

The Eocene–Oligocene Transition

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Abstract: A diverse array of fossil, geochemical and sedimentary data shows patterns of major change at or near the Eocene–Oligocene boundary, indicating a period of fundamental climatic and biotic reorganization on Earth. Multiple lines of evidence support the hypothesis that these changes signal major global cooling, especially at high latitudes, and rapid growth of semi-permanent ice-sheet on Antarctica in the early Oligocene. The quality and temporal resolution of Eocene–Oligocene fossil and sediment records and the diversity of climatic proxy tools have increased enormously in recent years, bringing a new level of detail to the study of this transition. The higher-resolution records have revealed that the climatic shifts across the Eocene–Oligocene boundary occurred in multiple stages that can be calibrated on orbital time-scales. Coupled with increasingly sophisticated computer models, these records have led to significant advances in our understanding of possible causal mechanisms and feedbacks driving this global shift. Here we review the wealth of evidence for Eocene–Oligocene climate change, summarize the current state of understanding, and highlight the key areas still requiring work that might guide the direction of future research. Obtaining a thorough understanding of this critical climatic transition is important for highlighting the mechanisms and sensitivities of Cenozoic climate, and addressing topical questions relating to the dynamics of global change during greenhouse–icehouse climate switching.

The transition from the Eocene to the Oligocene was a period of global change lasting about 500,000 years that marks a major step towards the development of the modern glaciated climate. Several decades of research (reviewed in this paper), which builds on work stretching back to the early 20th century, have revealed that this interval is associated with extinctions and evolutionary turnover, on land and in the oceans, and major shifts in geochemical and sedimentological proxies. These records provide strong evidence for a phase of oceanic reorganization, global cooling and the growth of the first semi-permanent continental-scale ice-sheets on Antarctica. The causative mechanisms of Eocene–Oligocene (E–O) climate change are widely debated, with much of the discussion centring on the relative roles of declining greenhouse gases and the opening of Southern Hemisphere oceanic gateways in permitting substantial ice build-up on Antarctica. Following Quaternary and Neogene models, attention is now being focused on defining the significance of orbital configurations, which affect the distribution of solar radiation received by the Earth, as well as the role of many possible feedbacks within the Earth System that may have interacted to give the record of E–O change that we see.

Terrestrial and shallow marine records of E–O climate change from around the world reveal significant biotic turnover in plants and animals across a range of latitudes that are linked to climatic

cooling, widespread regression and changes in the hydrological cycle. These records are sporadic, however, and the most complete archives are found in the deep-sea realm where sedimentation is often more continuous. Here, E–O environmental changes have left their mark as major shifts in microfossil communities, microfossil geochemistry, sedimentation and mineralogy. Much of the recent progress in understanding the E–O transition has come from palaeoclimate proxies derived from these marine records that are accessed through deep-sea coring.

A major problem has been that most Deep-Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) sites spanning the E–O boundary are condensed and/or interrupted by hiatuses, which have been attributed to an increase in ocean circulation vigour and glacioeustatic sea-level fall associated with climate change (Kennett & Shackleton 1976; Aubry 1991; Miller *et al.* 1991; Zachos *et al.* 1996). There has, therefore, been a shortage of sequences appropriate for continuous palaeoclimate analysis. Recent advances in drilling technology and methods of stratigraphic correlation have led to improved recovery of deep-sea Palaeogene sequences, and the quality of E–O sediment archives and derived proxy records has increased significantly. These newly available records, combined with continuously more sophisticated computer models, have led to advances in our understanding of the timing and mechanisms of

E–O climate change, and helped constrain theories on the feedbacks involved in the inferred cryosphere and biosphere responses.

Here we review the current state of understanding of the E–O transition. The account will begin with a discussion of the systematics of E–O boundary stratigraphic terminology. The core of the paper will review evidence for climatic change from (i) fossils and (ii) palaeoclimatic proxies. Finally, we provide a short synthesis summarizing progress to date and our vision of where future research is and should be directed.

Terminology, correlation and calibration

The E–O boundary is formally defined at the Global Stratotype Section and Point (GSSP) at Massignano, Italy, and corresponds to the extinction of the planktonic foraminiferal Family Hantkeninidae (see Coccioni *et al.* 1988; Nocchi *et al.* 1988; Premoli Silva & Jenkins 1993; Berggren *et al.* 1995). The boundary is a tie-point in the timescale of Cande & Kent (1995) where it is fixed at 33.7 Ma, although this figure is likely to be refined by astronomical tuning (Coxall *et al.* 2005; Gale *et al.* 2006; Jovane *et al.* 2006). We use the term ‘Eocene–Oligocene Transition’ (EOT) to encompass a phase of accelerated climatic and biotic change lasting 500 kyr that began before and ended after the boundary. This transition interval is most clearly recognized using deep-sea benthic foraminifera stable isotope data. In most records, it begins with a phase of relatively negative carbon isotopes and ends with a peak in both oxygen and carbon isotope ratios. Our definition of the transition interval excludes longer-term events that have sometimes been included in discussion of ‘terminal Eocene events’. We start with a clarification and revision of the nomenclature.

The $\delta^{18}\text{O}$ peak at the end of the transition interval coincides with the base of an Oligocene isotope Zone defined by Miller *et al.* (1991) as ‘Oi-1’, and is widely regarded as signalling a peak in glaciation on Antarctica (Fig. 1). There is some confusion in the literature regarding the meaning of Oi-1, despite the fact that it was clearly defined by Miller *et al.* (1991). Most workers use Oi-1 to identify the climax of the early Oligocene $\delta^{18}\text{O}$ excursion that lasted *c.* 400 kyr (Zachos *et al.* 1996; Coxall *et al.* 2005). As an isotope zone, however, Oi-1 extends between two peaks in the oxygen isotope record, and in fact spans much of the lower Oligocene, equivalent to several million years of time (Miller *et al.* 1991, Fig. 6, p. 6839). The base of the Oi-1 zone is defined in DSDP Site 522 by the maximum $\delta^{18}\text{O}$ value in benthic foraminifera *Stilostomella* spp. (Oberhänsli *et al.* 1984).

This occurs at 133.13 mbsf, which equates to 33.494 Ma on the geomagnetic polarity timescale of Cande & Kent (1995) (19.38% through C13n) (Miller *et al.* 1991; see summary by Vergnaud-Grazzini & Oberhänsli 1986). This level is slightly above the level of the abrupt shift to high $\delta^{18}\text{O}$ recorded in *Cibicides* spp. from the same site (133.59 m, *c.* 33.588 Ma), which represents the base of ‘Oi-1’ as identified by Zachos *et al.* (1996). Oi-1 does not correspond to or include an isotopic shift, as implied in some of the literature (e.g. Zachos *et al.* 2001, Fig. 2, p. 688; Gale *et al.* 2006, p. 412; Van Mourik & Brinkhuis 2005, p. 13).

The isotopic shift and the $\delta^{18}\text{O}$ maximum are clearly both important events that represent different climatic and environmental phases. Here we use the term ‘Early Oligocene Glacial Maximum’ (EOGM), advocated by Liu *et al.* (2004) and Tuo *et al.* (2006) (after Zachos *et al.* 1996) to identify the phase of maximum $\delta^{18}\text{O}$ (Oi-1 of Zachos *et al.* 1996), and to differentiate from Miller *et al.*’s (1991) isotope zone. The phase of rapidly increasing $\delta^{18}\text{O}$ that precedes the EOGM we refer to as the E–O ‘Shift’. In the type section (DSDP Site 522) and elsewhere (Zachos *et al.* 1996; Coxall *et al.* 2005), the Shift occurs over a period of several hundred thousand years and encompasses the E–O boundary. In some isotope records (see below), it is resolved as two or more steps (Fig. 1). The ‘E–O Transition’ in its strict sense, therefore, is equivalent to the ‘E–O Shift’. Under an alternative astronomical naming scheme (based on the 400 kyr cycle of Earth’s eccentricity) that has recently been proposed for the Oligocene glaciations (Wade & Palike 2005) the EOGM is referred to as event ‘84Eo C13n’.

Fossils

The fossil record across the E–O boundary has been periodically reviewed as knowledge has increased (Pomeroy & Premoli Silva 1986; Prothero & Berggren 1992; Prothero 1994; Ivany *et al.* 2003; Prothero *et al.* 2003) and new data continue to be published every year. While the E–O transition interval was not one of the ‘Big Five mass extinctions’ (Sepkoski 1986), it was nevertheless a time of substantial extinction and ecological reorganization in many biological groups. Some of these groups are vital for biostratigraphic correlation, so the disappearance or appearance of key taxa in the fossil record is often tied up with attempts to recognize the E–O boundary itself in different facies. Because of fundamental problems in precisely correlating stratigraphic sections across environments, oceans, continents and latitudes, the detailed sequence of biotic events is

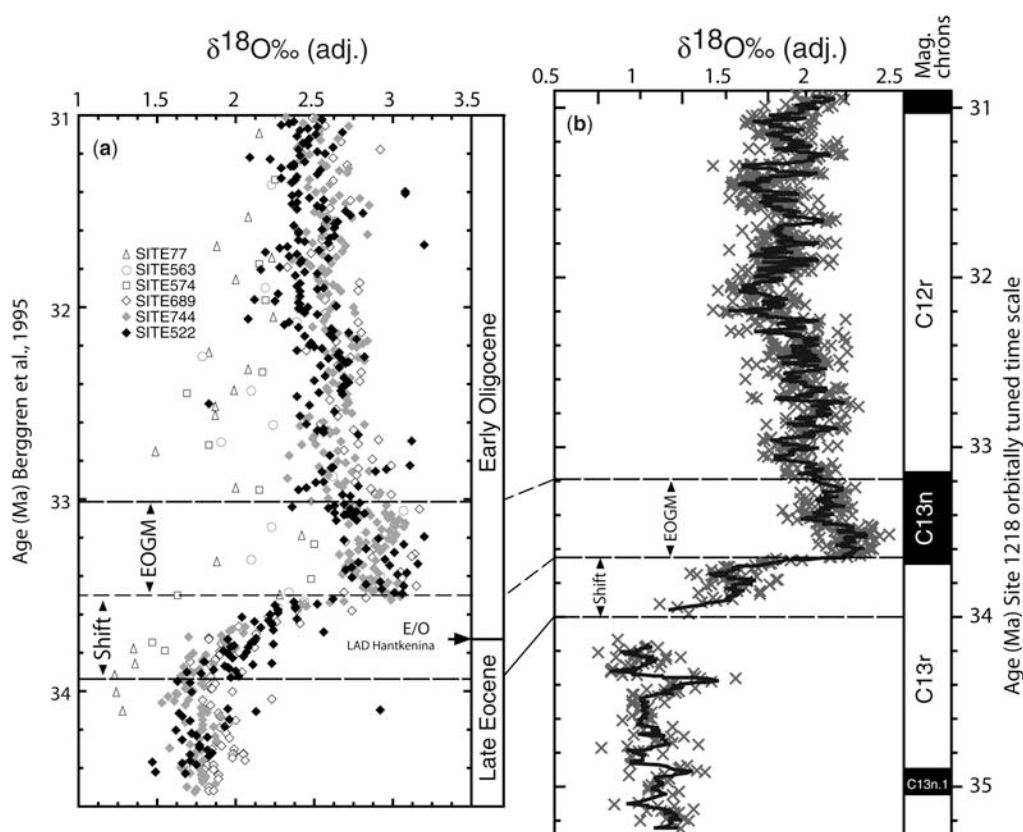


Fig. 1. Terminology, calibration and $\delta^{18}\text{O}$ signature of the Eocene–Oligocene Transition. (a) Benthic foraminifera $\delta^{18}\text{O}$ compilation (after Zachos *et al.* 2001) from mid- to high southern latitudes (diamonds) and the equatorial Pacific (other symbols) plotted on a common time scale (Berggren *et al.* 1995) showing the globally recognizable *c.* $\delta^{18}\text{O}$ 1.5‰ shift and positive $\delta^{18}\text{O}$ anomaly. The extinction of *Hantkenina* spp. has been identified in South Atlantic DSDP Site 522 (136.7 mbsf; Poore 1984) and is here calibrated (arrow) against the corresponding benthic $\delta^{18}\text{O}$ record (black diamonds). (b) *Cibicidoides* spp. $\delta^{18}\text{O}$ (+0.64) from ODP Site 1218 (3800 m water depth; Coxall *et al.* 2005) (5-point moving average trend line) plotted on an orbitally tuned timescale. We distinguish the interval of $\delta^{18}\text{O}$ 'Shift' (which is time equivalent to the Eocene–Oligocene Transition), from the early Oligocene $\delta^{18}\text{O}$ maximum, here referred to as the Early Oligocene Glacial Maximum (EOGM) (after Zachos *et al.* 1996; Liu *et al.* 2004). These features are also recognizable in the compilation. The site 1218 data gap corresponds with a zone of severe dissolution through which no calcareous benthic forams were available (see below). Lower $\delta^{18}\text{O}$ values at Site 1218 and other tropical sites suggest bottom-water temperatures *c.* 2 °C warmer than high southern latitudes. Species-specific adjustments have been applied (+0.64 or +0.4) to account for vital effects (after Zachos *et al.* 2001).

still not clear at high resolution (Ivany *et al.* 2003). However, it is likely that some of the extinctions are associated with the phases of rapid climatic change and sea-level fall across the E–O boundary and others may be associated with the maximum glacial conditions of the early Oligocene (EOGM, Fig. 1; corresponding to the base of the 'Oi-1' isotope zone of Miller *et al.* 1991). The radiation of more cold-adapted forms in many biotic groups probably began during this glacial period, and continued thereafter into the Oligocene. Ongoing efforts directed at relating patterns

of biotic turnover in different environments to the global isotope and palaeomagnetic record is likely to lead to greater clarity as work progresses.

Planktonic foraminifera

In the Global Stratotype Section at Massignano in Italy, the E–O boundary marker (the 'Golden Spike') is placed at the last occurrence of the planktonic foraminiferal Family Hantkeninidae (Nocchi *et al.* 1988; Premoli Silva & Jenkins 1993). This Family, although seldom dominant in planktonic

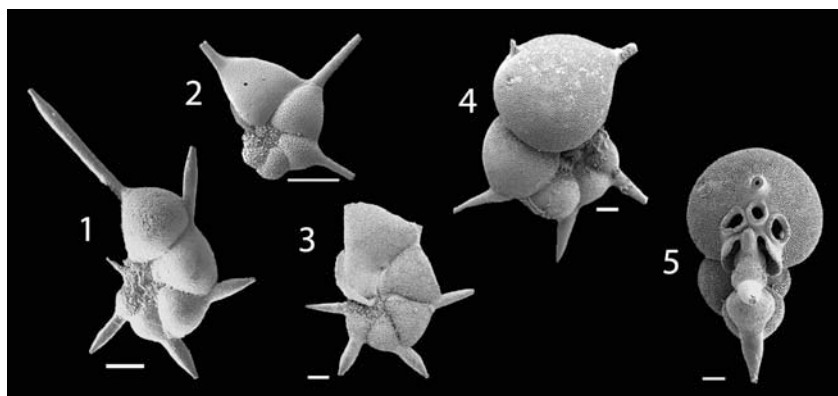


Fig. 2. SEM micrographs of species of the planktonic foraminiferal family Hantkeninidae that went extinct at the E–O boundary (see Coxall & Pearson 2006). (1) *Hantkenina alabamensis*; (2) *H. primitiva*; (3) *H. compressa*; (4) *H. nanggulanensis*; and (5) *Cribrohantkenina inflata*. Specimens are from various deep-sea sites. Scale bar = 100 µm. The extinction of these species denotes the Eocene–Oligocene boundary worldwide.

assemblages, is a very distinctive component of middle and upper Eocene pelagic carbonates worldwide (Fig. 2). Coccioni *et al.* (1988) recognized five species and two genera (*Hantkenina* and *Cribrohantkenina*) of Hantkeninidae at Massignano, although in their analysis they do not all persist to the boundary, and a similar set of species can be recognized in the Spanish sections such as that at Fuente Caldera (Molina 1986; Molina *et al.* 2006). The earlier suggestion by Blow (1979) that the extinction of *Cribrohantkenina* preceded *Hantkenina* (which was based on limited sampling) can now be discounted. Our own work (Coxall & Pearson 2006) suggests that the extinction of *Hantkenina* and *Cribrohantkenina* was essentially simultaneous and involved all five species. Moreover, it exactly coincides with the local extinction of another common species, *Pseudohastigerina micra* (Molina *et al.* 2006), or its dwarfing (Nocchi *et al.* 1986), and is close to the first appearance of a typically Oligocene form, *Globoquadrina tapuriensis* (Blow & Banner 1962; Coccioni *et al.* 1988; see also Keller 1983 and Keller *et al.* 1992). This means that the E–O boundary is one of the best-defined biostratigraphic levels of the Cenozoic for planktonic foraminifera and in the latest tropical subtropical biozonation it is used as the top of the topmost Eocene zone, E16 (Berggren & Pearson 2005). Although good stratigraphic sections with acceptable carbonate preservation are rare, there is as yet no evidence that the extinction of the Hantkeninidae was locally controlled or diachronous (as claimed by Van Mourick & Brinkhuis 2005), except in the high polar latitudes where the group only occasionally occurs during climatically favourable episodes.

