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From greenhouse to icehouse; organic-walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene

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Abstract

Dinoflagellates are an important component of the extant eukaryotic plankton. Their organic-walled, hypnozygotic cysts (dinocysts) provide a rich, albeit incomplete, history of the group in ancient sediments. Building on pioneering studies of the late 1970s and 1980s, recent drilling in the Southern Ocean has provided a wealth of new dinocyst data spanning the entire Paleogene. Such multidisciplinary studies have been instrumental in refining existing and furnishing new concepts of Paleogene paleoenvironmental and paleoclimatic reconstructions by means of dinocysts.

Because dinocysts notably exhibit high abundances in neritic settings, dinocyst-based environmental and paleoclimatic information is important and complementary to the data derived from typically more offshore groups as planktonic foraminifera, coccolithophorids, diatoms and radiolaria. By presenting case-studies from around the globe, this contribution provides a concise review of our present understanding of the paleoenvironmental significance of dinocysts in the Paleogene (65–25 Ma). Representing Earth's greenhouse–icehouse transition, this episode holds the key to the understanding of extreme transient climatic change. We discuss the potential of dinocysts for the reconstruction of Paleogene sea-surface productivity, temperature, salinity, stratification and paleo-oxygenation along with their application in sequence stratigraphy, oceanic circulation and general watermass reconstructions.
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1. Introduction

The Paleogene has by now emerged as representing a climatically highly dynamic period, which involved the Earth's transformation from a greenhouse to an icehouse state. It has become increasingly apparent that this transformation was not gradual, but instead was characterized by numerous extreme transient climatic events (see Zachos et al., 2001 for an overview). It has become generally appreciated that dinocyst paleoenvironmental analysis is a key element in understanding Paleogene paleoceanographic change and climate dynamics.

Dinoflagellates are single-celled, predominantly marine, eukaryotic plankton that typically occur as

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motile cells in surface waters (e.g., Fensome et al., 1996a), sometimes in astonishing concentrations (e.g., 'red tides'). Although most dinoflagellates are autotrophic, many dinoflagellates have heterotrophic lifestyles and may rank among the zooplankton. As part of their—often complex—life cycle, some dinoflagellates produce preservable organic-walled hypnozygotic resting cysts (dinocysts). In addition, (mainly vegetative) calcareous and siliceous cysts are known. The cyst part of the dinoflagellate life cycle is usually associated with sexual reproduction and is induced by particular surface water parameters, predominantly seasonal nutrient depletion, that only prevail for a brief period (Taylor, 1987). Typically, the motile stage does not preserve, but organic dinocysts are found from the late Triassic onwards (e.g., MacRae et al., 1996 and references therein).

Together with diatoms and coccolithophorids, dinoflagellates are among the most prominent marine primary producers in the oceans today and, as such, play an important role in the global carbon cycle (e.g., Brasier, 1985). Moreover, they were probably an important factor in the development of coral reef systems; the ecological success of scleractinian corals since the Triassic was probably a direct result of their acquisition of dinoflagellate symbionts, which allowed them to exploit nutrient-poor environments (Haeckel, 1894; Trench, 1987). Dinoflagellate symbionts are also known from some groups of extant and fossil planktonic foraminifera (e.g., Spero, 1987).

The strong interest in dinoflagellates also has economic reasons. In addition to their position at or near the base of the marine food chain, modern dinoflagellates are known to cause massive fish kills (e.g., Heil et al., 2001; Cembella et al., 2002), paralytic shellfish poisoning in humans, and constitute other harmful algal blooms (e.g., Backer et al., 2003). The high economic impact of these phenomena has stimulated extensive research in order to develop preventive measures (e.g., Taylor and Seliger, 1979; Hallegraeff, 1993; Fogg, 2002; abstracts in Matsuoka et al., 2003). Over the past decades, the importance of dinocyst analysis has been increasingly recognized in hydrocarbon exploration where dinocyst biostratigraphy has now emerged as a routine tool (see, e.g., Stover et al., 1996; Williams et al., 2004, for a summary of existing Triassic to Neogene dinocyst

biozonations). In many oil and gas provinces, such as the Paleogene of the North Sea Basin, they have yielded a higher stratigraphic resolution than calcareous microfossils (e.g., Gradstein et al., 1992). Remains of dinoflagellates are also major components of petroleum source rocks (Ayres et al., 1982) due to their ability to store lipids (Bold, 1973; Horner, 1985).

Over the past 30 years, organic-walled dinocysts have been increasingly employed as sensitive (paleo-) environmental indicators (e.g., Downie et al., 1971; Mudie and Harland, 1996; Wall et al., 1977; see overviews in, e.g., Dale, 1996; Pross et al., 2004). Generally, dinocyst (paleo-)ecology is best understood for Quaternary assemblages due to the high number of extant taxa that can be studied following an actuo-paleontological approach (e.g., Turon, 1981; Harland, 1983; de Vernal and Mudie, 1992; Harland and Long, 1996; Dale, 1996, 2001; Rochon et al., 1999; Targarona et al., 2000; Boessenkool et al., 2001; Marret and Scourse, 2002; Sangiorgi et al., 2002, 2003; Sprangers et al., 2004; see Matthiessen et al., submitted for publication for a detailed discussion). Such Quaternary studies have shown that organic walled cyst-producing dinoflagellates are indeed highly sensitive to even small changes in surface water characters. As the number of extant dinocysts decreases back in time, the process of relating dinocyst taxa to specific environmental parameters becomes more difficult for pre-Quaternary assemblages. Despite this drawback, building on actuo- and Quaternary studies, dinocyst-based 'deep time' paleoenvironmental reconstructions have become increasingly more realistic and sophisticated over the past decades. Moreover, recent ocean drilling, e.g., in the Southern Ocean, has provided a wealth of Paleogene dinocyst data boosting more integrated, multidisciplinary studies and interpretations (Brinkhuis et al., 2003a,b; Sluijs et al., 2003; Röhl et al., in press(a,b); Schellenberg et al., in press; Williams et al., 2004; Huber et al., in press; van Simaeys et al., submitted for publication; Stickley et al., in press). These and similar other recent efforts have led to considerable progress in Paleogene dinocyst paleoecology.

Considering the above, we here aim to provide a concise review of applied methodologies and illustrate the environmental and climatic signals currently recognized through Paleogene dinocyst studies, often also utilizing Quaternary examples. For this purpose,

we present a selection of Paleogene case studies from the northern and southern hemispheres, and include a brief introduction into the nature of the fossil dinocyst record.

2. The fossil dinoflagellate record

The earliest organic-walled cysts with firmly established dinoflagellate affinity are found in the mid-Triassic. To date, the oldest records have been described from Australia (late Anisian: Nicoll and Foster, 1994, Anisian/Ladinian: Helby and Stover in Goodman, 1987) and Arctic Canada (possibly late Early Triassic: Sarjeant in Goodman, 1987). Because

first lower-latitude records are slightly younger (early Carnian; Hochuli and Frank, 2000), it has been hypothesized that dinoflagellates forming organic-walled cysts developed in high-latitude settings (Stover et al., 1996). Biogeochemical evidence, however, suggests an origin of the dinoflagellate lineage in the Precambrian or early Cambrian (Fensome et al., 1996b; Moldowan and Talyzina, 1998). The late Silurian *Arpylorus*, long considered to be the earliest dinophycean cyst (Sarjeant, 1978), has recently been demonstrated not to be of dinoflagellate affinity and is probably an arthropod remain (LeHérissé et al., 2000).

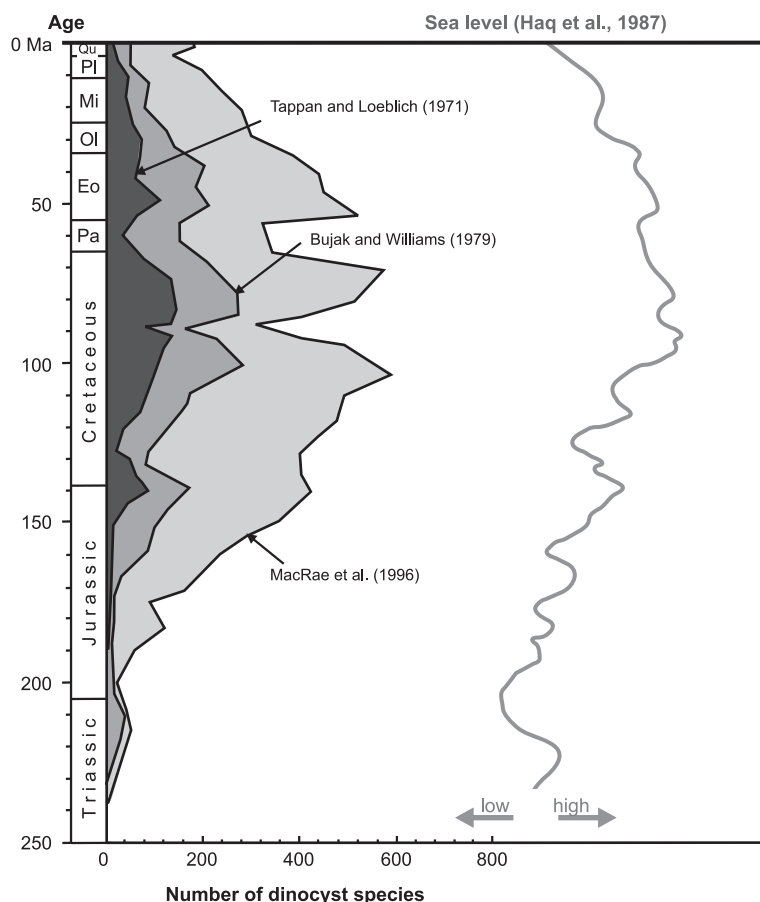While Triassic and early Jurassic cyst assemblages exhibit low species diversity and relatively simple

Fig. 1. Dinocyst diversity through the Mesozoic and Cenozoic. The concurrence with the sea level curve of Haq et al. (1987) has been proposed to be the result of the positive correlation between sea level and the degree of ecological variance in shelfal environments. Modified from MacRae et al. (1996).

cyst morphologies, there is a strong increase in both diversity and morphological complexity during the mid and late Jurassic (Tappan and Loeblich, 1971; Bujak and Williams, 1979; MacRae et al., 1996). This apparent reflection of evolutionary radiation extends well into the Cretaceous and can be visualized by plotting the number of cyst-based species for each age (Fig. 1). This plot shows diversity peaks in the mid-Cretaceous Albian (ca. 580 species), late Cretaceous Maastrichtian (ca. 570 species) and in the early Eocene (ca. 520 species). From the Eocene onward, the number of species declined steadily towards the modern value of 150–175 (MacRae et al., 1996; Head, 1996). The overall character of the cyst-diversity plot shows a strong correlation with the sea level curve of Haq et al. (1987), with high diversity corresponding to intervals of high sea levels and large shelf seas. This correlation probably reflects the higher ecological variance in shelfal settings as compared to open marine environments, allowing higher diversity among shelf-inhabiting groups, such as the organic-walled cyst producing dinoflagellates. It is worth noting, however, that dinocyst taxonomy is purely based on cyst-morphology. Since fossil cysts represent only a surviving structure of part of the life cycle of dinoflagellates (Fensome et al., 1996a), this taxonomy is artificial. Cysts of extant dinoflagellates can be traced back to the motile stage (theca) through laboratory experiments. The studies cited above refer to the cyst-based species numbers. These do not necessarily reflect the number of biological species because several modern dinoflagellate species are known to produce various cyst morphotypes depending on the physiochemical parameters of the water mass in which the theca develops. Furthermore, the cyst-based dinoflagellate 'diversity curve' is strongly biased by the species concepts of different authors. It is also strongly biased towards intervals and areas where there has been extensive hydrocarbon exploration. Moreover, it should be stressed that a diversity record of 'dinocysts' does not relate to the diversity of the group in general. Today, some 2000 species of aquatic dinoflagellates have been described from the Recent, while only a fraction (~ 15%, Head, 1996) of these include the formation of preservable organic-walled cysts as an obligatory part of their life cycle.

Although the fossil dinocyst record is primarily a marine one, Cretaceous and Cenozoic freshwater cyst assemblages are well known from a multitude of localities (e.g., Krutzsch, 1962; Batten and Lister, 1988; Batten et al., 1999). To date, the oldest unequivocal freshwater or brackish water cysts have been described from the late Jurassic/early Cretaceous of Australia (Backhouse, 1988). An even earlier appearance of freshwater dinoflagellates is suggested by nearly monospecific assemblages of suessioid cysts in the upper Triassic (Norian) of Germany (W. Wille, pers. comm., 2001).

3. Productivity trends

Reconstructions of eukaryotic productivity patterns in marine environments are of great interest because they are directly linked to important climate characteristics such as surface current patterns, upwelling systems, water mass mixing, surface winds and the global carbon cycle (e.g., Berger et al., 1989; Bertrand et al., 1996). For the reconstruction of marine eukaryotic productivity, both geochemical (e.g., Shimmield, 1992) and micropaleontological approaches are available. Information based on micropaleontological data has traditionally been obtained from benthic and planktic foraminifera, coccolithophorids, diatoms and radiolaria. However, the applicability of these groups for deciphering marine productivity is limited by the fact that most of their representatives occur in open marine environments. Hence, they render only little information on neritic settings where a major portion of modern marine primary productivity originates (Dale and Fjellså, 1994). Moreover, all the remains of these other groups are mineralized and thus prone to chemical dissolution, which limits their utility in paleoceanographic reconstructions, especially at high latitudes (de Vernal and Mudie, 1992). These restrictions do not apply to organic-walled dinocysts, although oxidation may hamper their recovery (see, e.g., Versteegh and Zonneveld, 2002; Reichart and Brinkhuis, 2003). They are not only abundant in neritic settings and resistant to chemical dissolution, but also extremely sensitive to even small changes in nutrient availability (e.g., Dale, 1996). Thus, they provide a promising tool for the reconstruction of productivity.

