North American mammalian diversity and Eocene–Oligocene extinctions

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Abstract.—Diversity and faunal turnover of North American land mammals are calibrated against the magnetic polarity time scale for million-year intervals for the latest Eocene through late Oligocene. A major, gradual Late Eocene decline in diversity, caused mostly by an extended period of extinction of archaic forms, seems to be related to the worldwide crisis known as the "Terminal Eocene Event." Along with other evidence of gradual changes in deep-sea microfossils, this evidence argues against a catastrophic explanation for late Eocene extinctions.

Faunal stability characterized the rest of the Oligocene except for a wave of extinctions in the mid-Oligocene (Chadronian-Orellan boundary, about 32.4 ma). This mid-Oligocene event is sudden and severe, occurring in less than 200,000 yr, based on estimates from sedimentation rates calibrated from magnetic polarity interval boundaries. The mid-Oligocene event is found in many paleoclimatic records, but not in all of them. It may be related to the completion of the Circum-Antarctic Current and to increased mid-Oligocene glaciation.

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Introduction

The Late Eocene and Oligocene were critical periods in earth history. During these times there were profound changes in world temperature (Savin 1977), global oceanic circulation (Kennett 1977, 1981), sea level (Vail et al. 1977), the carbonate compensation depth (CCD) (Van Andel 1975), marine biotas (Fischer and Arthur 1977; Cavelier et al. 1981), and land floras (Wolfe 1978). The Late Eocene–Oligocene was the turning point of Tertiary climatic evolution and set the stage for the development of the present-day oceans and climate.

This major change in world climate is also reflected in land mammals. The changes in the European faunas have recently been reviewed by McKenna (1983), Brunet (1977, 1979), Crochet et al. (1982), and Cavelier (1979). The major event, the "Grande Coupure" of Stehlin (1909), appears to take place near the Eocene-Oligocene boundary. Little detailed work has been done on changes in the North American mammalian faunas. Lillegraven (1972) discussed the diversity of Cenozoic mammals at the ordinal and familial level, but the time resolution of this study is only at the level of subepoch ("early," "middle," and "late" Oligocene). Savage and Russell (1983) have updated this com-

pilation, but the time resolution remains on the level of land mammal "ages," which average 3–5 ma in length. Black and Dawson (1966) reviewed the Late Eocene mammalian faunas of North America but did not discuss Oligocene faunas in detail. Other authors (Gregory 1971; Wilson 1972; Webb 1977) have discussed aspects of the Oligocene land mammal faunas in a more qualitative sense. The attempt at a synthesis by Clark et al. (1967) was also qualitative, but is now badly out of date.

Recent paleomagnetic studies (Prothero 1982; Prothero et al. 1983; Prothero 1985; Prothero, in prep.) have made it possible to calibrate the changes in North American Oligocene land mammal faunas more precisely and to correlate these changes with other changes in world climate. Fossil mammal collections with good stratigraphic resolution (particularly those of the Frick Collection of the American Museum of Natural History) have also made it possible to document taxonomic ranges much more precisely than in the past. It seems appropriate to review our knowledge of Oligocene mammal faunas and their temporal changes using this information, since there is so much current interest in the Oligocene and the significance of mid-Tertiary faunal turnovers.
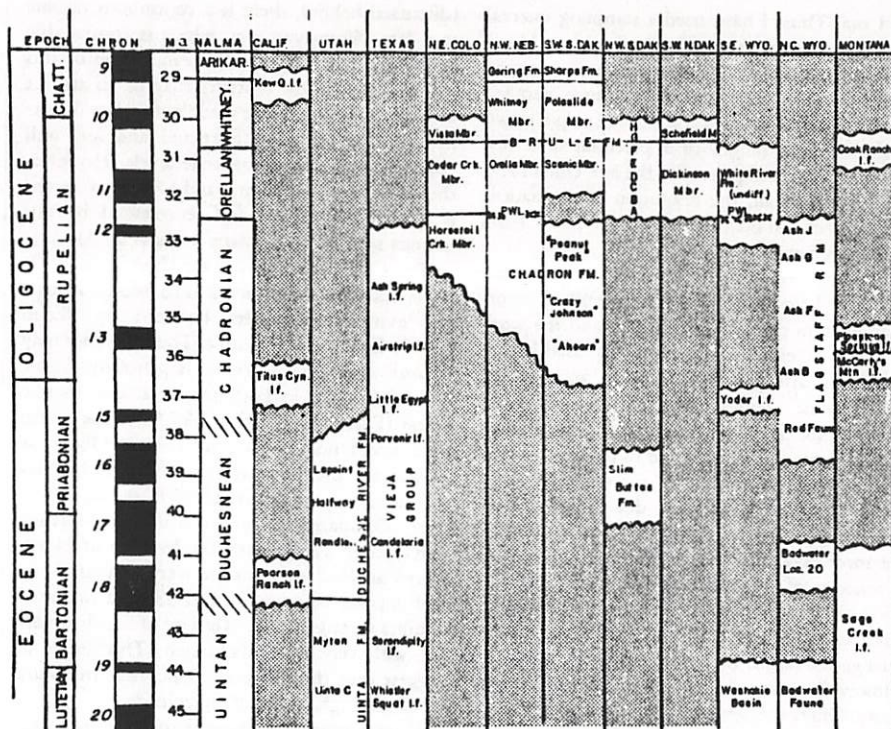
FIGURE 1. Correlation of Late Eocene–Oligocene rocks and faunas with the magnetic polarity time scale. Correlations based on Black and Dawson (1966), Wilson (1978, 1984), Prothero et al. (1983), Prothero (1982, 1985), and Emry et al. (1986). The Oligocene record is now almost completely studied magnetostratigraphically, and the precision and resolution are much better than the Late Eocene, where relatively little magnetostratigraphy has been carried out. Late Eocene correlations are thus more indirect, and this is reflected in the imprecision in faunal dating used in Figs. 2 and 3 and Table 1. ("Late Uintan" = 45–42 ma; "Early Duchesnean" = 42–39 ma; "Late Duchesnean" = 39–38 ma). Future work will certainly revise and refine Late Eocene correlations.