Another major extinction in the planktonic foraminiferal records can be found close to the last occurrence of the Hantkeninidae, namely the extinction of the *Turborotalia cerroazulensis* group, which in most taxonomies consist of three separate species (see Pearson *et al.* 2006 for a recent review). In the Massignano stratotype, this occurs just 60 cm below the Golden Spike, which equates to about 65 kyr (Coccioni *et al.* 1988; Berggren & Pearson 2005). It also narrowly predates the *Hantkenina* extinction at Fuente Caldera in Spain (Molina *et al.* 2006) and several deep-sea drilling sites in the North and South Atlantic and Indian Oceans (e.g. Poore 1984; Pearson & Chaisson 1997). The *T. cerroazulensis* group of species was very abundant and widespread. Both the Hantkeninidae and the *T. cerroazulensis* group existed for many millions of years before their eventual demise, which hints that their closely spaced extinctions were very likely more than coincidental and related to a prolonged phase of environmental disruption. Taken together, they represent one of the most obvious extinctions of the Cenozoic among planktonic foraminifera.

Boersma & Premoli Silva (1986) and Keller *et al.* (1992) noted that the long-term trend of planktonic foraminifera evolutionary turnover from the middle Eocene into the Oligocene largely involves extinction of warm-water, tropical, surface-dwelling species. The extinctions at and near the E–O boundary might therefore be due to rapid environmental change and cooling, and may also have been influenced by changing water mass stratification and patterns of biological productivity.

Unfortunately, it is still not possible to confidently (and precisely) locate the planktonic foraminifer

extinctions with reference to the stable isotope events (see below). Probably the best published record is DSDP Site 522 on the Walvis Ridge, South Atlantic, where the hantkeninid extinction (Poore 1984) occurs within the isotope shift that precedes the basal EOGM (see Fig. 1), but in Site 522 the planktonic foraminifera are somewhat dissolved and fragmentary. Another relevant section is ODP Site 925 in the tropical North Atlantic. Here the preservation is even worse (in hard limestone), but the hantkeninid extinction (Pearson & Chaisson 1997) occurs above a zone of dissolution and below the most prominent carbon isotopic shift that leads into the EOGM (Diester-Haass & Zachos 2003).

Nannofossils

The other calcareous group that is widely used for deep-sea biostratigraphy is the nannoplankton. Perch-Nielsen (1986) and Aubry (1992) documented a long-term decline in diversity from the middle Eocene into the Oligocene but little change is associated with the boundary interval itself. The only significant extinctions that occur near the E–O boundary interval are the stepped disappearance of rosette-shaped discoasters (Aubry 1992). The disappearance of *Discoaster saipanensis* at approximately 34.2 Ma (i.e. about 500 kyr before the boundary; Berggren *et al.* 1995) is preceded slightly by the extinction of another species, *D. bardiensis*. The former of these extinctions marks the boundary between nannofossil Zones NP20 and NP21. A more minor event, namely the extinction of *Pemmatoporella papillatum*, may be more closely associated with the E–O boundary itself (Varol 1998) but requires further study. Beyond that, no major changes to nannofossil assemblages have been reported, but there are significant biogeographic changes associated with the basal Oligocene glaciation and the onset of a relatively unstratified ocean around Antarctica, where nannoplankton locally disappear from the record (Hay *et al.* 2005).

Radiolaria

Although it has long been thought that radiolaria were largely unaffected by the E–O transition (e.g. Riedel & Sanfilippo 1986), a major turnover of tropical species has recently been described by Funakawa *et al.* (2006) from sites drilled in the Pacific. This turnover includes the extinction of several taxa and a corresponding sudden drop in diversity and radiolarian accumulation rates, and is combined with the expansion of cool-water cosmopolitan taxa. It appears to be closely associated with the stable isotope shifts that precede the

EOGM and awaits study in other areas, especially high latitudes.

Dinoflagellate cysts

Brinkhuis (1992), Brinkhuis & Biffi (1993) and more recently Van Mourik & Brinkhuis (2005) have reviewed the evolution of dinoflagellate cysts (dinocysts) across the Eocene–Oligocene boundary interval in Italy. Van Mourik & Brinkhuis (2005) present new data from the GSSP and a neighbouring sediment core (the 'Massicore'). Across the E–O boundary interval in Italy, two successive influxes of cool-water high-latitude species occur (Brinkhuis & Biffi 1993), the first of which correlates directly with the E–O boundary *sensu stricto* and the second with the onset of a more severe cold episode and inferred sea-level lowstand. Although these effects are local migrations, they may relate to the stepwise isotopic shifts that precede the early Oligocene glaciation and the maximum glaciation itself. A later event, identified in the Massicore, is the extinction of *Areosphaeridium diktyoplokum*, which occurs near the top of Chron C13n. This is several hundred thousand years younger than the $\delta^{18}\text{O}$ maximum.

Elsewhere, the record of dinocysts across the E–O boundary interval is patchy with the record from local basins probably affected by sea-level fall and changing local environments (e.g. Gedl 2004). Sluijs *et al.* (2003) have described the transition interval in the Southern Ocean where typical early Palaeogene assemblages are sequentially replaced with assemblages dominated by *Brigantidium*, which is interpreted as related to the onset of upwelling conditions in the water column. Records from the Weddell Sea and off Dronning Maud Land (Antarctic margin) show decreasing dinocyst diversity through the Eocene and at the E–O boundary, falling to only two species by the end of the early Oligocene (Mohr 1990). This pattern is thought to indicate development of cold surface waters.

Diatoms

Baldauf (1992) brought together deep-sea drilling data available at that time and identified a significant turnover in marine diatoms as occurring at the E–O transition, with a notable increase in diversity in the tropics. He interpreted this as being related to a decrease in the vertical stratification of the water column and an increase in the latitudinal thermal gradient. The most profound changes seem to have occurred in the higher latitudes, associated with the changes in high-latitude water masses across the E–O transition. For example, Suto (2006) noted a rapid diversification of *Chaetoceros* resting spores in the Norwegian Sea, which

they associate with a change from a stable water column with a constant nutrient supply in the Eocene to an unstable and more vertically mixed water column in the Oligocene. Similarly in the southern high latitudes, Olney *et al.* (2005) record an increase in cold-adapted species in the Oligocene of Antarctica, and Whitehead (2005) describes an increase in the diversity of benthic diatoms in the Oligocene associated with the increasing influence of the Antarctic polar current.

Benthic foraminifera

Benthic foraminifera occur in a range of environments and habitats, and the pattern of evolution differs markedly between these habitats. In abyssal and bathyal environments, there is little major change associated with the boundary interval itself (Thomas 1992; Coccioni & Galeotti 2003). Nevertheless, Diester-Haass & Zahn (2001) and Diester-Haass & Zachos (2003) record a sudden increase in the rate of accumulation of benthic foraminifera in deep-sea environments in various parts of the world, which they correlate to the rapid isotopic shifts and attribute to an increase in productivity associated with the more vigorous overturning of the earliest Oligocene ocean (see also Boersma 1986, for a similar suggestion). Thomas and Gooday (1996) also observe declining deep-sea benthic diversity and an increase in dominance of opportunistic phytodetritus-exploiting species (e.g. *Epistominella exigua* and *Alabaminella weddellensis*) that suggest a switch to a more unpredictable and seasonally fluctuating food supply, especially at high latitudes during the transition. Kaminski (2005) has recorded an acme of deep-water agglutinated species in the North Atlantic and Western Tethys during the E–O transition interval, one of several such events in the Palaeogene.

The pattern of turnover in smaller benthic foraminifera from shallower environments seems to contrast with the deep-sea record in that significant changes are more obvious. McGowran & Beecroft (1986) and McGowran *et al.* (1992) noted an abrupt turnover of neritic benthic foraminifera in Australia, which they linked to the sudden cooling and sea-level drop associated with the early Oligocene glaciation. The pattern is similar in the US Gulf Coast, although, as in Australia, it is complicated by facies changes across the boundary (Fluegeman 2003). A slightly delayed radiation of Oligocene shallow-water smaller benthic foraminifera in the US Gulf Coast was noted by Fluegeman (2003).

By far the most dramatic evidence for extinction and turnover occurs in larger foraminifera. These organisms were important carbonate producers

throughout the Eocene, where they were abundant and widespread. According to Kiessling *et al.* (2003) and Nebelsick *et al.* (2005), Eocene carbonate platforms, which are dominated by coralline algae and larger foraminifera, declined rapidly in the Late Eocene and across the E–O boundary interval, reaching a ‘post-Cambrian low’ in the earliest Oligocene. Unfortunately, continuous sections in carbonate facies are rare, possibly because of the sea-level drops associated with the glacial maximum. The most complete section available seems to be the Melinau limestone of Sarawak, which was studied in detail by Adams (1965). Adams *et al.* (1986) reviewed the Indo-Pacific records and noted a mass extinction of some important long-ranging genera and species, notably *Asterocyclina*, *Discocyclina* and some species of *Nummulites*. These events occur in the Melinau limestone associated with a brief switch to algal-dominated facies. The mass extinction has not been reliably correlated to isotope or magnetostratigraphy, nor has it been demonstrated how abrupt or gradual the extinctions were, but Adams *et al.* (1986) suggest a relation to the climate deterioration and sea-level fall across the E–O transition. The Americas were a different faunal province, but from limited evidence, the pattern may be similar; for example, Robinson (2003) has noted a rapid decline in larger foraminifera in the Caribbean that may be associated with the boundary interval.

Ostracodes

Benson (1975) suggested that the E–O transition to be the most significant in the Cenozoic history of ostracodes, but it is not clear how precisely this turnover correlates to the boundary events and to what extent different habitats were affected. Schellenberg (1998) found significant drops in diversity of ostracodes across the E–O boundary interval, and noted that the extinction seems to have been most severe among deposit-feeding species. In contrast, Dall’Antonia *et al.* (2003) found little variation in assemblages across the E–O boundary in the Massignano stratotype section, and found little change in either the shallow and deep records from the US Gulf Coast and Barbados respectively, except for some minor extinctions in both. Like benthic foraminifera, ostracodes lived in a wide variety of habitats and the Eocene turnover pattern probably varies between them.

Shallow marine invertebrates

The fossil record of shallow marine invertebrates across the E–O boundary worldwide is quite patchy, with the best records coming from North America and Europe. Dockery (1986) and

Dockery & Lozouet (2003) have described a major turnover of molluscs in the early Oligocene of the US Gulf Coast and Paris Basin, including the disappearance of many long-ranging forms, which they attribute to sea-level fall and global cooling. Dockery & Lozouet (2003) also document a major influx of European taxa into North America in the earliest Oligocene that may be related to changing water mass circulation in the North Atlantic. Squires (2003), Hickman (2003) and Nesbitt (2003) described a major and relatively abrupt turnover of marine molluscs in the earliest Oligocene in the western United States, in which over half of pre-existing genera disappeared. During these events, warm-water taxa suffered disproportionately, while cold-water forms radiated and expanded their ranges. The higher-latitude record from Alaska and Kamchatka (Oleinik & Marincovich 2003) is similar to the record further south. More recently, minor extinction and size reduction in veneroid bivalves has been described from the eastern United States (Lockwood 2005). Other events, both before and after the E–O boundary interval, are also in the record and some groups, while others such as the echinoids of the United States (Carter 2003) do not show an unusual extinction pattern.

The fundamental problem involved with shallow-water marine invertebrates (as with benthic foraminifera) is distinguishing global and local effects. The problem of sea-level fall associated with the transition is bound to have caused many local changes; far better geographic sampling would be necessary to distinguish local from global effects.

Terrestrial vegetation

There is clear evidence for major changes in terrestrial vegetation worldwide across the E–O transition, but the pattern of change varied from continent to continent and across the latitudes. The change in North American floras was recognized by Wolfe (1978) as the ‘Terminal Eocene Event’ and has been studied in more detail by Wolfe (1992, 1994) and recently by Liv *et al.* (2007). The dominant pattern in North America is for widespread replacement of the subtropical broad-leaved Evergreen vegetation of the Eocene with cooler, deciduous forms in the Oligocene, with regional extinctions, especially at higher latitudes. Similarly in the south, Patagonian floral records show the disappearance of tropical vegetation and the rise to dominance of subtropical and cool-temperate species from the middle Eocene of Early Oligocene (Palazzessi & Barreda 2007). In other places in North America, there was a diversification of desert species as aridity

increased in the continental interior (Yancey *et al.* 2003; Moore & Jansen 2005). In some areas such as the US Gulf Coast, there is less evidence for dramatic change (Oboh-Ikuenobe & Jaramillo 2003). Collinson (1992) has reviewed the botanical data from Europe, where there is a similar change to a more seasonal temperate flora accompanied by loss of tropical and subtropical taxa. These records suggest that the main phase of change shortly pre-dates the mammalian extinctions (discussed below) (see also Hooker *et al.* 2004).

The evolution of extensive North American grassland habitats, and associated mammalian radiation, has been linked with the Eocene–Oligocene Transition but the timing is controversial (Stucky 1992; Strömberg 2005 and references therein). A recent study suggests that the spread of this habitat, and the mammalian grazing ecology, occurred between the late Oligocene and Early Miocene, driven by post-EOGM climate changes that led to increased seasonal aridity (Strömberg 2005, 2006).

With regard to the tropics, Jaramillo *et al.* (2006) have recently produced a detailed composite floral record from Columbia and Venezuela, based on pollen and spore occurrences that produce an unprecedented view of long-term floral diversity. The most rapid phase of change in this record occurs around the E–O boundary interval, which Jaramillo *et al.* (2006) link to the environmental changes associated with the onset of Antarctic glaciation. The resolution, however, is too low to correlate floral changes with the events of the transition itself, as seen in detailed deep-sea records (see below).

Perhaps the most dramatic changes would be expected in the high southern latitudes close to the supposed expansion of Antarctic ice. Macrofloral and palynological evidence from Antarctica has been reviewed by Francis (1999) and Francis & Poole (2002). The E–O transition interval coincides with a change from evergreen forest to sparse tundra on the Antarctic Peninsula and Seymour Island, and Francis (1999) goes further to suggest that vegetation–climate feedbacks may have played a role in the rapid environmental changes at that time. Similar patterns are seen in the high northern latitudes, where there was widespread displacement of subtropical broad-leaved vegetation, especially at altitude (Wolfe 1994; Myers 2003).

