

The Marine Eocene-Oligocene Transition: A Synthesis

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ABSTRACT

Progressive global cooling and increasing seasonality brought on by a combination of tectonic and oceanographic factors led to a series of worldwide pulsed turnovers through the middle Eocene and into the Oligocene. Real patterns of evolutionary turnover are often obscured in shelf settings by regional tectonism and facies changes, but, as seen in this volume, progress is being made at seeing the global pattern through the regional overprint. Most taxonomic groups show significant perturbations at or near the middle/late Eocene boundary and near or shortly after the Eocene/Oligocene boundary. Other events were noted in some groups in the late middle Eocene, within the late Eocene, and later into the Oligocene. Difficulties in establishing good age control and correlating widely separated sections limit our ability to determine the degree to which these events were isochronous, but the strong similarity of records from disparate regions, environments, and taxonomic groups suggests that these turnovers were global and hence triggered by changes occurring on a global basis, such as climate cooling. Extinction seems to have played a more important role in low-latitude turnovers, while origination was a significant component at high latitudes. Warm-water taxa were, without exception, hit harder than cool-water taxa, particularly at the middle/late Eocene boundary. While cosmopolitan taxa are more likely to survive turnovers, at high latitudes the reverse is true, and at the Eocene/Oligocene boundary itself taxa seem to have been affected indiscriminately.

INTRODUCTION

It has been well over a decade since the 1989 Penrose Conference on the Eocene-Oligocene transition was convened (Prothero and Berggren, 1992). Since that time, much new information has come to light, and work that was initiated as a result of that first conference has come to fruition. This volume, based on the 1999 Penrose Conference (Prothero et al., 2000), offers the most up-to-date views on the nature of the Eocene-Oligocene transition from climatic, oceanographic, and paleontologic perspectives. The majority of the papers presented here are chosen to represent the varied and ongoing work in Eocene-Oligocene marine *shelf* sections, from which much of our macrofossil record comes, and to draw comparisons between these data and those from open-ocean and terrestrial sources. Additional papers focus on deep-sea and coastal-lowland-forest environments. As editors, we intend that this selection provide a comprehensive look at the patterns and processes that characterize the time period from the middle Eocene through the Oligocene, spanning geographic, taxonomic, and methodological boundaries to allow for a global, multidisciplinary perspective.

The transition from global “greenhouse” conditions of the early and middle Eocene to global “icehouse” conditions of the early Oligocene marks a turning point in Cenozoic Earth history. The early Eocene world is characterized by palm trees growing in Alaska (Scotese, 2002) and the northern Rocky Mountains (Greenwood and Wing, 1995), crocodiles living on Ellesmere Island well above the Arctic Circle

(Markwick, 1994), forests blanketing much of Antarctica (Case, 1988), and a host of unusual archaic taxa scattered across the marine shelves and continents (papers in Prothero and Berggren, 1992; Prothero, 1994). By the start of the Oligocene, changes in ocean circulation brought about by the opening of the passage between Australia and Antarctica, and the Drake Passage between South America and Antarctica, had resulted in progressive global cooling (Zachos et al., 1994), the extinction of hundreds of warm-water taxa (Dockery, 1986; Haas and Hansen, 1996), and the development of a continent-scale ice sheet on Antarctica (Zachos et al., 1992). Events associated with the Eocene-Oligocene transition in particular ushered in more modern climatic and biologic systems. The general oceanic and atmospheric circulation patterns of today were first established at this time. Groups that survived and radiated following the close of the Eocene are those that, for the most part, are still extant. During this interval, large shifts toward both warmer and cooler conditions occurred on both gradual and episodic time scales (Kennett and Stott 1991; Zachos et al., 1992; Zachos et al., 1993; Zachos et al., 1994; Lear et al., 2000; Ivany et al., 2000). Not surprisingly, the faunal and floral response to such changes was variable in both space and time, and some groups were more sensitive to change than others. Our goal here is to relate the latest information concerning climatic and oceanographic change associated with this transition, and to examine geographic and taxonomic patterns in biotic turnover that provide clues about where, when, and how fast these environmental changes are happening.

The papers in this volume are organized by geographic region. However, a number of recurring themes through the papers highlight the timing and magnitude of both climatic and biotic change. We felt it would be useful to synthesize that information in one place, and this summary chapter is structured in such a manner. We discuss, in sequence:

- The tectonic and paleogeographic setting of the Paleogene
- Specific issues related to the stratigraphy of shelf deposits, the topic of most of these studies
- Advances in recognizing and correlating boundary sections
- Trends in the expression of climate change
- Patterns of faunal and floral turnover, and
- A synthesis of pattern by latitude and environment

By necessity, all the papers offered in this volume are concerned with one or more of these issues, and

they offer a range of potential solutions to the problems of comparing sections both in space and in time through the Eocene-Oligocene transition.

This chapter is not meant to be a comprehensive literature review, but a summary of the topics covered in this volume. Clearly, there are many seminal papers published earlier on many of these subjects, and the reader is referred to papers in this volume for the relevant literature reviews.