Abbreviations: ARIKAR. = Arikareean; CHATT. = Chattian; l.f. = local fauna; M, Mbr. = Member; NALMA = North American land mammal "age"; WHITNEY. = Whitneyan. Epoch and Chron Correlations after Berggren et al. (1984).

Methods

The faunas used in this study, and their correlation with the magnetic polarity time scale, are shown in Fig. 1. Most of these faunas are directly calibrated by paleomagnetics (Prothero 1982, 1985, in prep.; Prothero et al. 1982, 1983). For faunas from localities that have not yet been sampled paleomagnetically but can be tied to areas that are (e.g., Rancho Gaitan local fauna, McCarty's Mountain local fauna), I have used the correlations of Emry et al. (1986). Some

faunas (e.g., Cypress Hills, Mink Creek, Pilgrim Creek), which are not yet sampled paleomagnetically, appear to span too much time or are too imprecisely correlated to be useful to this study (Emry et al., 1986). Their exclusion seems to make no significant difference in the results.

The ranges of mammalian taxa are plotted against their position on the magnetic polarity time scale in Fig. 2, based on the correlations given above and the data in Prothero (1982). In many cases, range data are too poor to resolve first or last occurrences more precisely than with-

TAXA	TEMPORAL RANGE

TAXA	TEMPORAL RANGE

and taxonomic data in this study are derived from Macdonald (1963, 1970), Black and Dawson (1966), Emry (1973), Wilson (1978, 1984, pers. comm.), Prothero (1982), and Emry et al. (1986). In addition, the following sources were consulted: Neoplagiaulacidae—Krishtalka et al. (1982), Ostrander et al. (1979); Didelphidae—Setogouchi (1979), Green and Martin (1976), Krishtalka and Stucky (1983); Leptictidae—Novacek (pers. comm.); Apternodontidae—McKenna (pers. comm.); Micropternodontidae—Russell (1960); Adapisoricidae—Lillegraven et al. (1981), Setogouchi (1978); Erinaceidae—Bjork (1975), Gawne (1968), Krishtalka and Setogouchi (1977); Soricidae—Repenning (1967), Krishtalka and Setogouchi (1977); Proscalopidae—Barnosky (1981); Pantolestidae—Cook (1954); Apternyidae—Clemens (1964); Epoicotheriidae—Rose (1978); Leporidae—Gawne (1978, pers. comm.); most Rodentia—Wood (1980); Cylindrodontidae—Emry (1981); Eomyidae—Setogouchi (1978), Korth (1981a); Ischyromyidae—Prothero (1982); Cricetidae—Martin (1980), Korth (1981b); Hyaenodontidae—Mellett (1977); Carnivora—Galiano (pers. comm.); Amphicyonidae—Dawson (1980), Emry and Hunt (1980), Hunt (pers. comm.); Mesonychidae—Emry (1981); Helaletidae and Tapiridae—Radinsky (1963); Hyracodontidae—Radinsky (1967); Amynodontidae—Wilson and Schiebout (1981); Rhinocerotidae—Radinsky (1967), Prothero (in prep.); Brontotheriidae—Emry (1981); Equidae—Emry (1981), Prothero and Shubin (in prep.); Leptochoeridae—Edwards (1976); Entelodontidae—Emry (1981), Wilson (1971); Tayassuidae—Woodburne (pers. comm.); Anthracotheriidae—Russell (1978), Macdonald (1956); Agriochoeridae—Emry (1981), Wilson (1977); Merycoidodontidae—Stevens (pers. comm.); Camelidae and Oromerycidae—Wilson (1974), Prothero (in prep.); Leptomerycidae—Black (1978), Storer (1981); Hypertragulidae—Emry (1978); Protoceratidae—Emry and Storer (1981), Patton and Taylor (1973).