Evidence from beyond America and Europe is sparser. Kemp (1978) reviewed the Australian palaeobotanical record and found a major change near the E–O boundary, with a trend towards lower diversity, higher seasonality and a spread of cool-temperate plants. Leopold *et al.* (1992) document significant changes in Asian floras, with

diversity reduction across the boundary interval. Ramussen *et al.* (1992) found little variation in North Africa. More recently, however, Pan *et al.* (2006) have suggested that the E–O transition was the most important step in the extinction of African palms (Arecaceae), although they continued to flourish on other continents.

Mammals

A mass extinction of mammalian faunas in Europe (principally known from records in the Paris and Hampshire basins) at approximately the E–O boundary was noted almost a century ago by Stehlin (1909) as the ‘Grand Coupure’ (great break). It represents a major turnover in both perisodactyls and artiodactyls (hoofed herbivores). This has recently been dated as approximately coinciding with the EOGM (Hooker *et al.* 2004) and the associated sea-level regression. Approximately 60% of taxa seem to have disappeared at this time and it has been argued that the extinctions were caused either by climatic deterioration or competition with immigrant taxa from Asia (Savage & Russell 1983). A major turnover of mammals in Mongolia at this time has also been linked to climatic change (Meng & McKenna 1998).

In North America, the mammalian record has long been confused because of a misalignment of the land mammal stages with the global stratigraphy (see Prothero & Swisher 1992 for discussion). It is now clear, however, that there was a more minor extinction, coinciding with the diversification of hypsodont mammals close to the E–O boundary (Stucky 1992), and there are similarities with the record in South America (Marshall & Cifelli 1989). There may be a similar pattern in Asia but the issue is further confused by uncertain chronology (see comments by Berggren *et al.* 1992). The Oligocene in general marks the time when representatives of modern land mammals became the dominant vertebrate life, including the appearance of the first primates and apes, but precise timing is problematic.

In the marine realm, it has long been recognized that the extinction of the archeocete whales such as the giant *Basilosaurus* occurred at or near the E–O transition (Fordyce 1992, 2003; Manning 2003) although there is no evidence for a substantial mass extinction (Fordyce 1992). The cold high-latitude water masses of the early Oligocene seem to have been a spur to the evolution of crown-group whales, and the first baleen whales are known from the early Oligocene (Fordyce 1992, 2003), most likely in parallel with increased Southern Ocean upwelling and increases in plankton abundance. In addition, it has been demonstrated that toothed whales (suborder Odontoceti), which include

dolphins and porpoises, underwent a significant increase in brain size with respect to body size near the E–O boundary (Marino *et al.* 2004).

Others

The amphibians and freshwater turtle records from North America seem to suggest declining diversity (Hutchinson 1992), possibly related to increasing aridity around the E–O boundary. Corsini *et al.* (2006) also identified changes in turtle carapace size that may be a response to E–O climatic change. A similar picture emerges from Europe (Rage 1986) where tropical taxa disappear in large numbers near the end of the Eocene. The first diversification of cat-like carnivores (mostly sabre-toothed) and other predators also occurs in the early Oligocene and is thought to coincide with the development of grassland habitats in central North America (Bryant 1996). Evidence for other tetrapods tends to be patchy and difficult to interpret (e.g. see Prothero & Emry 1996), although it may be noteworthy that there seems to have been a radiation of passerine birds in the early Oligocene (Mayr 2005).

Summary of palaeontological evidence

There is widespread evidence for enhanced extinction in many groups across the E–O boundary interval, followed either immediately, or after a slight delay, by renewed radiation in the Oligocene. Precise correlations to the isotope shifts, glacial maxima and magnetostratigraphy are still problematic in many groups. In several groups where there is sufficient age-discrimination, the extinctions seem to have been stepwise over a period of change that may equate to several hundred thousand years, starting before the stage boundary as formally defined and ending with the maximum glaciation that corresponds to the base of the Oi-1 isotope zone. It is interesting that in groups as diverse as foraminifera, primates, whales and birds, the Oligocene saw the diversification of recognizably modern taxa, whereas most of the Eocene forms are from ‘prehistoric’, now-extinct groups that lie outside of the modern lineages. This pattern almost certainly relates to the fact that the E–O boundary interval was one of the most profound periods of change that led to the modern climatic regime, the change that is widely described as the greenhouse–icehouse transition (Miller *et al.* 1991).

The close coincidence of widespread extinction and stepwise climatic changes seems to imply causal linkage, but the causes of extinction must be different in many groups. Possibilities include temperature change, sea-level fall and the associated exposure of the continental shelf, change in

biological production on land and in the oceans, water mass properties (especially at high latitudes but also in equatorial and upwelling areas), atmospheric and ocean chemistry, etc. The whole Earth System seems to have entered a period of prolonged change, a factor that makes the E–O boundary extinctions rather different from the more sudden mass extinctions at the end of the Cretaceous and probably at the end of the Permian as well. In the following sections, we will review the geochemical and other evidence for prolonged and interlinked changes in the Earth System at this time.

Proxies

Other than the occurrence of glaciomarine sediments on and around Antarctica (e.g. Barrett *et al.* 1989; Zachos *et al.* 1999), there is little direct evidence of E–O climate change. Therefore, climate-sensitive proxies are used to trace responses to climatic parameters indirectly. These proxies provide information on global temperature, ice volume, ocean productivity, water mass structure, circulation, carbon cycling, atmospheric carbon dioxide concentration and continental weathering. Many of the processes being recorded are related to the global carbon cycle, either as cause or effect, and have the potential to influence and be influenced by atmospheric CO₂ concentration. The search for cause and effect relationship is therefore similar to the lesser (but still-unresolved) problem of understanding glacial–interglacial climatic switching.

Other important techniques that are integral to modern E–O palaeoclimatic study are climate modelling on various scales and complexities, and time series analysis, the latter having the power to identify patterns of external orbital forcing on Milankovitch timescales. Tectonic evolution is also fundamental to the system and feeds into all questions related to E–O climate change. Descriptions and applications of the various proxies and modelling techniques that have been utilized in the study of the E–O transition are discussed below under headings that represent the principal process or parameter they are tracing. As with the discussion of fossil evidence, there is no way it can be completed in this discussion, but we can identify a snapshot of important and promising areas.

Ice, temperature and sea level

Benthic foraminifera oxygen stable isotopes – Undoubtedly, the most significant proxy for documenting E–O climatic change is benthic foraminifera $\delta^{18}\text{O}$. As classically demonstrated, the principal controls on benthic $\delta^{18}\text{O}$ are: (i) seawater temperature and, (ii) $\delta^{18}\text{O}$ of seawater (δ_w), which

changes during glaciations. The benthic $\delta^{18}\text{O}$ proxy, therefore, helps constrain deep-water temperatures and global ice volumes. Since the Southern Ocean was probably the dominant deep-water source from at least the Late Eocene (e.g. Wright & Miller 1993), benthic $\delta^{18}\text{O}$ also provides an estimate of high-latitude surface water temperatures.

As discussed above, studies of numerous deep-sea cores demonstrates the existence of an abrupt positive *c.* 1.2–1.5‰ shift in benthic $\delta^{18}\text{O}$ associated with the E–O boundary that builds to a sustained maximum at the base of the Oligocene (Fig. 1). This interval of maximum $\delta^{18}\text{O}$, which we refer to as the EOGM, is now widely believed to represent the maximum extent of the first semi-permanent ice sheet on Antarctica (e.g. Kennett & Shackleton 1976; Kennett 1977; Miller *et al.* 1987; Zachos *et al.* 1996, 1999, 2001; Lear *et al.* 2001; Coxall *et al.* 2005), 50% (or more) of the present Antarctic ice-sheet volume (Barker *et al.* 1999; DeConto & Pollard 2003a). Following termination of the EOGM, $\delta^{18}\text{O}$ recovered to a new equilibrium value that was on average 1‰ higher than the Late Eocene, suggesting subsequent deglaciation and stabilization of Oligocene ice volumes.

High resolution (2–10 kyr) $\delta^{18}\text{O}$ records have improved constraints on the timing, magnitude and structure of the E–O isotopic shift and $\delta^{18}\text{O}$ maximum and identified additional structure within it. These records demonstrate that the EOGM can be correlated fairly precisely to the base of magnetic Chron C13n with an estimated duration of 400 kyr (e.g. Oberhänsli *et al.* 1984; Miller 1985; Zachos *et al.* 1996; Coxall *et al.* 2005). The *c.* 1.5‰ $\delta^{18}\text{O}$ shift into the EOGM lasted about 500 kyr and occurred in two phases (Zachos *et al.* 1996; Coxall *et al.* 2005). Orbitally tuned records from equatorial Pacific ODP Site 1218 suggest that this involved two 40 kyr steps, separated by a well-defined 200 kyr-long plateau (Coxall *et al.* 2005) (Fig. 1b), although this is not a unique interpretation of the orbital evidence. The first step, which accounts for less than half of the total shift, and the plateau occur in reversed interval C13r and the second step was completed at approximately the base of C13n. This relationship to the magnetic reversal record holds up in DSDP Site 522 and ODP site 744 (Zachos *et al.* 1996). The step-form is remarkably similar to the pattern of non-linear ice growth simulated by a coupled GCM-ice sheet models (DeConto & Pollard 2003a, b), although it is of significantly greater magnitude than predicted by the model. At ODP Site 744 (Southern Indian Ocean), the EOGM comprises two pronounced peaks lasting approximately 100 and 150 kyr respectively. These have been interpreted as two distinct glacial maxima, termed Oi-1a and Oi-1b (Zachos

et al. 1996). These features are less well defined elsewhere. The termination of the EOGM is more difficult to define and correlate between sites than its initiation because it consists of a series of small stepped decreases in $\delta^{18}\text{O}$, totalling *c.* 0.5–0.6‰, interspersed with minor positive excursions spread over a few tens of thousands of years (Zachos *et al.* 1996; Coxall *et al.* 2005). Most of this decrease, however, occurs in the top of magnetochron C13n (which is where the upper boundary of the EOGM is placed), coincident with a decrease in glaciomarine sediments close to Antarctica (e.g. Wise *et al.* 1991).

Quantifying the relative contribution of temperature and ice growth to the *c.* 1.5‰ $\delta^{18}\text{O}$ shift is a problem, but separating the two effects is not a trivial issue. One method is to obtain independent palaeotemperature estimates using Mg/Ca ratios in order to extract the δ_w component. This method is summarized here but discussed fully by Lear (2007). Other methods that have been used include looking for covariance in deep-sea benthic and low-latitude planktonic foraminifera $\delta^{18}\text{O}$ records (e.g. Miller *et al.* 1991) and modelling of Antarctic ice-sheet sensitivity to climate change (Oerlemans 2004, 2005).

Magnesium calcium ratios and ice volume – Benthic foraminiferal Mg/Ca palaeothermometry has been useful for providing independent temperature estimates and, therefore, resolving temperature and ice volume contributions to $\delta^{18}\text{O}$ records in the Quaternary and early Cenozoic (Mashiotto *et al.* 1999; Lear *et al.* 2001, 2004; Martin *et al.* 2002; Billups & Schrag 2003). Surprisingly, existing E–O Mg/Ca records show no evidence of deep-water cooling. In fact, if anything they suggest a 2 °C warming (Lear *et al.* 2001, 2004; Billups & Schrag 2003) (Fig. 3a). Taken at face value, this suggests that the entire E–O $\delta^{18}\text{O}$ shift is attributable to ice growth. This implied ice volumes seem unrealistic for Antarctica alone (Coxall *et al.* 2005), and raises several possibilities: (i) that changes in the hydrological system (moisture supply) rather than cool temperatures were important for ice-sheet expansion (Lear *et al.* 2001) (cf the ‘snow gun hypothesis’, Prentice & Matthews 1991), (ii) there was more ice elsewhere; i.e. possible contemporaneous northern hemisphere glaciation, consistent with sedimentary and modelling (DeCouto & Pollard 2007) evidence, (Davies *et al.* 2001; Via & Thomas 2006; Eldrett *et al.* 2007), and/or (iii) that some additional factor acts to mask the Mg/Ca cooling signal, such as seawater pH and/or carbonate ion concentration (Billups & Schrag 2003; Lear *et al.* 2004).

The lack of a cooling signal in deep water proxy records is puzzling because, although cooling might not have been the trigger for E–O Antarctica

glaciation, it seems logical that widespread Antarctic glaciation would lead to local cooling in the vicinity of Antarctica in the early Oligocene (Zachos *et al.* 1996; Oerlemans 2005). A likely explanation for the lack of Mg/Ca evidence for cooling is that the extreme increase in deep ocean carbonate ion concentration/alkalinity associated with a 1 km deepening of the calcite compensation depth (see below), synchronous with the shift into the EOGM, masked the cooling (Lear *et al.* 2004; Coxall *et al.* 2005). Until these effects are better understood, the Mg/Ca record across the E–O should be interpreted cautiously.

Covariance of $\delta^{18}\text{O}$ in global benthic and non-upwelling tropical planktonic foraminifera (i.e. from regions with the most thermally stable surface waters) has been used as an indicator of global ice volume fluctuations in the Quaternary (e.g. Shackleton & Opdyke 1973). However, there is a general shortage of suitable low-latitude and/or high-resolution E–O planktonic records because of poor preservation of dissolution-susceptible planktonic shells in notoriously carbonate-poor deep-sea sequences of this age. Existing planktonic $\delta^{18}\text{O}$ records are mainly restricted to the mid- to high latitudes, i.e. DSDP Site 522 (Oberhansli *et al.* 1984), DSDP Sites 592 and 593 (Murphy & Kennett 1986) and ODP Site 744 (Stott *et al.* 1990; Barrera & Huber 1991). These show highly variable increases in planktonic $\delta^{18}\text{O}$, ranging from 0.5 to 1.5 times benthic $\delta^{18}\text{O}$, that reflect complex contributions of regional sea-surface temperatures, salinity, depth habitat and post-burial diagenesis effects, in addition to sea-level shift related to ice growth. Prentice & Matthews (1988) compared compilations of low-latitude planktonic and deep-sea benthic $\delta^{18}\text{O}$ during the Cenozoic. They concluded that benthic $\delta^{18}\text{O}$ primarily reflects deep-ocean temperature variation whereas tropical planktonic $\delta^{18}\text{O}$ show responses to Cenozoic ice volume and suggested the presence of a significant ice budget for the past 40 myr. The Prentice & Matthews (1988) record, however, lacks the detail necessary to resolve the pattern of change during the E–O transition. In any case, assumptions about the stability of low-latitude temperatures during major climatic transitions may be ill founded (Miller *et al.* 1991). Acquisition of high-quality planktonic isotope records from low and high latitudes, of the kind that have been produced from Eocene and Cretaceous ‘glassy forams’ (Pearson *et al.* 2001; Wilson & Norris 2001), therefore, are a priority for better constraining global sea-surface temperatures and E–O latitudinal thermal gradients.