To date, dinocyst-based identification of productivity variations in the Paleogene strongly relies on changes in the ratio of peridinioid (P) versus gonyaula-

coid (G) cysts of dinocyst assemblages. This approach, which has its basis in observations on Quaternary dinocyst assemblages (e.g., see overview in Reichart and Brinkhuis, 2003), is founded on the different life-styles and feeding strategies in dinoflagellates forming peridinioid and gonyaulacoid cysts. Using Modern *Protoperidinium* as an analog, P-cysts are considered to predominantly represent heterotrophic dinoflagellates that predominantly thrive on diatoms, whereas G-cysts mainly represent autotrophic dinoflagellates (e.g., Powell et al., 1992). This approach has however been criticised for various reasons (e.g., Dale and Fjellså, 1994). Most importantly, not all living peridinioid dinoflagellates are heterotrophic and the same holds probably true for extinct peridinioids (Dale and Fjellså, 1994). Because it is the heterotrophic rather than the peridinioid dinoflagellates that indicate eutrophic conditions, the assumption of a complete equivalence between the terms "peridinioid" and "heterotrophic" is a simplification that may produce erroneous results. Hence, Dale and Fjellså (1994) and Dale (1996) proposed the terms "H-cysts" and "A-cysts" for the cysts of heterotrophic and autotrophic dinoflagellates, respectively. Moreover, Dale and Fjellså (1994) drew attention to the fact that modern heterotrophic dinoflagellates also occur in places other than high productivity regions, such as sea-ice dominated settings, which could also lead to the misidentification of eutrophic areas (or to the identification of sea-ice). Despite these drawbacks, approaches to identify paleoproductivity trends in the Paleogene based on the feeding strategies of most peridinioid and gonyaulacoid dinoflagellates have been successfully applied. Even if an unknown portion of P-cysts do represent autotrophic rather than heterotrophic dinoflagellates, peridinioids still represent the closest approximation to heterotrophic dinoflagellates and can thus be used to reconstruct productivity.

Note that the concept of a G/P ratio was first introduced by Harland (1973) using the number of *species*. He suggested that low G/P values were associated with significant freshwater input. In later studies, some authors applied this G/P ratio but confused the number of species with the number of *specimens* (e.g., Hultberg, 1987).

The potential and limitations of dinocysts as productivity indicators in the Paleogene are discussed in the following paragraphs. For the benefit of clarity,

different aspects of productivity reconstructions (coastal settings, upwelling areas and open-ocean settings) are discussed separately.

3.1. Productivity in coastal and neritic settings

Dinocysts have been shown to yield a productivity signal in coastal and neritic settings of the Paleogene. Here, the abundance (specimens) of P-cysts (considered to represent predominantly heterotrophic dinoflagellates feeding on diatoms, other phytoplankton and organic detritus) plays a major role. For instance, Crouch (2001) and Crouch et al. (2003b) reconstructed productivity changes in neritic settings from the Paleocene/Eocene boundary interval in New Zealand based on the percentage of peridinioids (Fig. 2). High abundances of P-cysts were used to indicate phases of enhanced nutrient availability probably derived from stronger terrigenous input. Similar approaches were taken by, e.g., Eshet et al. (1994), Brinkhuis et al. (1998), van Mourik and Brinkhuis (2000) and van Mourik et al. (2001). In a related study on the dinocyst record of the Paleocene–Eocene Thermal Maximum (PETM), Crouch (2001) and Crouch et al. (2003a,b) recorded an acme of the tropical genus *Apectodinium* co-occurring with the prominent PETM negative carbon isotope excursion (Fig. 3). The *Apectodinium* event has been recorded in sections from the North Sea (Bujak and Brinkhuis, 1998 and references therein, Steurbaut et al., 2003), Greenland, Spitsbergen (e.g., Boulter and Manum, 1989; Nohr-Hansen, 2003), the Tethyan Ocean (N Africa, Austria, Tunisia, Uzbekistan, Pakistan, India; e.g., Köthe et al., 1988; Bujak and Brinkhuis, 1998; Crouch et al., 2003a), equatorial Africa (Jan du Chêne and Adediran, 1984), the eastern (e.g., Edwards, 1989) and northwestern U.S. (J. Lucas-Clark, pers. comm., 2003), Barents Sea, South America (Brinkhuis, pers. obs.) and New Zealand (Crouch, 2001), and is thus shown to be global in nature (Crouch et al., 2001). Although its paleoceanographic nature is not yet fully understood, the *Apectodinium* acme appears to be related to globally high sea-surface temperatures and a strong increase in nutrient availability in marginal marine settings (Crouch et al., 2001, 2003a). The latter view is based on the concept that the motile dinoflagellates forming *Apectodinium* cysts were probably heterotrophic and fed on organic
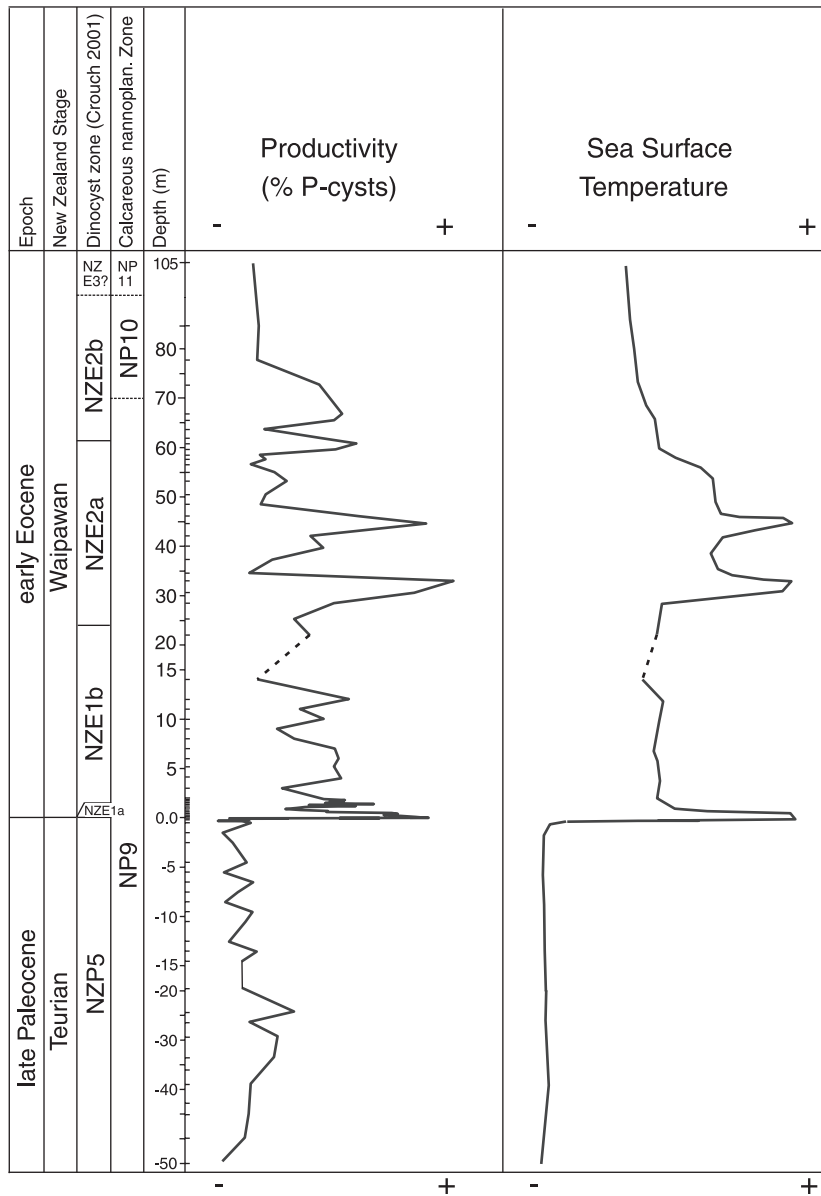
Fig. 2. Dinocyst-based SST and productivity reconstructions across the Paleocene–Eocene transition at the Tawanui section in New Zealand. The SST reconstruction is based on the percentage of species thought to be derived from low latitudes, whereas the productivity reconstruction is based on the percentage of peridinoioid (P) cysts. Modified from Crouch (2001).

detritus or other plankton that occurred in high abundances in marginal marine settings during this time interval. It is in agreement with other studies that show evidence of increased coastal productivity during the PETM (e.g., Speijer et al., 1996; Gavrilov et al., 2003).

Enhanced coastal and neritic productivity has also been reconstructed based on increased abundances of peridiniacean genera such as *Wetzeliella* spp. and *Deflandrea* spp. (e.g., Williams, 1977; Köthe, 1990; Brinkhuis, 1994; Brinkhuis et al., 1992; Powell et al., 1996; Firth, 1996; van Mourik et al., 2001). The high
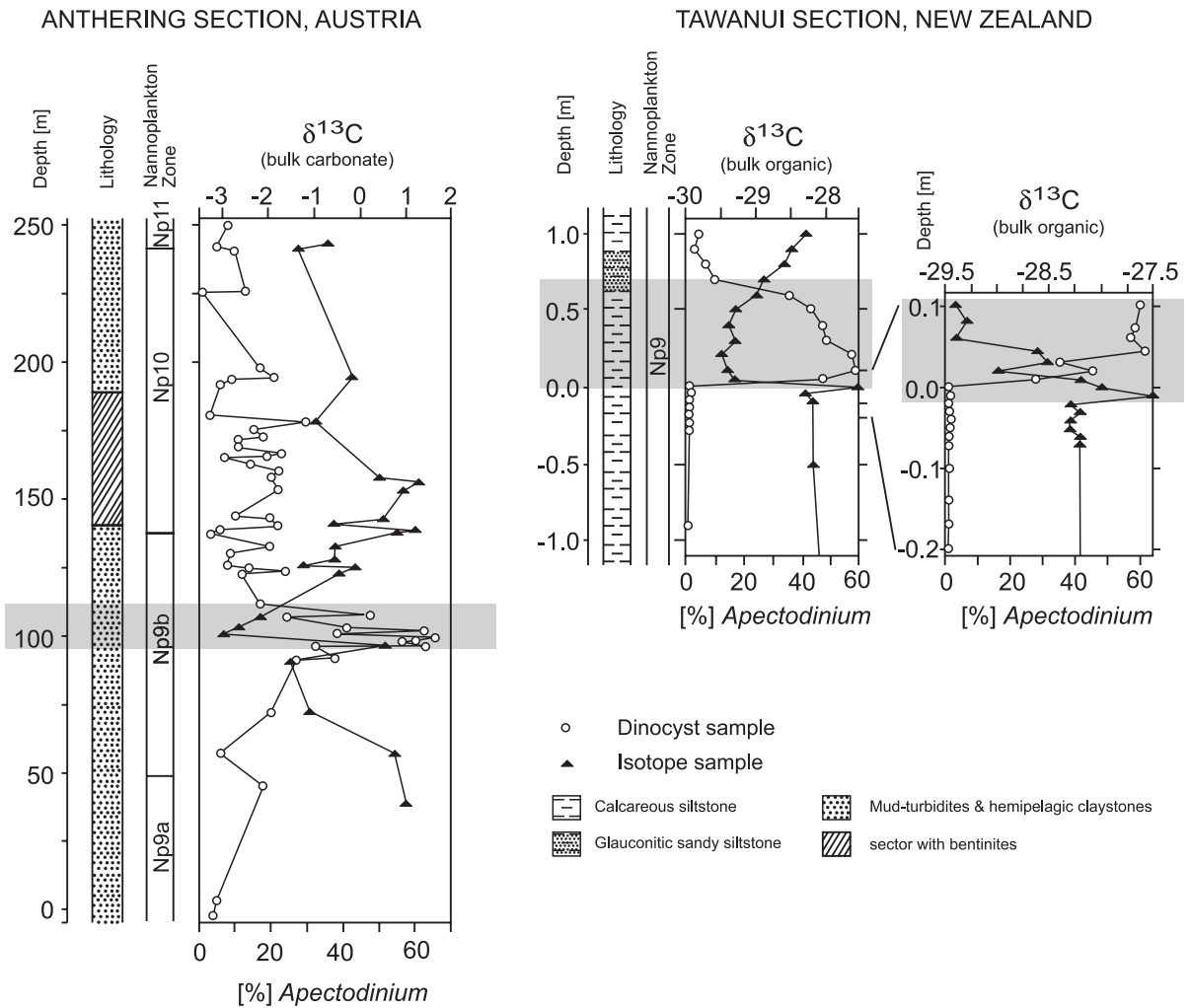
Fig. 3. Distribution of *Apectodinium* percentage and $\delta^{13}C$ isotope records through the Paleocene–Eocene transition from the Anthering section, Austria (left) and the Tawanui section, New Zealand (right). Shaded areas indicate *Apectodinium*-dominated dinocyst assemblages coincident with the carbon isotope minimum characterizing the PETM. Modified from Crouch et al. (2001).

abundance of these taxa in nutrient-rich environments may be due to a heterotrophic feeding strategy, as has been postulated based on the close morphological relationship of peridiniacean taxa with present-day *Protoperidinium* cysts, differing mainly in the number of cingular plates (Brinkhuis et al., 1992). In a multi-proxy study on marginal marine middle Eocene deposits in the Southern Ocean, Röhl et al. (in press-b) found that high abundances of *Deflandrea* spp. (sometimes monospecific) correspond to CaCO$_3$-

depleted sediments and an inshore, possibly brackish, eutrophic setting (see discussions below).

In a study on early Oligocene dinocyst assemblage variations from an epeiric setting in southern Germany, Pross and Schmiedl (2002) applied a statistical approach to identify productivity changes. The dinocyst dataset was subjected to Q-mode principal component analysis. The chosen four-component model explains 78.0% of the total variance of the dataset. The peridiniacean genera *Deflandrea*, *Rhom-*

bodinium and *Wetzeliella*, which are often used as productivity indicators (see above), plotted seperately from the monospecific *Thalassiphora pelagica* assemblage and exhibit highest factor loadings in samples below and above horizons dominated by the *T. pelagica* assemblage. Pross and Schmiedl (2002) interpreted high factor loadings of the *T. pelagica* assemblage to represent periods of enhanced stratification, eutrophication and productivity in the upper water column, and/or oxygen depletion in the lower water column (compare to Vonhof et al., 2000; Coccioni et al., 2000; see also discussion below). Increased abundances of *Deflandrea*, *Rhombodinium* and *Wetzeliella* are probably also linked to elevated nutrient availability, but in well-mixed waters rather than stratified (coastal) waters. Hence, it appears that dinocyst analysis can also yield information on productivity changes that are related to the structure of the water column.