FIGURE 3. Summary of diversity data listed in Fig. 2. S, (open bars) = sum of known taxa in interval i; Rm (patterned bars) = running mean (compensated for effects of turnover); E, (solid line) = extinction rate per million years; O, (dashed line) = origination rate per million years; L.U. = Late Uintan (42–45 ma); E.D. = Early Duchesnean (39–42 ma).

thus supports the subjective assessment based on visual inspection of Fig. 3. The late Uintan and Duchesnean "ages" and the Cha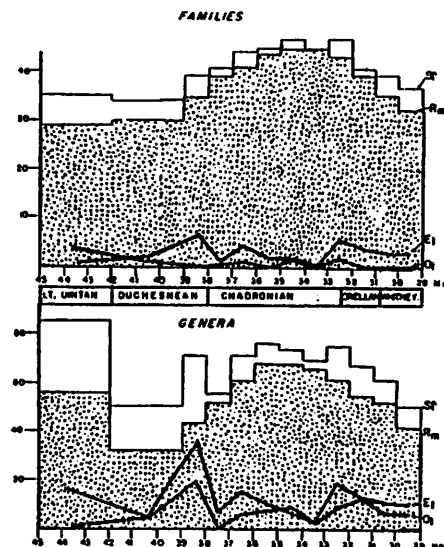dronian-Orellan boundary are periods of significantly high extinction, and the only unusual increase in originations occur in the Duchesnean.

Discussion

The trends shown by the data above have long been recognized by mammalian biostratigraphers in a qualitative sense. Lillegraven (1972) found a somewhat similar pattern in his quantitative studies on the ordinal and familial level. But the higher temporal and taxonomic resolution in the present data brings out two features that have not been previously discussed:

1. The gradual development and severity of the Terminal Eocene Event and the stability of the Chadronian fauna;

2. The abrupt nature of the extinctions at the end of the Chadronian.

The Eocene–Oligocene transition.—Black and Dawson (1966), Lillegraven (1972,) Wilson (1984), and Webb (1977) discussed the Eocene-Oligocene transition in North American land mammal faunas. Several elements combine to cause a drastic faunal change. The most important is the wholesale extinction of many archaic groups (i.e., those that are characteristic and dominant in the Paleocene and Eocene). These include mixodectids, microsyopids, taeniodonts, achaenodonts, uintatheres, nyctitheriids, anaptomorphine primates, sciuravid rodents, dichobunid artiodactyls, limnocyonid and "miacid" carnivores, mesonychids, hyopsodonts, isectolophid tapiroids, and the ceratomorph Hyrachyus. Black and Dawson (1966) have provided the most thorough review of the changes in the fauna during this transition. Other archaic groups, such as the lophiodontid perissodactyls, oromerycid artiodactyls, multituberculates, apaternyids, epoicotheres, and pantolestids, become extremely rare and finally disappear in the Chadronian. Dermopterans vanish from North America at the end of the Eocene, although there is still an extant form, Cynocephalus, in Asia. These archaic forms give way to a large number of taxa with a more modern aspect, labeled the "White River Chronofauna" by Emry (1981). The White River Chronofauna apparently remained quite stable until the Arikareean, except for the

also a short period of relative stability during the late Orellan and Whitneyan, after the effects of the mid-Oligocene event have receded.

Statistical significance of these turnover peaks was calculated using Raup and Marshall's (1980, formula 2) method for estimating the chi-square statistic. In the familial data, only two extinction peaks were statistically significant at the 95% confidence level (chi-square greater than 3.841 with 1 degree of freedom). These peaks occur in the late Uintan and the Chadronian–Orellan (32.4 ma). On the generic level, four extinction peaks were significantly above background: the late Uintan, early and late Duchesnean, and Chadronian–Orellan. Originations show a slightly different pattern. The early and late Duchesnean generic peaks and the late Duchesnean familial peak are the only ones significantly above normal. The stability of the Chadronian faunas, and of the late Orellan and Whitneyan faunas is corroborated by the fact that none of their E, or O, values are significantly above the critical value at the 95% confidence level. Statistical analysis

Table 1. Summary of diversity data from Fig. 2 (see Fig. 3).

	Late Uinta 42-45	Early Duches. 39-42	Midpoint of 1 ma time increment									
			38.5	37.5	36.5	35.5	34.5	33.5	32.5	31.5	30.5	29.5
Families (60 total)												
Total number (S)	36	34	39	41	44	45	41	45	47	41	37	34
First appearances (O)	2	6	7	2	4	2	2	0	2	0	0	0
Last appearances (E)	8	2	0	1	1	0	2	0	6	4	3	3
Origination rate (O)	0.67	2	7	2	4	2	2	0	2	0	0	0
Extinction rate (E)	2.7	0.67	0	1	1	0	2	0	6	4	3	3
Running mean (Rm)	29	30	35.5	39.5	41.5	44	45	45	43	39	35.5	32.5
Turnover rate (T)	1.7	1.3	3.5	1.5	2.5	1.0	2.0	0	4.0	2.0	1.5	1.5
			Units in families/ma									
Genera (227 total)												
Total number (S)	85	50	71	55	71	76	74	69	75	67	61	50
First appearances (O)	5	19	36	6	15	10	6	3	9	12	6	6
Last appearances (E)	53	15	20	1	6	8	8	3	18	13	11	10
Origination rate (O)	1.7	6.3	36	6	15	10	6	3	9	12	6	6
Extinction rate (E)	17.7	5.0	20	1	6	8	8	3	18	13	11	10
Running mean (Rm)	56	33	43	51.5	60.5	67	67	66	61.5	54.5	52.5	42
Turnover rate (T)	9.7	5.7	28	3.5	10.5	9	7	3	13.5	12.5	8.5	8
			Units in genera/ma									