Other temperature proxies – Much of the study of E–O palaeoclimates is limited by our ability to accurately determine temperature variability. As

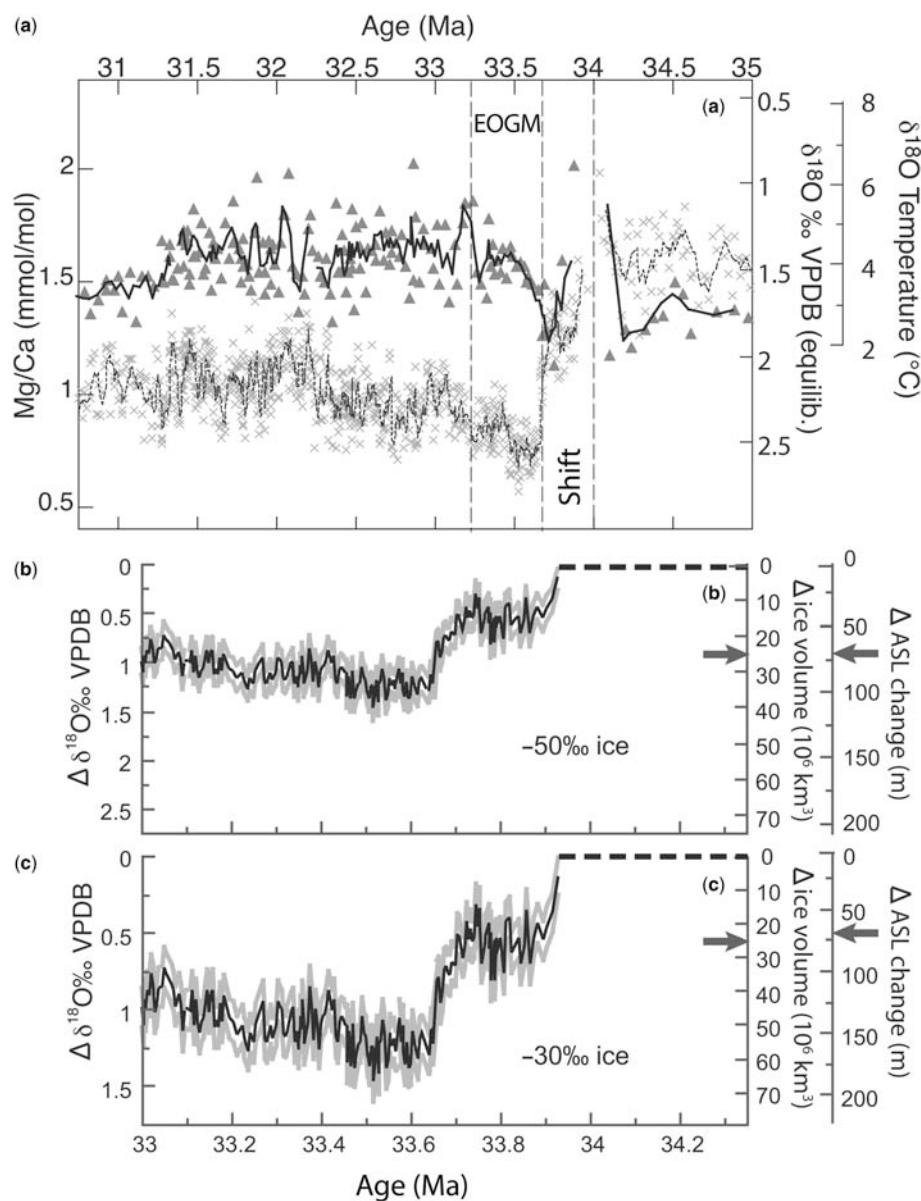


Fig. 3. Eocene–Oligocene benthic foraminifera palaeoclimate proxy records from ODP Site 1218 examining possible changes in sea level, ice volume and temperature (after Coxall *et al.* 2005). Data are plotted on the ODP Site 1218 orbitally tuned timescale. (a) $\delta^{18}\text{O}$ (crosses, 5-point moving average trend line) versus Mg/Ca (triangles, 3-point moving average trend line), in principle an independent palaeothermometer (*c.* 35 to 31 Ma) from ODP Site 1218 (Mg/Ca data from Lear *et al.* 2004). The records show no decrease in Mg/Ca across the E–O transition and into the EOGM. In fact, the Mg/Ca data show an increase from latest Eocene to earliest Oligocene suggesting either bottom-water warming or that Mg partitioning into benthic foraminiferal calcite is sensitive to factors other than temperature (e.g. increasing pH with CCD deepening, see Fig. 7). $\delta^{18}\text{O}$ temperatures shown apply to a world free of continental-scale ice-sheets ($\delta^{18}\text{O}_w = -1\text{‰}$ Standard Mean Ocean Water (Kennett & Shackleton 1976). Equilibrium calcite values = $\delta^{18}\text{O}_c + 0.64\text{‰}$ (Kennett & Shackleton 1976). (b) & (c) Estimated global ice budgets and glacioeustatic sea-level fall associated with onset of Antarctic glaciation for ice with oxygen isotope values of -50‰ and -30‰ , assuming that all of the $\delta^{18}\text{O}$ increase associated with Oi-1 is attributable to increased ice volume. Arrows indicate modern Antarctic ice volume (*c.* $25.4 \times 10^6 \text{ km}^3$) and apparent sea-level fall (ASL, defined as eustasy plus the effects of water loading on the crust) (70 m) estimated for the Eocene–Oligocene Transition by sequence stratigraphy (Pekar *et al.* 2002).

discussed above, the deep-sea climate proxy records used routinely across the E–O interval that are temperature sensitive are also affected by other factors such as changing global ice volume and possibly alkalinity related to CCD shift and or changes in atmospheric $p\text{CO}_2$. The range of additional independent palaeotemperature proxies is limited for this time interval because of preservation issues, but there are several that provide information about E–O changes especially in continental regions.

Palaeobotanical assemblage associations (see above) and leaf margin analysis document significant cooling in the Late Eocene to Early Oligocene of Saxony, Germany (Roth-Nebelsick *et al.* 2004). $\delta^{18}\text{O}$ variations in low latitude shallow-marine molluscs and fish otoliths also indicate E–O cooling, and increased seasonality (i.e. cooler winters) (Kobashi *et al.* 2001; Ivany *et al.* 2000). Elsewhere in Northern Europe, summer palaeotemperature estimates for continental freshwater derived from rodent tooth enamel, molluscs and fish otoliths, suggest a fluctuating mesothermal climate during Eocene Oligocene time (Grimes *et al.* 2005) but no clear evidence for climatic cooling. Cooling in this record, however may be masked by the large error bars associated with the mean fresh water $\delta^{18}\text{O}$ estimates (5–6‰) because other continental records derived from fossil bone and tooth enamel indicate a large drop in mean annual temperatures of *c.* 8°C over 400 kyrs (Zanazzi *et al.* 2007). In the latter study, continental cooling appears to have been delayed in time with respect to the marine changes by *c.* 400 kyrs. Sedimentary records from the Tibetan Plateau provide additional evidence for cooling and aridification in continental Asia precisely at the time of the Eocene–Oligocene Transition (Dupont-Nivet *et al.* 2007).

In the future, organic biomarkers, such as TEX₈₆ (TetraEther indeX of tetraethers with 86 carbon atoms), a proxy for determining sea-surface temperature from the fossilized membranes of marine archaea (or Archaeobacteria) (Schouten *et al.* 2002), may prove useful for obtaining accurate temperature reconstructions. Recent recovery of well-preserved organic biomarkers of early Palaeogene age from Tanzania (van Dongen *et al.* 2006) suggests that such temperature estimates are not far off (Pearson *et al.* 2007).

Sea level – Widespread glaciation of Antarctica at the E–O boundary, and possibly elsewhere, would have resulted in a significant drop in global sea level proportional to the magnitude of ice growth. Identification and quantification of E–O eustatic change, therefore, is important for understanding this climatic event. Although there are doubts concerning the relative contributions of temperature and ice volume to the $\delta^{18}\text{O}$ record, it is generally considered that Antarctic ice volume

achieved at least 50% of its present development at the E–O boundary (Barker *et al.* 1999; DeConto & Pollard 2003a). Associated sea-level fall has been estimated at 30–90 m by Miller *et al.* (1991) and modelled more conservatively at 40–50 m by DeConto & Pollard (2003a). The classic Cenozoic sea-level curves, based on sequence stratigraphy, failed to recognize sea-level fall close to the E–O boundary and place the largest change in the middle Oligocene (e.g. Vail & Hardenbol 1979; Haq *et al.* 1987). However, there are large uncertainties in dating and correlation in these early reconstructions and recent sequence stratigraphic studies on the New Jersey continental margin have identified evidence for a prominent eustatic lowering, indicating as much as 70 m absolute sea-level fall, coincident with the EOGM (Miller & Mountain 1996; Pekar & Miller 1996; Pekar *et al.* 2002). Eustatic change is further supported by covariance between benthic and tropical planktonic $\delta^{18}\text{O}$ records (Miller *et al.* 1991). Evidence of significant E–O sea-level fall has been also been recorded on the West African margin (Séranne 1999), in the North Sea region (Vandenbergh *et al.* 2003) and Southern Australia (McGowran *et al.* 1992), although these studies do not provide estimates of the magnitude of change.

Surprisingly, E–O sea-level fall does not appear to be ubiquitous, and in other regions there is little or no evidence for large-scale change, even in quasimarine continental facies that should be very sensitive to change. For example, estuarine sedimentary records from the Hampshire Basin, UK, suggest maximum relative sea-level fall of 15 m (Gale *et al.* 2006) and in Mississippi, USA, the stratigraphy has been interpreted as indicating sea-level highstand at the E–O boundary with evidence for increasing water depth across the transition (Echols *et al.* 2003). These studies question the extent of E–O sea-level change and/or suggest that it coincided with widespread tectonic activity that masked the full magnitude of eustatic response. The lack of consensus and quantitative agreement of benthic proxies is one of the current areas of disagreement regarding the E–O transition and there is still scepticism among some workers over whether there was any global change in sea level, and thus, ice volume, at all (Hay *et al.* 2005).

Carbon cycling and productivity

Marine carbonate carbon stable isotopes – Deep-sea benthic foraminifera and bulk carbonate sediment $\delta^{13}\text{C}$ reflect regional and local changes in surface to deep organic carbon cycling as well as global changes in organic and inorganic carbon

burial as carbon moves between the lithosphere, oceanic and atmospheric reservoirs. The commencement of Oligocene glaciation was accompanied by an oceanwide positive $\delta^{13}\text{C}$ anomaly of up to 1.0‰ (e.g. Zachos *et al.* 1996, 2001; Diester-Haass & Zachos 2003; Coxall *et al.* 2005) (Fig. 4). The shift into the $\delta^{13}\text{C}$ anomaly was also rapid (several hundred kyr) and stepwise (Coxall *et al.* 2005), with peak values recorded at the base of the EOGM. ODP Site 1218 records show a distinctive $\delta^{13}\text{C}$ ‘overshoot’ of typical early Oligocene values followed by a longer recovery phase

(400–600 kyr) to near pre-excursion values (Fig. 4b). The long recovery is probably a response to the rapid deepening of the oceanic carbonate compensation depth (see below) (Coxall *et al.* 2005; Zachos & Kump 2005). In the high-resolution record from ODP Site 1218, the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ step-shifts are similar in form, but $\delta^{13}\text{C}$ lags by *c.* 10 kyr (Coxall *et al.* 2005). A lag between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was also recognized in Site 522 records (Zachos *et al.* 1996). This pattern had reversed by the Oligocene because spectral analysis shows a phase lag of $\delta^{18}\text{O}$ to $\delta^{13}\text{C}$ of *c.* 8 kyr with respect to

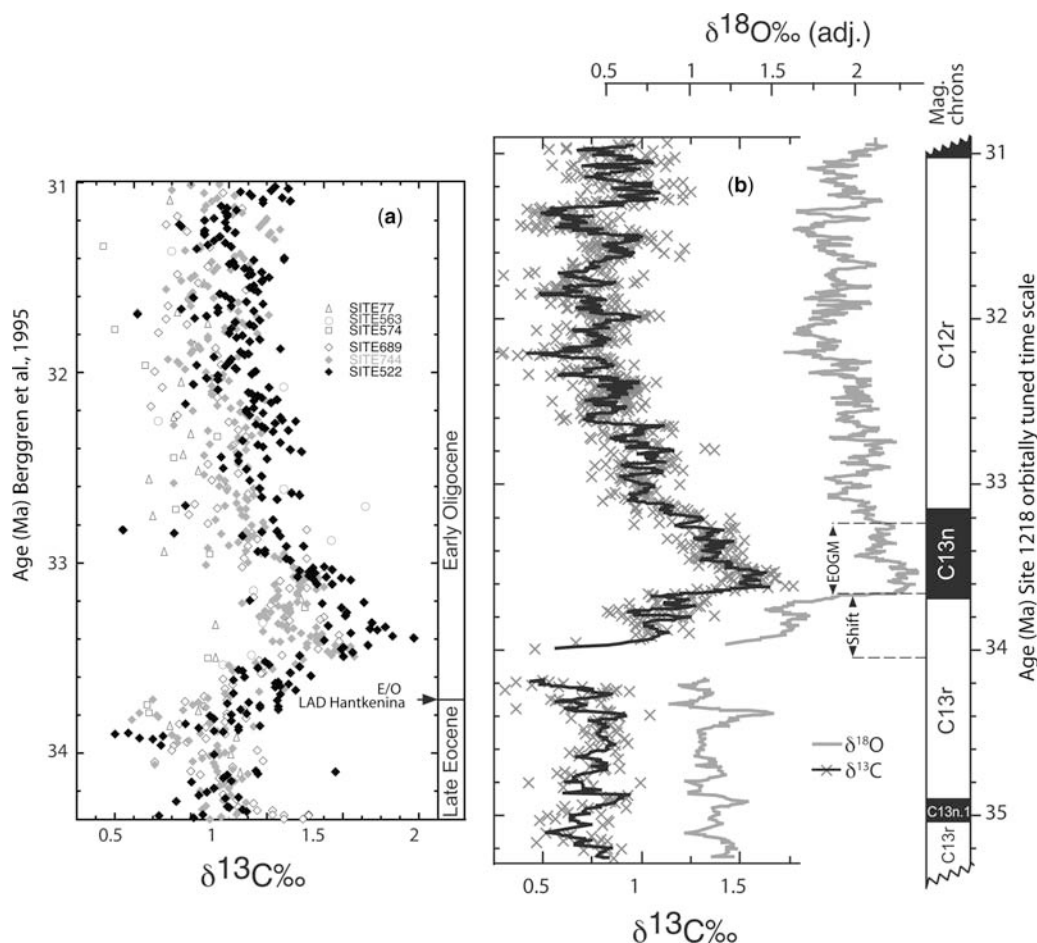


Fig. 4. Benthic foraminifer $\delta^{13}\text{C}$ from deep-sea drill sites across the Eocene–Oligocene Transition. (a) Compilation (after Zachos *et al.* 2001) from mid- to high southern latitudes (diamonds) and the equatorial Pacific (other symbols) plotted on a common timescale (Berggren *et al.* 1995) showing the globally recognizable *c.* 1‰ shift and positive excursion. Note that the two figures are plotted on different timescales. The E–O boundary, as identified by Poore (1984), is shown in relation to the Site 522 data (see Fig. 2). (b) $\delta^{13}\text{C}$ (crosses) from ODP Site 1218 (Coxall *et al.* 2005) plotted on an orbitally tuned timescale and compared to $\delta^{18}\text{O}$ (5-point running mean from Fig. 2), the isotope ‘Shift’ and the EOGM. A stepped pattern of change, including an intermediate plateau, is clear in the Site 1218 $\delta^{13}\text{C}$ record. There is also an indication of step features in the compilation, especially Site 522.

the 40 kyr band, suggesting that the response of the global carbon cycle may have helped force changes in early Oligocene climate (Coxall *et al.* 2005).

One hypothesis regarding the carbon isotope anomaly relates it to a temporary increase in the ratio of organic carbon/CaCO₃ burial rates because of enhanced marine export production, brought about by climate-induced intensification of wind stress, upwelling and oceanic turnover (e.g. Shackleton & Kennett 1975; Diester-Haass 1992, 1995; Zachos *et al.* 1996 and references therein – see below). In addition, the supply of production-limiting nutrients, especially iron, is likely to have increased in response to sea-level fall and enhanced continental weathering, as has been suggested during Quaternary glacial/interglacials (e.g. Martin 1990). Observations are also compatible with recent modelling studies that suggest the $\delta^{13}\text{C}$ shift reflects reorganization of the carbon cycle in response to a rapid drawdown of carbon dioxide related to increased biological production and CCD deepening (Zachos & Kump 2005). Qualitative and quantitative proxy evidence for these parameters and processes is presented in more detail below.