3.2. Productivity in oceanic upwelling areas

Upwelling is an important component of the marine circulation pattern. Because areas of upwelling are connected to increased nutrient availability, they represent a prime source of biological productivity in today's oceans. Moreover, upwelling systems have climatic significance. On a global scale, they play an important role in the partitioning of CO_2 between the ocean and atmosphere, thus affecting the concentration of atmospheric greenhouse gases (e.g., Sarnthein et al., 1988). On a regional scale, they exert a strong control on the atmospheric moisture flux to adjacent land masses (e.g., Rognon and Coudé-Gaussen, 1996). In turn, upwelling areas are the result of oceanic or atmospheric circulation features and may be used for the reconstruction of these patterns. The identification of upwelling in the sedimentary record plays an important role in paleoproductivity and paleoclimate studies. Due to the upwelling-related formation of phosphate deposits, they also have economic significance.

Dinocyst-based identification of upwelling regions in the Paleogene uses the P/G cyst ratio of dinocyst assemblages is used in a similar manner to the reconstruction of productivity in proximal settings. In an analysis of high-latitude North Atlantic dinocyst assemblages from the Eocene and early Oligocene,

Firth (1996) reconstructed paleoproductivity events, possibly caused by upwelling, from the distribution patterns of *Deflandrea* spp. and *Phthanoperidinium* spp. The correlation between abundance peaks of these two genera and diatom- and radiolarian-rich biosiliceous oozes (high abundances of diatoms and radiolarians are among the primary food sources for present-day heterotrophic dinoflagellates) supports the idea that dinoflagellates forming *Deflandrea* and *Phthanoperidinium* cysts may have been heterotrophic (cf. Brinkhuis et al., 1992), and allows reconstruction of high-productivity episodes in intervals where primary biosilica is not preserved.

Records indicating oceanic upwelling in the Paleogene of the Southern Ocean are largely absent. High relative abundances of peridinioid cysts in the spatially relatively well covered Paleocene and Eocene in this region are usually interpreted to reflect a supply of nutrients from land (e.g., Goodman and Ford, 1983; Wrenn and Hart, 1988; Mao and Mohr, 1995; Brinkhuis et al., 2003b; Sluijs et al., 2003). The scarcity of data that suggest Paleogene upwelling in the Southern Ocean could be due to a relatively sparse geographical and temporal resolution of existing datasets, along with the primarily shallow marine setting studied thus far. Alternatively, this situation may indicate that upwelling intensity in the early Paleogene of the Southern Ocean was indeed relatively low. Unraveling the Paleogene upwelling history of the Southern Ocean using dinocyst analysis has so far been hindered by (1) the absence of data from deep water sites and (2) the absence of early Oligocene records altogether as a result of winnowing by the initiation of strong bottom-water currents related to the onset of Antarctic glaciation, and/or the opening of deep Southern Ocean gateways (see discussions in McMinn, 1995; Brinkhuis et al., 2003a,b).

The abovementioned studies indicate that the relative and absolute numbers of peridinioid cysts can provide information about (changes in) trophic levels of ancient water masses. However, P/G ratios do not allow to distinguish between upwelling-related and runoff-related productivity. Hence, the P/G signal may potentially lead to paleoenvironmental misinterpretations. This problem can be reduced if dinocyst datasets are considered from multiple perspectives and interpretations are based on an inter-
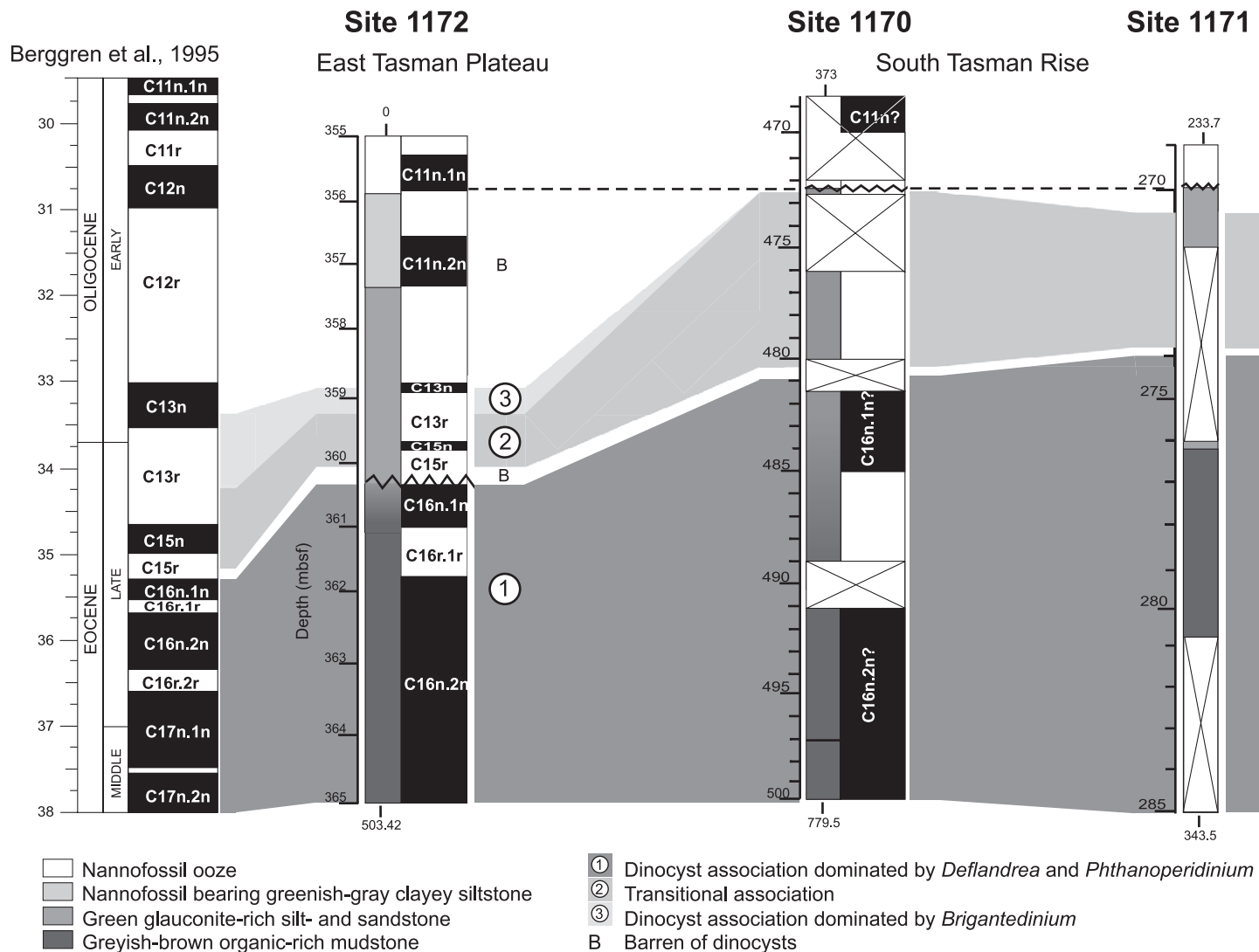
Fig. 4. Dinocyst assemblage distribution across the Eocene–Oligocene transition in ODP Leg 189 Sites 1170–1172 off Tasmania, southwestern Pacific Ocean. Coinciding with accelerated subsidence in the latest Eocene, the *Deflandrea*- and *Phthanoperidinium*-dominated assemblages of the early Paleogene are replaced by representatives of *Brigantedinium*. Based on the results of a multi-proxy approach, this assemblage change has been interpreted to reflect a shift from an environment characterized by runoff-related nutrient supply towards the establishment of an upwelling system. Modified from Sluijs et al. (2003).

disciplinary (i.e., multi-proxy) approach. Early Paleogene dinocyst assemblages in sediments from Ocean Drilling Program Leg 189 around Tasmania (South Tasman Rise, East Tasman Plateau) often consist of peridinioid cysts, indicating very high trophic levels (Brinkhuis et al., 2003b; Sluijs et al., 2003). This situation prevailed into the latest Eocene when rapid subsidence of the Tasmanian Gateway initiated (Stickley et al., in press). Coinciding with this deepening is a changeover from assemblages dominated by *Deflandrea, Vozzhennikovia* and *Phthanoperidinium*, to assemblages dominated by representatives of *Brigantedinium* (Fig. 4). The integrated multi-proxy (lithological, geochemical, grain size and diatom) data indicate that e.g., *Deflandrea* and *Phthanoperidinium* cysts were representing relatively shallow marine heterotrophic dinoflagellates that were in this case closely tied to an ancient deltaic setting and organic-rich facies (see Brinkhuis et al., 2003a,b; Sluijs et al., 2003, Röhl et al., in press-b for further discussion). Blooms of *Brigantedinium*, an extant protoperidinioid genus, are well-known from upwelling regions (Rochon et al., 1999; Reichart and Brinkhuis, 2003) and their motile stage feed on diatoms. Based on the above information, Sluijs et al. (2003) interpreted the latest Eocene assemblage change in the Tasmanian region to reflect a shift from an environment characterized by runoff-related nutrient supply towards the establishment of an upwelling system. Alternatively, the *Brigantedinium* blooms may reflect sea ice conditions, similar to the situation in modern high latitude oceans (e.g., Wall et al., 1977; Dale and Fjellså, 1994; Rochon et al., 1999).

3.3. Open-ocean surface productivity

Variations in organic matter content of sediments are widely considered to be a good proxy for primary productivity (e.g., Suess, 1980; Emerson and Hedges, 1988). In open ocean settings with generally low sedimentation rates, oxidation of organic matter is often intensive. Because dinocysts are among the most resistant organic particles and also represent important primary producers in the upper water column, they can potentially provide a good record of surface productivity in oceanic environments if they are preserved.

However, to date, there have been only few attempts to reconstruct open-ocean surface productivity changes in the Paleogene based on dinocysts. Blooms of *Thalassiphora pelagica* in upper Eocene hemipelagic and pelagic sediments from central Italy have been ascribed to a marked productivity increase and/or cooling of surface waters, possibly triggered by meteor impacts and related feedback mechanisms (Vonhof et al., 2000; Coccioni et al., 2000). This interpretation is corroborated by $\delta^{13}C$ data from the sections studied (Vonhof et al., 2000).

4. Sea surface temperature trends

Sea surface temperature (SST) is widely considered to be the most important parameter for describing environmental conditions of past oceans and is a crucial factor in paleoclimate modelling (e.g., Wefer et al., 1999). To date, paleo-SST estimations are mostly derived from stable oxygen isotope and magnesium/calcium analysis on calcareous microfossils, and/or quantitative analysis of the latter. The applicability of this approach to high-latitude and sub-calcite compensation depth settings, however, is often hindered by carbonate dissolution. Moreover, calcareous microfossils are usually rare in sediments formed in neritic settings. In this context, dinocysts provide an interesting avenue for SST reconstructions. They are resistant to chemical dissolution and reach high abundances in proximal and distal settings. As in any other group of microorganisms, temperature has a strong control on their growth rate and thus plays an important role in the distribution of dinoflagellate species (de Vernal et al., 1994). Mounting evidence also indicates that dinoflagellates are particularly sensitive to temperature changes compared to other microfossils, making them an excellent tool for SST reconstructions (de Vernal et al., 1993, 1994, 1998, 2000, 2001; Versteegh, 1994; Versteegh and Zonneveld, 1994; Rochon et al., 1998; Grøsfjeld et al., 1999; Devillers and de Vernal, 2000; Boessenkool et al., 2001; Sangiorgi et al., 2002, 2003). Consequently, both quantitative (including transfer-function) and qualitative approaches have been developed to evaluate SST signals in present-day and fossil Quaternary dinocyst assemblages.

Various Paleogene dinocyst assemblage studies have used qualitative cyst information to infer paleo-SST trends. They are based on an empirical and/or statistical differentiation of dinocysts into warm-water, temperate and cold-water elements. Changes in the abundances of the respective elements are then interpreted in terms of a temperature signal.

The approach of evaluating the relative contributions of high/mid-latitude (i.e., cool to temperate) versus low-latitude (i.e., warm) water taxa was originally developed to detect SST variations in the late Eocene and early Oligocene of central Italy (Brinkhuis and Biffi, 1993). It has subsequently been applied to other Paleogene dinocyst records, such as the Oligocene of central Italy (Brinkhuis, 1994), and the early Paleogene of the Southern Ocean (Crouch, 2001; Brinkhuis et al., 2003a,b; Sluijs et al., 2003; Huber et al., in press). It has also yielded reconstructions of SST trends across the Cretaceous–Paleogene (K/P) boundary section at El Kef, Tunisia, at that time located in the western Tethys, and other K/P boundary sections, including Boreal sites (Brinkhuis et al., 1998; Galeotti et al., 2004). To infer paleo-temperature trends for the K/P interval, Brinkhuis et al. (1998) followed three interrelated approaches. Detrended correspondence analysis was used to identify SST-related environmental changes and to identify temperature-sensitive species. At the same time, the apparent latitudinal preference of taxa were identified based on literature data. For example, *Palynodinium grallator* and *Membranilarnacia polycladiata* represent typical high-latitude taxa, whereas *Senegalinium bicavatum* is recorded in low latitudes. This enabled the authors to assess the relative contribution of high/mid-latitude versus low-latitude/Tethyan taxa and to evaluate the distribution pattern of rare taxa with very clear latitudinal preferences. Recent analysis and integration of benthic foraminifer and dinocyst records from the El Kef K/P boundary indicated an influx of taxa from high/mid-latitudes, marking a short-term (~ 0.5 kyr) cooling pulse at the K/P boundary (Fig. 5; Galeotti et al., 2004). This was followed by an episode of pronounced warming that was in turn followed by two more cool-warm cycles before relatively stable warm conditions were reestablished. Galeotti et al. (2004) discuss simulations with fully coupled three-dimensional climate models (e.g., Huber and Sloan,

2001), in which incoming solar radiation was reduced to nearly zero, caused by the sulfate aerosols generated by the K/P bolide impact ('impact winter'; e.g., Pope et al., 1997). These simulations show that subsequent cooling of both surface and deeper waters resulted in profound changes in ocean circulation. Both theory and the field observations at El Kef (dinocyst and foraminiferal species from high/mid-latitudes) indicate the invasion of watermasses with a distinct Atlantic signature into the western Tethys as a direct result of the impact winter (Galeotti et al., 2004).