TECTONIC AND PALEOGEOGRAPHIC SETTING FOR THE EOCENE AND OLIGOCENE

Paleogeographic and paleoclimatic reconstructions (Scotese, 2002) portray the Eocene world with a wide Tethys Sea, which extended from the western Indian Ocean, through the Mediterranean, to between North and South America. During this interval, India collided with the south-central Asian coastline, coinciding with realignment of the Pacific midocean ridge system. South America, Australia and Antarctica were still connected as remnants of Gondwana, and North America and Europe were intermittently connected by the Bering land bridge. Thus both the southern and northern hemispheric oceanic circulations were significantly different from today's pattern. Eustatic sea levels were high (Vail et al., 1991), and the only circumglobal circulation occurred around the equator. Across-latitude circulation was severely restricted. A drop in global sea level around the Eocene/Oligocene boundary resulted in the Tethys becoming more restricted. But more significantly, Antarctica separated from both Australia and South America, generating the first circum-Antarctic current and the deep-water circulation originating from the Antarctic (Berggren and Prothero, 1992; Diester-Haass and Zahn, 1996; Exon et al., 2002).

In this volume, papers that focus on changes in seaway paleogeography and oceanic circulation patterns bear particular relevance to the Gulf of Mexico, Caribbean Sea, and Atlantic Ocean. Iturralde-Vinent (this volume) uses stratigraphic techniques to understand the changes in the Caribbean Seaway during the Eocene-Oligocene transition. He documents shifts from free exchange between Tethyan and Pacific faunas earlier in the Paleogene to more restricted exchange near the boundary, related to tectonism and uplift in the Caribbean. The biogeography of benthic foraminiferal assemblages allows Robinson (this volume) to add more data supporting the progressive restriction of circulation between the Gulf of Mexico and the Caribbean Sea during the Eocene. In addi-

tion, Florida was more insulated from the rest of the Gulf Coast by the northeast-flowing Suwannee Current, which prevented many Tethyan mollusks from crossing the gap between Florida and the central Gulf. Dockery and Lozouet (this volume) record the arrival of characteristic Tethyan forms in western Alabama and Mississippi near the Eocene/Oligocene boundary, which indicates breaching of that divide as sea level fell.

Another line of evidence for a rapid change in oceanic circulation is illustrated by Scholl et al. (this volume) from the depositional patterns of the deep-sea Meiji sediment body in the northernmost Pacific Ocean. The pelagic sediments of the Meiji body accumulated along the northern flank of the Emperor Seamounts chain beginning in Oligocene time. From its bathymetric setting, depositional form, and textures, Scholl et al. (this volume) conclude that the deposition of the Meiji body was initiated by changing oceanographic circulation in the early Oligocene that brought cold, dense, and salty abyssal waters into the North Pacific.

THE NATURE OF SHELF DEPOSITS

In comparison with records from the deep sea, shelf sections can be difficult to work with due to their time-transgressive nature and regional variation of sedimentation rates, and the lithologic heterogeneity and intense bioturbation of many deposits. Eustatic sea-level fluctuations and active tectonics result in substantial and frequently undetermined disconformities (Ager, 1993; Posamentier and Allen, 1993). Faunal correlation along shelves, and with the deep-sea record, is also complicated by provinciality and the very poor record of planktonic taxa in nearshore environments. The next step, interpreting apparent faunal turnover across temporal units and with continental deposits, is often fraught with difficulties and inconsistencies. Sequence boundaries offer consistent, traceable surfaces with which to correlate sections, but they may not be the same age everywhere, particularly in updip versus downdip sections. In addition, the amount of time missing at sequence boundaries varies from place to place depending on where on the shelf the section is located (Christie-Blick, 1991).

Condensed sections, which are isochronous everywhere on the contiguous shelf, offer one solution to the problem of correlating disparate shelf sequences (Loutit et al., 1988). In addition, biostratigraphically useful pelagic fossils are more frequently preserved in deeper-water condensed strata, adding to their value in correlation (e.g., Echols et al., this vol-

ume; Robinson, this volume). Terrestrial palynomorphs can also be preserved in marine shelf sediments (e.g., Oboh-Ikuenobe and Jaramillo, this volume; Yancey et al., this volume), offering a way to correlate terrestrial with marine records. Despite their limitations, therefore, shelf sediments can provide a valuable (and often the only) link between terrestrial and deep-sea sections.

Interpretation of apparent faunal turnover events can be complicated by correlative changes in lithology and hence paleoenvironment, making it unclear whether the turnover is real or simply facies-controlled (Holland, 1995). Collecting assemblages from a range of localities up and down a contiguous shelf can allow comparison of faunas drawn from the same lithology across a probable transition, thereby minimizing this potential bias, but this is an option only when both updip and downdip sections are available. The issue of facies change becomes particularly important when boundaries are recognized based on faunal turnovers but those faunas are facies-specific. The dramatic middle-late Eocene turnover in mollusks of the Pacific Northwest provides a good illustration: the transition from the warm shallow-marine faunas of the Cowlitz Formation to the cooler, deeper-water faunas of the Lincoln Creek and Keasey formations was also accompanied by a large facies shift toward fine-grained tuffaceous sediments (Hickman, this volume; Nesbitt, this volume). It is unclear in this case how much of the turnover was brought on by global cooling and how much simply reflected a facies shift due to regional tectonics. Papers by Fluegeman (this volume) and Echols et al. (this volume) offer an additional example from the U.S. Gulf Coast, where the Eocene/Oligocene boundary had been traditionally placed at the lithologic and faunal break between the Jackson and Vicksburg Groups. While the faunas of the Jackson and Vicksburg Groups are distinct, the contact between them has recently been shown to be time transgressive (Jaramillo and Oboh-Ikuenobe, 1999). With close examination of the faunas across the boundary in several geographic areas, these authors found that the boundary as defined by the disappearance of *Hantkenina* spp. occurs below the Jackson-Vicksburg contact in some areas and above it in others.

