

# EVOLUTION OF TERTIARY MAMMALS OF NORTH AMERICA

VOLUME 1:  
TERRESTRIAL CARNIVORES, UNGULATES,  
AND UNGULATELIKE MAMMALS

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## 2 Tertiary vegetation of North America as a context for mammalian evolution

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### INTRODUCTION

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This chapter is an attempt to summarize the Tertiary history of the vegetation of North America as a context for mammalian evolution. From the point of view of a mammalian paleontologist, and presumably from that of the other mammals they study, plants are important chiefly as sources of food and as partial creators of the habitats in which mammals live. Ideally, for any given time and place we would like to be able to describe the quantity and variety of food resources provided by plants and also the aspects of vegetational structure that correspond to mammalian habitat types. What were the mechanical and chemical properties of food resources such as leaves and fruits? How important were seasonal fluctuations in their availability? What was the height of the vegetation? How dense was it? How many species were in it? How many types of vegetation were in the regional mosaic? How big were the patches? At a larger spatial scale, to what degree was North American vegetation divided into discrete vegetation types and floral provinces? Answering most of these questions is difficult for most times and places in the Tertiary of North America because of the nature of the paleobotanical record.

The Tertiary paleobotanical record consists largely of dissociated leaves, fruits and seeds, and pollen. There is very limited direct evidence for the shape and habit of the plants that produced these parts, their potential as mammalian food, or their seasonal pattern of flowering, fruiting, and leafing. Much of what we know (or think we know) about Tertiary vegetation is based on analogy with living relatives. That is, species identified in the fossil record are assumed to be similar to their closest living relatives in size and growth habit, and to have preferred similar climate and vegetation types. This is why most descriptions of the past vegetation of North America are filled with the generic names of plants. To the extent possible I avoid floristic analogies in this summary, both because the paleozoological audience presumably will not find these analogies particularly meaningful and because there are persistent questions about the accuracy of this method of vegetational and climatic reconstruction (see later). However, much information is lost if such information is excluded entirely, especially when considering Neogene vegetation.

Where floristic data are the only type available for a particular time and region I have included common names for the nonbotanical reader.

The problems with floristic analogy have been detailed by numerous recent authors, most persuasively by Wolfe (1979). These are the main points: (1) many taxonomic identifications of fossils are incorrect, (2) evolution within lineages may have resulted in extinct and living species having different climatic tolerances, growth forms, etc., and (3) extant taxa do not necessarily occupy the full range of climatic or vegetational situations they can tolerate because of Pleistocene glaciation, anthropogenic disturbance, or other factors. Any or all of these factors could result in a misinterpretation, and points 1 and 2 apply with greater force to older fossil assemblages. The reliability of paleoclimatic inference based on floristic analogy is thought to be increased by considering many species (e.g., Hickey, 1977; Hickey et al., 1988) and by restricting analogies to taxa that are currently diverse, widespread, easily recognized by traits preserved in fossils, and relatively uniform in their climatic tolerances (Wing and Greenwood, 1993).

In response to the difficulties with floristic analogy, some workers have turned to physiognomic aspects of fossil assemblages to infer vegetation and climate. These characteristics include the percentage of species with entire-margined leaves (Wolfe, 1979), as well as the size of leaves and their apical, basal, and overall shape. In living floras these features are highly correlated with temperature and rainfall (Wing and Greenwood, 1993; Wolfe, 1993; Gregory, 1994), and thus with vegetation type. Although inferences about paleoclimate and vegetation based on foliar physiognomy are generally consistent with other lines of evidence, there are questions about the precision of the technique and its validity with older floras. The physiological bases for correlations between leaf form and climate are poorly understood, as are the possible confounding effects of soil type and phylogeny. An additional problem from the point of view of the paleomammalogist is that foliar physiognomic correlations only give information about climate. The habitats and resources available to mammals have to be inferred through an additional step which requires us to assume that ancient vegetation was

similar in its structure and trophic resources to extant vegetation growing in a similar climate. This assumption is tenuous for early Tertiary vegetation that contained many extinct lineages, and also for vegetation types without close living analogues, such as the mid-latitude, subtropical forests of the Eocene.

An additional source of information about Tertiary vegetation lies in the local distribution of fossil plants in the sediments. Unlike vertebrate remains, most plant parts are quickly degraded if they are not buried by sediment. Plant fossils, particularly the compressed leaves that make up the bulk of the Tertiary record in North America, are not easily transported long distances, and consequently much of the fossil record of plants is composed of samples that each represent a small area and a short interval of time (e.g., Gastaldo, 1988; Burnham, 1993a; Johnson, 1993). Although such samples represent a tiny proportion of the regional flora, they can preserve some aspects of the local mosaic of source vegetation. Samples of semiautochthonous to autochthonous plant assemblages should provide reasonably good estimates of the local diversity, species composition, and relative abundances of species in the source vegetation (Burnham, 1989a; Burnham, Wing, and Parker, 1992; Burnham, 1993b).

Closely spaced quarry sites in the same horizon can provide information on small-scale heterogeneity in the composition and richness of wet floodplain paleovegetation (e.g., Hickey, 1980; Wing, Alroy, and Hickey, 1995), and may provide the basis for inferences about the canopy size of some taxa (Burnham, 1993b), although detailed lateral studies of this type are still rare. However, the autochthonous nature of these assemblages precludes their revealing much about the vegetation of drier or better drained areas that were presumably the habitat of most mammals. The same constraints apply to plant fossils derived from peats or coals, except that the vegetation of such edaphically unusual habitats may be even less representative of the region as a whole. Ironically, the sedimentary environments that preserve the most information about the distribution and abundance of plant species on ancient floodplains may record a habitat that was little used by mammals and not similar to terra firma vegetation.

Plant fossil assemblages preserved in large lakes are another major component of the Tertiary record of North American vegetation. Lakes receive some plant debris from inflowing streams as well as from the lake margins, so they have the potential to represent several types of vegetation, although taphonomic studies show that few plant parts are transported long distances, even in areas with steep topography (Drake and Burrows, 1980; Spicer, 1981; Spicer and Wolfe, 1987). Lacustrine assemblages may yield a fairly complete list of the woody plant species occupying a local lake basin, but because all of the fossils have been transported to the bottom of the lake, they preserve little information on the spatial mosaic of the original vegetation. Inferences about the source vegetation for lacustrine assemblages come largely from physiognomic and floristic analyses.

