemblages has no equivalent in the modern Mediterranean. Today this species accounts for less than 5% of the Mediterranean associations (Meier & Willems, 2003), similar to its abundance in the Pliocene record here. It is proposed that conditions similar to those in modern oceans, with high amounts of *C. albatrosianum* (Wendler *et al.*, 2002a; Tanimura & Shimada, 2004; Vink, 2004), prevailed in the Mediterranean during the late Tortonian and early Messinian.

C. elongatum, a common species in the eastern Mediterranean today, and which occurs for the first time in the basal Pliocene sample, might be seen as an Atlantic newcomer.

T. heimii is the most abundant calcareous dinoflagellate species in the present-day Mediterranean Sea (e.g. Zonneveld *et al.*, 2001; Meier & Willems, 2003). This species, which can be traced back to the K/T boundary (Hildebrand-Habel *et al.*, 1999), occurs in the material only sporadically and with very low relative and absolute abundances (<2 cysts mg⁻¹). The only exceptions are in two of the upper Messinian samples (Fig. 2) where this species accounts for 22% and 54% of the assemblage. However, in total, this species remains rare over the Messinian salinity crisis and after the restoration of marine conditions with the beginning of the Pliocene. Until now it remains unclear why, and when, *T. heimii* started to dominate the Mediterranean calcareous dinoflagellate assemblages.

L. granifera and *C. stella*, which increase in proximity to the Messinian salinity crisis, are either very scarce or not present (*C. stella*) in the modern Mediterranean (Meier & Willems, 2003).

Only one specimen of *L. granifera* was reported from a survey of surface samples taken throughout the Mediterranean by

Meier & Willems (2003). However, this species is abundant in the S1 sapropel (c. 8–30% of the assemblages) (Meier *et al.*, 2004), an environment which is therefore closer to the basal Pliocene environment. The other species linked to the S1 sapropel, *C. levantinum*, is not present in the samples. Compared to the present Mediterranean, which is characterized by oligotrophic, high saline water masses with strong east–west gradients (Meier *et al.*, 2004), the Mediterranean during S1 deposition was marked by enhanced fresh-water discharge and consequently increased nutrient concentration (Meier *et al.*, 2004). A similar situation, but far much severe, is proposed to have occurred during the basal Pliocene in the eastern Mediterranean, when huge amounts of fresh water spread out over the re-establishing Mediterranean (e.g. Diester-Haass *et al.*, 1998; Rouchy *et al.*, 2001). The species that apparently benefits most from this configuration in both settings is *L. granifera*. Interestingly, this did not lead to sapropel formation in the earliest Pliocene, suggesting sufficient ventilation of the deeper water masses.

The low relative abundance of *C. albatrosianum* mentioned above, a feature of this basal Pliocene assemblage, is in common with the modern Mediterranean ones. Furthermore, *L. urania* and *C. elongatum*, which are common in the eastern Mediterranean today, peak (*L. urania*) or appear for the first time (*C. elongatum*) in the Pliocene material.

L. urania and *C. elongatum* have a strong affinity with oligotrophic waters of elevated salinities, such as in the modern eastern Mediterranean, where these species form large parts of the calcareous dinoflagellate assemblages (Meier *et al.*, 2004). Today *L. urania* is restricted almost entirely to the high saline (c. 39 psu) and oligotrophic eastern Mediterranean Sea and only a few specimens have been recorded from the Tyrrhenian Sea (Meier *et al.*, 2002, 2004; Meier & Willems, 2003). Even though *L. urania* and *C. elongatum* are present within the basal Pliocene samples they remain scarce. *L. urania* is restricted to the eastern Mediterranean today, it has also been reported from the Miocene Indian Ocean (Streng *et al.*, 2004), but not from the Atlantic. This gives the species a Tethyan rather than an Atlantic signature. Therefore, it is suggested, in agreement with Meier & Willems (2003), that some specimens of *L. urania* survived the salinity crisis within the Mediterranean. It is unclear when *L. urania* established its dominant position in the eastern Mediterranean.

Explanation of Plate 1.