Figure 4. Details of the mid-Oligocene event (Chadronian-Orellan transition). Important faunal ranges, speciation events, and dwarfing intervals are shown for two key sections in eastern Wyoming. PWL = Persistent White Layer. Sedimentation rate for Chron CIIr reversed magnetochron is 133 m/ma at Douglas and 98 m/ma at Lusk. Using these rates, the time represented between the last appearance of oromerycids and Yoderimys, and the last appearance of Brontotheriidae is about 200,000 yr at Lusk, and 137,000 yr at Douglas.

second wave of extinction at the end of the Chadronian (discussed below). Many living families, including the leporids, canids, camelids, heteromyids, sciurids, rhinoceroids, and soricids, first appear during this "modernization". (Lillegraven 1972). There is also a peak of apparent immigration of groups, particularly from Asia (Simpson 1947; Webb 1977) during the Eocene-Oligocene transition.

Contrary to the popular image of the Terminal Eocene Event as a single, short, catastrophic event in the oceans (Ganapathy 1982; Alvarez et al. 1982; Asaro et al. 1982), the Oligocene diversity data for land mammals presented above suggest a more complicated, extended transition. The majority of archaic groups were gone by the early Duchesnean (about 42 ma), well before the Eocene-Oligocene boundary (according to Berggren et al. 1985). There is a consequent diversity low during the early Duchesnean which is not replaced until the late Duchesnean. The actual Eocene-Oligocene boundary in North America (the late Duches-

near-earliest Chadronian) is marked more by immigration of new taxa and diversification of local groups, and only to a lesser extent by a second wave of extinction of archaic groups. This hardly corresponds to the pattern of diversity that would result from a single asteroid collision (as suggested by Ganapathy 1982; Alvarez et al. 1982; Asaro et al. 1982), where a large number of groups would be extinguished indiscriminately. Instead, the diversity pattern strongly suggests that the turnover is due to faunal interchange between Asia and North America. The Eocene-Oligocene transition marks the end of endemism in European mammals as well (Cavelier et al. 1981; Brunet 1977, 1979). European mammalian faunas show a gradual transition in the Late Eocene leading to the Grande Coupure (Crochet et al. 1982). It is probably not coincidence that the drying up of the Turgai Straits across central Asia, which separated eastern and western Asia in the Late Eocene, is believed to have occurred near the Eocene-Oligocene boundary (Heissig 1979; McKenna 1975,

1983), so far as the timing of this event can be resolved.

This picture of Late Eocene–Early Oligocene deterioration, diversity low, and gradual replacement also emerges from the studies of deep-sea microfossils and benthic molluscs. Hansen (1984) reports a continuous decline in Gulf Coast bivalve diversity through the Late Eocene, with a much larger event at the Middle/Late Eocene boundary than at the Terminal Eocene Event. According to marine micropaleontologists (Haq and Lohmann 1976; Corliss 1981; Keller 1983a, b; Corliss et al. 1984; Snyder et al. 1984), the record of foraminiferans and calcareous nannoplankton shows no catastrophic change at the Eocene-Oligocene boundary. Instead, there is a pattern of gradual turnover and replacement spaced out over nearly 5 ma that cannot be explained by a single catastrophic event (Corliss et al. 1984).

The Mid-Oligocene event.—In contrast with the Eocene–Oligocene transition, there has been relatively little discussion of the Chadronian–Orellan transition. In the past, the only taxon to generate significant attention was the titanotheres, but recent work has shown that many other groups disappear at nearly the same time. As indicated in Fig. 4, the Chadronian–Orellan transition is dominated by a wave of extinctions, particularly of archaic forms, which are characteristic of the Eocene and Early Oligocene. In addition to the titanotheres, these include pantolestids, epoicotheres, paramyid and cylindrodont rodents, and oromerycid artiodactyls. There are also numerous generic and species-level changes. The first appearance of leptauchenine oreodonts and eumyine cricetid rodents (both important in the later Oligocene) occurs during this transition, and rapid dwarfing took place in the oreodont *Miniochoerus* (Lander 1977; Prothero 1982). The genus then stabilized through the rest of the Orellan.