Marine productivity – Variations in palaeo-marine productivity and export production provide important information about global carbon cycling and the causal/feedback roles they play in regulating climate. Significant effort has been focused on obtaining proxy records of E–O productivity changes. Commonly used methods include benthic foraminifera and other marine micro- and macro-fossil accumulation rates, opal/carbonate accumulation, carbonate dissolution indices, carbonate $\delta^{13}\text{C}$ and marine barite accumulation (e.g. Salamy & Zachos 1999; Diester-Haass & Zachos 2003; Averyt *et al.* 2005). Fossil accumulation rate proxies are thought to vary in direct response to standing biomass in the water column and phyto-detritus availability at the sea floor but can be biased by age model problems (Diester-Haass & Zachos 2003). Carbonate dissolution indices (based on foraminiferal shell fragmentation) provide insight into primary production because dissolution is affected by the rain ratio of organic carbon/CaCO₃ (Diester-Haass & Zachos 2003).

Palaeoproductivity proxy data point towards a sharp increase in export production associated with the E–O transition, especially in the southern high latitudes. Benthic and planktonic foraminifera, radiolaria, fish debris, echinoderms and ostracodes all show significant increases in accumulation rate in parallel with the isotopic shifts into the EOGM, in both Southern Ocean (Ehrmann & Mackensen 1992; Diester-Haass 1995, 1996; Diester-Haass & Zahn 1996; Salamy & Zachos 1998) and mid- and low-latitude regions (Diester-Haass & Zahn 2001; Diester-Haass & Zachos 2003; Vanden Berg &

Jarrard 2004). Other reports, however, find no evidence for increased productivity in equatorial regions (Nilsen *et al.* 2003; Schumacher & Lazarus 2004) suggesting that there was considerable regional variation in circulation and productivity responses to the climate change outside of the Southern Ocean region. The highest-resolution records suggest that the increase in productivity was initiated during the isotopic shift, i.e. during the E–O transition, and was sustained for at least the duration of the EOGM (Salamy & Zachos 1999; Diester-Haass & Zachos 2003).

Records from the Southern Ocean suggest that net productivity increased by several-fold in response to the EOGM (e.g. Baldauf & Barron 1990; Salamy & Zachos 1999) with evidence for increased seasonality in the delivery of organic matter to the sea floor (Thomas & Gooday 1996; Schumacher & Lazarus 2004) that may have facilitated more rapid burial of organic carbon. Calcareous primary producers, dominant in the Late Eocene, were partially replaced by opaline organisms suggesting a trend toward seasonally greater surface divergence and upwelling. A corresponding increase in organic carbon content has not been widely recorded, but organic content is generally very low in Palaeogene-age deep-sea sediments because of rapid post-burial consumption, and the signal may not be preserved (Curry *et al.* 1995). Increases in carbonate accumulation proxies is complicated by the major deepening of the CCD synchronous with the onset of the E–O shift, thus, integration of multiple independent proxies is important for differentiating productivity signals from secondary processes, such as dissolution related to lysocline shift.

Other productivity proxies such as barium, reactive phosphorus and nitrogen isotopes may provide complementary evidence for changes in export production that are independent of carbonate dissolution issues. For example, Nilsen *et al.* (2003) concluded that although biogenic silica production/preservation increased during the E–O transition in equatorial Atlantic ODP Site 925, barium and reactive phosphorus suggested no change in productivity or nutrient burial, implying that the increased opal production was relative and occurred at the expense of carbonate production.

The cause of worldwide increased palaeoproductivity from the Late Eocene to the Oligocene is attributed to ocean mixing/circulation changes that increased the availability of nutrients in surface waters. Whether this was driven by increased latitudinal thermal gradients stimulating stronger winds, upwelling and mixing, or reorganization of global circulation related to the opening and closing of tectonic ocean gateways is still a matter of much debate (Diester-Haass 1996; Diester-Haass & Zahn 1996;

Salamy & Zachos 1999; Diester-Haass & Zahn 2001; Diester-Haass & Zachos 2003; Hay *et al.* 2005). Either way, the result of the widespread palaeoproductivity increase, and a phase of increased organic carbon burial, might have led to a lowering of oceanic and atmospheric CO₂ that could have played a key role in E–O climate change by: (1) directly forcing the extreme transient cooling and glaciation, and/or (2) providing a positive feedback that further contributed to global cooling once the transition was initiated (Diester-Haass & Zachos 2003; Zachos & Kump 2005).

Atmospheric carbon dioxide

Changes in the partial pressure of atmospheric carbon dioxide ($p\text{CO}_2$) is thought to be a primary driver of climate over Phanerozoic time (Raymo 1991; Berner 1992; Crowley 2000) and especially during transitions into and out of glaciations (e.g. Barnola *et al.* 1987; Petit *et al.* 1999; Royer *et al.* 2004). General circulation models of Palaeogene climate have been used to show that continuous depletion of $p\text{CO}_2$, amplified by Milankovitch forcing and ice-albedo feedbacks, could cause significant temperature reduction resulting in permanent continental ice-sheets in high latitudes (e.g. DeConto & Pollard 2003a, b; Pollard & DeConto 2003a; Zachos & Kump 2005). Reconstructing E–O $p\text{CO}_2$, therefore, is a primary goal for constraining the links between climate and radiative forcing of the Earth's surface temperatures through the E–O transition.

A variety of proxies are used to estimate $p\text{CO}_2$ during the early Cenozoic including: isotope ratios of marine carbonates or soil carbonates; stomatal density/index in fossil leaves; alkenone proxy in organic biomarkers; boron isotopic ratios in fossil surface-dwelling foraminifera (see Royer *et al.* 2001; Boucot & Gray 2001 for reviews). These are discussed further below. In addition, models have been used to simulate CO₂ variations over Phanerozoic time. Such models are based on changes in carbon burial on land (due to the evolution of land plants) and weathering changes (caused by organic acids in soils) (e.g. Berner 1990) and suggest a general decline in the early Cenozoic. Although there is a good first-order agreement between model results and proxy CO₂ estimates on long timescales (Berner 1990, 1997; Crowley 2000; Berner & Kothavala 2001; Royer *et al.* 2007), the records mostly lack the detail and accuracy to fully resolve the magnitude and timing of decline during the E–O transition and other key climatic events.

Fossil stomata proxies – The palaeobotanical approach for determining past CO₂ concentration is based on the inverse relationship between leaf

stomatal density and $p\text{CO}_2$ in some types of plants (e.g. Beerling *et al.* 1993). Application of this method using early Cenozoic plant fossils has yielded conflicting results. Stomatal counts on the gymnosperms *Ginkgo biloba* and *Metasequoia glyptostroboides* suggest that $p\text{CO}_2$ was stable at between 300 and 450 parts per million (ppm) by volume during the Eocene and Neogene (Royer 2001; Royer *et al.* 2001), whereas results of a later study on *Ginkgo* suggest a decrease in $p\text{CO}_2$ at the E–O boundary (Retallack 2002). Stomatal densities in fossil leaves from three dicotyledon angiosperm taxa (*Eotrigonobalanus furcinervis*, *Laurophyllum pseudoprinceps* and *Laurophyllum acutimontanum*) suggest that $p\text{CO}_2$ was higher during the Late Eocene than during the Early Oligocene (Roth-Nebelsick *et al.* 2004). These differing results indicate large uncertainties in the method and probably different stomatal responses to $p\text{CO}_2$ in different species. This is not surprising because, although stomatal density may decrease somewhat systematically in laboratory experiments with increasing $p\text{CO}_2$, the response on evolutionary timescales is unknown and the calibration curve used to calculate $p\text{CO}_2$ with the stomatal indices are subject to wide uncertainties especially at higher than pre-industrial values (Roth-Nebelsick *et al.* 2004). Consequently, results using stomatal proxy methods should be interpreted cautiously.

Boron isotopes – The boron-isotope ratios of planktonic foraminifera have been used to estimate the pH of surface-layer seawater, which is in turn used to estimate $p\text{CO}_2$ (e.g. Pearson & Palmer 1999, 2000; Hřnisch & Hemming 2004). Results suggest an erratic decline in $p\text{CO}_2$ from 3000–4000 ppm between 55 and 40 Myr ago to 1000 ppm for the Late Eocene but are based on various assumptions (see e.g. Pagani *et al.* 2005a). Data for the E–O transition are lacking but values are suggested to have decreased by at least a factor of two by the Miocene (Pearson & Palmer 2000).

Alkenones – $p\text{CO}_2$ estimates using the carbon stable isotope composition of marine alkenones indicate a similar pattern of $p\text{CO}_2$ decline through the Palaeogene and Neogene to the boron isotope method, but there are also significant differences (Pagani 2002; Pagani *et al.* 2005b). Results suggest that $p\text{CO}_2$ ranged between 1000 to 1500 ppm in the middle to Late Eocene then decreased in several steps during the Oligocene, reaching 'modern' levels by the latest Oligocene. In detail, the alkenone record shows that $p\text{CO}_2$ remained high across the E–O boundary and into the lower Oligocene and began falling rapidly at c. 32 Ma (Pagani *et al.* 2005b).

Palaeosol estimates – $p\text{CO}_2$ estimates based on palaeosols isotopic data support a pattern of higher

concentrations during the Eocene and Oligocene compared to the Neogene (e.g. Cerling 1991, 1999; Ekart *et al.* 1999; Lowenstein & Demicco 2006).

In summary, despite some discrepancies, independent proxies largely support a pattern of higher than modern (2 to 5 times) atmospheric $p\text{CO}_2$ in the Late Eocene, falling through the Cenozoic and reaching near-modern values in the lower Miocene. Possible causes are reduced sea-floor spreading (Berner 1990), increased silicate weathering (Raymo & Ruddiman 1992; Ruddiman *et al.* 1997) and increased organic carbon burial (Diester-Haass & Zachos 2003). Although there is a suggestion of a trend towards decreasing $p\text{CO}_2$ through the Eocene (Pearson & Palmer 2000; Pagani *et al.* 2005b), the alkenone data suggest that $p\text{CO}_2$ remained high (1000–1500 ppm) until after the E–O climatic transition, possibly following termination of the EOGM (Pagani *et al.* 2005b). This questions the proposed relation between $p\text{CO}_2$ and the initiation of glaciation on Antarctica (DeConto & Pollard 2003a). However, none of the proxies or age correlations are perfect (e.g. Pagani *et al.* 2005a; Roth-Nebelsick *et al.* 2005) and despite the issues of timing it is still possible that the $p\text{CO}_2$ decrease was a critical factor that allowed expansion of ice-sheets on Antarctica.

Carbonate and the CCD

The carbonate compensation depth (CCD) is the depth in the ocean at which the supply of carbonate produced in surface waters is balanced by dissolution. The CCD is sensitive to ocean fertility, acidity and $p\text{CO}_2$ and, thus, is closely linked to global climate. Cenozoic palaeodepth reconstructions showing the distribution of carbonate sediments across the ocean basins reveal a general increase in deep-sea carbonate content in the Oligocene compared to the Eocene associated with a major global deepening of the CCD (Van Andel 1975; Thunell & Corliss 1986) (Fig. 5a). The deepening was most extreme in the eastern equatorial Pacific (estimated at 1200 m, Rea & Lyle 2005) but has also been recorded in the Atlantic Ocean (c. 1 km; Hsü *et al.* 1984; Moore *et al.* 1984) and the Indian Ocean (max. 700 m; Peterson & Backman 1990), indicating that it was a global phenomenon reflecting large changes in ocean palaeochemistry. The effect of the CCD deepening was to more than double the area of sea-floor available for CaCO_3 deposition (Rea & Lyle 2005).

Recent CCD proxy records from equatorial Pacific ODP Site 1218 have provided improved constraints on the timing of the CCD shift and its relation to the EOGM (Coxall *et al.* 2005). These

records show a very rapid increase in CaCO_3 content and CaCO_3 mass accumulation rate (MAR) close to the E–O boundary (Fig. 5b). The shift occurred in parallel with the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ increase, and shows the same two-step structure, indicating that deepening CCD shift was synchronous with the climatic shifts that preceded the EOGM. Data and model simulations suggest that under Pleistocene conditions, the increase in deep-sea carbonate ion concentration associated with a 1-km deepening of the global lysocline yields a drawdown of atmospheric CO_2 of less than 25 ppm (Sigman & Boyle 2000; Zeebe & Westbroek 2003). Thus, E–O CCD deepening is unlikely on its own to have caused glaciation through the reduction of $p\text{CO}_2$. More likely, the glaciation triggered the CCD shift. The CCD probably deepened to compensate for a reduction in the global ratio of CaCO_3 to organic carbon burial, as suggested by the calcite $\delta^{13}\text{C}$ increase. The observed increase in the carbonate saturation state of the deep ocean could have been achieved in various ways, which may have acted in combination: (1) a shift in the locus of carbonate sedimentation from the shelf to the deep sea (Berger & Winterer 1974; Opdyke & Wilkinson 1989; Coxall *et al.* 2005); (2) a rapid increase in the amount of calcium entering the oceans (Rea & Lyle 2005); (3) an increase in global siliceous (at the expense of calcareous) plankton export production (e.g. Thunell & Corliss 1986; Harrison 2000). The biomineral shift hypothesis is supported by microfossil evidence from the Southern Ocean and elsewhere that demonstrates increased opal accumulation in the early Oligocene (e.g. Diester-Haass & Zahn 1996; Salamy & Zachos 1999; Diester-Haass & Zachos 2003). The relative importance of these hypotheses can be tested using biogeochemical models such as developed in Zachos & Kump (2005).

Also of note is an interval of severe carbonate dissolution in the top of magnetic Chron C13r that pre-dates the CCD shift (Fig. 5b). At ODP Site 1218, CaCO_3 content of the sediment and CaCO_3 MAR fall to zero for an interval of c. 0.6 m (~200 kyr) close to the base of the shift into the EOGM. In fact, the precise timing of the base of the $\delta^{18}\text{O}$ shift is lost in this record because there are no benthic calcitic foraminifera for analysis. A similar interval of dissolution, correlative with upper Chron C13r, occurs at DSDP Site 522 (Zachos *et al.* 1996), Equatorial Atlantic ODP Site 925 (Diester-Haass & Zachos 2003) and ODP Site 1265 (Liu *et al.* 2004; Tuo *et al.* 2006). This suggests a temporary shallowing of the CCD immediately before the build-up to the EOGM, the significance of which has yet to be established.