Shifts in the large-scale distribution of temperature-sensitive cyst-forming dinoflagellates are also documented for the PETM (Bujak and Brinkhuis, 1998; Crouch et al., 2001, 2003a). This brief (ca. 220 kyr) episode at ca. 55 Ma is marked by profound global warming, a major negative carbon isotope excursion (CIE) recorded in the terrestrial and marine realm, and dramatic biotic response (e.g., Kennett and Stott, 1991; Koch et al., 1992; Thomas and Shackleton, 1996; Norris and Röhl, 1999; Zachos et al., 2001, 2003; Bowen et al., 2002). With regard to the dinocyst record, the PETM shows a global acme of the tropical genus *Apectodinium* in the mid- to high latitudes of both hemispheres that is synchronous with the CIE (Fig. 3; Crouch, 2001; Crouch et al., 2001). Global dinocyst acmes have not been recorded from any other time period, which indicates the intensity of this event. Apparently, PETM warming and accompanying changes in nutrient availability enabled *Apectodinium* to dominate mid and high latitudes, while many cooler-water dinocyst taxa were reduced. By the end of the PETM, declining temperatures caused the end of the bloom *Apectodinium*-producing dinoflagellates in mid- and high latitudes and vacant niches were filled by newly evolving taxa (Bujak and Brinkhuis, 1998).

Another large-scale migration of temperature-sensitive dinocysts has recently been documented from the mid Oligocene. Species of the genus *Svalbardella* are mainly known from the upper Eocene and lower Oligocene of Spitsbergen (Manum, 1960), the Norwegian-Greenland Sea (Manum et al., 1989; Poulsen et al., 1996), the Labrador Sea (Head and Norris, 1989) and off western Tasmania (Brinkhuis et al., 2003a). Hence, its geographical distribution suggest that *Svalbardella* is a representative of cold-water
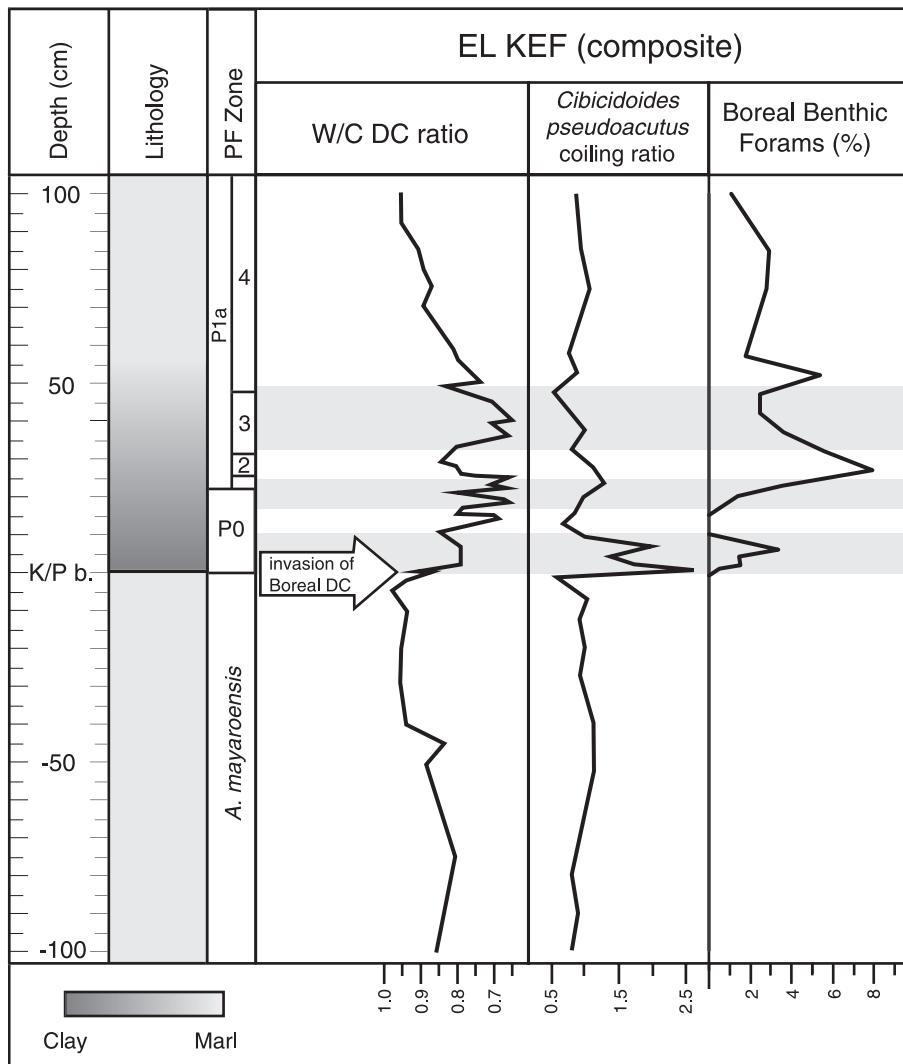
Fig. 5. Dinoflagellate cyst (DC) and benthic foraminiferal records across K/P boundary of El Kef (W/C = warm/cold). Cooler intervals recognized in dinocyst assemblages (shaded bands) coincide with the invasion of boreal benthic foraminifera, and a shift in coiling ratio of benthic foraminifera *Cibicidoides pseudoacutus* (indicating a bioprovincial reorganization and/or a temperature change). Galeotti et al. (2004) postulate that this cooling pulse was associated with a distinct Atlantic watermass invading the western Tethyan Realm after the K/P boundary bolide impact. Modified from Galeotti et al. (2004).

environments (Head and Norris, 1989; Brinkhuis et al., 2003a). Dinocyst distribution patterns in several mid- and low-latitude sections in both hemispheres show that representatives of this genus are conspicuously present (up to 10% of the total dinocyst assemblages) in a distinct interval correlative to the upper part of magnetosubchron C9n (Fig. 6; van Simaeys et al., submitted for publication). The inter-polation between horizons of magnetostratigraphic polarity changes allows the occurrence of this cold water taxon to be constrained to an interval from ∼ 27.65 to ∼ 27.15 Ma and a duration of ∼ 500 ka. The timing of this *Svalbardella* event coincides with one of the major benthic foraminiferal $\delta^{18}O$ cooling events near the top of magnetochron C9n known as the Oi-2b event (Miller et al., 1991, 1998; Fig. 6). The
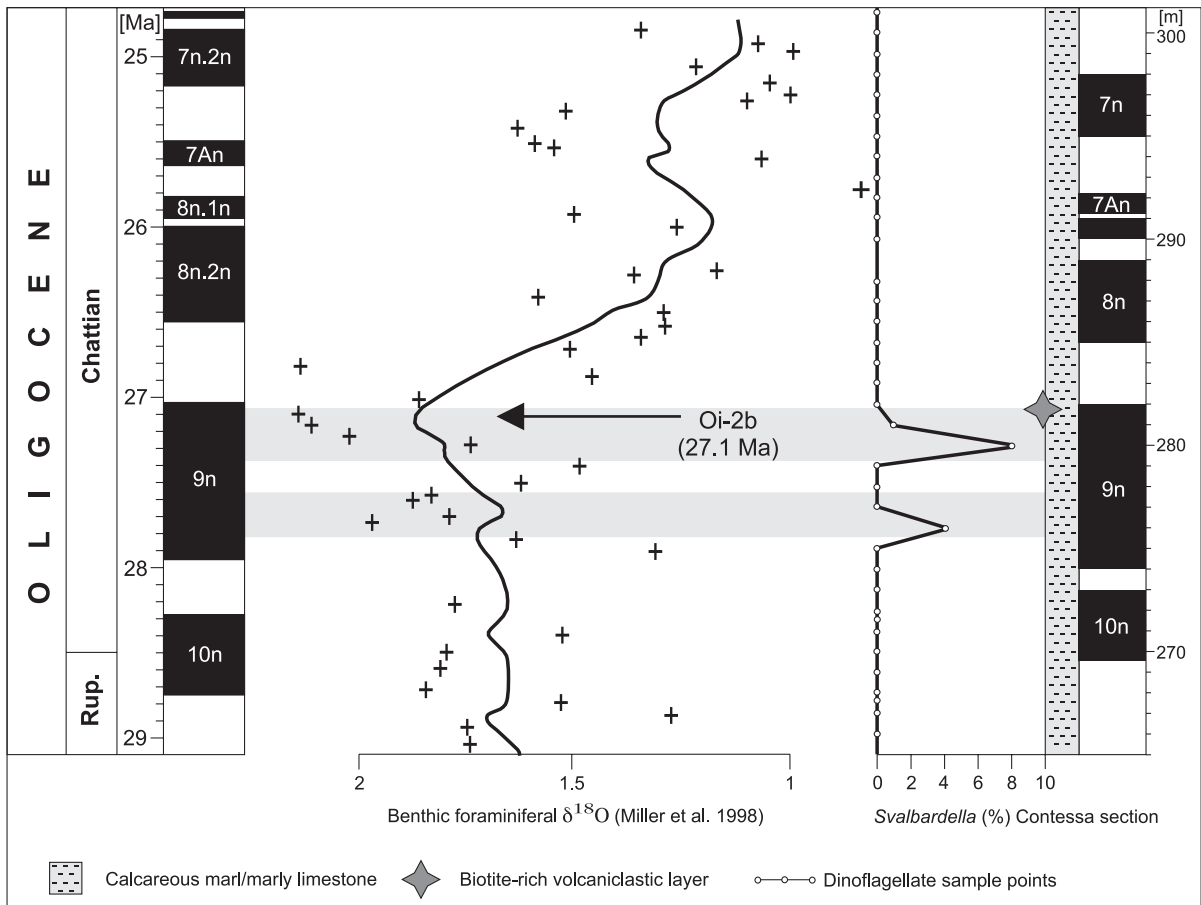
Fig. 6. Distribution of the genus *Svalbardella* in upper Oligocene sediments from the Contessa section, central Italy. The occurrence of this cold-water taxon is synchronous with a major benthic foraminiferal $\delta^{18}O$ maximum (Oi-2b event) near the top of magnetochron C9n. The globally synchronous *Svalbardella* abundance in the upper part of magnetochron C9n coincides with the Oi-2b event, and has been interpreted to indicate distinct atmospheric global cooling and concomitant Antarctic ice-sheet growth. Modified from van Simaeys et al. (submitted for publication).

concomitant occurrence of the global *Svalbardella* event with the Oi-2b event favours a scenario of distinct surface water and atmospheric cooling in both hemispheres and concomitant Antarctic ice-sheet growth during that time (van Simaeys et al., submitted for publication).

Another example from the Eocene involves the spatial distribution of the Antarctic-endemic (and bipolar) dinocyst assemblage, the so-called 'Transantarctic Flora' (Wrenn and Beckmann, 1982). This assemblage has been widely recognized at sites with a paleolatitude south of ~ 60°S and can be readily distinguished from assemblages with more cosmopolitan or tropical affinities (e.g., Lentin and Wil-

liams, 1976; Wrenn and Hart, 1988; Brinkhuis et al., 2003a,b; Sluijs et al., 2003, and references therein). Recently, Brinkhuis et al. (2002b, 2003c) and Huber et al. (in press) modeled the distribution of the Transantarctic Flora in the Australo–Antarctic realm using a fully coupled general circulation model (GCM). Given their newly reconstructed surface circulation, they defined a threshold temperature value of 5 °C below which cosmopolitan species would not thrive and only members of the Antarctic-endemic assemblage would occur. Brinkhuis et al. (2002b, 2003c) and Huber et al. (in press) showed that the modeled biogeographical distribution of the Transantarctic Flora mirrors the
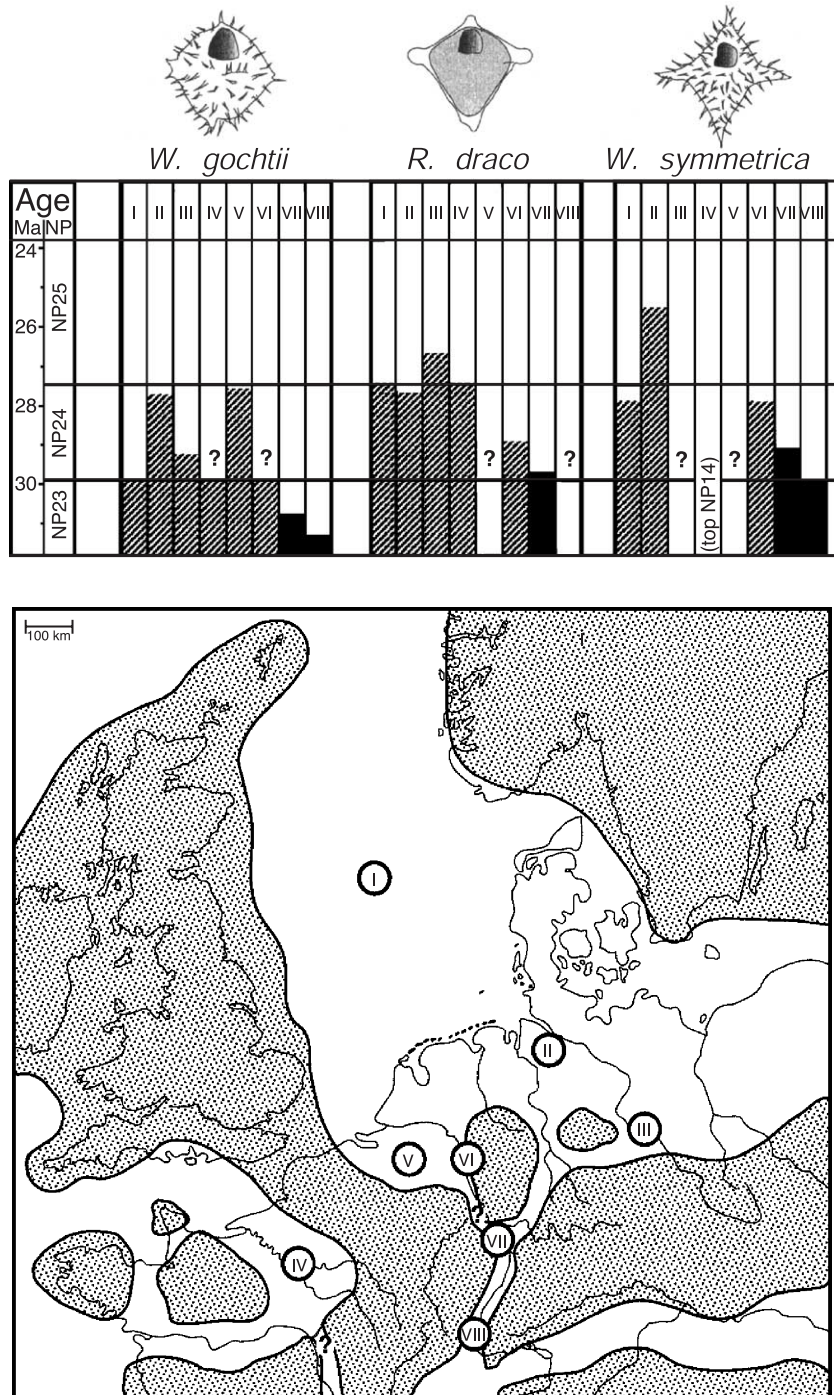
Fig. 7. Early Oligocene paleogeography of northwestern Europe and associated patterns in last occurrences for the species *Wetzeliella gochtii*, *Rhombodinium draco* and *Wetzeliella symmetrica*. Modified from Pross (2001a).