Rare and unusual facies also pose correlation dilemmas. Gammon et al. (this volume) describe geographically extensive biosiliceous beds within late Eocene shallow-shelf limestones in Western Australia. These beds consist of bioclastic concentrations of siliceous sponge spicules that have Mesozoic-Tethyan

taxonomic affinity. Today such lithistid-hexactinellid assemblages occur only in deep water. However, in the Eocene shelf of Australia they flourished at neritic depths because of elevated amounts of silica-rich, land-derived nutrients and calm, warm waters. Likewise, taxa relegated to the deep sea today are found in Eocene shallow-marine deposits of the Antarctic Peninsula (Aronson et al., 1997).

ADVANCES IN IDENTIFYING AND CORRELATING BOUNDARY SECTIONS

A significant limitation with respect to studies of the Eocene-Oligocene transition is our ability to (1) agree on a defining characteristic for particular chronostratigraphic boundaries; (2) recognize them in our respective sections; and (3) correlate our sequences with others in different areas. These concerns, of course, are not unique to the Eocene-Oligocene interval, but characterize all studies based on stratigraphic sections. Berggren et al. (1992) presented a substantial review of the issues surrounding Paleogene geochronology and made strides toward an age reassessment of the Eocene/Oligocene boundary. Those estimates were fine-tuned in Berggren et al. (1995), with an age assessment of the boundary at 33.7 Ma, and their revised and updated Cenozoic geochronology is the time scale we use in this volume.

The currently accepted marker for the Eocene/Oligocene boundary in a stratigraphic section is the last appearance of the planktonic foraminifer *Hantkenina* spp., as seen in the type section of Massignano, Italy. However, Brinkhuis (1992) showed that the relative rarity of *Hantkenina* caused this criterion to place portions of the type upper Eocene Priabonian Stage into the Oligocene, as per the Signor-Lipps effect (Signor and Lipps, 1982). Consequently, Berggren et al. (1995) suggested using the Last Appearance Datum (LAD) for the *Turborotalia cerroazulensis/cunialensis* group instead, or in addition, because of the higher probability of their being better preserved in a section. While the two events may eventually be shown to have been synchronous, at present the LAD of the *T. cerroazulensis/cunialensis* group, defining the P17/P18 planktonic foraminiferal zonal boundary, is about 0.1 million years younger than the LAD of *Hantkenina* spp. that defines the actual Eocene/Oligocene boundary.

The long-recognized concern associated with biostratigraphically recognized boundaries, that the first (FAD) and last appearances of taxa may not be geographically synchronous, is expanded upon in a number of the papers in this volume. Coccioni and

Galeotti (this volume), for example, make clear that the disappearance of the benthic foraminifer *Nuttallides truempyi* was diachronous and occurred earlier at high latitudes than at low. This also was true of calcareous nannofossils, which appear to be temperature-limited and hence not globally synchronous in their FADs and LADs (Wei and Wise, 1990; Vandenberghe et al., this volume). Since the Eocene-Oligocene transition marks a profound cooling trend, temperature limitation and the resulting diachronous nature of faunal events become particularly significant problems.

Magnetic stratigraphy provides an entirely independent check on other types of correlation. Using magnetostratigraphy pinned to radiometric dates, and to known microfossil zones, Prothero (this volume) presents a higher resolution chronostratigraphy of shelf sediments along the western North American coast than previously available. Without this resolution, the studies of faunal and floral turnover, extinction and originations would be difficult to place in a global context.

Chemostratigraphy is another approach that is becoming more and more useful for the Cenozoic. While geochemical tools have become widely accepted as useful for correlation, workers seem to have resisted employing them to define particular chronostratigraphic intervals. This is changing with the recent acceptance of the carbon isotope anomaly formerly known as the LPTM (late Paleocene thermal maximum) as the recognized marker for the Paleocene-Eocene boundary (Aubry et al., 1998; Röhl et al., 2000). For the Eocene-Oligocene transition, the large step toward more positive oxygen isotopic compositions of marine carbonate has been recognized across a globally wide range of sections, latitudes, and environments. This is the so-called Oi1 event (Miller, 1992), which marks the rapid expansion of ice on Antarctica in what is now considered the earliest Oligocene (Zachos et al., 1992). Recognition of this isotopic shift in boundary sections, and the extent to which it reflects ice growth and not temperature change, can help constrain the age of particular deposits and correlate disparate sections. Geochemical excursions may well prove to be the ideal tool for recognizing global isochronous time planes on which to hang our sections and avoid the problem of diachroneity of biostratigraphic events. Strontium isotope stratigraphy, too, is especially useful in marine sections from the late Eocene into the Oligocene because the steep slope of the marine reservoir curve can allow for very precise age determinations, assum-

ing no problems with diagenesis or freshwater influence (DePaolo and Ingram, 1985; McArthur et al., 2001).