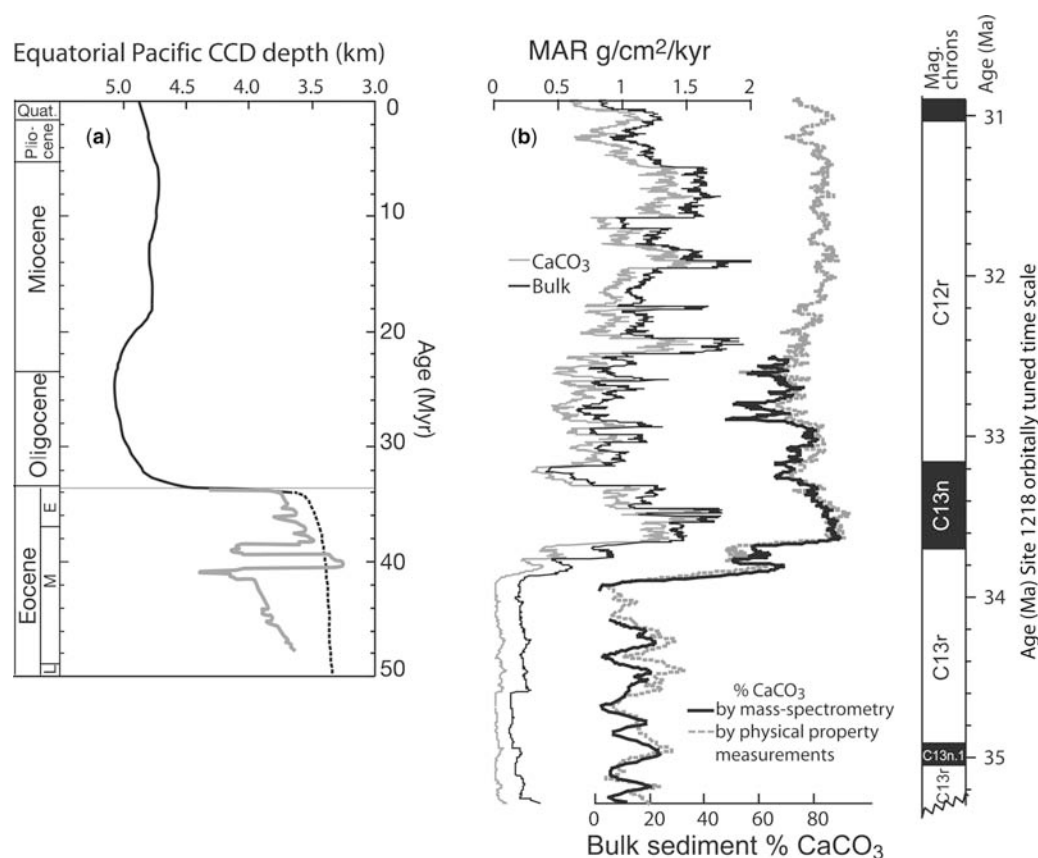


Fig. 5. Deep-sea records showing changes in the Eocene–Oligocene equatorial Pacific Calcite Compensation Depth (CCD). (a) Long-term Cenozoic record of CCD depth from 50 Ma to Present sediments based on carbonate mass accumulation rate (MAR) (after Tripathi *et al.* 2005). Black line is the CCD depth reconstructed from classic low resolution Deep Sea Drilling Project records (modified from Van Andel 1975). Grey line is the revised E–O CCD history based on ODP Leg 199 sediments. (b) High-resolution %CaCO₃ and CaCO₃ MAR (5-point running means) across the E–O transition from ODP Site 1218 (palaeodepth c. 3800 m) (Coxall *et al.* 2005) on an orbitally tuned timescale. The records show that CCD deepening (increase in CaCO₃) occurred (i) faster than previously documented, (ii) in two 40 kyr steps. The timing of CCD deepening is synchronous with the stepwise $\delta^{18}\text{O}$ shift into the EOGM (Coxall *et al.* 2005).

Weathering and sediments

Changes in the flux, nature and chemistry of deep-sea marine sediments indicate the style and intensity of contemporaneous weathering and the possible sources of incoming sedimentary material, all of which vary with climate.

Glaciomarine sediments – The most direct evidence of E–O Antarctic glaciation is the occurrence of glaciomarine sediments, i.e. water-lain glacial tills (including ice-rafted debris), sands and diamictites (coarsely sorted boulder- to sand-sized grains), on or close to Antarctica and elsewhere. These sediments represent material that was scraped off and entrained by moving ice and subsequently

deposited at the front of retreating glaciers or transported offshore by icebergs. The pattern of early Cenozoic glaciomarine sedimentation as recovered in deep-sea cores indicates several episodes of expansive continental glaciation during the Oligocene and several short-lived episodes in the Late Eocene in east Antarctica (e.g. Barrett *et al.* 1989; Wise *et al.* 1991; Breza & Wise 1992; Zachos *et al.* 1992, 1999). There is now also glaciomarine evidence for a regionally extensive West Antarctica ice-sheet of E–O age (Birkenmajer 1996; Gilbert *et al.* 2003; Birkenmajer *et al.* 2005; Ivany *et al.* 2006). These records suggest that the Oligocene glaciation was not restricted to East Antarctica and, thus, imply an extreme climatic response to the forcing

factors that facilitated high-latitude ice expansion in the earliest Oligocene (Ivany *et al.* 2006).

Information for the Northern Hemisphere is limited. Results from recent drilling on Lomonosov Ridge, central Arctic Ocean, recovered the first evidence of ice-rafted debris from the middle Eocene, *c.* 35 Myr earlier than previously thought (Moran *et al.* 2006). These sediments are interpreted as indicating Arctic cooling and significant ice coverage coincident with Antarctic glaciation and are used in support of arguments for bipolar symmetry in early Cenozoic climate change (e.g. Tripathi *et al.* 2005). Understanding of the extent of Arctic glaciation and pattern of climatic change, however, remains limited because carbonate sediments, including calcitic microfossils that provide important geochemical climate proxies, are missing from Lomonosov cores, and the Late Eocene and Oligocene fall in a hiatus (Moran *et al.* 2006). Further drilling, therefore, is necessary to corroborate the initial findings from Lomonosov Ridge and obtain appropriate stratigraphic coverage of the E–O Transition. Recent reports of stratigraphically extensive ice rafted material in the Late Eocene to early Oligocene from the Norwegian–Greenland Sea add support to the idea of contemporaneous Northern Hemisphere glaciation (Eldrett *et al.* 2007). However, these records cannot determine the extent of glaciation, i.e. whether the material was deposited by icebergs calving off small ephemeral glaciers or larger ice-sheets.

Strontium isotope ratios – Variations in marine carbonate $^{87}\text{Sr}/^{86}\text{Sr}$ during the Cenozoic represent changes in the balance of Sr inputs from hydrothermal flux and continental weathering (e.g. Palmer & Edmond 1992; Richter *et al.* 1992; Reilly *et al.* 2002). Therefore, as well as providing a useful stratigraphic tool (e.g. Burke *et al.* 1982), $^{87}\text{Sr}/^{86}\text{Sr}$ has the potential to record information on various processes relevant to climate change, especially concerning weathering shifts related to longer-term variations in atmospheric CO_2 . The pattern of post-Eocene $^{87}\text{Sr}/^{86}\text{Sr}$ shows a general increase in values with a series of stepped increases in the rate of Sr isotopic variation superimposed. The first of these steps occurs around the Late Eocene to early Oligocene (Hess *et al.* 1986; Miller *et al.* 1991; Mead & Hodell 1995; Zachos *et al.* 1999; Reilly *et al.* 2002). Although changes in hydrothermal flux and carbonate weathering are thought to have contributed to the general $^{87}\text{Sr}/^{86}\text{Sr}$ increase over the last 100 myr, increased riverine inputs due to enhanced continental weathering are believed to have been responsible for the larger-scale isotopic variation (e.g. Reilly *et al.* 2002; Lear *et al.* 2003).

The cause of the inferred enhanced weathering is controversial. This is in part because of

differences in identifying the timing of the Sr shift (see Reilly *et al.* 2002) and has been attributed to: tectonic uplift of the Himalayan Plateau, which increased elevation and altered exposure of rock lithologies (e.g. Raymo & Ruddiman 1992); initiation of Antarctic glaciation, whereby increased ice-sheet growth resulted in increased mechanical and chemical weathering of continental rocks (Miller *et al.* 1991; Zachos *et al.* 1999; Zachos & Kump 2005); or a combination of these processes (Mead & Hodell 1995; Reilly *et al.* 2002).

Clay mineralogy – Variations in clay mineralogy indicate changes in depositional environment and provide insight into erosional processes related to climate. Cenozoic clay mineral records show a general trend towards illite–chlorite-dominated assemblages and a reduction in smectite and kaolinite. This is thought to reflect an increase in the rock-derived supply and a decrease in soil-derived supply of clay minerals to the ocean (Chamley 1986), although the pattern is also affected by local conditions. The shift begins in the Late Eocene and has been recorded in marine sediments globally (Chamley 1986; Ehrman & Mackensen 1992; Diester-Haass *et al.* 1993; Robert *et al.* 2002; Gale *et al.* 2006). Close to Antarctica, the illite–chlorite shift has been interpreted as recording a switch from a climate typified by alternating wet and dry seasons resulting in predominantly chemical erosion, to intensified physical (mechanical) weathering by glaciers on eastern Antarctica under a cooler climate (Ehrman & Mackensen 1992; Diester-Haass *et al.* 1993; Zachos *et al.* 1999; Robert *et al.* 2002). Antarctic environmental magnetic records support this hypothesis. For example, Ross Sea sediments show a decrease in detrital magnetite during the early Oligocene, which is interpreted as indicating a shift to a cooler, drier climate leading to reduced chemical weathering of igneous rocks on Antarctica (Sagnotti *et al.* 1998; Wilson *et al.* 1998). The environmental magnetic records and clay mineral behaviour is thus consistent with other evidence for widespread cooling and glaciation of Antarctica in the earliest Oligocene. These records also constrain the timing of glacial activity on Antarctica in the Late Eocene and suggest intensification of glaciation in the basal Oligocene.

Osmium isotopes – Os isotope variation in seawater ($^{187}\text{Os}/^{188}\text{Os}$), as recorded by marine sediments, is believed to reflect the contribution of Os to the oceans from continents (rivers) and submarine alteration, and the influx of extraterrestrial material (cosmic dust). The long-term Cenozoic record of $^{187}\text{Os}/^{188}\text{Os}$ variation shows a pattern of

increasing values that was probably caused by some combination of changes in weathering or increased influx of cosmic dust (Peucker-Ehrenbrink *et al.* 1995; Pegram & Turekian 1999; Peucker-Ehrenbrink & Ravizza 2000). The increasing numbers of detailed Os isotope records across the E–O transition provide good evidence for the global influence of glaciation on the supply of Os to the ocean (Ravizza & Peucker-Ehrenbrink 2003; Dalai *et al.* 2006).

Bulk sediment $^{187}\text{Os}/^{188}\text{Os}$ records from the Atlantic and Pacific reveal a *c.* 30% stepwise shift towards higher values in the early Oligocene after a minimum in the Late Eocene (Pegram & Turekian 1999; Ravizza & Peucker-Ehrenbrink 2003; Dalai *et al.* 2006). The stepwise shift is interpreted as coinciding with the growth and decay of major ice-sheets. Comparison of E–O $^{187}\text{Os}/^{188}\text{Os}$ records with high-resolution benthic foraminiferal $\delta^{18}\text{O}$ from Site 1218 (Coxall *et al.* 2005) suggests that Os flux to the oceans decreased during cooling and ice growth, whereas subsequent decay of ice-sheets and deglacial weathering drove seawater $^{187}\text{Os}/^{188}\text{Os}$ to higher values, i.e. higher $^{187}\text{Os}/^{188}\text{Os}$ values occur following termination of the EOGM. The post-EOGM $^{187}\text{Os}/^{188}\text{Os}$ shift is interpreted to represent an increase in radiogenic Os to the oceans derived from the weathering of easily erodible glacial moraines following termination of the glaciation (Ravizza & Peucker-Ehrenbrink 2003; Dalai *et al.* 2006). It is suggested that $^{187}\text{Os}/^{188}\text{Os}$ remained high through the Oligocene because subsequent cyclic variations in ice volume regularly replenished sediment supply (Ravizza & Peucker-Ehrenbrink 2003).

Dust – Aeolian grains in pelagic clays, i.e. wind-blown dust particles, show an increase in mean grain size beginning in the Late Eocene close to the E–O boundary. This has been attributed to more vigorous atmospheric circulation associated with the climatic reorganization (Rea *et al.* 1985; Ravizza & Peucker-Ehrenbrink 2003; Vanden Berg & Jarrad 2004). A more controversial idea is that cosmic dust flux in the Late Eocene may have contributed to global cooling and the EOGM by supplying bio-essential trace elements to the oceans and thereby resulting in higher ocean productivity, enhanced burial of organic carbon and drawdown of atmospheric CO_2 (Dalai *et al.* 2006).

The sedimentary and geochemical evidence for changes in weathering associated with the E–O transition is consistent with other proxies that indicate widespread glaciation. Weathering- CO_2 climate feedbacks undoubtedly play a role in forcing or moderating climate but their importance is widely debated (Volk 1987; Kump *et al.* 2000; Lear *et al.* 2004).

Late Eocene impacts

The discovery of three bolide impact craters (Chesapeake Bay, Toms Canyon and Popigai; e.g. Poag 1995; Bottomley *et al.* 1997) and associated breccia and ejecta deposits in the Late Eocene has provoked speculation that the biotic turnover and climatic cooling associated with the E–O boundary was triggered by the impact of an extraterrestrial body or bodies (e.g. Keller 1986; Vonnhof *et al.* 2000). Recent age correlation of the impact sites shows that they all occurred within magnetic Chron C16n.2n (Poag *et al.* 2003), which precedes the E–O boundary by about 2 million years, and may have formed part of a ‘comet shower’ (Poag *et al.* 2003). Minor extinction episodes and assemblage shifts among planktonic foraminifera (e.g. Keller 1986) and dinocysts (Vonnhof *et al.* 2000) and a negative $\delta^{13}\text{C}$ excursion associated with the impact horizons at several sites (Poag *et al.* 2003) has been taken as evidence for global-scale long-term environmental disturbance related to the impacts. However, it seems unlikely that the impacts had a major influence on the Earth’s biosphere at the E–O boundary and they are discounted here as a possible cause of the climatic transition. It is possible, however, that climatic disruption caused by atmospheric dust loading associated with the Late Eocene impacts, coupled with an ice-albedo feedback mechanism that amplified impact-induced climatic cooling, may have contributed to global cooling in the run-up to the E–O transition (Vonnhof *et al.* 2000).

Cyclostratigraphy and Milankovitch cyclicity

Orbital dynamics that affect the amount and distribution of incoming solar radiation received by the Earth are thought to have been the principal ‘pace-maker’ of Quaternary climate cycles, forcing the repeated growth and decay of continental glaciers (Imbrie *et al.* 1984). The effects of orbital fluctuations in the early Cenozoic, however, when climate boundary conditions differed and global ice volumes may have been significantly less than in the Quaternary, have been difficult to resolve. One problem has been uncertainties in tracing astronomical solutions that predict the position of individual cycles back into the Palaeogene (Laskar 1999). However, much progress has been made recently, and astronomical models have been extended back to the early Oligocene and beyond (Laskar *et al.* 2004; Pälike *et al.* 2004), allowing orbital tuning of E–O records (Coxall *et al.* 2005; Gale *et al.* 2006; Jovane *et al.* 2006).

Improved deep-sea core recovery and automated quasi-continuous core and downhole logging analysis have resulted in a number of E–O climate proxy records, including magnetic susceptibility, percent carbonate and benthic $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, of sufficient resolution for resolving patterns of cyclic variation on Milankovitch timescales (e.g. Mead *et al.* 1986; Hartl *et al.* 1995; Zachos *et al.* 1996; Coxall *et al.* 2005; Jovane *et al.* 2006; Gale *et al.* 2006). Changes in surface productivity and bottom-water redox conditions in response to climate are thought to be responsible for the observed periodicity in sediment physical property records, whereas fluctuating ice volumes and behaviour of the global carbon cycle are thought to be the major climatic control on $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ respectively (Zachos *et al.* 1996).

Spectral analysis of ODP Site 1218 $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ records, which are the highest-resolution E–O time series available, show that all Milankovitch periods are encoded (i.e. *c.* 20, *c.* 40, *c.* 100 and *c.* 400). Power is concentrated at the obliquity (40 kyr) frequency for $\delta^{18}\text{O}$ and at the 400-kyr eccentricity frequency, with a weaker 40 kyr component for $\delta^{13}\text{C}$ (Coxall *et al.* 2005). A similar *c.* 40 kyr spectral peak was recognized in DSDP Site 522 $\delta^{18}\text{O}$ records (Zachos *et al.* 1996). In the Oligocene, a phase lag of $\delta^{18}\text{O}$ with respect to $\delta^{13}\text{C}$ of *c.* 8 kyr in the 40 kyr band suggests that the response of the global carbon cycle helped to force climate changes in early Oligocene climate rather than reacting to it (Coxall *et al.* 2005). As in Neogene records, the clear *c.* 40 kyr spectral peak in $\delta^{18}\text{O}$ is probably associated with changes in Earth's tilt axis and is consistent with a strong high-latitude (ice volume) influence on global climate (e.g. Imbrie *et al.* 1984). A new 13-million-years-long record from ODP Site 1218 for the entire Oligocene, which includes the E–O dataset, confirms this pattern and identifies 405, 127 and 96 kyr Earth's eccentricity and 1.2-million-year obliquity cycles pacing periodically re-occurring glacial and carbon cycle events throughout the Oligocene (Pälike *et al.* 2006).