field observations. Hence, they concluded that the spatial distribution of the Eocene 'Transantarctic dinocyst Flora' was restricted to relatively low temperatures and the nature of Southern Ocean watermass distribution and circulation.

Recently, a significant warming event termed 'the middle Eocene Climatic Optimum' (or MECO; Bohaty and Zachos, 2003) was identified by stable oxygen isotope studies in the late middle Eocene of the Southern Ocean, including Site 748 on Kerguelen Plateau. The pelagic carbonate deposits from this location contain high concentrations of well preserved dinocysts (HB, AS, pers. obs.), which is unusual for deep marine settings. Preliminary results indicate strong assemblage variations across the MECO, with acmes of various cosmopolitan species and declining numbers of representatives of the 'Transantarctic Flora'.

On a more regional scale, Pross (2001a) investigated the spatial distribution patterns of the peridinioid taxa *Wetzeliella gochtii*, *Wetzeliella symmetrica* and *Rhombodinium draco* in the Oligocene of western and northwestern Europe. The last occurrences (LOs) of these taxa proved to be diachronous, with localities from the Northwest European Tertiary Basin exhibiting younger LOs than the southernmost localities (Fig. 7). The maximum time differences are ∼ 4.5 Ma in *W. symmetrica*, ∼ 3.6 Ma in *W. gochtii* and ∼ 3 Ma in *R. draco*. Because these differences seem too large to be explained by dating inconsistencies and because other dinocyst taxa, such as *Phthanoperidinium amoenum* and *P. comatum*, have isochronous LOs with regard to nannoplankton ages, the LO diachronism was argued to represent a real phenomenon. Pross (2001a) explains this phenomenon by paleoceanographic changes within the gateway connecting the Northwest European Tertiary Basin and the Tethys via the Rhône and Upper Rhine Grabens. An influx from the South of possibly less nutrient-rich, less or more saline, or warmer water masses (or a combination of these factors) may have led to an earlier and stronger environmental deterioration for *W. gochtii*, *W. symmetrica* and *R. draco* at the southernmost localities. In contrast, dinocyst assemblages in the Northwest European Tertiary Basin were not affected by this environmental change until later and to a lesser extent, therefore exhibiting the youngest LOs of these species. Similar studies involving diachronous FOs and

LOs of Eocene dinocyst have been successfully related to progressive changes in SSTs in the North Sea Basin and the NE Atlantic (J.P. Bujak, pers. comm.).

In summary, the SST control over the Paleogene spatial dinocyst distribution has become well established. To date, dinocyst-based SST reconstructions are shown to be especially important for higher-latitude and neritic environments, where the application of approaches based on calcareous microfossils is often problematic.

5. Salinity trends

Salinity, together with temperature, determines the density of water masses and thus represents an important component controlling thermohaline circulation. To date, methods for determining paleo-salinity have predominantly utilized oxygen isotopes and ecological preferences of foraminiferal assemblages (see Wolff et al., 1999 for a detailed discussion). As salinity is a prime factor controlling osmotic exchanges in microorganisms, it also plays a role in the distribution of dinoflagellates (e.g., de Vernal et al., 1994). Salinity levels may also affect the cyst morphology of dinoflagellate species (Wall et al., 1973; Wall and Dale, 1974; Lewis et al., 1999, 2003). This may result in multiple cyst-based taxa for one theca-based species.

Morphological changes in dinocysts as a result of low salinity or other environmental stress were first described by Wall et al. (1973) and Wall and Dale (1974) based on Holocene material from the Black Sea. They observed that in low-salinity environments as compared to normal-salinity assemblages an increased number of dinocysts with reduced processes, variations in septal development and a cruciform rather than a rounded endocyst. Moreover, changes in archeopyle formation have also been attributed to salinity fluctuations (Wall et al., 1977). The hypothesis that salinity was a factor in determining process length in various chorate dinocysts has been corroborated by recent studies on *Lingulodinium machaerophorum*/*L. polyedrum* (e.g., Nehring, 1994a,b), *Operculodinium centrocarpum* (e.g., de Vernal et al., 1989; Matthiessen and Brenner, 1996) and *Spiniferites* spp. (e.g., Dale, 1996; Ellegaard, 2000; Lewis et al., 1999, 2003). The suggestion that a cruciform endo-

cyst may indicate the influence of a low-salinity environment has also been corroborated by Dale (1996) and a recent study on cruciform *Spiniferites* cysts from a lacustrine setting in northern Greece (Kouli et al., 2001). Taking these hypotheses a step further, Brenner (2001) used process length variations in *O. centrocarpum* to reconstruct Holocene salinity changes in the Baltic Sea.

In terms of cyst formation, the morphological changes are probably related to an early rupture of the outer membrane surrounding the dinoflagellate theca and cyst (Kokinos and Anderson, 1995). Laboratory findings, however, indicate a more complex relationship between cyst morphology and salinity. Although it has been shown that the process lengths in *Lingulodinium machaerophorum* are reduced at low salinities (Lewis and Hallet, 1997), monoclonal cultures of this taxon can develop different process lengths even under stable salinity conditions (Kokinos and Anderson, 1995). Similarly, the development of different morphotypes in *Spiniferites membranaceus* and *S. ramosus* also occurs under stable salinity (Lewis et al., 1999). Hence, salinity is probably not the only factor controlling these morphological changes and other parameters of environmental stress may also be involved. These findings are supported by a study on late Quaternary dinocysts from the Black, Marmara and Aegean Seas (Mudie et al., 2001). For *L. machaerophorum*, there emerged no clear statistical relationship ($R = 0.33$) between process length and salinity as inferred from the foraminiferal signal. Moreover, there was a weak inverse correlation between salinity and relative abundance of *Spiniferites cruciformis* ($R = -0.61$) and also between salinity and the percentages of a specific morphotype of *S. cruciformis* ($R = -0.67$), with the degree of velum development decreasing with lowered salinity. Other *S. cruciformis* morphotypes did not correlate with salinity. Kouli et al. (2001) recorded *S. cruciformis* together with the freshwater species *Gonyaulax apiculata* in lacustrine sediments. They suggest that *S. cruciformis* is a freshwater species and that any occurrences in (brackish) marine environments, with the exception of specimens with strongly reduced ornamentation, may be due to transportation, short-lived freshwater surface conditions and/or tolerance of the species to brackish conditions. Mudie et al. (2002), using material from

the Marmara and Black seas, followed an actuopaleontological approach towards a paleosalinity quantification. Their data are compatible with Kouli et al. (2001) as they show *S. cruciformis* to co-occur with taxa found in freshwater environments and also use *S. cruciformis* to reconstruct brackish water environments (∼ 7–18 practical salinity units) and freshwater input from glacial lakes.

Among Paleogene and Neogene dinocyst taxa, members of the *Homotryblium* complex (i.e., many taxa of the family Goniodomaceae such as *Eocladopyxis*, *Heteraulacacysta*, *Polysphaeridium*; see Fensome et al., 1993) are widely considered to be characteristic of restricted settings with increased salinity (see Brinkhuis, 1994 for a detailed discussion). This attribution is due to morphological similarities with the extant high-salinity indicator *Polysphaeridium zoharyi* and the group's empirically derived preference for low- to mid-latitude, inner neritic environments (Reichart et al., 2004). In a study on early Oligocene dinocysts from a neritic setting in southern Germany, Pross and Schmiedl (2002) interpreted alternating intervals dominated by *Homotryblium tenuispinosum*/*H. floripes* and *Thalassiphora pelagica*, respectively, to indicate alternations between high- and low-salinity conditions. This distribution pattern was explained through a model invoking repeated environmental changes from relatively dry to relatively humid conditions and stratification (Fig. 8). High abundances of *H. tenuispinosum* and *H. floripes* reflected drier periods where reduced runoff, in combination with strong evaporation, led to increased salinity in nearshore settings. Periods of maximum runoff were indicated by high abundances of *T. pelagica*, interpreted to reflect reduced salinity in the surface waters, increased productivity, salinity stratification and resulting oxygen depletion in the deeper water column (Fig. 8). Similarly, Köthe (1990) interpreted intervals of high *Homotryblium* abundances in the Oligocene and Miocene of northwest Germany to indicate high-salinity conditions.

Acmes of *Homotryblium tenuispinosum* have also been recorded alongside high abundances of the freshwater algae *Pediastrum* spp. which indicates a brackish setting (S. van Simaeys, pers. comm., 2003). Its co-occurrence with *Pediastrum* implies that the *Homotryblium* motile cell was tolerant of a wide range
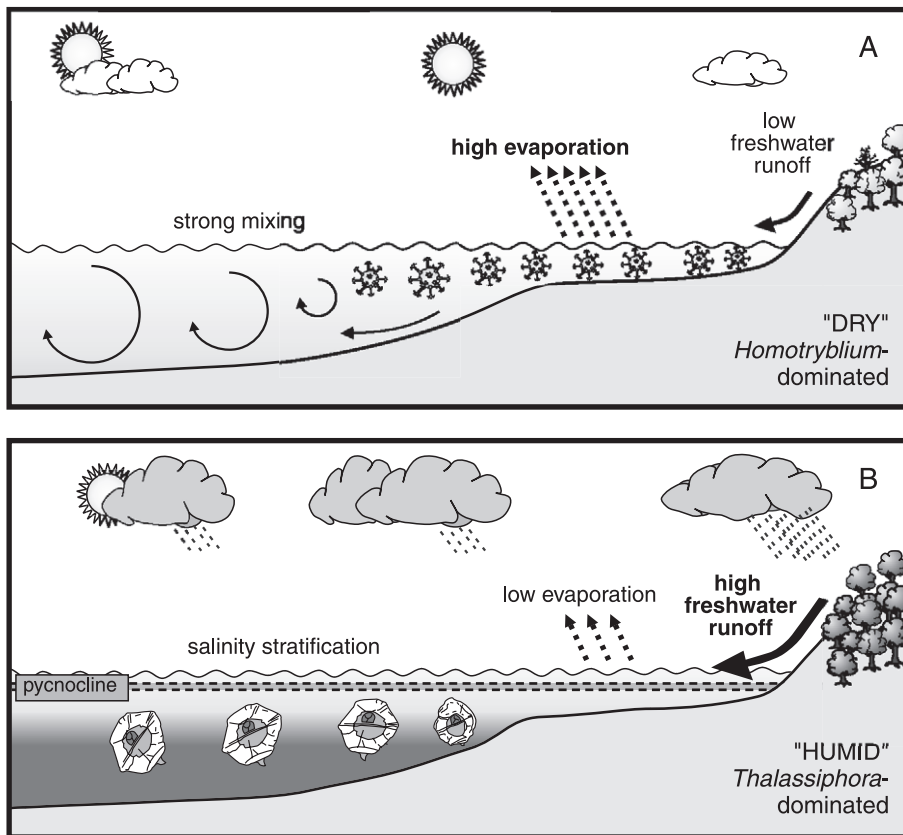
Fig. 8. Schematic model for the response of cyst-forming dinoflagellate populations to climate-induced oceanographic changes in the lower Oligocene of southern Germany. (A) During relatively dry periods (dominance of *Homotryblium tenuispinosum*), reduced runoff and strong evaporation caused high sea surface salinity. (B) During relatively humid periods (dominance of *Thalassiphora pelagica*) high freshwater discharge lead to increased nutrient input, salinity stratification and a decrease in bottom water oxygenation. See text for further explanation. Modified from Pross and Schmiedl (2002).

of salinities, similar to extant *Pyrodinium bahamense* (the thecal stage of the dinocyst *P. zoharyii*).

Based on the aforementioned studies, the analysis of the distribution pattern of *Homotryblium* and allied genera can yield information on salinity conditions in the Paleogene. Although most available records suggest an affinity of *Homotryblium* to hypersaline environments, there are indications that the genus may also have favoured abnormally low-salinity conditions. Because *Homotryblium* first occurs in the early Paleocene (Iakovleva et al., 2001) and has a last occurrence in the mid-Miocene (Brinkhuis, 1994), it provides a valuable tool in dinocyst-based salinity reconstructions for most of the Paleogene.