In addition to the raw diversity data, nonquantitative differences in the fauna are quite revealing. Two groups of low-crowned forest browsers, the titanotheres and oromerycids, become extinct. The mole-like epoicotheres also vanish, although the proscalopine moles persist. However, the Orellan faunas include very few animals that show major ecological differences from typical late Chadronian faunas. The dom-

inant Orellan groups are the same as those dominant in the late Chadronian: oreodonts, leptomerycid artiodactyls, rabbits, horses, camels, and rhinos such as *Hyracodon* and *Subbyracodon*. The only noticeably high-crowned group to appear in the Orellan is the leptauchenine oreodonts, and they are scarce until the Whitneyan. The paramyid-cylindrodont-dominated rodent fauna of the Chadronian is replaced by a eumyine cricetid fauna of the Orellan, Whitneyan, and Arikareean. Although eumyine cricetids are more advanced in their jaw musculature than paramyids or cylindrodonts, they are not more high-crowned. On the other hand, the abundant ischyromyid rodents are unaffected by the transition. It appears that the rapid and severe environmental stresses at the Chadronian-Orellan boundary selectively affected only the archaic
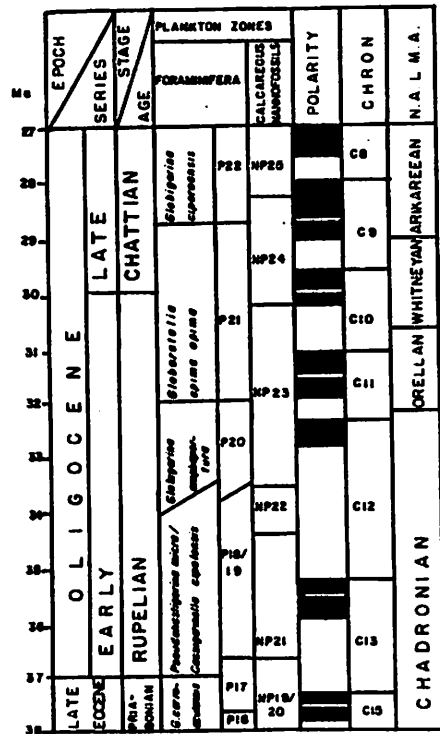

Figure 5. Comparison of North American chronology with the European chronology and the magnetic polarity time scale, based on the work of Berggren et al. (1985).

Table 2. Comparison of terminal Eocene and mid-Oligocene events.

Climatic record	Terminal Eocene Event 36–38 ma	Mid-Oligocene Event 31–33 ma	Source
Terrestrial records:			
North American land mammals	Major extinction and migrations	Major extinction, dwarfing	This paper
North American land reptiles	Drop in diversity, decreased temperature tolerance	Diversity low	Hutchinson (1982)
European land mammals	Grande Coupure (17 generic extinctions, 20 originations, 25 unaffected)	Sannoisian-Stampian event (7 generic extinctions, 6 originations, 39 unaffected)	Brunet (1977), McKenna (1983)
North American land floras	Minor drop in temperature	Major drop in temperature, decreased equability	Wolfe (1978)
European land floras	Major drop in temperature	Not yet recorded	Cavelier et al. (1981)
North American paleosols	Humid climates become subhumid	Subhumid climates become subarid	Retallack (1983)
Marine diversity:			
Marine benthic faunas	Major decrease in diversity	Increasing diversity	Cavelier et al. (1981)
Phytoplankton diversity	Major decrease in diversity	No recorded change	Fischer and Arthur (1977)
Dinoflagellate diversity	No change	Small decrease	Fischer and Arthur (1977)
Braarudosphaera ooze	None recorded	Several	Percival (1984)
Planktonic foraminifers	Gradual diversity decrease	Abundant cool water forms	Keller (1983a, b)
Marine chordates	Small decrease in diversity	No recorded change	Fischer and Arthur (1977)
Geochemical evidence:			
Benthic mollusc $\delta^{18}O$	2.5‰ increase	Gradual decrease	Cavelier et al. (1981)
Benthic foram $\delta^{18}O$	1.2‰ increase	1.0‰ increase	Savin (1977)
Planktonic foram $\delta^{18}O$	2.0‰ increase	Slight increase	Savin (1977)
Planktonic foram $\delta^{13}C$	Small decrease	Large decrease	Cavelier et al. (1981)
Geological and oceanographic events:			
Paleotemperature curve	5°C decrease	3°C decrease	Savin (1977)
Sedimentation rate	Major decrease	Slight increase	Cavelier et al. (1981)
Carbonate compensation depth (CCD)	Big decrease	No change recorded	Cavelier et al. (1981)
Sedimentary hiatuses	Major increase	Major decrease	Cavelier et al. (1981)
Sea-level change	Small drop	Major drop	Vail et al. (1977), Poag and Schlee (1984)
Explosive volcanism	Small increase	Large increase	Axelrod (1981)
Cosmic/extraterrestrial	Ir anomaly (?)	Not recorded	Alvarez et al. (1982), Ganapathy (1982)
Oceanic events	Development of psychrosphere; first sea ice; beginning of circum-Antarctic circulation; opening of Greenland-Norway passage and Arctic exchange with Atlantic; Turgai Straits dry up	Major Antarctic ice advance; deep-water circulation between Antarctica and Tasmania	Kennett (1977, 1981), Keigwin and Keller (1984), Miller et al. (1985), Miller and Fairbanks (1983), Murphy and Kennett (1985), Heissig (1979), Berggren (1982)