Scanning electron (SEM) images and one light microscope image. **figs 1–2.** *Calciadinellum albatrosianum* (sample PIS182, upper Tortonian, apical view): **1**, open cyst with polygonal archaeopyle; **2**, closed cyst with polygonal delineated operculum. **figs 3–4.** *Calciadinellum operosum* (sample RF17a, upper Messinian): **3**, paratabulated cyst with well-developed crystal ridges and large pores; **4**, lateral view, closed cyst with blocky crystallite ridges and reduced pores. **figs 5–8.** *Leonella granifera* (sample JMR158): **5**, basal Pliocene, side apical view, SEM image, spherical cyst with round operculum; **6**, sample RF17a, upper Messinian, side apical view, SEM image, cyst with open archaeopyle; **7**, basal Pliocene, side view, SEM image, cysts with open archaeopyle and coarser surface crystallites. **8**, light optical view under crossed nicols. **figs 9–11.** *Caracomia stella* Streng *et al.*, 2002: **9**, sample RF17a, upper Messinian, apical view, open cyst with large polygonal archaeopyle; **10**, sample JMR158, basal Pliocene, side apical view of closed cyst, with delineated archaeopyle suture; **11**, sample RF17a, upper Messinian, side view of open cyst. **fig. 12.** *Lebessphaera urania* (sample PIS136, upper Tortonian), lateral view of closed cyst, operculum suture visible in the upper part. **figs 13–15.** *Rhabdotherax* spp. (upper Messinian): **13**, sample PIS126, spherical closed cyst with shorter blocky spines; **14**, sample PIS108, closed cyst with long spines; **15**, sample PIS126, spherical cyst with reduced blocky spines. **fig. 16.** *Pernambugia tuberosa* (sample RF17a, upper Messinian), closed spherical cyst with pyramid-like cyst surface crystals. **figs 17–18.** *Pirumella parva* (sample PIS68, upper Messinian): **17**, side apical view, elongated cyst with small round archaeopyle; **18**, spherical closed cyst, no operculum suture visible. **fig. 19.** *Thoracosphaera heimii* (sample PIS41, upper Messinian), spherical cyst with small round archaeopyle, irregular surface crystals. **fig. 20.** *Pirumella loeblichii* (sample PIS180, upper Tortonian), spherical cyst with irregularly arranged surface crystals. **fig. 21.** *Calciadinellum elongatum* (sample JMR158, basal Pliocene), elongated cyst with open paratabulated archaeopyle. **fig. 22.** *Melodomoncula berlinensis* (sample RF17a, upper Messinian), lateral apical view of open cyst. **figs 23–24.** *Bicarinellum tricarineloides* (sample RF17a, upper Messinian): **23**, side apical view of open cyst; **24**, same cyst, apical view.

CONCLUSIONS

The impact of the Messinian salinity crisis on Mediterranean calcareous dinoflagellate assemblages was analysed from the Pissouri Basin on Cyprus. Time slices before, during and after the salinity crisis were investigated. The main objective of this paper was to investigate longer-term palaeoenvironmental changes in relation to the Messinian salinity crisis in the eastern Mediterranean based on calcareous dinoflagellates. The dominance of *C. albatrosianum* and its high absolute and relative abundance during the late Tortonian and early Messinian is unlike modern Mediterranean Sea associations. It is most similar to the modern tropical Atlantic (Vink *et al.*, 2002). Changing environmental conditions caused by the separation of the Mediterranean Sea from the Atlantic Ocean, superimposed by short-term (precession-controlled) variability, led to the replacement of *C. albatrosianum*-dominated assemblages by *L. granifera*-dominated ones after the salinity crisis. At the same time the species diversity changed from low diverse, almost monospecific associations during the late Tortonian and early Messinian, through relatively highly diverse associations during the late Messinian, to low diversity ones again during the basal Pliocene. With the re-filling of the Mediterranean Basin, just after the Miocene/Pliocene boundary, the Atlantic element *C. elongatum* occurs for the first time and contributes to a more modern character of the Pliocene associations. The basal Pliocene calcareous dinoflagellate assemblage most closely resembles those of the Holocene S1 sapropel but still differs from the present Mediterranean ones. The final changes to current Mediterranean calcareous dinoflagellate associations must have taken place after the disappearance of the more or less monospecific earliest Pliocene association. Finally, it can be said that the Messinian salinity crisis did not lead to a permanent removal of oceanic calcareous dinoflagellate taxa from the Pissouri Basin. Most of the dinoflagellate cyst species of this period are still present in the modern Mediterranean and they can be interpreted as re-immigrants to the Mediterranean from the Atlantic. The exception is *L. urania*, which must have survived the salinity crisis in the Mediterranean.