6. Proximal–distal trends

Due to the general life strategy of organic cyst-forming dinoflagellates (e.g., commonly involving neritic settings) and the adaptation of many species to specific surface water conditions, marine dinoflagellate assemblages show a strong proximal–distal signal. Hence, the dinocyst assemblages from the sediments can be used to reconstruct the influence of inshore waters in a more offshore locality (Brinkhuis, 1994), despite possible taphonomic problems such as long-distance transport (e.g., Dale and Dale, 1992).

In a pioneering study on the inshore–offshore distribution pattern of modern dinocysts, Wall et al.

(1977) attributed different cyst taxa to specific locations within neritic to oceanic transects. Their classification is based on the presence or absence of taxa considered to be typical for oceanic settings and on relative changes in species composition from nearshore to offshore. The results of Wall et al. (1977) have been corroborated by many later studies (e.g., Edwards and Andrle, 1992; Dale, 1996) and can be summarized as follows: (1) Oceanic settings are characterized by the occurrence of *Impagidinium*. The environmental preference of this genus seems so clearly defined that even the occurrence of a few specimens may indicate an oceanic environment (Dale, 1996). Hence, if one assumes that *Impagidinium* has not changed its ecological preference since it first appeared in the Cretaceous, its occurrence can provide a tool to differentiate distal, oligotrophic settings from other, more proximal environments. (2) Species of *Nematosphaeropsis* and *Tectatodinium* indicate a neritic to oceanic environment; and (3) the occurrence of most other cyst taxa are representative of coastal to neritic settings.

Based on the premise that many dinoflagellate species are adapted to specific surface water conditions and utilizing literature information such as Wall et al. (1977), Brinkhuis (1994) presented a schematic model for the composition of gonyaulacoid (predominantly autotrophic) dinocyst assemblages along a proximal–distal transect as given by Eocene/Oligocene sections in northeast Italy (Fig. 9). He proposed a sequence of optimum abundances along an inner neritic to outer neritic and finally oceanic transect of the *Homotryblium*, *Areoligera*/ *Glaphyrocysta*, *Operculodinium*, *Enneadocysta*/*Spiniferites*, *Nematosphaeropsis*/*Cannosphaeropsis* and *Impagidinium* groups (Fig. 9). This classification scheme has subsequently been applied and modified in other studies on Paleogene dinocysts (e.g., Crouch, 2001; Pross and Schmiedl, 2002; Röhl et al., in press-b). In a multi-proxy study on marginal marine Eocene deposits in the Southern Ocean, Röhl et al. (in press-b) showed that the relative abundance of *Enneadocysta* spp. positively correlates with the $CaCO_3$ content of the neritic sediment, which suggests a slightly more offshore, less eutrophic setting (Fig. 10). In turn, high abundances of *Deflandrea* spp., corresponding to more $CaCO_3$-depleted sediments, indicate a more inshore setting. According to

Röhl et al. (in press-b), the dinocyst assemblage and $CaCO_3$ content variations represent astronomically forced, sea-level driven cycles within the Milankovitch bands.

Studies on the distribution pattern of Recent dinocysts have shown that—apart from nutrient availability and water temperature (e.g., Matsuoka, 1992; Dale, 1996)—cyst diversity strongly depends on the stress in ecosystems (e.g., Patten, 1962; Bradford and Wall, 1984). As stress is often related to relative shoreline proximity, the dinocyst diversity signal may thus also be broadly used as an indicator of the latter. This approach has been taken in several Paleogene dinocyst studies. A study on early Oligocene assemblages from an epicontinental basin in Central Europe revealed a rise in mean dinocyst diversity values with increasing distance from the shoreline (Pross and Schmiedl, 2002). Maximum mean values of the Shannon-Wiener information index $H(S)$, which was used to characterize the diversity of dinocyst assemblages, occurred in the center of the basin at a distance of ~ 15 km from the paleo-shoreline. Assemblages from more intermediate and proximal settings exhibited consistently decreasing $H(S)$ values. The same picture emerged for the equity index (E), which was used to describe the equity within dinocyst assemblages (Pross and Schmiedl, 2002). Hence, the diversity of dinocyst assemblages can render information on stress, and hence onshore–offshore trends in epicontinental settings.

6.1. Sequence stratigraphic application

In view of the above, the composition of dinocyst assemblages and dinocyst diversity can serve as an indicator for watermass composition, which is closely associated with shoreline proximity. Thus, changes in assemblage composition and diversity may be used to determine transgressive–regressive phases and can be related to changes in relative sea level. This has led to the successful application of dinocyst studies in sequence stratigraphy starting with Haq et al. (1987). As noted earlier in this paper, a species diversity plot for Mesozoic to Cenozoic dinocysts shows striking similarities to the general trend of the sea level curve of Haq et al. (1987), with high diversity corresponding to high sea level and vice
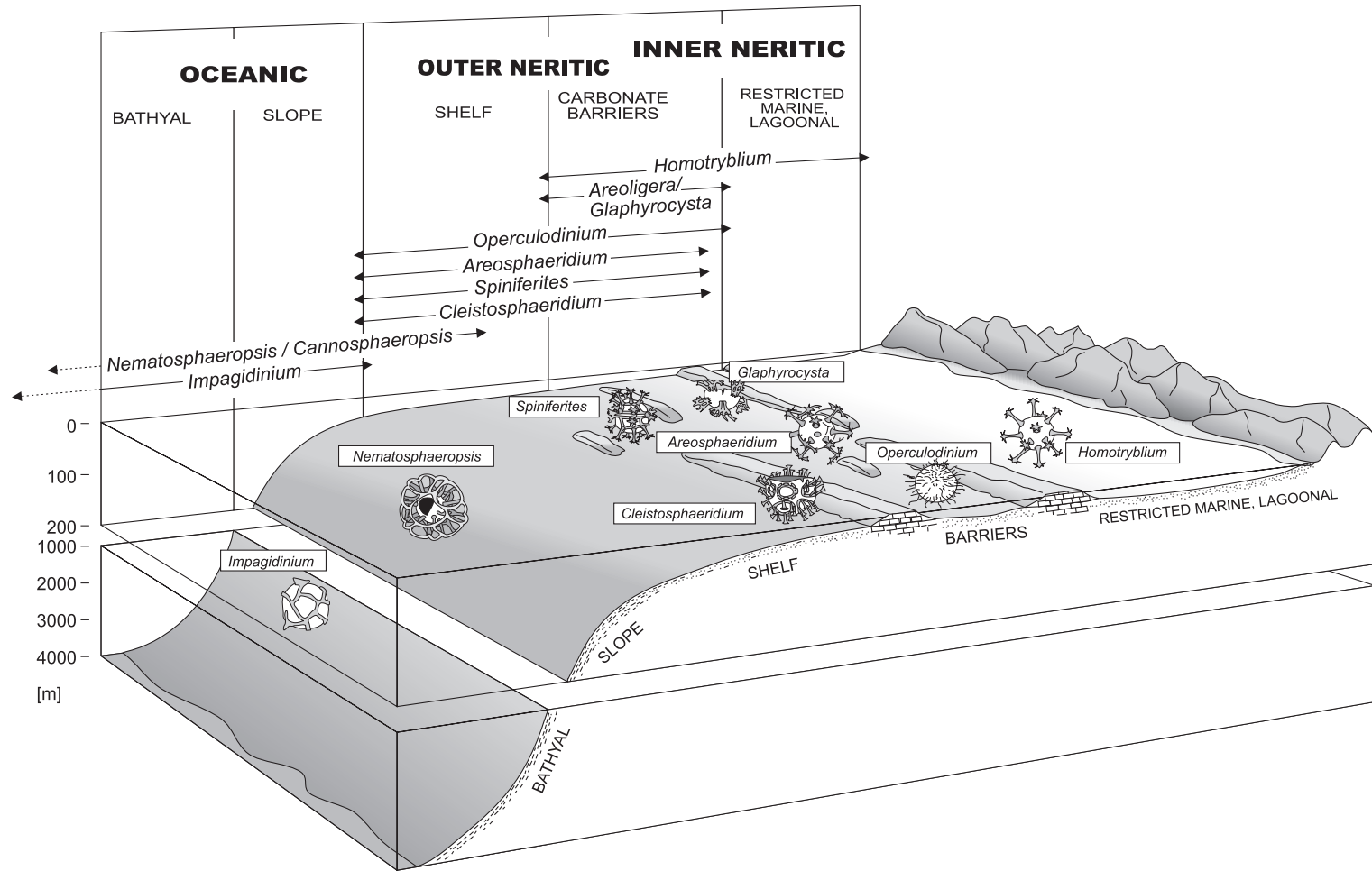
Fig. 9. Schematic model for the distribution of dinocyst associations along a proximal–distal transect during the late–Eocene and early Oligocene in central Italy. Modified from Brinkhuis (1994).
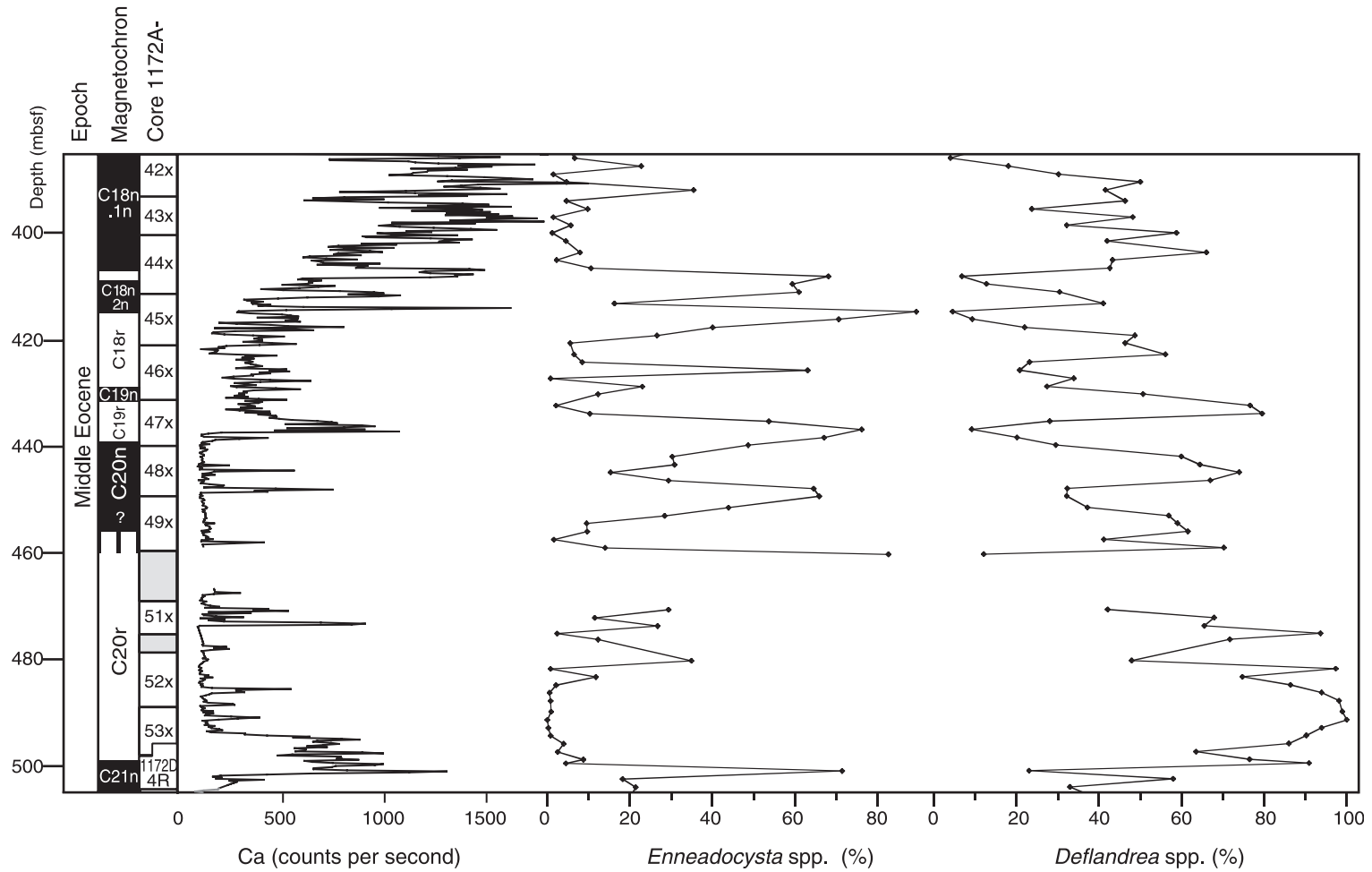
Fig. 10. High-resolution XRF calcium intensity (in counts per second) and the distribution of *Deflandrea* spp. and *Enneadocysta* spp. through a middle Eocene interval of ODP 189 Site 1172 in the Tasman Sea. The dinocyst assemblage and CaCO₃ content variations are thought to represent astronomically forced, sea-level driven cycles within the Milankovitch bands. Modified from Röhl et al. (in press (b)).

versa (Fig. 1). Existing dinocyst-based reconstruction of sea-level changes can be subdivided into (1) studies primarily utilizing differences in assemblage composition and (2) studies evaluating the diversity and abundance signal within assemblages.