groups and did not cause any noticeable morphologic change (Prothero 1982) in response to environmental stress (except possibly for dwarfing in *Miniochoerus* noted above). There are a

number of speciation events at or near the boundary (Fig. 4), but they do not reflect fundamental changes in ecology. There is no apparent increase in tooth crown height at this time,

despite the evidence from paleosols of increased grassland habitats (Retallack 1983). This evidence, along with the apparent stasis in most Oligocene mammal species (Prothero and Shubin 1983), suggests that species were not passively tracking environmental changes. Instead, they have some sort of homeostatic mechanism that prevents this flexibility, and the entire fauna responds to crisis by extinction of archaic groups and speciation within established groups. They do not seem to generate an immediate morphological response, such as higher-crowned teeth for increased grazing. A fully savannah-adapted grazing mammal fauna does not really appear until the Arikareean (Webb 1977).

The Chadronian–Orellan transition apparently took place over a very short span of time, judging from paleomagnetically calibrated sequences in eastern Wyoming (Fig. 4). These sequences preserve the transition in detail, with good stratigraphic data for all the taxa concerned. Calculation of sedimentation rates from the paleomagnetic time planes suggests that most of the range terminations took place within an interval of 200,000 yr at most. This event is clearly not an artifact of missing section, since the range terminations are spread out over tens of meters of section. If there were significant gaps, most of the ranges should be truncated along the planes of these unconformities.

Correlation with Other Events

Although most of the North American Oligocene land mammal record is now calibrated against the magnetic polarity time scale, most other Eocene–Oligocene records are not. In citing age determinations from other authors, one must determine the basis of their usage of the terms "Late Eocene," "Early Oligocene," and so on. Much of the older literature is badly out of date with respect to age determinations. For example, all but the most recent radiometric dates must now be recalculated using the new decay constants (Dalrymple 1979). In addition, a controversy has erupted over the absolute age of the Eocene–Oligocene boundary (Armentrout 1981; Glass and Crosbie 1982; and others). I will not discuss this debate further here, since it is discussed elsewhere (Prothero et al. 1982, 1983; Berggren et al. 1985; Prothero 1985). Fortunately, the calibration of the North American continental sequence with the magnetic polarity time scale permits direct correlation (Fig. 5) with the marine zonation of Lowrie et al. (1982, 1984). This circumvents much of the normal confusion that might surround such correlations. It also allows direct comparison with the marine microfossil sequence, where the Eocene–Oligocene boundary has been defined by convention.

Lowrie et al. (1982) and Poore et al. (1982, 1984) found that the Eocene–Oligocene boundary occurs between anomalies 13 and 15 of the magnetic polarity time scale. Using the La Breque et al. (1977) or Berggren et al. (1984) version of the time scale, this corresponds to an age of about 36.5 ma. In the North American continental record, several paleomagnetically sampled sequences appear to span this part of the magnetic polarity time scale. One of these sequences, the Vieja Group of Trans-Pecos Texas (Testarmata and Gose 1979), has been reinterpreted by Prothero et al. (1982, 1983), placing the earliest Chadronian Little Egypt local fauna near the top of anomaly 15 or the base of Chron C13R reversal (Fig. 1), which would make it latest Eocene. Thus, the Eocene–Oligocene boundary occurs in the early Chadronian. As discussed above, the major Uintan–Duchesnean change in the North American mammalian fauna takes place in the latest Eocene, slightly before the Terminal Eocene Event. Nor is the later Eocene decline in marine faunas an instantaneous event right at the end of the Eocene. The extinctions used to recognize the Eocene–Oligocene boundary are apparently the culmination of a series of Late Eocene faunal changes. Their most severe manifestation is the Terminal Eocene Event. The many changes taking place at the end of the Eocene (summarized in Table 2) have been thoroughly discussed elsewhere (Cavelier et al. 1981; Frakes 1979; Kennett 1981; Van Couvering et al. 1981; Corliss et al. 1984) and will not be reviewed here.