Radiometric dates bracketing fossiliferous horizons are the decisive factor in refining chronologies. New $^{40}\text{Ar}/^{39}\text{Ar}$ dates accompanied by paleomagnetic and floral correlations have resulted in the first reliable chronostratigraphy of both interior and lowland paleofloras that span the Eocene-Oligocene transition in the Pacific Northwest (Myers, this volume). Climate data obtained from whole-flora leaf morphologies produced a sequence of temperature and precipitation data that can be directly compared with the shelf and deep-marine record. Latest middle Eocene (39–38 Ma) lowland-forest data indicate a cooling of 3–4°C was followed by an unusual period of warming around 35 Ma. The terminal Eocene cooling produced ~6°C decline in mean average temperatures combined with a pronounced seasonality of rainfall (Myers, this volume). This climate change was not as severe as previously inferred (Wolfe, 1994), but it does correspond closely with the shallow-marine invertebrate record from the northeastern Pacific.

CLIMATE CHANGE ASSOCIATED WITH THE EOCENE-OLIGOCENE TRANSITION

We will not attempt to review here the voluminous and growing literatures on the deep-marine record of changes across the Eocene-Oligocene transition. We instead refer the reader to useful reviews by Miller (1992) and Zachos et al. (1993, 1994) and to papers in the previous Eocene-Oligocene Penrose Conference volume (Prothero and Berggren, 1992). Oceanic paleotemperatures are generally derived from the stable isotopic compositions of biogenic carbonate, which presumably reflect the temperature of the water in which the organism grew, and/or from biologic inference based on the affinities of organisms present at any given time in a sequence. When such information is derived from a marine source, a recorded change in the temperature of water may reflect a true global pattern of global cooling and/or the growth of polar ice caps, or it may be associated with regional changes in circulation. These factors are clearly not unrelated on a large scale, nevertheless, local and regional changes in upwelling or circulation can produce dramatic changes in the temperature of the water in a given area that may not be indicative of what is happening elsewhere. Buening et al. (1998) present an example of this phenomenon in their reconstruction of paleotemperatures from southeastern New Zealand based on the oxygen isotope values

of fossil brachiopod shells. The cooling they see across the Eocene/Oligocene boundary is more than they expected, given the presence of warmer-water taxa on the north and west sides of the island. They reconcile the difference by proposing that the cooling reflected the development of a cool current that flowed up from Antarctica and past the east side of the island, while the north and west remained warm. The current itself was likely due to the presence of ice on Antarctica, and so was related to global climate change, but the difference between the east and west sides of the island was more a function of regional variation in ocean circulation.

High-resolution $\delta^{18}\text{O}$ data obtained from foraminifera along the Gulf Coast shelf produced unusual and intriguing results. Hurley and Fluegeman (this volume) compared their isotope curves with the planktic:benthic foraminifera ratio curve over the 1.7 million years of the P14 planktonic foraminiferal zone. They found an inverse similarity between the two curves and concluded that the isotope pattern did not result from changes in seawater temperatures per se, but from fluctuating ice volumes in the late middle Eocene reflecting 17 inferred glacio-eustatic cycles.

The range of seasonal variation is particularly important in controlling the biogeographic distributions of organisms and yet this variable is generally not accessible from oceanographic data sources. Advances in our ability to microsample accretionary biogenic materials, such as bivalve shells and fish otoliths, have allowed for reconstruction of seasonal variation from high-resolution stable isotopic analysis. Ivany et al. (2000; this volume) recognize an increase in the seasonal range of temperature variation across the Eocene/Oligocene boundary in the U.S. Gulf Coastal Plain as inferred from microsampling and oxygen isotopic analysis of otolith carbonate, and they infer a link with the associated faunal turnover. Data from shelf sections such as these will become increasingly important for constraining this variable, as long-lived marine taxa are generally not recovered from deep-sea sections.

Ultimately, the Eocene-Oligocene transition can most likely be traced back to tectonics—plate motion and the effects it had on oceanic circulation, and mountain building and the effects it had on atmospheric composition. The conventional story, and it is undoubtedly more complicated than presented here, is that the progressive isolation of Antarctica caused by the rifting away of Australia, Tasmania, and South America led to the development of circum-Antarctic

circulation in the Southern Ocean. Recent analyses suggest that this isolation began with the opening of the Drake Passage, possibly at the middle/late Eocene boundary at 37 Ma (Diester-Haass and Zahn, 1996). The final event was the separation of East Antarctica from Tasmania at 33.5 Ma (Exon et al., 2002), which allowed for ocean waters to continuously circulate around Antarctica, rather than be deflected up to warmer climes. This caused the water and the continent it circled to cool down, eventually leading to the growth of continental ice sheets. It also generated the psychrosphere, the cold bottom-water currents that sink from the Antarctic surface waters and flow at abyssal depths all the way to the North Atlantic and North Pacific.

The second part of the story comes with the proposed links among tectonics, continental weathering, and climate change. The hypothesis proposed by Raymo et al. (1988) is that the uplift of the Tibetan Plateau led to increased rates of chemical weathering of silicate minerals, thus removing large quantities of CO₂ from the atmosphere. Reduced atmospheric CO₂ produced a significant and geologically rapid cooling of the planet. The drawback of this explanation is that the process, while probably important in the Neogene, is not likely to have played a significant role in Eocene-Oligocene cooling because the Himalayan orogeny had only just gotten underway. Zachos et al. (1999) propose an alternative mechanism to explain the trend toward more radiogenic strontium in the marine reservoir, a strong piece of evidence used by Raymo and colleagues to support their hypothesis. Zachos et al. (1992) suggest instead that Eocene-Oligocene cooling and ice growth on Antarctica increased the rate of chemical weathering itself, thereby causing the observed trend in strontium isotopes and, in theory, also causing further climate cooling by the drawdown of CO₂. The issue remains largely unresolved, and is perhaps one of the most interesting in the earth sciences today (see also papers in Chemical Geology volume 161). Clearly, though, tectonics, ocean circulation, and atmospheric composition all play a role in the long-term Cenozoic cooling trend that began in the middle Eocene.