Based on changes in the composition of dinocyst assemblages, Brinkhuis and Biffi (1993) and Brinkhuis (1994) reconstructed sea-level fluctuations of different magnitudes across the Eocene/Oligocene transition in Italy. An increase of outer neritic to oceanic taxa (such as species of *Nematosphaeropsis* and *Impagidinium*) was interpreted to indicate a sea level rise, whereas increasing abundances of neritic to coastal taxa were interpreted to denote a regressive trend. The results indicate a latest Eocene episode of low sea level (correlated to the boundary of the third-order cycles TA4.2 and TA4.3 of Haq et al., 1988) and a pronounced earliest Oligocene sea-level fall (correlated to the TA4.3/4.4 type 1 se-

quence boundary of Haq et al., 1988). These major events were accompanied by cooling as reflected by increased abundances of higher-latitude species, which supports the idea of glacio-eustatic control on the late Eocene/Oligocene sea-level curve. Minor fluctuations, in contrast, were not connected to cooling as shown by the dinocyst signal and were interpreted to be the result of local to interregional tectonics (Brinkhuis, 1994). Similarly, Peeters et al. (1998) were able to discriminate between tectonically and eustatically driven sea-level change in the Eocene/Oligocene Pindos Basin, Greece. Powell et al. (1996) developed a dinocyst-based "sequence biostratigraphy" for late Paleocene/early Eocene sections from southeast England. Based on the proximal–distal signals of different dinocyst groups similar to those defined by Brinkhuis (1994) and additional information from other accompanying aquatic palynomorphs, Powell et al. (1996) proposed
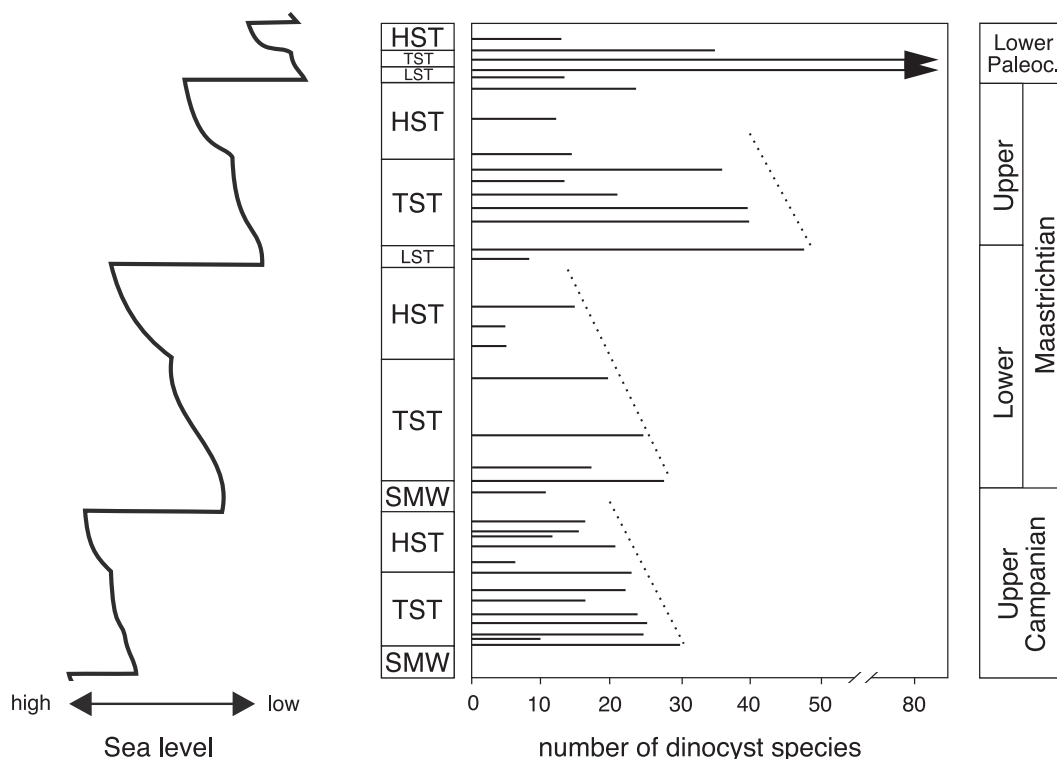

Fig. 11. Dinocyst diversity correlated to the sequence stratigraphy in the upper Cretaceous and lower Paleocene of the southern United States. Diversity maxima occur at the base of the transgressive system tracts (TST), whereas diversity minima fall within the lowstand system tracts (LST). HST = highstand system tract, SMW = shelf margin wedge. Modified from Moshkovitz and Habib (1993).

eight sequences in the studied sections that could be correlated to the well-established sequence stratigraphy of the North Sea Central Graben. Similar approaches have been taken by Zevenboom et al. (1994), Zevenboom (1996), Wilpshaar et al. (1996), Iakovleva et al. (2001) and Van den berghe et al. (2003).

In a study on the sequence stratigraphic significance of dinocysts in the Lower Oligocene of Belgium, Stover and Hardenbol (1994), took a similar approach and could show that the number of dinocyst species increased rather abruptly in the transgressive systems tract above the underlying sequence boundary. Once established, species numbers remained relatively constant into the early highstand deposition and increasingly deteriorated during late highstand deposition. The majority of dinocyst range bases were positioned in transgressive systems tracts, which can probably be attributed to a widening of shelfal dinoflagellate habitats, fostering the evolution of new dinoflagellate taxa. Accordingly, range tops were predominantly found in highstand systems tracts.

For the upper Cretaceous and lowermost Paleogene of the southern U.S., a similar relationship between dinocyst diversity and sea level change has been postulated (Habib and Miller, 1989; Habib et al., 1992; Moshkovitz and Habib, 1993). Minimum species numbers occurred in lowstand deposits and maximum species numbers were observed at the base of transgressive systems tracts (Fig. 11). The evaluation of dinocyst species numbers to determine sea-level change has been especially useful for establishing a sequence stratigraphic framework for the Cretaceous/Paleogene boundary interval, because dinoflagellates did not undergo a mass extinction as calcareous microfossils (Habib et al., 1992).

In summary, the dinocyst signal shows a strong proximal/distal differentiation as a result of dinoflagellate sensitivity to the wide range of physiochemical characteristics of neritic watermasses along the inshore−offshore transect. Through the formation of benthic resting cysts in most cyst-producing dinoflagellates, there is also a link to water depth. The proximal/distal signal is expressed by changes in assemblage composition, assemblage diversity and cyst abundances. The strong expression of the proximal/distal signal in dinocyst assemblages has led to the successful application of dinocyst studies in sequence stratigraphy.

7. Stratification

Most dinoflagellate cysts species are known from shallow marine (i.e., shelfal) settings. This is because dinoflagellates need to be able to return to the photic zone after excystment, which limits the maximum water depth of the habitat and inhibits occurrences of most cyst-forming species in the open ocean. Recently, however, assemblages dominated by the typical restricted marine, lagoonal species *Polysphaeridium zoharyi* were recorded in Pleistocene open-oceanic sediments from the Arabian Sea (Reichart et al., 2004). *P. zoharyi* represents the cyst stage of *Pyrodinium bahamense*, a harmful dinoflagellate known from lagoons that is tolerant of strong salinity fluctuations (see Section 5). Conspicuously, the *P. zoharyi* blooms were recorded in sediments deposited during warm interstadials following strong Heinrich events (Fig. 12). Reichart et al. (2004) postulated that rapid warming in the North Atlantic region immediately following the Heinrich events led to a decrease of the winter monsoon intensity in the Arabian Sea. In turn, this resulted in the interruption of deep mixing that had persisted during glacial times in the Arabian Sea. The weakening of the winter monsoon predated the subsequent strengthening of the summer monsoon and ongoing evaporation resulted in the development of very high sea surface salinity and a shallow and unusually strong pycnocline in the Arabian Sea. Reichart et al. (2004) termed this phenomenon 'hyperstratification' (Fig. 13). The strong pycnocline provided a virtual seafloor, enabling *P. zoharyi* to complete its life cycle prior to sinking into deep water. This 'hyperstratification', in combination with high sea surface salinity, provided optimum living conditions for *P. zoharyi* in open-ocean environments (Reichart et al., in press). Although hyperstratified conditions as described from the Quaternary of the Arabian Sea have not (yet) been identified by dinocysts in the pre-Quaternary, dinocysts with high-salinity affinities such as *Homotryblium* are well known to dominate lagoonal settings in the Paleogene (see Section 5).
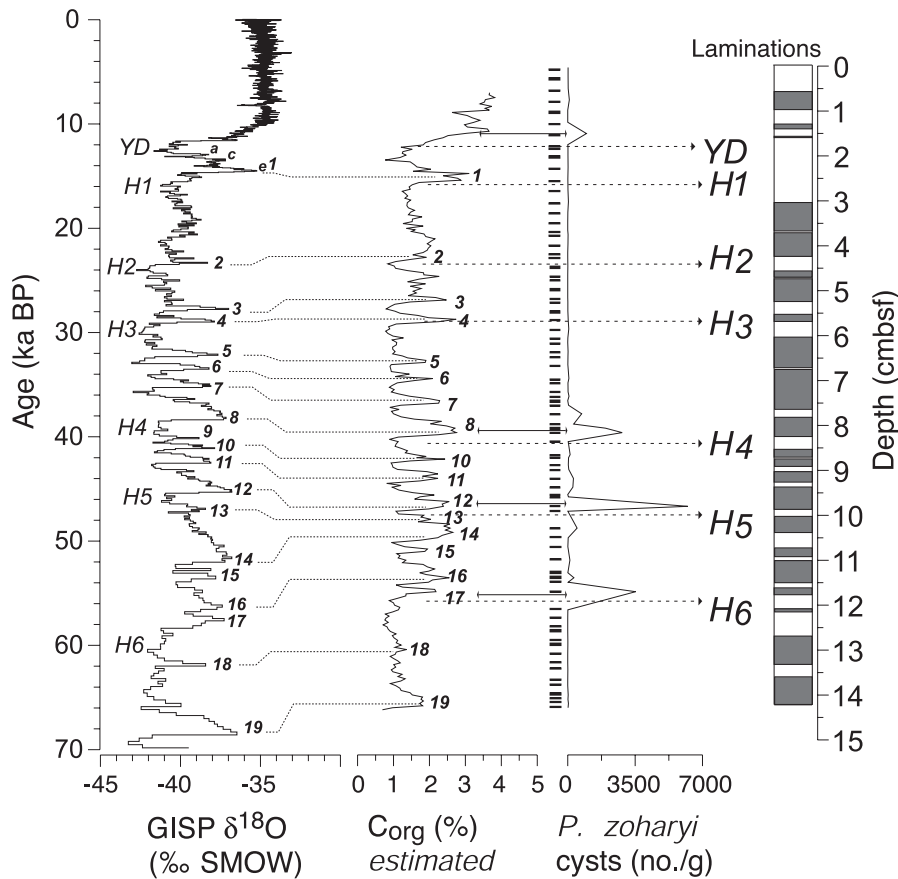
Fig. 12. Correlation between the oxygen isotope record of the GISP2 Greenland ice core, the predicted organic carbon record (see Reichart et al., 2004), and abundance of *Polysphaeridium zoharyi* cysts. Numbers 1–19 refer to interstadials, H1–H6 refer to Heinrich events 1–6, YD refers to the Younger Dryas. Laminated intervals are indicated in grey. Position of palynological samples are indicated by thin horizontal lines next to the *P. zoharyi* record. Solid lines with arrows indicate events characterized by *P. zoharyi*. Modified from Reichart et al. (2004).

Thus, they have the potential to record hyperstratified open-ocean conditions during this time interval and it is possible that some of the presumed Oligocene deep marine records of abundant *Homotryblium* may actually represent such processes (e.g., Stover, 1977).

8. Bottom water and water column oxygenation

Reconstructing the oxygenation of marine sediments has long been a focus of geologists because of the relevance of low-oxygen conditions in the formation of hydrocarbons. Moreover, oxygen availability is a prime factor in controlling diversity and

abundance of, particularly, benthic biota, and it can also provide paleoceanographic, paleogeographic and paleoclimatic information. Consequently, various paleontological, sedimentological and geochemical approaches have been developed to reconstruct the oxygenation of marine sediments (cf. Allison et al., 1995).

Studies on modern dinoflagellates have shown that oxygen availability exerts a strong control on cyst germination, with anaerobic conditions completely inhibiting the excystment of most taxa (Anderson et al., 1987). Because dinocysts in shelf environments typically reach the sea floor before excystment (Dale, 1983) and are therefore exposed to bottom water conditions, cyst assemblages in shelf environments

Interglacial   **Glacial**

a) winter monsoon

b) strong winter monsoon (stadial)

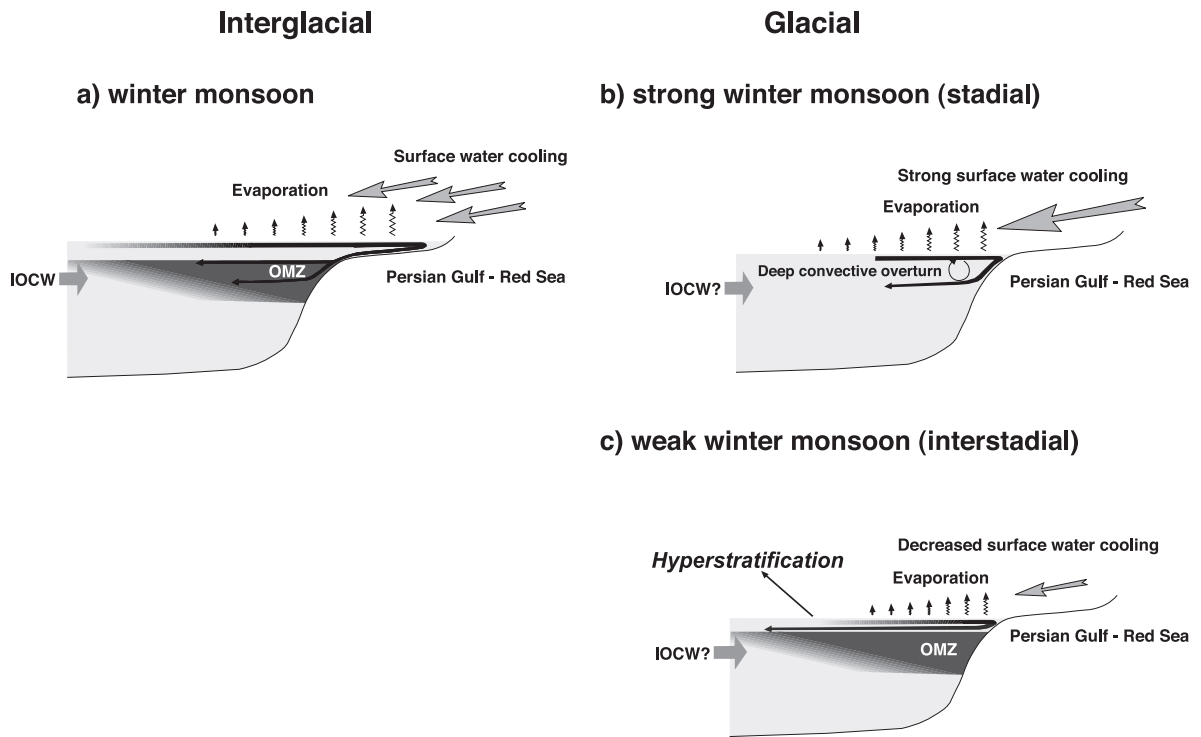### c) weak winter monsoon (interstadial)

Fig. 13. Schematic representation of surface and intermediate water circulation during interglacial (present) and glacial times in the Arabian Sea. The present-day (a) circulation of the intermediate water is dominated by the inflow of relatively oxygen-poor Indian Ocean Water (IOCW) and inflow at depth of warm and saline water from the Persian Gulf and Red Sea. The two glacial scenarios represent full stadial conditions (b) and the transition from stadial to interstadial (c). The brief periods of hyperstratification at stadial–interstadial transitions are inferred from the *Polysphaeridium zoharyi* data. Modified from Reichart et al. (2004).

may well bear a benthic oxygenation signal. Although shelves are usually well-ventilated, several studies on fossil dinocyst assemblages from Jurassic, Cretaceous and Paleogene organic-rich shelf sediments have revealed changes that possibly relate to variations in benthic oxygenation. Sediments deposited under low-oxygen conditions showed reduced cyst diversities and shifts within cyst assemblages (Jarvis et al., 1988; Marshall and Batten, 1988; Leckie et al., 1992; Pross, 2001b; Bucefalo-Palliani et al., 2002).