Volcanic source material increases the potential for silicification, but a great many volcanoclastic assemblages are still derived from wet fluvial or lacustrine settings. Air fall tuffs can preserve plant material in situ, either in the form of forest floor litter or as standing trunk fields (e.g., Dorf, 1951, 1964; Burnham and Spicer, 1986). Ash falls may entomb upland forests or the litter layer underneath such

forests, but in the long term these deposits would likely be destroyed by erosion. Even in known volcanic areas (e.g., Yellowstone, Challis Field) most plant fossils appear to be derived from lowland vegetation, rather than from the slopes, and this is particularly true of autochthonous assemblages (Fritz, 1986; Yuretich, 1984). At least one major Tertiary assemblage of fruits and seeds, the middle Eocene Clarno flora of central Oregon, represents concentration and deposition of plant debris in a volcanic mudflow and may contain a substantial component of allochthonous remains (Manchester, 1994). Studies of recent volcanic eruptions have shown that in areas some distance from the source, ash falls may preserve an accurate record of pre-eruption forest vegetation in nonswamp settings (Burnham and Spicer, 1986). At least theoretically, plant assemblages preserved by ash falls could retain physiognomic, floristic, and positional information about nonswamp vegetation, and thus hold the greatest hope for making reliable, detailed inferences about the vegetational context of fossil mammals. To date no studies have demonstrated this potential, although the Miocene ash deposits of the Great Plains might provide a test case.

Fossil pollen provides another major source of data on the Tertiary vegetation of North America. The great strength of the palynological record is its wide distribution and high stratigraphic density. Palynological assemblages vary in the degree to which they represent regional as opposed to local vegetation. In general, pollen and spores are derived from a wider area than megaflores from the same depositional environment, but under forest canopies even pollen assemblages are dominated by grains derived from vegetation no more than hundreds to thousands of meters away (Farley, 1989, 1990). The greatest weakness of the palynological record is that pollen and spore taxa generally correspond to genera or families of plants, so changes in vegetational composition across space or through time are blurred. The interpretation of palynological assemblages relies almost entirely on floristic analogy at this high taxonomic level, there being no equivalent to leaf physiognomy for pollen. Nevertheless, pollen assemblages are important for reconstructing the history of North American vegetation because for many times and regions they are the only available source of information. Palynological data also are the main tool for resolving short-term or rapid changes in floras because megaflores seldom occur in sufficient stratigraphic density to resolve events that are less than tens or hundreds of thousands of years apart.

## TERTIARY VEGETATIONAL HISTORY OF NORTH AMERICA

The vegetation of North America has undergone dramatic changes during the Tertiary in response to physiographic modification of the continent, global climatic variation, and plant and animal evolution. The most notable changes were the shift from broad-leaved evergreen to broad-leaved semideciduous or deciduous vegetation during the middle Tertiary, the development of grasslands in the late Tertiary, and the increasing importance of evergreen conifer forests, especially in northern and montane regions. Global climatic cooling and widening of the North Atlantic during the Tertiary also had a profound effect on floral composition by

reducing interchange across Beringia and the North Atlantic and splitting the early Tertiary Boreotropical Flora into fairly distinct North American and Eurasian provinces (Wolfe, 1975; Tiffney, 1985a, 1985b).

No part of the continent escaped substantial modification of its vegetational cover during the Tertiary, but the southeastern United States, parts of the Pacific Coast, and some upland areas of Mexico have been cited as areas with climates and floras somewhat similar to those that were widespread in the earlier Tertiary (MacGinitie, 1969). Other areas, notably the Rocky Mountains and northern midcontinent, have been subject to the greatest climatic and/or physiographic change, and have also experienced the greatest vegetational change (e.g., Leopold and Denton, 1987; Leopold, Liu, and Clay-Poole, 1992). Thus the history of vegetational change in North America is in fact a collection of semi-independent, although linked, histories of separate areas.

Our ability to reconstruct regional floras and vegetation is in direct proportion to the number, geographic spread, and environmental range of well-dated paleobotanical localities from a given time interval, and therefore poorly sampled intervals may falsely appear to be times during which provincial differences were reduced. Because of the importance of semi-independent changes in different regions, I have divided the discussion of each Tertiary epoch into sections treating five regions: the East Coast, the Mississippi Embayment and Gulf Coast, the Great Plains and eastern Rocky Mountains, the western Rocky Mountains and Pacific Coast, and the Arctic region including Alaska. The quality and quantity of fossil assemblages vary greatly among these regions.

The East Coast of North America has a very poor Tertiary megafossil record, although a number of palynofloras have been described. The Mississippi Embayment and Gulf Coast hold many Paleocene through Oligocene megafossil assemblages preserved in clays and lignites, but these local deposits have proved difficult to correlate with one another, and the Neogene is poorly known. Paleogene palynofloras of this area have also received considerable study. Like the Mississippi Embayment, the Great Plains and eastern Rockies have produced many Paleocene and Eocene megafossil assemblages. These derive from a fairly wide array of depositional settings, and generally can be correlated through litho- or biostratigraphy. In the later Eocene and Oligocene volcanic settings were important in preserving plant megafossils, but the region has far fewer Neogene assemblages. The most complete set of Tertiary megafloras in North America comes from the Pacific Northwest area of the United States, where deposition in coastal and volcanic settings has preserved numerous floras of every Tertiary epoch except the Paleocene. Paleobotanical assemblages in Nevada and California also are sparse in the Paleocene, but more common in the Eocene through Pliocene. Floras from Arctic North America also span the whole Tertiary, but with the bulk of the localities being from southern Alaska.

The floras on which this summary is based are listed in the chapter appendix. The paleogeographic positions of the floras, and the inferred vegetational boundaries, are presented in reconstructions for each epoch (Figures 2.1–2.4). These paleovegetational maps are highly generalized, each being based on floras spanning millions of years, and with great variability in the quality and number

of data points between regions. Nevertheless, some visual representation of vegetational change through time is desirable, and I hope the maps will serve as a starting point for further refinements. The rotation of present coordinates to Tertiary positions was accomplished with PGIS-Mac, which was also the source for paleogeography.