Time-series analysis of other datasets shows similar patterns. Spectral analysis of astronomically tuned terrestrial illitic clay data from the Hampshire Basin, UK, identifies strong *c.* 400 kyr eccentricity and 41 kyr obliquity frequencies, with a smaller peak at around 100 ka (Gale *et al.* 2006). Illite is interpreted to have formed in palaeosols through repeated wetting and drying in response to high seasonality. The obliquity frequency cyclic variation probably reflects changes in sea level driven by minor fluctuations in the volume of Antarctic ice. Longer-term environmental magnetic records from the E–O stratotype in Massignano, Italy, reveal cycles of *c.* 405 kyr (Jovane *et al.* 2004, 2006) as

a robust feature through the Late Eocene and into the Oligocene. External forcing by orbital parameters at eccentricity frequencies has also been detected in E–O Southern Ocean (Diester-Haass & Zahn 1996) and low-latitude productivity proxies (Nilsen *et al.* 2003), suggesting that orbital forcing caused a sedimentary response to global climate change from at least Late Eocene.

The dominance of the long Milankovitch periods in these records is unexpected because the climate system response predicted by insolation calculations based on the traditional Milankovitch summer insolation hypothesis (Loutre *et al.* 2004) is for the dominance of climatic precession and obliquity, with only a very minor contribution by Earth's eccentricity periods. Modelling experiments using a carbon cycle box model coupled to models with orbital variations suggest that the explanation for this phenomenon at least for $\delta^{13}\text{C}$ records is amplification of the 405 kyr cycle due to the long residence time of carbon in the oceans (*c.* 0.1 million years) (Pälike *et al.* 2006).

In summary, time-series analyses performed on early Oligocene datasets have revealed that 40 and 400 kyr Milankovitch cycles are a pervasive feature of isotopic and other climate proxy records, as in much of the Neogene (e.g. Zachos *et al.* 1997; Paul *et al.* 2000), and further support the presence of ice-sheets responding to orbital fluctuations during this time period.

Deep-water circulation

The history of deep-water formation and circulation provides important information about global thermal gradients and circulation regimes. Today, and for much of the later Cenozoic, the near-freezing conditions at high northerly and southerly latitudes produce the most dense *in situ* water masses that sink to fill the deep ocean basins. During the early Cenozoic, however, when the high latitudes were warmer, the Southern Ocean and even mid-latitudes are thought to have played greater roles in deep-water formation (e.g. Miller & Fairbanks 1985; Kennett & Stott 1990; Wright & Miller 1993). Considerable effort has been put into trying to reconstruct E–O deep-water circulation history using a variety of different techniques. Early reconstructions that utilized $\delta^{18}\text{O}$ (temperature), $\delta^{13}\text{C}$ (water mass age) and sediment distribution suggest that the Southern Ocean was the dominant source of deep water for the Late Eocene, with pulses of bipolar deep-water formation, i.e. an additional Northern Hemisphere-sourced deep-water component, from the earliest Oligocene (e.g. Wright & Miller 1993 and references therein). This is supported by sedimentary

and seismic evidence that indicates the occurrence of early Oligocene-age sediment drift deposits reflecting a southern-flowing deep-water mass in the North Atlantic (Kidd & Hill 1987; Davies *et al.* 2001) and North Pacific (Scholl *et al.* 2003). Deep-sea benthic foraminifera also provide indications of bottom-water conditions. The gradual faunal changes in lower bathyal benthic foraminiferal assemblages observed in the Southern Ocean and elsewhere have been interpreted as suggesting that the cold, high-latitude-sourced deep waters became established gradually as a result of progressive cooling of surface waters at high latitudes (Thomas 1992; Takata *et al.* 2007).

Neodymium isotopes – Additional evidence for northern-sourced deep water is provided by neodymium isotopes. Nd isotopic variations in seawater (ϵ_{Nd}) reflect local Nd supply to the ocean through weathering of continental rocks. Deep-water masses sinking in a particular region therefore carry a ϵ_{Nd} signature characteristic of the proximal Nd source (e.g. Goldstein & Jacobsen 1988; Via & Thomas 2006 and references therein). This signature is preserved in the teeth and bones of fossil fish (e.g. Wright *et al.* 1984) and can be extracted to provide a useful tracer of deep-water influences on geological timescales. Nd isotope data from E–O sediments indicate that the initial transition to a bipolar mode of deep-water circulation, involving the onset of Northern Component deep-water formation, occurred in the early Oligocene (Scher & Martin 2004; Via & Thomas 2006). Such data seem to imply substantial cooling and/or ice growth in the Northern Hemisphere at the climax of the E–O transition.

Mechanisms and modelling

The cause of the E–O climate transition is still widely debated and will doubtless remain so, because such complex shifts in the Earth System probably do not have a single identifiable cause. The most widely held explanations for the fundamental climatic shift and initiation of the EOGM are that it was caused by (i) cooling of Antarctica due to changes in ocean circulation controlling poleward heat transport, (ii) a gradually forced threshold response to declining atmospheric carbon dioxide levels. New drill sites and high-fidelity proxy records are important for exploring these hypotheses by documenting patterns of change across the planet. Computer models, however, which are becoming ever more sophisticated in their ability to couple ocean, atmosphere, cryosphere and biosphere climatic parameters, have a valuable role in hypothesis testing and allow exploration of climate behaviour that includes

a range of complex forcing and feedback mechanisms operating on global scales. Here the high-quality proxy records provide essential boundary conditions for constraining the models. The following section summarizes evidence for and against the possible mechanisms of E–O climate change including the results of modelling studies, but we emphasize that there is still more that we ‘don’t know’ than that which we ‘know’.

Ocean gateways – One classical hypothesis suggests that E–O glaciation was achieved through thermal isolation of Antarctica following the tectonic opening of ocean gateways between Antarctica and Australia (Tasmanian Passage) and Antarctica and South America (Drake Passage), which led to the organization of the Antarctic Circumpolar Current (ACC) (Kennett *et al.* 1975; Kennett 1977; Murphy & Kennett 1986). This idea draws on foraminiferal isotopic evidence from deep-sea drill cores, principally from the Tasman Sea, that suggests a shift from warm to cold currents close to the E–O boundary and a shift from calcareous to biosiliceous microfossils in the early Oligocene. The theory has been extended recently following a new campaign of deep-sea drilling in the Tasman Sea region (Shipboard Scientific Party 2001; Exon *et al.* 2004). Renewed support for the hypothesis that thermal isolation of Antarctica was the principal cause of E–O climate change is also provided by the results of (GCM) simulations that suggest the opening of Drake Passage and the organization of an ACC would have reduced southward oceanic heat transport and facilitated cooling of Southern Ocean sea-surface temperatures (Toggweiler & Bjornsson 2000; Nong *et al.* 2000).

This view, however, remains controversial. An alternative interpretation of siliceous microfossil distribution from the region, principally dinocysts and diatoms that are abundant in productive polar regions, suggests that the Tasman Gateway opened two million years before permanent glaciation at about 35.5 Ma and that, although possibly a factor contributing to the changes, this tectonic event probably was not the cause of the E–O climatic shift (Stickley *et al.* 2004). Moreover, an alternate coupled ocean–atmosphere GCM challenges the idea that the opening of the Tasmanian Passage contributed to Antarctic thermal isolation by interrupting the southward flow of warm tropical waters, because model simulations suggest that warm waters did not penetrate to high latitudes in the first place (Huber *et al.* 2004). This interpretation is supported by another set of GCM simulations which suggest that the opening of Southern Ocean gateways plays a secondary role in this transition, relative to pCO_2 concentration (DeConto & Pollard 2003a, b). Similarly, in an assessment of

the potential influence of the ACC on Antarctic glaciation, it was concluded that the presence of biosiliceous biofacies in the early Oligocene cannot be used as evidence for the existence of a continuous deep-reaching front, in the form of an ACC, and that colder SSTs were an effect of glaciation rather than the cause (Barker & Thomas 2004). According to this study, Eocene–Oligocene deepening of the Tasmanian gateway and timing of glaciation are coincidental.

Precise timing of the opening of these tectonic gateways is necessary for assessing their importance as possible mechanisms of E–O climate change. However, there are differences and uncertainties in the age estimates of events, especially for the opening of Drake Passage. Using tectonic plate reconstructions, Lawver & Gahagan (2003) suggested that a deep-water passage opened in the Tasman Seaway close to the E–O boundary (c. 33 Ma), and that the Drake Passage may have been open by 31 Ma. The authors recognize a major change in circulation at this time, with increased production of Antarctic Bottom Water, but they are cautious about linking this change directly to the early Oligocene glaciation because there is not a great deal of evidence to support vigorous ACC until the Miocene (Rack 1993).

Using geophysical-modelling techniques, Livermore *et al.* (2005) and Eagles *et al.* (2006) estimate Drake Passage opened near to the E–O boundary (34–30 Ma) and suggest that this tectonic event was the trigger for rapid onset of early Oligocene glaciation. Geochemical proxy data (Latimer & Fillipelli 2002) and opal accumulation records (Diekmann *et al.* 2004) from the Agulhas Basin have also been interpreted as evidence for Drake Passage opening to deep ACC flow close to the E–O boundary at around 32–33 Ma. The Livermore *et al.* (2005) kinematic model predicts that initial opening of the Drake Passage occurred in the middle Eocene, which is considerably earlier than previous estimates, and suggest that flow of deep water through a series of restricted basins may have contributed to gradual cooling through the middle Eocene.

Nd isotopes also provide constraints on the timing of Drake Passage opening. Scher and Martin (2006) interpret Nd records from Agulhas Ridge as indicating an influx of shallow Pacific water in the late middle Eocene at c. 41 Ma, suggesting that a connection through Drake Passage was already open and probably facilitating complete circum-Antarctic circulation by the Late Eocene, i.e. before the opening of the Tasman Seaway. Based on this timing, the authors conclude that Drake Passage opening could not have initiated the EOGM glaciation and propose circulation/productivity linkages as a mechanism for declining

atmospheric carbon dioxide that may have been the primary cause.

Despite recent and ongoing research into these questions, opinions on the role of circulation changes in the initiation of E–O climate change remain divided. There appears to be a variety of evidence to suggest that Southern Ocean gateways had opened by the E–O boundary and that some form of proto-ACC, which might have had a direct impact on Antarctic climate, had been established by the earliest Oligocene. Alternatively, new interpretations of microfossil records and alternative GCM simulations suggest that circulation changes leading to thermal isolation of Antarctica did not play a primary role in initiating glaciation. Considering these issues, Barker and Thomas (2004) outline ideas for future work. They suggest that future efforts should be focused on obtaining: (i) better definition of the properties of oceanic fronts, (ii) Cenozoic atmospheric $p\text{CO}_2$ proxy records, (iii) further developments in models of Antarctic glaciation, (iv) marine geology studies, including grain-size, geochemical and mineralogical as a way of examining bottom-water circulation patterns, and (vi) reappraisal of palaeontological records previously interpreted as evidence for an ACC.

Declining carbon dioxide and orbital geometry – The second widely held hypothesis is that E–O Antarctic glaciation was triggered by a threshold response to declining atmospheric $p\text{CO}_2$, consistent with proxy records (see above), in combination with a planetary orbital configuration that favoured accumulation of annual snow. Modelling experiments have bolstered support for this hypothesis. In one set of simulations, sudden glaciation was forced by gradually declining $p\text{CO}_2$ (DeConto & Pollard 2003a). The results suggest that a threshold may be reached whereby ice-sheet height/mass-balance feedbacks cause isolated ice-caps to expand rapidly, eventually coalescing into a continental-scale ice-sheet (Fig. 6). Comparison of ODP Site 1218 proxy records with an orbital template reveals that the beginning of the shift into the EOGM coincides with a rare orbital configuration comprising a phase of low eccentricity and low-amplitude change in obliquity, favouring cool austral summers and permitting accumulation of summer snow that probably tipped the balance towards glaciation (Coxall *et al.* 2005) (Fig. 7). Further model sensitivity experiments suggest that the range of atmospheric CO_2 variability needed to induce such a rapid transition in the presence of orbital forcing is 2 to 4 times pre-industrial levels (Pollard & DeConto 2005). The pattern of step-change in geochemical proxy records substantiates the model prediction of a non-steady mode of ice-sheet growth but the magnitude of the $\delta^{18}\text{O}$

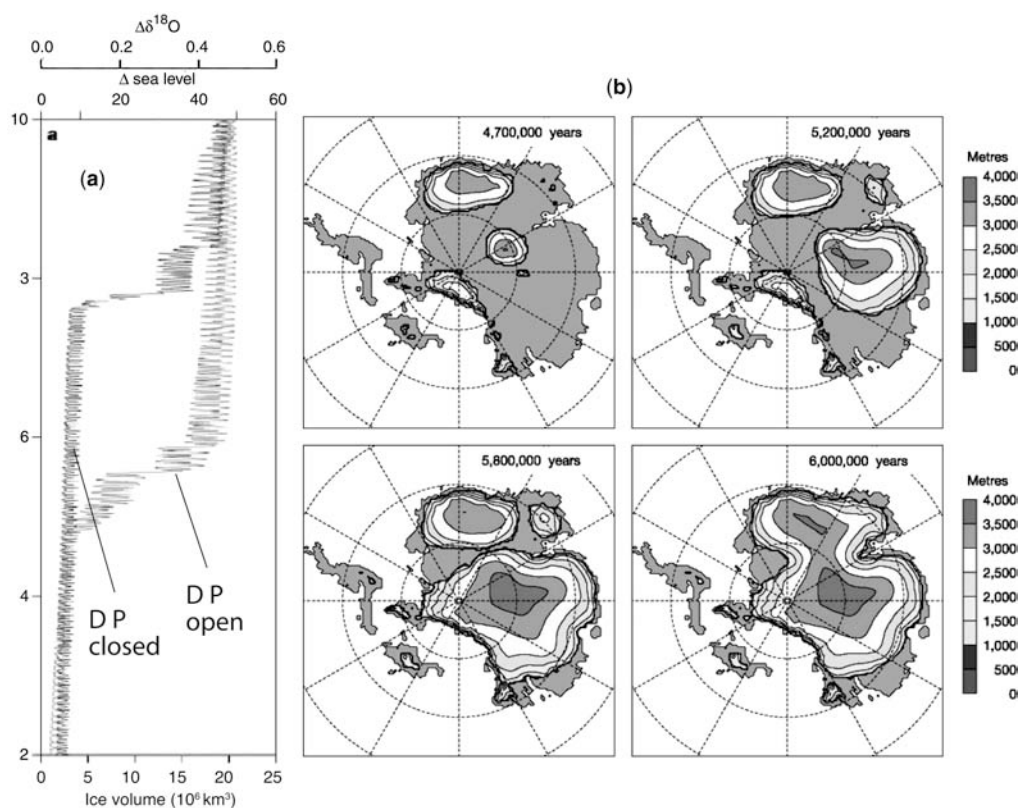


Fig. 6. A General Circulation Model simulation of the glacial inception and early growth of the East Antarctic Ice Sheet (reprinted from DeConto & Pollard (2003a) with permission from authors and Nature Publishing Group). (a) Model simulation of the transient climate-cryosphere response to a prescribed decline in CO_2 from 4 times to 2 times the pre-industrial atmospheric level over a 10-million year period. Ice volume, equivalent changes in sea level ($\Delta\text{sea level}$) and the mean isotopic composition of the ocean ($\Delta\delta^{18}\text{O}$) are shown for two pairs of simulations: (i) Drake Passage (DP) open; (ii) DP closed (global climate model ocean heat transport coefficient increased in the Southern Hemisphere). Equivalent sea-level changes were calculated according to the global ocean-area fraction in the 34-million-year palaeogeography (0.731). $\Delta\delta^{18}\text{O}$ was calculated assuming a 0.0091 change in $\delta^{18}\text{O}$ per 1 m change of sea level. (b) Modelled ice-surface elevations for four time slices during the E–O transition in a 10-million-year simulation (DeConto & Pollard 2003a). The simulation predicts that as CO_2 declined through the Palaeogene, the gradual lowering of the Antarctic snowline began intersecting areas of high topography, first producing small, isolated ice-caps (4.7 and 5.2 million years). As CO_2 continued to fall, height/mass-balance feedbacks were initiated suddenly, producing larger dynamic ice-sheets that alternately coalesced and separated in response to orbital forcing (5.8 million years). With further decline of CO_2 , a single, large EAIS became a more permanent feature, almost insensitive to orbital forcing, with very little summer melting, and accumulation zones reaching sea level around most of the continent (6.0 million years).

response is underestimated by the model (Coxall *et al.* 2005).