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APPENDIX A: Annotated listing of calcareous dinoflagellate taxa found in the investigated material

Division **Dinoflagellata** (Bütschli, 1885) Fensome *et al.*, 1993
 Subdivision **Dinokaryota** Fensome *et al.*, 1993
 Class **Dinophyceae** Pascher, 1914
 Subclass **Peridiniphyceae** Fensome *et al.*, 1993
 Order **Peridiniales** Haeckel, 1894
 Suborder **Peridiniineae** Autonym
 Family **Peridiniaceae** Ehrenberg, 1831
 Subfamily **Calciodinelloideae** Fensome *et al.*, 1993

Bicarinellum tricarinelloides Versteegh, 1993 (Pl. 1, figs 23, 24)
Calciodinellum albatrosianum (Kamptner, 1963) Janofske & Karwath, 2000 (Pl. 1, figs 1, 2)
Calciodinellum elongatum (Hildebrand-Habel *et al.*, 1999) Meier *et al.*, 2002 (Pl. 1, fig. 21)
Calciodinellum operosum Deflandre, 1947 (Pl. 1, figs 3, 4)
Caracomia stella (Gilbert & Clark, 1983) Streng *et al.*, 2002 (Pl. 1, figs 9–11)
Lebessphaera urania Meier *et al.*, 2002 (Pl. 1, fig. 12)
Melodomuncula berlinensis Versteegh, 1993 (Pl. 1, fig. 22)
Pernambugia tuberosa (Janofske & Karwath, 2000) Hildebrand-Habel *et al.*, 1999 (Pl. 1, fig. 16)
Pirumella parva (Bolli, 1974) Lentin & Williams, 1993 (Pl. 1, fig. 17–18)
Pirumella loeblichii (Bolli, 1974) Lentin & Williams, 1993 (Pl. 1, fig. 20)
Rhabdothorax spp. (Kamptner, 1937) Kamptner, 1958 (Pl. 1, figs 13–15)
 Order **Thoracosphaerales** Tangen in Tangen *et al.*, 1982
 Family **Thoracosphaeraceae** Schiller, 1930 emend. Tangen in Tangen *et al.*, 1982
Thoracosphaera heimii (Lohmann, 1920) Kamptner, 1944 (Pl. 1, fig. 19)
Leonella granifera (Fütterer, 1977) Janofske & Karwath, 2000 (Pl. 1, figs 5–8)

According to the new phylogenetic ideas of Gottschling *et al.* (2005) and the close relationship of *Leonella* and *Thoracosphaera*, *L. granifera* is grouped under Thoracosphaerales rather than under Calciodinelloids, as previously. The light optical appearance of the cysts is identical to that of typical *L. granifera*. However, upon SEM analysis it appears that most of the *L. granifera* cysts differ from the type in the absence of pores in the outer cyst surface and by a characteristic wall surface with epitaxially grown crystals. Since the whole spectrum of intermediate forms is also observed, the observed morphological variation is interpreted as a slight diagenetic overprint. This morphological variation of *L. granifera* was also observed in other Neogene Mediterranean samples (e.g. Keupp & Kohring, 1993; Kohring, 1993).

APPENDIX B

Table B1 shows the count data and calculated diversity data for all analysed samples.