## PALEOCENE (SEE FIG. 2.1)

### East Coast

The only published Paleocene megafossil reports from the mid-Atlantic Coast are of pinaceous seed cones from the nearshore marine Aquia Formation of Virginia (Miller, 1977). Palynofloras derived from core and outcrop samples in Virginia (Frederiksen, 1979a; Gibson et al., 1980) and South Carolina (Frederiksen, 1980a) have been studied, although generally from a biostratigraphic rather than floristic or paleoecological perspective. Lithologies and microfossils of most samples suggest open shelf to nearshore marine deposition. Broadly speaking, these palynofloras are similar in composition to those of the Gulf Coast.

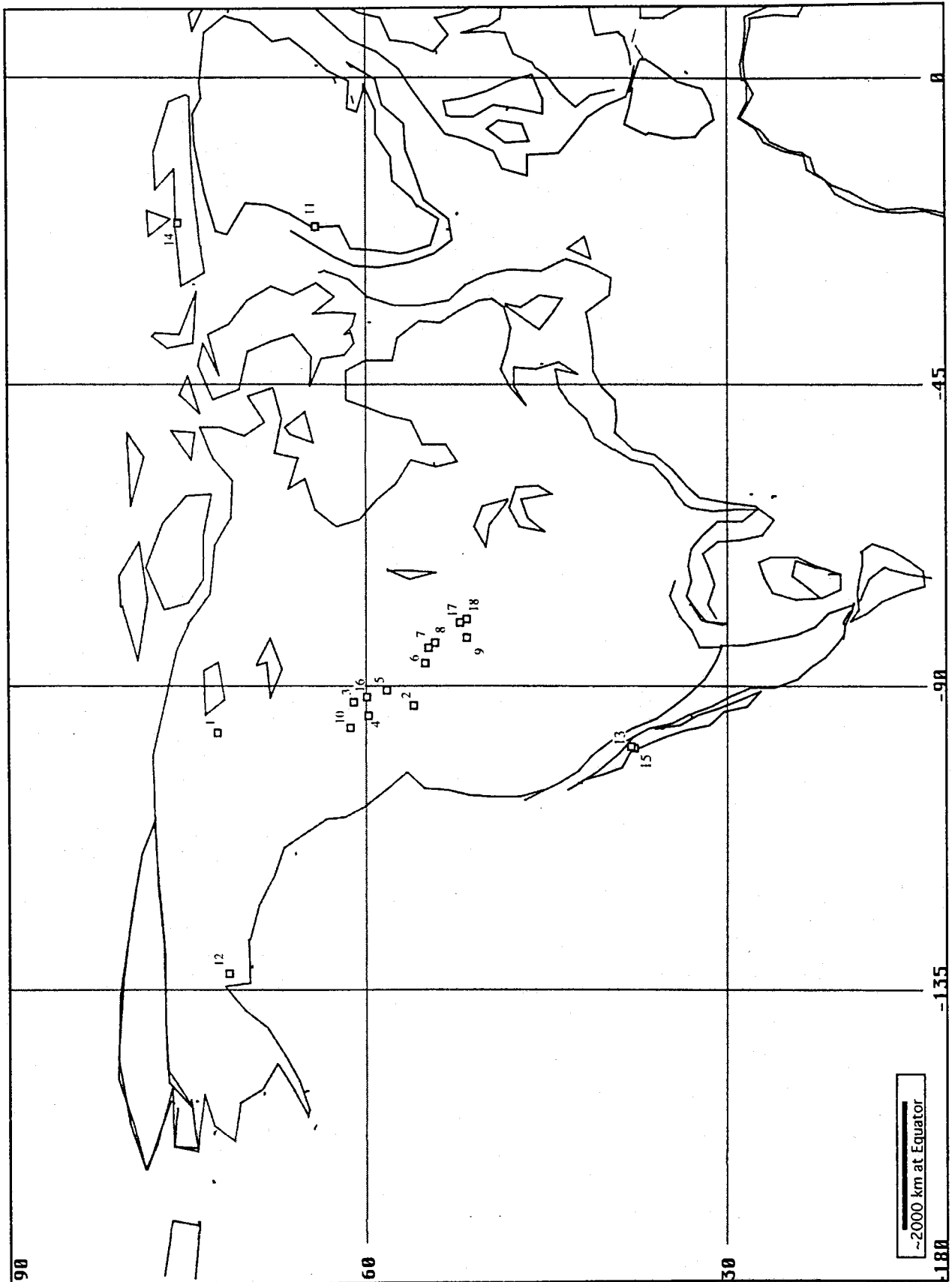
### Mississippi Embayment and Gulf Coast

Most of the Paleocene megafossil assemblages of the Mississippi Embayment and Gulf Coast area are from coastal or fluvio-deltaic environments including lagoons, oxbow fills, and channel sands. These rocks are part of the Midway and Wilcox Groups (e.g., Berry, 1916a), which have more recently been divided into a series of formations, including the Naheola, Nanafalia, Tuscahoma, Naborton, Porters Creek Clay, Rockdale, Seguin, and Clayton Formations (Fairchild and Elsik, 1969; Tschudy, 1973). In many areas the fossil plants are found in clay lenses associated with lignite deposits that presumably formed in lowland swamp settings. Several assemblages from near Naborton, Louisiana, are probably late Paleocene (Tschudy, 1973, 1975). Wolfe (1978) interpreted these as being derived from tropical forest vegetation based on leaf size and percentage of entire-margined forms. However, the assemblages are small and poorly preserved, leaving some question about this vegetational reconstruction.

There are a number of reliably dated Paleocene palynofloras from the Mississippi Embayment, most of which appear to be from the middle or latter part of the epoch (e.g., Elsik, 1968a, 1968b; Srivastava, 1972; Christopher et al., 1980). Pollen types similar to that of living chestnuts are common in many of these palynofloras, and diversity is generally lower than in subsequent Eocene palynofloras (Frederiksen, 1988, 1994). Diversity of Gulf Coast palynofloras increased slowly during the first half of the Paleocene, then decreased sharply at the very end of the epoch (Frederiksen, 1994).