A biogeochemical modelling study that was used to investigate the role of the carbon cycle in the glaciation process also supports a drawdown of CO_2 as a likely initial forcing mechanism (Zachos & Kump 2005). The models were able to reproduce the observed positive excursions in the mean $\delta^{13}\text{C}$ of inorganic marine carbon and biogenic sediment accumulation rates by simple CO_2 balancing feedbacks in the climate system associated

with ice-sheet coverage, silicate weathering rates, and increased global carbon burial. However, the post-EOGM timing of the stepped reduction in $p\text{CO}_2$, as suggested by recent proxy records, questions this proposed relation between $p\text{CO}_2$ and the initiation of Antarctic glaciation (Pagani *et al.* 2005b).

Additional forcing and feedback mechanisms – A range of additional climate models is providing further insight into the importance of other forcing and feedback mechanisms on E–O climate

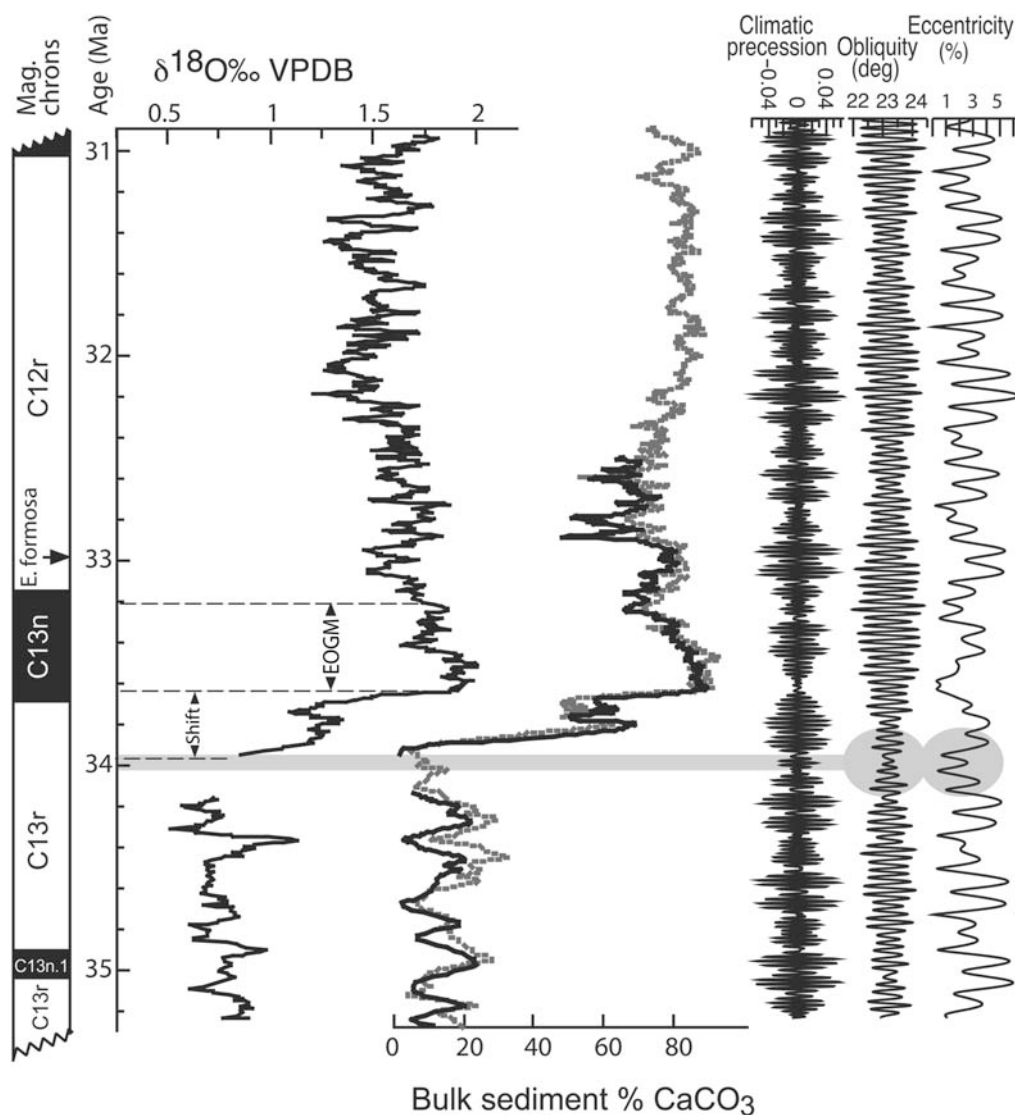


Fig. 7. ODP Site 1218 glacial and CCD proxy records during the Late Eocene to Early Oligocene showing the orbital pacing of Eocene–Oligocene climate change. Comparison of the records indicates that stepwise growth of Antarctic ice-sheets (benthic foraminifera $\delta^{18}\text{O}$ increase), was synchronous with CCD deepening in the equatorial Pacific and occurred during an eccentricity minimum and interval of low-amplitude obliquity change (grey shading) favouring cool summers (Coxall *et al.* 2005).

change. For example, modelling has suggested that changes in Antarctic vegetation (i.e. needle leaf forest to tundra) could have caused positive feedbacks through changes in albedo that would have played a significant role in the rapid glaciation (Thorn & DeConto 2006). Other experiments have shown that geothermal heat flux could strongly influence aspects of Cenozoic Antarctic evolution such as ice-sheet basal hydrology, sediment deformation and discharge that appear to increase

orbital variability of ice-sheet behaviour (DeConto & Pollard 2003a,b; Pollard *et al.* 2005). Models have also suggested that non-linear Antarctic ice-sheet transitions involving hysteresis have played important roles in many of the observed patterns of $\delta^{18}\text{O}$ change (Pollard & DeConto 2005). The hysteresis effect in this context relates to the sudden transitions in ice-sheet size between multiple stable states as a geometric consequence of the intersection of ice-sheet surfaces with typical

spatial patterns, such as topography and coastline geography (Pollard *et al.* 2005). The results of these simulations suggest that the E–O global climate shift may have been sensitive to the particular Antarctic conditions operating at the time. Even so, it would be wise to consider Northern Hemisphere changes as well (e.g. Moran *et al.* 2006; Eldrett *et al.* 2007; DeConto & Pollard 2007).

Change in ocean structure and circulation – An alternate view of E–O climate change is presented by Hay *et al.* (2005). These authors suggest that the transition from an Earth without perennial polar ice to one with quasi-permanent polar ice could have taken place rapidly only if both polar regions became extensively ice-covered in a short time. Since there is currently only limited evidence for rapid E–O Northern Hemisphere glaciation, Hay *et al.* (2005) suggest the global transition to an ice-dominated climate system must have been gradual. Their explanation relates the observed changes in climate proxy data to changes in ocean structure and deep-water circulation, specifically attributing the E–O $\delta^{18}\text{O}$ shift to three factors: (1) a major component of the $\delta^{18}\text{O}$ shift is related to temperature, representing the filling of the deep ocean with cold water and development of a ‘psychrosphere’ (Kennett & Shackleton 1976); (2) a secondary part is attributed to the formation of permanent sea-ice in the Arctic and perhaps around Antarctica, with only minor growth of an East Antarctic ice-sheet; (3) a large part of the $\delta^{18}\text{O}$ shift change may be related to changes in alkalinity and decrease in the pH of seawater as a result of uptake of CO_2 by the ocean from the atmosphere. This hypothesis rests largely on the lack of contemporaneous E–O sea-level change interpreted from earlier sea-level reconstructions but loses power in light of reconstructions that link sequence boundaries implying sea-level fall with global $\delta^{18}\text{O}$ increases (e.g. Pekar *et al.* 2002).

Synthesis

The weight of fossil and climate proxy evidence strongly indicates the Late Eocene to Early Oligocene as a time of major global climate change, with many implications for marine and terrestrial ecosystems. Unlike the Cretaceous–Palaeogene or Permian–Triassic boundaries, there is no indication of a sudden catastrophic event; rather, fossil records document a pattern of enhanced yet gradual turnover signalling adjustment to changes in food and nutrient availability, habitat and climate regime.

Terrestrial biotas suggest significant and varied environmental change across the latitudes, including cooling, increased aridity and increased seasonality. These changes are consistent with a scenario of

reduced thermal gradients, strengthening of zonal winds and changes in precipitation patterns that might result from cooling of one or both poles. Most floral, and other terrestrial, fossil records, however, lack the time resolution to correlate them precisely with the EOGM as recorded by marine records. Evolutionary turnover is recorded in many terrestrial organisms, with highly varied ecologies, which indicates a variety of external-forcing mechanisms. The clear signal from the terrestrial realm is that there was no ‘Terminal Eocene Event’. Instead, the transition was marked by a series of gradual extinctions and speciations, before and after the E–O boundary, that suggest interplay of environmental selection pressures at variable intensities.

Patterns of evolutionary turnover in the pelagic realm suggest changes to ocean thermal structure, food availability and ocean temperatures. Phytoplankton show patterns of gradual turnover and replacement by cosmopolitan, cold-tolerant species. Tropical micro-zooplankton experienced more extinction than other groups, although not on a wide scale, and there was significant reduction in tropical plankton diversity, especially among the radiolaria. These records support the hypothesis of increased oceanic turnover, a reduction in tropical pelagic niches and more intense high-latitude, equatorial and coastal upwelling associated with the climatic shift into the EOGM. These records can be tightly correlated with the proxy records of Antarctic glaciation and show extinctions within the isotopic shift that precedes the EOGM (i.e. planktonic foraminifera and shallow-water benthics), as well as major changes in plankton communities during the EOGM. Deep-sea benthic communities appear to have survived relatively unchanged. Some even benefited from increased food availability because of increased ocean mixing and higher surface ocean productivity. Diversification of large plankton-feeding whales, in parallel with increased opal accumulation, suggests that other elements of the pelagic ecosystem were responding to an expanding nutritional opportunity that arose during the EOGM.

Shallow marine environments appear to have suffered severely during the E–O transition, which brings support to the hypothesis that there was significant sea-level fall associated with the E–O climatic transition. Collection and correlation of fossil records from these types of environments may help further constrain the problem of identifying and quantifying evidence for sea-level change associated with the EOGM.

Multiple proxies support the idea that the biotic changes were associated with major climatic and oceanographic reorganization brought about by widespread glaciation on Antarctica and possibly in the Northern Hemisphere. The causal

mechanism for this fundamental shift is controversial. The most popular explanations are that glaciation was caused by (i) cooling of Antarctica due to plate tectonic reorganization and related changes in ocean circulation controlling poleward heat transport and (ii) a threshold response to declining atmospheric $p\text{CO}_2$. Models and proxy records are being interpreted very differently to bring support to both theories. In our view, the balance is tipped in favour of the idea that the Eocene–Oligocene climate transition was forced by a gradual change in a key parameter (i.e. $p\text{CO}_2$) past a switching point, rather than rapid forcing, which caused a shift towards conditions favourable for ice accumulation and leading to the geologically sudden build-up of the Antarctic ice-cap. This mechanism seems to provide the most parsimonious explanation linking up proxy data observations, orbital configurations and complex carbon system and biosphere feedbacks. The effects were not instantaneous, however, and were spread over a timeframe of several hundred thousand years. On the other hand, it is difficult to dismiss the tectonic separation of Antarctica leading to geographic isolation as pure coincidence. Most likely, the E–O transition, which represents a very significant shift in the Earth System, was caused by some complex combination of forcing factors rather than a single identifiable cause.

Incoming datasets have a tendency to raise new, more focused questions that direct future research. For example, $\delta^{18}\text{O}$ and Mg/Ca proxies and the problems associated with separating temperature and ice volume effects have peaked interest in the possibility of contemporaneous Northern Hemisphere glaciation. This highlights the necessity for future deep-sea drilling to target the Northern Hemisphere, particularly Arctic, sediments that will resolve this question. In addition, future drilling should aim to sample sediments close to Antarctica that might provide further constraints on the timing and extent of Antarctic glaciation. Recognition of the synchrony of CCD deepening and the $\delta^{18}\text{O}$ shift into the EOGM has raised questions about the importance of deep-ocean alkalinity changes as a primary cause or effect of the climatic transition. Attention to these issues has also prompted studies into the role of deep-water alkalinity and carbonate ion concentration on the Mg/Ca palaeotemperature proxy (see Lear 2007).

In the future, production of high-resolution records will be vital. First, these are essential for resolving leads and lags between ice fluctuations and carbon cycling. This has already been achieved in one site (e.g. Coxall *et al.* 2005) but needs to be duplicated elsewhere. Secondly, high-resolution records on 1000-yr timescales are necessary to assess the importance of orbital

spacing of climate, and identify changes in the influence of different forcing periods during the transition from a (relatively) ice-free to a glaciated climate state. The Site 1218 record, which combines various proxies, represents an important step towards this goal and should provide a model for future high-resolution studies.

In summary, the improved resolution of incoming proxy records together with the variety of additional proxies that provide independent checks on key climatic parameters are providing better constraints for modelling E–O climate change scenarios. These data allow us to test hypotheses on climate change mechanisms that incorporate many factors. Model outputs force us to cross-check data interpretations, seek new ways of constraining key processes and, in some cases even re-evaluate the principles underpinning proxies. In particular, new SST estimates from ‘glassy forams’ and the TEX₈₆ method will be important in this respect and recent data for other time periods (Pearson *et al.* unpublished) are already much closer to the modelled view of warmer poles and tropics under greenhouse conditions. Only then can the influence of global extinction patterns on climate itself start to be understood.

Still requiring further study is the question of the relative importance of changing ocean circulation patterns (as a consequence of the opening of Southern Ocean tectonic gateways) and threshold-global cooling related to gradually declining atmospheric CO_2 . Resolving this issue requires improved proxy records of atmospheric CO_2 at sufficient resolution to resolve leads and lags that reveal the primary forcing mechanism. Future efforts should be concentrated on refining the calibrations and reducing assumptions to produce more accurate $p\text{CO}_2$ estimates and obtaining higher-resolution time series that can be accurately correlated with glaciation and carbon cycle proxies, not forgetting the power of multiple proxies to bring conciliation. In addition, there is a great need to expand floral and faunal datasets that document climatic and biotic changes in the terrestrial realm, and to more accurately correlate them with marine records. A fundamental hole in our understanding is the extent of climate change and ice growth in the Arctic region during the E–O transition. Efforts could be focused on identifying and accessing records on the Arctic margins and locating suitable deep-sea drilling targets in the Arctic Ocean basin where mid-Cenozoic sediments are preserved.

At the time of writing (August 2006), there is a need for refinement of $p\text{CO}_2$ proxies, expansion of datasets and improved understanding of high northern latitude and continental E–O climate change. Future application of new and existing proxies, recovery of additional high-quality sediment

archives from the oceans and continents and more-complex models that integrate chemical and biological processes across the Eocene–Oligocene Transition will no doubt yield exciting results and should rapidly advance the field of palaeoclimatology as a whole.

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