Did the late Eocene impact events have any demonstrable effects on global climate? Poag et al. (this volume) make a case for periods of greenhouse warming associated with impact events. They base their arguments on the oxygen isotopic compositions of benthic foraminifera taken from a deep shelf section in Virginia immediately overlying the Chesapeake Bay impact structure. In addition, they

document a negative $\delta^{13}\text{C}$ signal in many sections worldwide that they speculate may be related to impact event perturbations of the global carbon cycle. This is in contrast to data obtained from the 35.5 Ma impact horizon in an ODP core from Maude Rise (high latitude, Southern Ocean) and an equivalent horizon from the midlatitude, type section at Massignano, Italy (Vonhof et al., 2000). Oxygen isotope values from the impact horizon indicate accelerated global cooling, within an already deteriorating climate trend. This is accompanied by a marked peak in the relative abundance of the dinoflagellate *Thalassiphora pelagica* at both Maud Rise and Massignano, indicating cooling and increased productivity.

It is interesting to note that these two impact hypotheses predict opposite effects: Poag et al. (this volume) suggest that an impact caused a brief warming episode (or at least that it temporarily suspended global cooling), while Vonhof et al. (2000) argued that it caused global cooling. Disentangling potential causes for an observed climatic trend can clearly be difficult, and simple correlation of events in time is not enough to establish causality. In fact, it remains unclear how impacts of the size of Popigai and Chesapeake Bay could cause such long-term and global effects (either warming or cooling). While there were undoubtedly severe short-term regional effects from these impacts, in all likelihood they produced relatively insignificant long-term global effects in comparison to the overall climatic trends of the Eocene-Oligocene transition.

Recently, Fawcett and Boslough (2002) have suggested that the cooling of the late Eocene could have been due to a ring of impact debris around the Earth, which casts a shadow and shades the tropics for about 100,000 years. There are several problems with this hypothesis. First of all, post-impact late Eocene was marked by *warming*, not cooling (as Poag et al. (this volume) attribute to impact debris. Finally, the effects take much longer than 100,000 to develop after the impact, and persist for longer than 100,000 years.

PATTERNS, TIMING, AND INFERRED CAUSES OF FAUNAL TURNOVER

Climatic change during the Eocene-Oligocene transition had profound effects on global biotic communities, as many of the papers in this volume demonstrate. The nature and magnitude of these biotic changes can often be even more informative than physical or geochemical indicators in understanding the nature and timing of the climatic changes.

The Biotic Record

Because many higher taxa are characterized by particular and distinct ecologies (e.g., mode of life, feeding strategy, developmental pathway, and so on), establishing the taxonomic expression of a turnover interval can be helpful in determining the proximal and ultimate cause(s) of the event. Here we discuss the major groups represented within this volume and the patterns they typify across the Eocene-Oligocene transition.

In the record of Eocene-Oligocene benthic foraminiferal assemblages, pulses of extinction can be noted at the end of the middle Eocene and/or at or close to the Eocene/Oligocene boundary in the Tethys and Paratethys in Italy (Coccioni and Galeotti, this volume), Israel (Barbieri et al., this volume), the circum-Alpine region (Nebelsick et al., this volume), southern Australia (McGowran et al., 1992), in the Caribbean (Robinson, this volume), and the U.S. Gulf Coast (Gaskell, 1991; Fluegeman, this volume). In both the Caribbean and the Gulf Coast, there are indications that the turnover generally associated with the boundary may in fact have been taking place in the earliest Oligocene (Fluegeman, this volume; Robinson, this volume), and therefore perhaps have been associated with Oi1 cooling.

Mollusks are abundant, ecologically diverse, and well skeletonized and therefore well preserved. Thus they are the primary marine-shelf faunal component for which there are good data across the Eocene-Oligocene transition. The U.S. Gulf Coastal Plain records arguably one of the best sections of fossiliferous Paleogene sediments in the world, and the mollusks there have been intensively studied for more than a century and a half (synthesized in the works of Palmer and Brann, 1965, 1966; Dockery, 1982; and MacNeil and Dockery, 1984). One place in the world that rivals the Gulf in the nature of its molluscan fossils is the Paris Basin and associated regions in France. Dockery and Lozouet (this volume) present a comparison of these two spectacularly diverse sequences. In the Gulf Coast, there is substantial molluscan taxonomic turnover at group-level boundaries throughout the Paleogene (Dockery, 1986). In both regions, the greatest turnover is near the Eocene/Oligocene boundary, with more than 95% of Gulf Coast mollusk species going extinct, among them several long-ranging and abundant Paleocene and Eocene forms. In the U.S. Atlantic Coastal Plain, limited outcrops and poor preservation have made molluscan faunas difficult to record and analyze. Using what is available, Campbell and Campbell (this volume) found

close taxonomic affinities of these faunas to the Gulf Coast assemblages, and noted the similar stepwise extinction patterns across the middle/late Eocene and late Eocene/Oligocene boundaries. In addition they observe that no taxa endemic to the region survive from one stratigraphic unit to the next.