### Great Plains and eastern Rocky Mountains

The Fort Union Formation has produced megafossil and palynofloral assemblages from hundreds of localities distributed across North Dakota, Montana, and Wyoming (e.g., Dorf, 1940; Brown, 1962; Tidwell, Ash, and Parker, 1981; Hickey, 1977, 1980; Pocknall, 1987; McClammer and Crabtree, 1989; Crane, Manchester, and Dilcher, 1990; Johnson and Hickey, 1990; Johnson, 1992). Paleocene fossil localities in this region span the whole epoch, and



**Figure 2.1.** Paleocene vegetation of North America. Numbers indicate the positions of Paleocene floras. Name, age, present coordinates, literature citation, and inferred paleovegetation are given for each number in the chapter appendix. See text for details.

also provide the most detailed record of change in plant life across the K/T boundary and during the earliest Paleocene. Paleocene formations with broadly similar lithologies have also produced numerous assemblages in Alberta and Saskatchewan (Berry, 1930, 1935; Bell, 1965; Christophel, 1976; McIver and Basinger, 1993), and in Colorado and New Mexico (Knowlton, 1922, 1930; Brown, 1962; Ash and Tidwell, 1976; Tidwell, Thayne, and Roth, 1976; Wolfe and Upchurch, 1987). During the Paleocene much of the interior area east of the Rockies was occupied by wide basinal or marginal marine lowlands; topography was low, drainage was poor, and swamps were widespread (Flores, 1981, 1983). The relatively homogeneous features of the preserved landscape may account in part for the homogeneity and low diversity of the floras.

In the northern Rockies floral assemblages derived from carbonaceous shales or clastic rocks associated with coals generally are dominated by the deciduous bald-cypress family conifers (Taxodiaceae) *Glyptostrobus* and *Metasequoia*. Swamp vegetation of this type evidently existed almost to the shores of the Arctic Ocean (Sweet and Braman, 1992). Dicotyledons frequently were important though subdominant elements in such settings, and presumably formed an understory element in the forest. As far north as the U.S./Canadian border some of these dicot tree/shrubs, for instance members of the tea and laurel families, were probably evergreen, but deciduous dicots in the birch and witch hazel families were more common. The herbaceous layer was composed largely of ferns, large horsetails, and gingerlike monocots. Vegetation of alluvial ridges had more species of dicotyledonous trees and shrubs than did that of the backswamps, many belonging to deciduous temperate zone families of today such as the walnuts, birches, elms, sycamores, witch hazels, oaks, dogwoods, and katsura tree. In spite of some familial-level similarity between Paleocene and Recent floras it should be emphasized that most Paleocene species do not belong to extant genera, and many may represent extinct families. Palms were rare through most of the Paleocene in areas north of southern Wyoming and were absent north of southern Montana (Brown, 1962). Megafloral assemblages from southern Canada are generally similar to those from the northern United States, showing dominance by conifers and a low diversity of deciduous dicotyledons (Christophel, 1976; McIver and Basinger, 1993).

Recent work has pointed out the dissimilarity between floras of the northern and southern Rockies in the Paleocene. Swamp assemblages from northern New Mexico and southern Colorado generally lacked taxodiaceous conifers; alluvial ridge vegetation was more diverse than in the north and possessed more species with entire-margined leaves belonging to living families with subtropical to tropical distributions such as laurels (Wolfe and Upchurch, 1986). Palynofloras derived from coals in the Raton Basin are 75–80 percent angiosperm pollen, including palms and diverse dicots, with conifers only accounting for 1–2 percent of pollen grains (Fleming and Pierce, 1994). Fossil wood suggests dicots were important elements in the vegetation of the Big Bend region in Texas during the Paleocene (Wheeler, 1991).

### Western Rocky Mountains and Pacific Coast

Two major floras of the Pacific Northwest that were once thought to be Paleocene (Swauk and Chuckanut) more recently have been assigned to the Eocene (Newman, 1981; Johnson, 1984), leaving little or no information about Paleocene vegetation in this area. In southern California, a latest Paleocene palynoflora and megaflora have been recovered from the Silverado Formation (Gaponoff, 1984; Wing, unpublished data). The Paleocene latitude of this area may have been as far south as southern Baja California. The stream-side elements of the flora are similar at a high taxonomic level to roughly coeval floras from the Fort Union Formation (members of the birch and witch hazel families predominate); taxodiaceous conifers are rare in the palynoflora and absent from the megaflora. The palynoflora is similar in composition to late Paleocene floras from the Gulf Coast area, containing a variety of forms belonging to higher taxa that currently have temperate to tropical distributions (Gaponoff, 1984). The Elsinore flora, also from the Silverado Formation, but on the east side of the Santa Ana Mountains, has been interpreted to represent a fairly moist savanna forest growing under seasonal precipitation on a well-watered floodplain (Axelrod, 1979). This conclusion is based on the presence of ferns, palms, notophyllous to mesophyllous dicot leaves, and clay minerals deemed to be the product of weathering under a seasonally dry, warm climate.

### The Arctic and Alaska

Late Paleocene megafloras have been described from the Chickaloon and Tolstoi formations of southern Alaska by Wolfe (1966, 1977). The leaf physiognomy of these assemblages is similar to that seen in the vegetation of some upland subtropical areas and northern Florida, and probably reflects a mixed evergreen and deciduous broad-leaved forest. Two species of palm were recovered (Wolfe, 1972). Based on the dominance of non-entire-margined leaves, mid-to late Paleocene floras from Greenland (Koch, 1963) may represent somewhat cooler climate and more deciduous forests than those of southern Alaska, although this may reflect cooler global climate during the mid-Paleocene rather than a geographic difference between coeval floras.

Megafloral collections from the North Slope of Alaska (Spicer, Wolfe, and Nichols, 1987) and Ellesmere Island (Hickey et al., 1983) demonstrate that forests grew well within the Arctic Circle in the late Paleocene. The species present were entirely deciduous, and the diversity of the assemblages is low. These have been termed Polar Broad-leaved Deciduous forests by Wolfe (1985). Palynological and geochemical analysis of the extensive late Paleocene coals in the Stenkul Fiord area of Ellesmere Island have demonstrated that the peat swamp vegetation was dominated by taxodiaceous conifers (McIntyre et al., 1994), particularly in the latest Paleocene when temperatures were rising in middle and high latitudes.