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Sample	<i>C. albatrossianum</i>				<i>C. operosum</i>				<i>C. elongatum</i>				<i>C. stella</i>				<i>L. granifera</i>				<i>L. urania</i>				<i>M. berlinensis</i>				<i>B. tricarinaloides</i>				<i>P. parva</i>				<i>P. tuberosa</i>				<i>Rhabdohorax</i> spp.				<i>P. loeblichii</i>				<i>T. heinii</i>				Unidentified		Total no. of Dinos	Diversity
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%														
JMR 158	7	1	1	0	11	2	18	2	626	87	11	2	2	0	0	0	0	0	0	0	38	5	0	0	0	0	0	0	6	1	721	-1.37																								
RF 5c	7	24	1	3	0	0	7	24	3	10	2	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	31	29	2.82																									
RF 7	1	20	0	0	0	0	0	0	2	40	0	0	1	20	0	0	0	0	0	0	0	0	0	0	0	0	0	1	20	5	4.33																									
RF 8a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4.61																									
PIS 12	0	0	0	0	0	0	2	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3.91																										
PIS 18	2	22	0	0	0	2	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	33	9	3.78																											
PIS 20	2	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3.91																										
PIS 25	1	33	1	33	0	0	1	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	4.61																										
RF 17	1	33	0	0	0	2	67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	33	9	3.78																											
RF 17a	5	20	0	0	0	4	16	4	16	0	0	2	8	8	32	0	0	1	4	1	4	0	0	0	0	0	0	0	25	3.12																										
RF 17b	66	94	0	0	0	4	6	0	0	0	0	0	0	0	0	0	0	0	1	100	0	0	0	0	0	0	0	0	70	0.58																										
PIS33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	4.61																										
PIS34	0	0	0	0	0	0	0	0	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4.61																										
PIS35	1	11	0	0	0	0	1	11	7	78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	3.09																										
PIS38	1	50	0	0	0	0	0	0	1	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4.61																										
PIS41	5	38	0	0	0	0	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	54	0	13	2.94																										
PIS42	1	17	0	0	0	0	5	83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	3.26																										
PIS43	1	50	0	0	0	0	0	0	1	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4.61																										
RF 25	15	83	0	0	0	0	0	0	1	6	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6	0	18	2.35																										
RF 31	11	58	0	0	0	0	1	5	7	37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	2.5																										
PIS 58	23	70	0	0	0	0	1	3	0	0	0	0	3	7	0	0	2	5	0	0	1	3	0	0	2	6	5	15	33	2.13																										
PIS 62	9	21	1	2	0	0	3	7	21	50	0	0	3	7	0	0	2	5	0	0	1	2	0	0	0	0	2	5	42	2.39																										
PIS 68	2	12	0	0	0	0	1	6	7	41	0	0	0	0	0	0	3	18	0	0	0	0	0	0	0	0	4	24	17	3.2																										
RF 39a	212	97	0	0	0	0	1	0	4	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	219	-0.61																										
RF 44	19	83	1	4	0	0	1	4	2	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	2.11																										
PIS 108	172	93	0	0	0	0	0	0	2	1	2	1	0	0	0	0	0	0	0	0	2	1	0	0	3	2	4	2	185	-0.25																										
PIS 124	27	90	0	0	0	0	1	3	0	0	1	3	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	30	1.64																										
PIS 125	123	97	0	0	0	0	0	0	1	1	2	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	127	-0.07																										
PIS 126	102	87	1	1	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	3	3	0	8	7	1	1	117	0.39																											
PIS 127	62	97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	2	0	64	0.61																											
PIS136	154	89	0	0	0	0	16	9	0	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	174	-0.14																										
RF67	151	92	1	1	0	0	7	4	2	1	3	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	165	-0.10																										
RF68	188	83	0	0	0	0	23	10	10	4	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	226	-0.19																										
RF 72	352	96	0	0	0	0	2	1	7	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	1	365	-1.10																											
PIS 176	212	99	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	214	-0.70																										
PIS 177	147	97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	1	1	151	-0.27																											
PIS 178	372	99	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	375	-1.27																										
PIS 179	370	97	0	0	0	0	2	1	0	0	3	1	0	0	0	0	0	1	0	2	1	0	0	0	2	1	0	0	380	-1.17																										
PIS 180	444	94	0	0	0	0	8	2	1	0	0	0	0	0	0	0	3	1	0	0	0	8	2	6	1	0	0	470	-1.25																											
PIS 181	527	100	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	528	-1.65																										
PIS 182	395	98	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	4	1	0	0	0	0	0	402	-1.28																										
sum:																													5248																											

Appendix 2. Count data and calculated diversity data.

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