A trio of papers on the western North American molluscan faunas shows a similar pattern of pulsed faunal turnover at the stage level, with significant events at the middle/late Eocene boundary, near the Eocene/Oligocene boundary, and at the early/late Oligocene boundary (Hickman, this volume; Nesbitt, this volume; Squires, this volume). As in the Gulf Coast, tropical taxa were particularly hard hit during turnovers. Farther north, in the Kamchatka Peninsula, the same middle/late Eocene and terminal Eocene turnovers occurred, and once again warm-water taxa suffered preferentially. Interestingly, while Alaskan faunas responded similarly to middle-late Eocene events, they were seemingly unaffected by Eocene/Oligocene boundary extinctions (Oleinik and Marincovich, this volume). In all regions, there was a notable radiation of new taxa that either migrated from higher latitudes or are endemic. The Eocene/Oligocene boundary marks the end of the characteristic shallow-marine Tethyan fauna in North America and the northern Pacific Ocean.

Ostracodes, too, can be useful indicators of oceanographic change. Schellenberg (1999) documents significant drops in species richness associated with the Eocene/Oligocene boundary at several sites in the Southern Ocean. Associated with the diversity drop is a transition from dominantly deposit-feeding to dominantly filter-feeding forms. This indicates a trend toward low-oxygen condition, for filter feeders are better able to move water over their bodies and hence exchange oxygen more efficiently.

The pattern of echinoderm diversity through the Eocene and into the Oligocene does not seem to consistently follow that of the mollusks and benthic foraminifera. Nearly all regions considered show an overall decline in echinoid diversity from the middle Eocene to the Oligocene, but the specifics of the patterns differ among the regions (Carter, this volume). Unlike that of other invertebrate groups, the diversity of echinoids in the southeastern United States actually increased from the middle to the late Eocene, then declined into the early Oligocene (Carter, this volume). Carter suggests that the record of echinoid diversity across the shelf was primarily controlled by facies effects, specifically the relative proportions of carbonate versus siliciclastic sediment and the balance

between muddy and sandy substrates. Conversely, in the Pacific Northwest, Burns and Mooi (this volume) point out that sand dollars in the Oligocene were significantly different from those in the Eocene, implying an Eocene/Oligocene boundary turnover. Based on paleobiogeography, they suggest that the Oligocene fauna may have had its origins at higher latitudes, consistent with the molluscan data. Other echinoderms have a less complete record due to poorer preservation potential, and so patterns can be only tenuous. The diversity and abundance of crinoids, asteroids, and ophiuroids in marine shelf sediments actually seem to have increased at high southern latitudes through the Eocene. Aronson et al. (1997) report unusual echinoderm-rich faunas near the top of the Eocene section on Seymour Island on the Antarctic Peninsula, potentially in response to the decrease in predation pressure associated with climatic cooling. In the Pacific Northwest, however, crinoids disappeared from shallow water at the end of the Eocene (Burns and Mooi, this volume).

The record of terrestrial vertebrates through the Eocene-Oligocene transition was covered in some detail by papers in Prothero and Berggren (1992) and Prothero and Emry (1996). Here, we add contributions regarding the record of marine vertebrates. Manning (this volume) records an unexpected pattern of FADs and LADs for marine vertebrates along the U.S. Gulf Coast, although he cautions that both the temporal and the stratigraphic record is poor. He noted an end-Eocene extinction of several Tethyan forms, such as the archeocete whale *Basilosaurus*, giant sea snakes, and the sawfish, *Proprius*. However, all other marine vertebrate groups show a gradual change, often at subspecific level, across the boundary or no change at all. On a global scale, Fordyce (this volume) reviews whale diversity, extinctions, and originations across the boundary. At the family level, there was an initial rapid appearance of grades and clades in the Ypresian-Lutetian interval (early to middle Eocene), and a second radiation near the Eocene/Oligocene boundary. Eustatic sea-level fall substantially reduces the available record of marine mammals for the early Oligocene. No archaic cetaceans ranged into the Oligocene, and new data show a complex pattern for the Oligocene radiation of cetaceans around the Pacific Ocean, including the oldest odontocetes from the Priabonian in Washington. Fordyce (this volume) concludes that this diversity pattern resulted from the restructuring of food resources during a period of oceanic cooling.

PALEOBIOLOGY OF TURNOVER

Turnover events are characterized by some combination of disappearance of old forms and/or appearance of new forms (Allmon, this volume), and hence can affect taxonomic diversity in several ways. It is conceivable that a boundary could be marked by 100% turnover of the fauna but have no associated change in diversity (number of taxa) across that boundary. Stepwise turnover of shelf communities through the Eocene and Oligocene seems to characterize nearly all the records reported here, with particular pulses at the middle/late Eocene boundary and near the Eocene/Oligocene boundary. In order to understand these events better, it is important to consider diversity in combination with either origination or extinction (or both). As an example, Campbell and Campbell (this volume) point out that the record of molluscan diversity in the Atlantic Coastal Plain tends to be characterized more by pulses of extinction than by pulses of origination. The Gulf Coast seems to be distinguished by both (Dockery, 1986). But in Alaska, origination actually exceeds extinction (Oleinik and Marinovich, this volume). All these turnovers, however, may have been roughly of the same magnitude.