### Summary

There is now abundant evidence that bolide impact(s) at the end of the Cretaceous had a major effect on terrestrial vegetation in North

America. Palynofloras derived from the first few centimeters above the Iridium-abundance horizon at sites in the eastern Rockies/Great Plains region tend to show unusual domination by ferns, although there is local and regional variation in the pattern (Tschudy et al., 1984; Nichols et al., 1986; Lerbekmo, Sweet, and St. Louis, 1987; Johnson et al., 1989; Sweet and Braman, 1992). Fern abundance is consistent with vegetational devastation followed by regrowth of early successional species because ferns are frequently early colonizers in subtropical and tropical environments. In megafloras as in palynofloras, there are local differences in the pattern of extinction and recovery. Fern abundance peaks and a pattern described as "quasisuccession" have been described based on megafloral and cuticular remains recovered from several sections in the Raton Basin of southern Colorado and northern New Mexico (Wolfe and Upchurch, 1986, 1987). Quasisuccession refers to a pattern of gradually increasing abundance and diversity of flowering plants during the first several hundred thousand years of the Paleocene.

Johnson (1992) and Johnson and Hickey (1990) have demonstrated 70 percent extinction in leaf megafloras across the K/T boundary in western North Dakota; these high levels of extinction are based on samples that are tightly controlled in terms of stratigraphy, depositional environment, and sample size. However, similarly detailed studies have not been completed in other areas, making it difficult to distinguish between local and regional extinction. Diversity and angiosperm dominance increase much more quickly in North Dakota than in the Raton Basin (within a few meters of the K/T boundary), but it is not clear whether this reflects real differences in the vegetational histories of the two regions or differences in sampling regimes and depositional rates.

The long-term effects of the K/T bolide impact(s) on the terrestrial vegetation of North America also remain highly controversial. Wolfe (1987a) suggested that vegetation of the northern Rockies was "anomalously deciduous" throughout the Paleocene – that is, the preferential extinction of evergreen lineages at the K/T boundary left a vegetation that had more deciduous species than would be expected for vegetation growing under climatic conditions which are thought to have been warm temperate to subtropical. The traditional explanation for the relatively low diversity of many Paleocene assemblages, and the dominance of inferred deciduous species, has been that climates in the interior of North America were seasonally cool (e.g., Hickey, 1980). Studies in both the Gulf Coastal Plain and the northern Rockies demonstrate that floral diversity increased very slowly through the first half of the Paleocene, a period of roughly 5 million years (Frederiksen, 1994; Wing, Alroy, and Hickey, 1995). Oxygen isotope data from DSDP cores indicate that Paleocene oceans were cool compared to those of the Cretaceous and Eocene (e.g., Miller, Fairbanks, and Mountain, 1987), and although continental indicators of paleoclimate agree with this trend, faunas and floras from the northern United States do contain some frost-sensitive forms through most of the Paleocene. At present it is difficult to determine if the low diversity of Paleocene vegetation

in North America represents a long "echo" of K/T boundary disturbance, a period of cool climate, or a combination of the two effects.

Whatever the explanation, Paleocene vegetation of the north temperate latitudes had low diversity compared with the Late Cretaceous or early Eocene, and many of the genera were widespread and abundant in assemblages from Alaska to the northern Rockies to Greenland and Europe. The low diversity, floristic homogeneity, and high percentage of non-entire-margined species in the early and mid-Paleocene (Puercan–early Tiffanian) is consistent with broad-leaved deciduous vegetation with only a small admixture of evergreen broad-leaved trees. Swamp vegetation of the time was dominated by taxodiaceous conifers in northern regions, but by palms and other angiosperms in the southern part of North America.

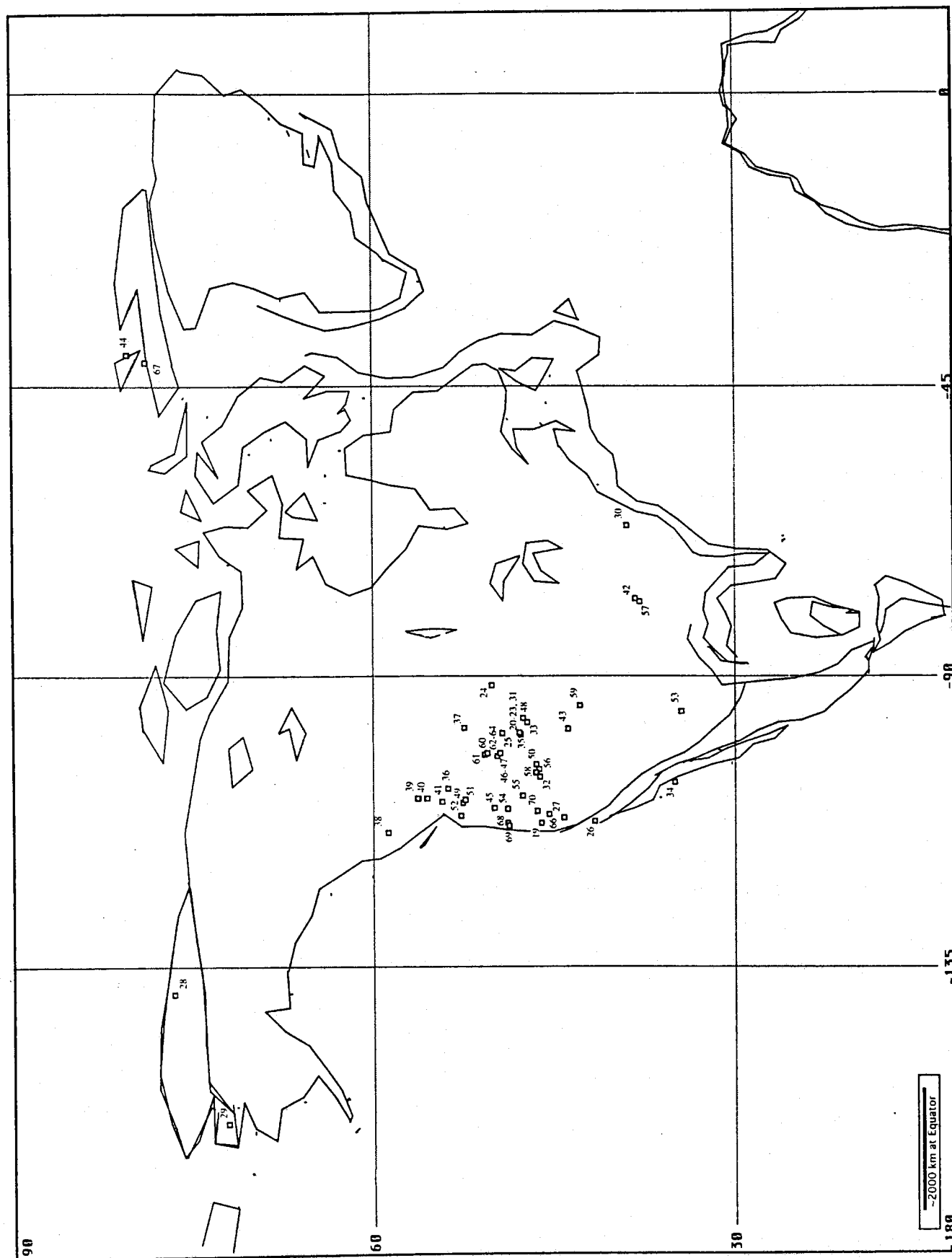
Global and North American climate warmed near the end of the Paleocene (Wolfe, 1978; Miller, Fairbanks, and Mountain, 1987; Wing, Bown, and Obradovich, 1991), moving vegetational zones northward and thus increasing the diversity and probably the structural complexity of forests over much of North America during the early Eocene. Recent studies have shown that a pronounced but short-lived period (100,000 years?) of extreme warming took place at the very end of the Paleocene, coincident with the earliest Wasatchian faunas (Kennett and Stott, 1991; Koch, Zachos, and Gingerich, 1992). This Terminal Paleocene Event is associated with a brief decrease in floral diversity in both the Gulf Coastal Plain and the northern Rockies (Frederiksen, 1994; Wing, Alroy, and Hickey, 1995), which may have been the result of midlatitude extinctions of temperate deciduous lineages (Wing, 1996). In general, however, the increase in temperature and decrease in temperature seasonality that took place in the later Paleocene should have resulted in less annual fluctuation in leaf and fruit production, and hence a less seasonal supply of resources for small mammals. In some areas, decreasing temperature seasonality might have been offset by increasing seasonality in precipitation (Wing and Bown, 1985). Global warming in the late Paleocene and early Eocene also permitted increased exchange of species across the North Atlantic, and perhaps Beringia as well (Tiffney, 1985a, 1985b; Frederiksen, 1994).