The Chadronian–Orellan event took place between anomalies 11 and 12 of the magnetic polarity time scale, or at about 32.4 ma. This event falls near the top of the Globigerina ampliapertura Zone (P20) and near the top of nannoplankton zone NP23 (Fig. 5). Although this event occurs in the late Rupelian (Early Oligocene), it is usually referred to as "middle Oligocene" in the literature. Wolfe (1971) called it the "Oligocene deterioration" and Berger (1982) called it the "mid-Oligocene oxygen shift." A "mid-Oligocene event" shows up in some records but not in others (Table 2). For example, there is a slight turnover in European mammal faunas between the late Sannoisian Ronzon fauna and the early Stampian Villebramar fauna (Brunet 1977; McKenna 1983). Retallack (1983) documents a major shift in paleosols from the same sections that produce much of the North American Oligocene land mammal record. Chadronian paleosols are predominantly subhumid open woodland but changed to a mixture of semiarid woodland and savannah in the Orellan. Collinson et al. (1981) have shown that the paleobotanical changes in southern England support a model of continuous cooling throughout the Late Eocene, with two major floristic changes before the end of the Eocene. Norris (1982) has found a similar pattern of early to mid-Oligocene cooling in palynofloras from northern Canada. The North American paleobotanical record (Wolfe 1978) shows a minor decline at about 40 ma (the end of the Eocene) and a major decline at about 32 ma (recalibrated with the new constants). Wolfe (1971) first referred to the latter major event as the "Oligocene deterioration," but later (1978) coined the term "Terminal Eocene Event" for the 32 ma floral change. Calibration of the polarity time scale (Prothero et al. 1982, 1983; Prothero 1985) indicates an age of 36.5–37.0 ma for the end of the Eocene. The event that Wolfe originally christened the "Terminal Eocene Event" is actually the mid-Oligocene event.

Marine diversity shows relatively little abrupt change in the mid-Oligocene (Stanley 1984a, b), except for a Braarudosphaera layer or two, which are interpreted as signs of environmental stress. Leg 73, Site 522 of the Deep Sea Drilling Project encountered Braarudosphaera oozes in zones P20-21 and NP23–24 in the South Atlantic (Poore et al. 1982; Percival 1984). Keller (1983a, b) has recently documented a dramatic shift to colder-water foraminiferal assemblages during the mid-Oligocene. Of the oxygen isotope records, the benthic foraminiferan $\delta^{18}O$ shows a mid-Oligocene change comparable to that of the Terminal Eocene Event, but the planktonic foraminiferans and benthic molluscs do not. The planktonic foraminiferan $\delta^{13}C$ change is much bigger in the mid-Oligocene than at the end of the Eocene. Keigwin and Keller (1984) and Miller et al. (1985) interpret the combined isotopic and faunal evidence to indicate a major increase in continental Antarctic ice volume and corresponding global cooling in the mid-Oligocene. However, Murphy and Kennett (1985) interpret the isotopic evidence as indicating that the mid-Oligocene Antarctic ice sheet was not permanent.

Of the geological changes in the mid-Oligocene, the most dramatic is a significant sea-level drop. If the sea-level curves of Vail et al. (1977) are approximately correct, eustatic sea level dropped more in the mid-Oligocene than at the end of the Eocene (Kerr 1984; Poag and Schlee 1984). Miller et al. (1985) attribute this sea-level drop to increased Antarctic glaciation.

The sedimentation rate curve and the CCD curve, however, show no significant mid-Oligocene event, and the percentage of mid-Oligocene hiatuses actually decreases. However, the accumulation of eolian material in the Pacific increases substantially between 38 and 30 ma, indicating increased atmospheric circulation at this time (Janacek and Rea 1983). Explosive vulcanism increased significantly in the Late Oligocene. This is even apparent in the North American mammal-bearing sections, which show increasing volcaniclastic content through the Orellan, Whitneyan, and Arikareean.

Thus, the paleoclimatic indicators of the mid-Oligocene are a confusing mixture of signals. Some show no change, and others show changes as severe as, or in some cases more severe than, those at the end of the Eocene. Interpretation of the significance of the mid-Oligocene event is in some ways more complicated than interpreting the Terminal Eocene Event.

Perhaps the most consistent explanation is suggested by the diversity data for fossil mammals and planktonic foraminiferans (Keller 1983a, b). Both exhibit an extended drop in diversity and increased turnover rates at the end of the Eocene and then a second abrupt drop in diversity in the mid-Oligocene. This suggests that the changes during the Late Eocene and Oligocene represent a stepwise process. The initial break at the end of the Eocene is the most severe,

but the fauna recovered somewhat through the Early Oligocene, only to decline again in the mid-Oligocene. This is in good agreement with the stepwise drop of the paleotemperature curve (Savin 1977) and the two-step drop in sea level (Vail et al. 1977). The mid-Oligocene drop in diversity may not have been as severe as the Terminal Eocene Event because the Early Oligocene faunas were already survivors of this first climatic crisis.

A number of explanations have been proposed for the stepwise changes in climates and faunas in the Late Eocene and Oligocene. Kennett (1977, 1981) and Murphy and Kennett (1985) have suggested that the initial development of the psychrosphere (cold bottom water) and significant sea ice occurred at the end of the Eocene as a result of opening of the shallow water passage between Antarctica and Australia. The opening of the passage between Greenland and Norway, which allows circulation between the Arctic and North Atlantic Oceans, is also believed to have occurred near the Eocene-Oligocene boundary (Talwani and Eldholm 1977; Berggren 1982; Miller and Fairbanks 1983). Thus, the severity and length of the Terminal Eocene Event may be due to the fact that it is the net effect of two slowly developing tectonic events that radically altered global oceanic and atmospheric circulation.