A common thread that seems to be present in the studies of Atlantic, Gulf, and European mollusks is that *diversity loss* is most significant at the middle/late Eocene boundary, yet the *turnover* in the fauna is greater near the Eocene/Oligocene boundary (Dockery and Lozouet, this volume; Campbell and Campbell, this volume). This implies, in the framework of faunal turnovers presented by Allmon (this volume), that while extinction was greatest at the middle/late Eocene boundary, it was not accompanied by much in the way of origination. The late Eocene fauna is simply a whittled-down version of the middle Eocene biota. At the end of the Eocene, turnover in the fauna was more complete such that not only did many forms suffer extinction, but many new taxa appeared for the first time in the early Oligocene. The result is that the Oligocene fauna is recognizably and distinctly different from the Eocene one, despite the fact that extinction alone might have been greater at the middle/late Eocene boundary.

On the Pacific Coast, the end of the middle Eocene is similar in that it marks a very large drop in molluscan diversity, but here turnover as well is virtually complete—taxonomic overlap between the units above and below is near zero (Hickman, this volume; Nesbitt, this volume; Squires, this volume). Near the Eocene/Oligocene boundary, turnover is compara-

tively severe and the percent extinction larger (Hickman, this volume)

The greater turnover experienced in the Pacific Northwest at the middle/late Eocene boundary in comparison with the Gulf Coast may be a function of its higher latitude, for warm, equable, environments there in the middle Eocene may have been more severely affected by cooling than those at lower latitudes. Farther north in the Pacific, on the Kamchatka Peninsula, middle-late Eocene turnover was also significant, but first appearances were more important than extinctions (Oleinik and Marinovich, this volume)—the exact opposite of the pattern from the Gulf Coast. Likewise, the Eocene/Oligocene boundary marks the most significant diversity drop there. In contrast, as mentioned earlier, the middle/late Eocene and Eocene/Oligocene boundaries in Alaska (Oleinik and Marinovich, this volume) are not so much marked by extinction, but by origination!

An ever-present question associated with any given turnover is how much of the taxonomic change is evolutionary (true origination and extinction) and how much is simply migration out of or into a given area. Dockery and Lozouet (this volume) consider this issue for the U.S. Gulf Coast and find that in many cases the extinctions at the Eocene/Oligocene boundary were truly extinctions (at least in the Western Hemisphere), rather than emigrations. In addition, they maintain that turnover was rapid enough near the Eocene/Oligocene boundary and without a significant loss in diversity, that the first appearances must have included a substantial amount of immigration from elsewhere, rather than evolution *in situ*. Interestingly as well, the new taxa that appeared in both the Gulf and western Europe are very similar, if not identical (Dockery and Lozouet, this volume), suggesting an open biogeographic connection at that time. The presence of these characteristic Tethyan forms in the basal Oligocene of Mississippi suggests to them that the source of larvae was to the east, in the vicinity of the Paris and Aquitaine Basins in France. Biogeography is a factor that is relevant in other ways, too. Campbell and Campbell (this volume), in their comparison of turnover in mollusk genera restricted to the Carolinas versus those more globally distributed, not surprisingly find that endemic genera were more likely than widespread ones to suffer extinction during turnovers. At the species level, however, even widespread taxa suffered greatly near the Eocene/Oligocene boundary (only a single species survived the transition), suggesting a severe and global event. Interestingly, at high

latitudes in the North Pacific, the more cosmopolitan taxa seem to have been more strongly affected by extinction than those with restricted distributions (Oleinik and Marinovich, this volume). Cosmopolitan taxa, in fact, were replaced by more endemic genera throughout the Eocene-Oligocene transition. In this case, the widespread taxa tended to have ranges that extended to warmer, lower latitudes. Their selective loss suggests that thermal tolerance may play a more important role than degree of endemism in determining survival probability at high latitudes.

CAUSES FOR TURNOVER?

In narrowing down the cause for a particular turnover, one of the possible strategies would be to ask whether the turnover itself is local or global. Do faunal events recognized in shelf sections match those noted on other continents or in open ocean (benthic or planktonic) assemblages? Fluegeman (this volume) points out that the pattern of turnover in benthic foraminifera, for example, is often not in phase with that in the deep sea because neritic taxa tend to be more sensitive to local and regional forcing factors, while the driving forces behind change in deep-sea benthics are more likely to be global. In the U.S. Gulf Coast, however, the similarity of the benthic foraminiferal record (e.g., Gaskell, 1991; Fluegeman, this volume) to that in southern Australia discussed in McGowran et al. (1992) suggests that this may not be the case for Eocene-Oligocene turnovers (Fluegeman, this volume). The similarity of molluscan extinction patterns across the middle/late Eocene and the Eocene/Oligocene boundaries in the Gulf and Atlantic Coastal Plains, Europe (Campbell and Campbell, this volume; Dockery and Lozouet, this volume), and the Pacific (Nesbitt, this volume; Hickman, this volume; Squires, this volume; Oleinik and Marinovich, this volume) also indicates a more global event. Nevertheless, several authors point out the importance of facies changes in influencing the patterns recovered in their sections. Care should be taken to constrain the turnovers as carefully as possible in time and space so that local versus global control can be evaluated.