## EOCENE (SEE FIG. 2.2)

### East Coast

Few Eocene plant megafossils have been recovered from the East Coast. Fruits similar to the mangrove palm *Nypa*, and of a probable mangrove belonging to the poinsettia family, have been described from the Nanjemoy Formation, a set of early Eocene nearshore marine sediments in Virginia (Mazer and Tiffney, 1982). These fossils closely resemble roughly coeval species from Egypt and Britain, demonstrating that some plant genera were distributed across the North Atlantic (Tiffney, 1985a, 1985b). Eocene palynofloras have been described from Virginia and South Carolina, and also demonstrate the similarity of floras across the North Atlantic (Frederiksen, 1979a, 1980a).

**Figure 2.2.** Eocene vegetation of North America. Numbers indicate the positions of Eocene floras. Name, age, present coordinates, literature citation, and inferred paleovegetation are given for each number in the chapter appendix. See text for details.





### Mississippi Embayment and Gulf Coast

Some of the most diverse and best preserved Eocene megafloras in North America come from the Wilcox, Claiborne, and Jackson Groups. The sediments in these formations were mostly deposited in fluvio-deltaic or coastal plain settings such as oxbow fills, lagoons and coastal marshes, and swamps (Frederiksen, 1981). Diverse assemblages with many notophyllous entire-margined species indicate somewhat dry, warm-temperate to subtropical vegetation (Dilcher, 1973) or dry tropical vegetation (Wolfe, 1978, 1985), depending on interpretation. There were also substantial climate-induced fluctuations in vegetational physiognomy and diversity through the Eocene (Wolfe and Poore, 1982; Frederiksen, 1980b, 1980c, 1988).

Generally speaking, taxodiaceous conifers are not important in Mississippi Embayment palynofloras or megafloras, even in swampy or lignitic facies (Frederiksen, 1981). Some conifers that are presently typical of temperate seasonal climates are known in palynofloras (e.g., hemlock, fir) and megafloras (podocarps) (Gray, 1960; Dilcher, 1969). These have been construed by some to be remains transported from Appalachian or Ozark uplands with a cooler climate (Frederiksen, 1985), but recent studies of pollen and leaf transport (e.g., Spicer and Wolfe, 1987; Farley, 1989) imply that such long-distance transport is unlikely to be an important source of fossils, particularly megafossils. If these "temperate" conifers were a part of local vegetation on Eocene floodplains in the Mississippi Embayment, there are two probable explanations: These genera evolved greater cold tolerance during the Tertiary (i.e., they did not prefer cool climates in the Eocene), and/or climates in the area were equable enough to permit the co-occurrence of taxa requiring frost-free conditions with those preferring cooler temperatures.

The physiognomy of the dicot leaf assemblages, the presence of palms, and the overall floristic composition place fairly high limits on winter low temperatures, and strong or prolonged winter freezing is very unlikely (Wing and Greenwood, 1993). A middle Eocene flora from eastern Texas that occurs in the same sediments with Bridgerian mammals documents the presence of a mangrove flora, including the highly frost-intolerant mangrove palm, *Nypa*, that is now restricted to southeast Asia (Westgate and Gee, 1990).

Although megafloras from the Eocene of the Mississippi Embayment are typically dominated by dicot leaves probably derived from trees, it is noteworthy that these deposits have also produced the oldest grass megafossils. Tens of specimens from the early Eocene Buchanan Clay Pit in western Tennessee represent a morphologically advanced grass, supporting the hypothesis, based on dispersed pollen records, that the grass family originated no later than the Maastrichtian (Crepet and Feldman, 1991).