Changes in dinocyst assemblages as a response to oxygen depletion at the sediment surface and in the water column of epeiric settings have been observed in early Oligocene sediments (Pross, 2001b). Dinocyst assemblages from oxygen-depleted intervals within the Mainz Embayment, SW Germany, are characterized not only by reduced dinocyst diversities, but also by high abundances of *Thalassiphora*

pelagica. The relative abundance of this species correlates inversely with the availability of bottom-water oxygen, as inferred from benthic foraminifera, and strong, probably runoff-induced stratification. Apparently, *T. pelagica* could successfully cope with this set of environmental parameters where others failed. Noting the unusual morphology of *T. pelagica* and studying its morphological variability quantitatively, Pross (2001b) proposed a model linking all aspects of the phenomenon. *T. pelagica* is characterized by a wing-like membrane on the dorsal side of most specimens, which may have facilitated a holoplanktic life cycle in contrast to most other cyst-producing dinoflagellates. Pross (2001b) interpreted the observed distribution pattern to mirror the effect of bottom-water oxygen depletion on dinoflagellates with a benthic resting cyst stage (Fig. 14). In his model, excystment of these other taxa was inhibited or reduced, leading to a decrease in dinocyst diver-
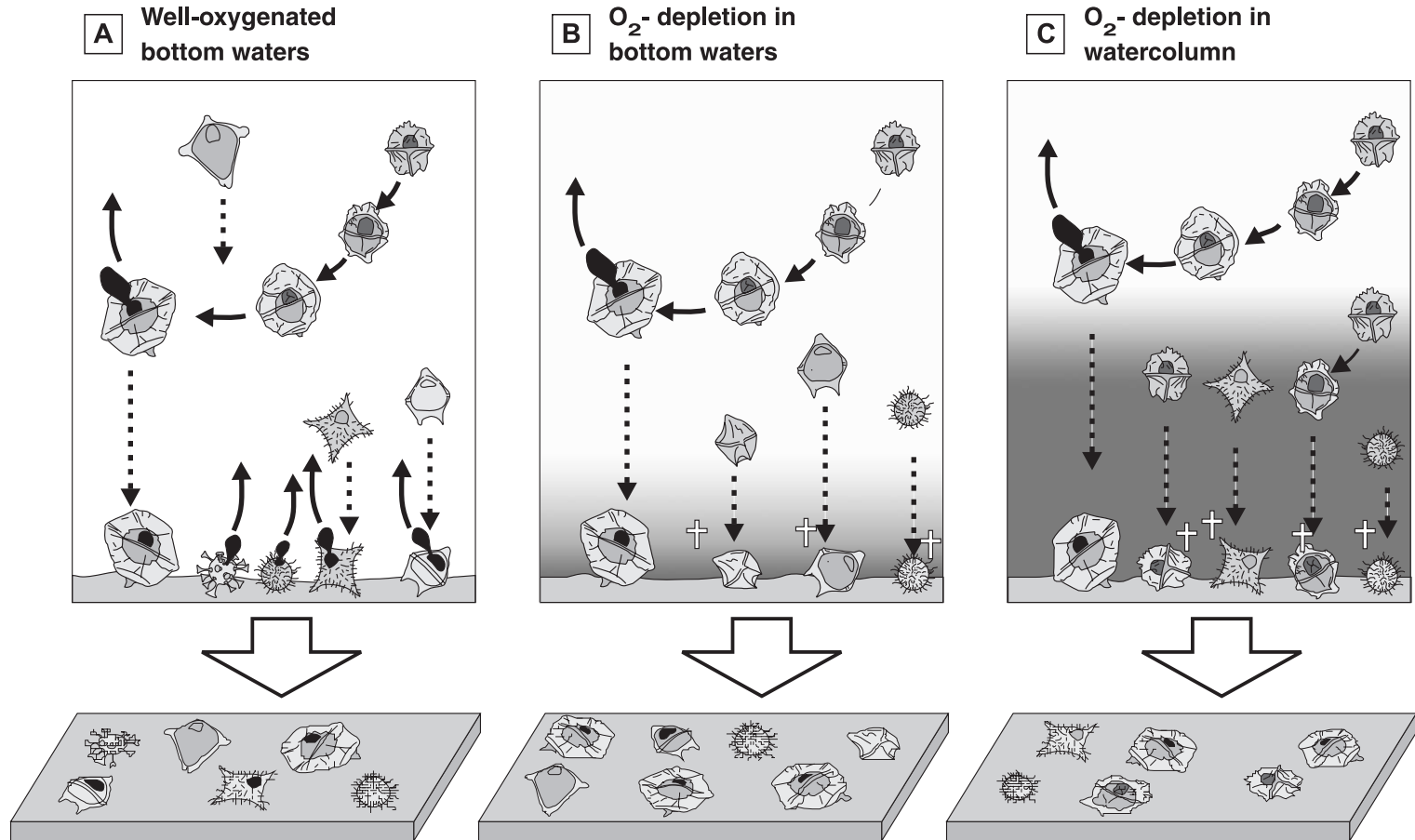
Fig. 14. Schematic model showing reaction of cyst-forming dinoflagellate populations to varying oxygenation levels in the lower Oligocene of the Mainz Basin in southern Germany. (A) During well-oxygenated intervals, dinoflagellates are able to excyst at the seafloor, diversity of cyst-forming dinoflagellates is relatively high and resulting dinocyst assemblages are relatively diverse. (B) Oxygen depletion at the sea floor prohibits excystment and causes dinocyst diversity to decrease. *Thalassiphora pelagica* is not affected because it excysts in the water column. (C) Oxygen depletion higher in the water column also prevents completion of the *T. pelagica* life cycle, leading to the preservation of ontogenetically early cyst morphotype. See text for further explanation. Modified from Pross (2001b).

sity. *T. pelagica*, in contrast, was not affected because it excysted mainly in the water column. Moreover, the distribution of different *T. pelagica* morphotypes (which Pross, 2001b considered to represent different stages within the cyst part of the *T. pelagica* life cycle; see also von Benedek and Gocht, 1981), appear to be linked to oxygen availability. Horizons with the strongest oxygen depletion and highest *T. pelagica* abundances are also characterized by highest abundances of *T. pelagica* specimens interpreted to represent an early, unfinished stage in cyst formation. This distribution pattern is interpreted to reflect the extension of low-oxygen conditions higher in the water column, so that even a holoplanktic taxon such as *T. pelagica* was affected. The completion of the *T. pelagica* life cycle was prevented, which led to the preservation of ontogenetically young morphotypes in the sediment. The model proposed by Pross (2001b) requires a concept for the formation of *T. pelagica* cysts that differs from that known from modern cyst-forming dinoflagellates. However, processes of encystment other than those known from extant forms are possible given the complexity of the dinoflagellate group and the fact that cyst morphogenesis is incompletely known even in most extant cyst-producing dinoflagellate species (Kokinos and Anderson, 1995). In addition, the realization of the model depends on three key environmental factors. Firstly, to yield a benthic signal, dinocysts other than *T. pelagica* must reach the sea floor prior to germination. Based on the sinking rates as observed in modern dinocysts (Anderson et al., 1985; Heiskanen, 1993) and derived from modeling (Sarjeant et al., 1987), this requires water depths not exceeding 150–200 m. Moreover, low-oxygen conditions must temporarily extend into the water column and low-energy hydrodynamic conditions are necessary for the thanatocoenosis on the sediment surface to provide an integrated picture of the biocoenoses in the water column above. These factors can be assumed to be realized in low-oxygen shelf settings. However, further work seems necessary to verify the applicability of this model to dinocyst assemblages from other oxygen-deficient shelf environments and other intervals of the Paleogene. Alternatively, the combined signals might reflect extreme surface salinities, in this case lowered salinities. It is conceivable that

an increase in runoff led to reversed density stratification, which obstructed deep ventilation and increased eutrophication of the surface layers, and provided conditions that only *T. pelagica* could cope with. A scenario of strongly abnormal salinity and only *T. pelagica* thriving under these conditions is similar to the record of *Polysphaeridium zoharyi* from the Arabian Sea, where very high sea surface salinity and hyperstratification prevailed following Heinrich events (Reichart et al., 2004; see Section 7). In the case of the lower Oligocene from the Mainz Embayment, however, low salinities (i.e., brackish conditions) would have prevailed instead of high salinities (i.e., hypersaline conditions). The strong salinity change(s) may have invoked the observed strong morphological variability in *T. pelagica*, perhaps in a similar manner to that observed in extant *Lingulodinium machaerophorum*. Fossil examples of such extreme morphological changes—comparable to that observed in *T. pelagica*—are known from *Galeacysta etrusca* during the Messinian salinity crisis in the Mediterranean (Corradini and Biffi, 1988) and have also been observed globally in the '*Cordosphaeridium fibrospinosum* complex' sensu Brinkhuis and Schiøler (1996) during the late Cretaceous and Paleogene.

9. General reconstruction of watermasses and paleoprovincialism

The global spatial differentiation of dinocyst assemblages (i.e., provincialism) depends on the physiochemical characteristics of the water masses in which the thecal stage developed, and on surface water circulation patterns. Dinocyst provincialism in the fossil record, first recognized in Mesozoic sediments (Norris, 1965; Lentin and Williams, 1980; Goodman, 1987), can be used to trace the direction, origin and intensity of surface currents in the past. For instance, assemblages in a given region that are under the influence of equatorially derived surface currents will become strongly altered if subjected to the influence of a current from high latitudes. Hence, the high diversity in Paleogene dinocyst assemblages may serve as a powerful tool to reconstruct surface water circulation patterns. A good example of provincialism is the distribution of the Antarctic-endemic

dinocyst assemblage ('Transantarctic Flora' of Wrenn and Beckmann, 1982) during the Eocene. As outlined above (see Section 4), this assemblage has been widely recognized at sites with a paleolatitude south of ∼ 60 °S and can be readily distinguished from assemblages with more cosmopolitan or tropical affinities (Lentin and Williams, 1976; Wrenn and Hart, 1988; Brinkhuis et al., 2003a,b; Sluijs et al., 2003 and references therein). Hence, the relative amount of Antarctic-endemic versus cosmopolitan taxa can be used to reconstruct the direction and origin of surface currents in this region. Recently, Brinkhuis et al. (2002a,c) and Huber et al. (in press) showed that along the eastern margin of Australia and in New Zealand high percentages of members of the 'Transantarctic Flora' are recorded in lower Paleogene deposits. Based on these and other (Antarctic-endemic) paleontological data from the region, and supported through the results of fully coupled General Circulation Model runs, these authors postulate that during the early Paleogene a northward, Antarctic-derived surface current flowed along the east coast of Australia, rather than the present-day southward East Australian Current.

10. Concluding remarks

Based on combined actuo-paleontological and empirical approaches, organic-walled dinoflagellate cysts provide a powerful tool for the reconstruction of marine environments in the Paleogene. Quaternary studies have demonstrated that organic-walled cyst-producing dinoflagellates are sensitive to even the slightest changes in the physiochemical parameters of surface watermasses, indicating their potential for Paleogene studies. Moreover, the cysts are particularly abundant in sediments that were deposited in neritic settings. These factors make the environmental signal that can be derived from dinocysts important, and complementary to the information derived from the traditionally used calcareous and siliceous microfossil groups such as foraminifera, calcareous nannoplankton and radiolaria.

Throughout the paper, we illustrate that dinocysts are indeed highly sensitive indicators for changes in surface water productivity, temperature, and salinity in a wide variety of Paleogene marine settings. In addition, dinocyst assemblages show a pronounced proximal–distal differentiation, which is of relevance for paleoenvironmental reconstructions involving transport, runoff, and sea level change. Finally, recent work indicates that dinocysts may also be useful tools for the reconstruction of surface water eutrophication, stratification, and ventilation of bottom waters and the water column, and are vital for the reconstruction of Paleogene ocean circulation. Altogether, past and ongoing studies have increasingly confirmed the relevance of Paleogene dinocyst analysis for unravelling the mechanisms underlying the Earth's greenhouse–icehouse transition.

Future studies in the still relatively young, but evolving field of organic-walled dinoflagellate cyst (paleo)ecology will result in a refinement of existing approaches, and ultimately yield further increase in both data quality and (paleo)environmental interpretations. In this respect, the results from multi-proxy approaches have proven to be essential. Future studies will certainly also explore the use of molecular geochemical applications of dinocysts.

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