Selectivity of extinction in terms of the type of fauna affected can be especially useful for determining the cause(s) of a particular episode or interval of turnover. A recurrent theme within the molluscan records of the Eocene-Oligocene transition seems to be that warm-water taxa suffered preferentially in comparison with cool-water taxa, particularly at the middle/late Eocene boundary turnover. Hansen

(1987, 1992) argues for a correlation between Gulf Coastal Plain turnovers and temperature based on the selective loss of warm-water taxa. Dockery and Lozouet (this volume) acknowledge temperature as a factor in the extinctions as well, but imply it to be less important than sea level. For the Pacific Coast, Nesbitt (this volume), Hickman (this volume), and Squires (this volume) point out the strong bias against warm-water and tropical taxa at the middle/late Eocene boundary in particular, and the same is true in the North Pacific (Oleinik and Marinovich, this volume).

Dockery (1986) and Dockery and Lozouet (this volume) also note that the molluscan faunal turnovers in the U.S. Gulf Coast correlate well with Type 1 sequence boundaries, and on that basis suggest a correlation between major sea-level falls and molluscan turnovers. Gaskell (1991) documents the same relationship for Gulf Coast benthic foraminifera. Their inferred mechanism by which sea level would affect diversity is through loss of habitable area and change in circulation patterns that force biogeographic change. While it is clear that the relationship with sea level exists in the Gulf, the widespread selective loss of warm-water taxa through the middle-late Eocene and into the Oligocene in a number of other areas strongly argues for temperature being a dominant causal factor in the extinctions globally.

In bathyal environments, the productivity regime and degree of oxygenation of the bottom seem to be particularly important factors in faunal turnover. Barbieri et al. (this volume) note a significant transition at the middle/late Eocene boundary in benthic foraminiferan assemblages that they link to a shift from oxygenated, oligotrophic conditions to oxygen-limited and nutrient-rich conditions. The same trend toward highly productive surface waters is seen near the Eocene/Oligocene boundary in bathyal (Coccioni and Galeotti, this volume) and abyssal sediments based on benthic foraminiferal abundances and carbon isotopic work (Diester-Hass, 1995; Thomas and Gooday, 1996; Salamy and Zachos, 1999; Diester-Hass and Zahn, 2001; Diester-Hass and Zachos, this volume). Increases in paleoproductivity of ocean waters was likely linked to cooling and concomitant changes in ocean circulation, leading to an increase in upwelling intensity.

As to whether the documented late Eocene bolide impacts (e.g., Poag et al., this volume) caused any response in the faunas at the time, there does not seem to be any obvious correlation between impacts and extinction peaks in the U.S. Gulf Coast (Hansen,

1987). In the Carolinas, where the effect plausibly would have been more severe, the problem of poor preservation makes the issue difficult to resolve (Campbell and Campbell, this volume). Robinson (this volume) notes an extinction of lesser magnitude in the benthic foraminiferan record in the Caribbean during the late Eocene. However, poor age constraints do not allow precise correlation with impact or other events. Given that the papers in this volume and others suggest major pulses of extinction at the end of the middle Eocene (well before the impacts) and the early Oligocene (well after), it is unlikely that the Chesapeake Bay or Popigai impacts had a significant effect on the global biota.

NEW AVENUES FOR RESEARCH

Since the proceedings volume of the first Penrose Conference on the Eocene-Oligocene transition was published (Prothero and Berggren, 1992), new avenues for research have opened up through the development of more refined techniques for investigating processes across an epoch boundary. Higher-resolution chronostratigraphy utilizing radiometric dating techniques, chemo-, magneto-, and sequence stratigraphy, microsampling of shell material for stable isotope investigations, and leaf morphology analysis have allowed us to focus on biotic and climatic changes occurring on progressively fine time scales. However, much work remains to be done in correlating boundary sequences across paleobiogeographic gaps. We all aspire to better age constraints so that we can place a virtual golden spike to mark the Eocene-Oligocene transition in each of our respective sections. Such precision will finally allow us to compare data across provincial boundaries, across oceans, and between taxa.

We see a number of new fruitful directions for research:

—Correlate marine and continental data to better resolve how climatic change affects coastal plain and inland/upland communities and determine whether turnovers are synchronous

—Refine the time scale of climatic change in different regions to determine the degree to which they correlate and how the magnitude of change varies geographically

—Explore latitudinal diversity trends, and how they respond to global climate change

—Investigate ecological and taxonomic selectivity across transitions in order to learn more about cause

—Deconvolve the relative contributions of in situ evolutionary change, true extinction, and migration

- Collect more faunal and environmental data in geographical regions that are less well represented
- Solve the ice volume versus temperature conundrum of oxygen isotopes, perhaps with progress being made using trace elements (e.g., Lear et al., 2000)
- Use biogeography of assemblages to better understand ocean circulation and thermal gradients

As Allmon (this volume) states, "Biologically defined boundaries—times of appearances and/or disappearances of taxa—have been fundamental to stratigraphic paleontology and geology for almost 200 years." This observation sets the stage for topics explored in this volume. Stratigraphic boundaries are nearly always associated with or defined by local and regional extinctions and originations, which themselves are often the result of environmental change. Recognizing the geologic cause(s) of such change, refining its temporal and geographic expression, and understanding the biological response to it, are our goals. As investigations move toward better temporal resolution of events using nonbiotic signatures, we are allowed freedom to disentangle the biotic events from their climatic and/or tectonic causes. Precise stratigraphic correlations continue to be the blueprint from which we work, and as paleontologists we can now utilize new geochemical tools to investigate faunal and floral responses to climate change. We hope this will help us to better understand the complexities associated with the study of climate change and the associated biological response to the past, as well as in our own immediate future.

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