Palynofloras from the Mississippi Embayment have also been studied extensively from both biostratigraphic and paleoecological perspectives (Frederiksen, 1988, and references therein). Generally these palynofloral analyses have supported reconstruction of the vegetation as seasonally dry and subtropical or paratropical rather than full tropical. Palynofloral diversity increased very rapidly during the early Eocene, surpassing the levels achieved during the Paleocene (Frederiksen, 1994). Major shifts in palynofloral composition occurred during the middle Eocene, when mesic

Paleocene "holdovers" became extinct and xerophytes, shrubs, herbs, and grasses became more diverse and abundant along with an overall decline in diversity. These changes in composition have been interpreted as the result of a decrease in rainfall or an increase in the seasonality of rainfall, and have been compared in their severity to the floral changes associated with the earliest Oligocene temperature decline (Frederiksen, 1988).

### Great Plains and eastern Rocky Mountains

The Eocene vegetational history of the Rocky Mountain area has been the subject of several reviews that are more detailed than the one given here (Leopold and MacGinitie, 1972; Axelrod and Raven, 1985; Wing, 1987). Eocene megafloral assemblages from the region have been recovered from a wide variety of depositional settings including fluvial swamps, alluvial ridges, small and large lakes, and ash falls. Palynofloras are known from all of these environments, as well as from coals (e.g., Pocknall, 1987; Farley, 1989, 1990). Generally, assemblages from fluvial settings predominate in rocks from the early Eocene, whereas volcanic and lacustrine assemblages are better known from later in the Eocene, particularly in the volcanic areas of western Wyoming and Idaho (e.g., Thunder Mountain and Salmon floras of Idaho).

Broad-leaved evergreen vegetation with some admixture of deciduous species was the dominant forest type over the entire region during the Wasatchian and Bridgerian except in areas with cool montane or seasonally dry to arid climates. Although palms and other subtropical to tropical plant groups were common in many places, the diversity and physiognomy of most assemblages from the northern Rockies is not consistent with full tropical vegetation. During the earliest Eocene, floodplain swamps were still dominated by deciduous taxodiaceous conifers, but conifers appear to have been replaced by dicots and palms in most of the region during the later early and middle Eocene (e.g., Nichols, 1987).

Throughout the Eocene deciduous broad-leaved species belonging to modern temperate groups (e.g., sycamores, poplars, birches) were locally important in some fluvial depositional environments, especially in sediments deposited in or near channels. In the intermontane basins of the northern Rockies, the continued importance of deciduous dicots during the thermal maximum of the Tertiary probably reflects seasonal dryness induced by orogeny and volcanism to the west, as well as seasonal fluctuation in light and temperature. This seasonal aridity began as early as the Clarkforkian in some areas (Wing and Bown, 1985), and is well documented by the late early and middle Eocene floras of the Green River Formation as well as in floras from other parts of Wyoming (MacGinitie, 1969; Leopold and MacGinitie, 1972; Wing, 1987). MacGinitie (1969) referred to this subtropical dry vegetation as savanna woodland, although he specified that grasses did not play an important role. Presumably such forests were somewhat open, but the composition of the herbaceous vegetation is unknown. Ferns may have been an important element, although pollen attributable to herbaceous dicots and grasses also occurs in rocks of this age in North America (Frederiksen, 1981). Woody xerophytes may also have been significant elements in low-stature vegetation of drier areas (Leopold, Liu, and Clay-Poole, 1992).

Early and middle Eocene forests of the volcanic uplands in westernmost Wyoming, Idaho, and Nevada were apparently quite distinct from those in the intermontane basins to the east (Axelrod, 1966, 1968). The Yellowstone assemblage, for instance, contains a diverse mixture of evergreen and deciduous broad-leaved taxa along with pinaceous and taxodiaceous conifers. Leaf size and margin features, and the presence of fossil wood with subdued or absent growth rings, are consistent with less seasonal precipitation than prevailed in the Bighorn Basin just to the east (Wheeler, Scott, and Barghoorn, 1977, 1978; Wing, 1987), and the same can be said in comparing the Wind River Flora in the southern Absarokas with samples from the eastern Wind River Basin. Some sort of vegetational boundary probably extended roughly north-south through western Montana, western Wyoming, and perhaps into Utah, separating wetter montane forests from the developing dry deciduous forest of the continental interior. However, late Eocene palynofloras from British Columbia are similar to roughly coeval Jackson Group palynofloras from the Mississippi Embayment (36.5 to 37.7 Ma), and are said to indicate a humid subtropical climate (Rouse and Mathews, 1987), implying that some floristic similarity was maintained between the two regions, at least at the high taxonomic level resolved in palynofloras.

The presence of sharp floristic and probably vegetational boundaries in the Rocky Mountain region was not recognized clearly before the 1980s. Some of the Eocene floral "phases" described by Leopold and MacGinitie (1972) may relate more to paleogeography than they do to temporal change. For example, sites documenting the earlier phases of more mesic vegetation were located in western areas that probably had a higher paleoelevation and were under the climatic influence of the Pacific Ocean (Wing, 1987). Although Eocene drying was regional or subcontinental in scope, local variation in severity and time of onset make it difficult to define phases of floral development that are applicable across the whole Rocky Mountain region.

Late Eocene Chadronian megaflores are known from several parts of the Rocky Mountains, including southwestern Montana (Becker, 1969), northern Utah (Axelrod, 1966), central Wyoming (Leopold and MacGinitie, 1972; Wing, 1987), southern Colorado (MacGinitie, 1953; Manchester, 1994; Nichols, 1987), and New Mexico (Meyer, 1992). Most of the Chadronian floras indicate some variety of subhumid or montane vegetation, probably depending as much on elevation as on age. The Montana collections represent mixed coniferous and broad-leaved deciduous forest with some possibly subhumid taxa like *Mahonia* (Oregon grape holly) and juniper (Becker, 1969). The floras from Utah and New Mexico reflect varieties of conifer-dominated montane forest with a low diversity of mostly deciduous dicots (Axelrod, 1966; Meyer, 1986). The Chadronian megaflores from central Wyoming is derived from fissure-fill deposits in the White River Group, so that comparisons with other floras are made difficult by differences in taphonomic setting. However, leaves from the fissure-fill are all very small, and may represent subhumid vegetation. Palynological assemblages from the same region are relatively low in diversity and commonly contain pollen of pine and deciduous broad-leaved trees and shrubs, sometimes including woody xerophytes like mormon tea (*Ephedra*

(Leopold and MacGinitie, 1972; Leopold, Liu, and Clay-Poole, 1992). Unlike modern dry-climate vegetation in North America, pollen of grasses and herbs is very rare in Chadronian palynological assemblages (Leopold, Liu, and Clay-Poole, 1992). Seasonal aridity during the Chadronian is further supported by fossil wood from an area adjacent to the Chadronia Pocket vertebrate locality in western Nebraska, which shows strongly seasonal growth patterns. Several of the taxa present have living relatives in seasonally dry climates (Wheeler and Landon, 1992). Paleosols in the Big Badlands of South Dakota also offer strong support of declining precipitation beginning in the Chadronian (500–900 mm precipitation/year) and continuing through the Oligocene to less than 500 mm/year by the Arikareean (Retallack, 1992).