On the basis of recently studied cores from near Australia, Murphy and Kennett (1985) have shown that deepwater circulation over the South Tasman Rise between Tasmania and Antarctica commences during the mid-Oligocene event. The initiation of deepwater circulation caused a major decoupling and thermal divergence between equatorial and polar waters. This, in turn, stimulated ice cap formation and sea-level change. The major change in circulation also caused turnover in the oceanic carbon, as shown by the carbon isotope record. It appears that the mid-Oligocene event is as severe and profound as the Terminal Eocene Event. The completion of Circum-Antarctic circulation took place in the late Oligocene or early Miocene, when the Drake Passage opened between Antarctica and South America (Barker and Burrell 1977).

Recently, several hypotheses involving extraterrestrial causes for extinctions have attracted considerable attention. Fischer and Arthur (1977)

first postulated a 32-ma cycle between "polytaxic" and "oligotaxic" episodes in the world ocean. The mid-Oligocene event falls at one of the "oligotaxic" peaks, but the Terminal Eocene Event is not explained by their model. Alvarez et al. (1982), Asaro et al. (1982), and Ganapathy (1982) attributed Eocene-Oligocene extinctions to extraterrestrial impacts, indicated by iridium anomalies and microtektites. But there are many problems with the dating of these, as Berggren et al. (1985) have thoroughly documented. Kyte (1984) has shown that none of the Eocene-Oligocene iridium layers is significantly above the background noise level. If any microtektite dates can be believed, they seem to indicate an Early Oligocene age (about 34 ma, or about the age of the North American strewn field), which corresponds to no known extinction event on either land or sea. Recent evidence of multiple microtektite layers (Keller et al. 1983a, b) make it likely that there were frequent showers of extraterrestrial matter in the Late Eocene and Oligocene. Keller et al. (1983a, b) attribute the concentration of microtektites to dissolution at hiatuses. Even if the microtektite layers do represent discrete events, their distribution bears no resemblance to the pattern of faunal change seen on both land and sea.

In short, catastrophic hypotheses have little support in the Eocene-Oligocene fossil record, as detailed above. The Eocene-Oligocene transition in land mammals spanned at least 6-7 ma and seems to be related to the major faunal interchange between Europe, Asia, and North America at that time. The mid-Oligocene event was more abrupt (lasting less than 200,000 yr) but hardly catastrophic in its effect on the fauna. Most of the change is due to the extinction of groups that were dominant in the Eocene. These patterns are also seen in the marine microplankton (Keller 1983a, b) and strongly contradict the catastrophist models. If the geochemical and tektite evidence for extraterrestrial impacts eventually proves to be real, the biosphere took little notice.

Raup and Sepkoski (1984) have reported a cycle of extinctions of 26 ma. Several authors have attempted to explain these cycles by the sun's vertical oscillation in the galactic plane (Rampino and Stothers 1984; Schwartz and James 1984) or by an unseen companion star to

the sun initiating comet showers (Davis et al. 1984; Whitmire and Jackson 1984). As Hallam (1984) has shown, the relevance of these speculations depends greatly upon the accuracy of their dating, and Hallam documents some serious problems in this regard. Specifically, none of these models explains why there is both a protracted Late Eocene event (from about 37 to 42 ma) and a mid-Oligocene event (30-32.5 ma). In addition, Kitchell and Pena (1984) have shown that the apparent periodicity reported by Raup and Sepkoski (1984) can be simulated by a stochastic autoregression model, which casts doubt on some of these deterministic explanations.

Extraterrestrial hypotheses founder on an even more difficult problem than dating. They do not take into account the profound oceanographic and climatic changes that are well documented in the Late Eocene and Oligocene, which must have affected the biota. These changes include the formation of deep bottom water, the opening of deepwater passages due to continental separation, and major changes in sea level, the CCD, and in oceanic circulation. Clearly these changes are much more strongly affected by plate configuration and ice volume changes than they are by the influx of extraterrestrial matter. The faunal, floral, and climatic changes discussed above are also much more in accord with a model that takes into account the profound but protracted nature of oceanographic change. Much further work is needed to test these hypotheses, but for the present, any explanation of mid-Tertiary extinctions must explain not only biotic crises but also the profound oceanographic and climatic changes that occurred at this time.

Conclusion

A detailed study of Oligocene land mammal diversity in North America shows the following features:

1. A gradual Late Eocene drop in diversity resulting from extinction of archaic groups and immigration of new groups;

2. Faunal stability through the Oligocene, except for a mid-Oligocene (about 32 ma) wave of extinctions.

This two-step faunal change is seen in many other paleoclimatic, paleoceanographic, and faunal records. It seems to be related to the devel-

opment of the Circum-Antarctic Current and to the concomitant development of Antarctic glaciation.

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