The best known of the Chadronian floras is Florissant, an assemblage derived from volcanic lake sediments that has been collected for over a century. MacGinitie (1953) inferred Florissant megafossils to represent two types of vegetation: a broad-leaved deciduous forest confined to stream course areas and a scrub forest/grass vegetation that occupied steeper topography and interfluvies. Lakeside vegetation included large taxodiaceous trees of the genus *Sequoia*. Recent reexamination of Florissant megafossils has resulted in a substantial revision of the botanical affinities of the assemblage and reduced the apparent relationship between Florissant and living floras of northern Mexico and Central America (Manchester, 1994). Florissant fossils include fragments of what may be *Stipa* (MacGinitie, 1953; Thomasson, 1986), a tropical to temperate grass commonly occurring in moderately dry climates.

Paleotemperature estimates for Florissant have also served as a starting point for inferring the late Eocene elevation of the Rockies in southern Colorado. Paleoelevation is determined from fossil floras by comparing mean annual temperatures estimated from coastal (presumably sea-level) and inland floras. An elevation for the inland flora is calculated by dividing the difference in temperature estimates by the lapse rate of temperature with elevation. Paleoelevational estimates for Florissant have varied from 1 to 4 km depending on the lapse rate and temperature estimates used in the calculation, but more recent work has favored elevations in the 2–3 km range, suggesting that by the Chadronian, southern Colorado had already attained an elevation close to the modern level (MacGinitie, 1953; Gregory and Chase, 1992; Meyer, 1992; Gregory, 1994; Wolfe, 1994a).

Several small megaflores collections from New Mexico (Red Rock Ranch, Hermosa, Hillsboro) appear to be latest Eocene in age and may represent dry subalpine vegetation (Axelrod and Bailey, 1976; Meyer, 1986). Small sample size and low diversity make vegetational interpretation of the southernmost late Eocene floras of the region difficult.

#### Western Rocky Mountains and Pacific Coast

Megaflores assemblages from the Pacific Coast area are derived from deltaic, fluvio-deltaic, and lacustrine environments (Burnham, 1989b, 1994). Coals are common in some units, such as the Puget Group. Inland floras are most often derived from volcanic lacustrine beds. Important Eocene megafossil assemblages are known from British Columbia (e.g., Princeton, Joseph Creek), Washington State (Puget Group, Swauk, Chuckanut), Oregon (Clarno localities,

Alvord Creek), and California (Montgomery Creek, Susanville, Chalk Bluffs); some of these were summarized by Wolfe (1987b).

Many Pacific Coast Eocene floras have leaf physiognomic characteristics and levels of diversity similar to those of living wet tropical forests. In general, assemblages are dominated by entire-margined, presumably evergreen dicots. Leaf sizes are notophyllous, mesophyllous, and in some place even megaphyllous. Palms are a common element in many assemblages. Diversity can be remarkably high (>40 species from a single small floodplain site in the Puget Group [Burnham, 1994]). Several hundred miles inland occurs one of the most diverse North American Tertiary fossil assemblages – the silicified fruits, seeds, and leaves from the Clarno Nut Beds (Manchester, 1981, 1994). This Uintan (43–44 Ma) flora contains over 170 species, and the living relatives of Clarno taxa belong to families with everything from temperate to tropical distributions, for example, the banana family, chocolate family, sycamore family, and grape family (Manchester, 1994). Clarno shares a number of genera with the Eocene London Clay flora of England (Tiffney, 1985a, 1985b).

In some inland areas, altitudinal effects are more noticeable. Floras from south-central British Columbia, eastern Washington, Idaho, and Nevada show cooler climate vegetation dominated by pinaceous and cupressaceous conifers, although evergreen and deciduous dicots were diverse at most well-sampled sites except those inferred to represent the highest paleoaltitudes (Axelrod, 1966, 1968; Wolfe, 1987b; Wolfe and Wehr, 1987). Attempts to reconstruct the late Eocene paleoaltitude of northeastern Nevada based on megaflores have yielded estimates with a large degree of error, but centered around elevations close to those seen today (Povey, Spicer, and England, 1994). High late Eocene paleoelevations in Nevada (and presumably Idaho) are part of the orographic explanation of the dry or seasonally dry climates inferred from Chadronian floras and paleosols in the eastern Rockies and western Great Plains.

In northern California, megafossil assemblages also indicate diverse broad-leaved evergreen vegetation that was probably analogous in many ways to some extant tropical forests. The early Eocene Chalk Bluffs flora has a number of species with relatives in seasonally dry parts of Mexico and Central America (MacGinitie, 1941), which could imply somewhat drier conditions than prevailed in coastal Washington. However, the middle to late Eocene Susanville assemblage in northern California is notable for extremely large leaves, many of them with drip tips, suggesting a wet climate. The early Eocene Montgomery Creek assemblage, also in northern California, demonstrates that some near-channel fluvial vegetation in this region was low in diversity and dominated by deciduous members of the birch family.

Recent work on middle Eocene (Lutetian or early Bartonian equivalent) palynofloras from southern California (e.g., Ardath Shale, Mission Valley Formation) has revealed many taxa related to the plant families that are today most speciose in seasonally dry climates, but fern spores and conifer pollen are also diverse (Frederiksen et al., 1983; Frederiksen, 1989). An early middle Eocene megaflores from the Torrey Formation north of San Diego has some taxa in common with coeval floras in northern California and the Rocky Mountains, and although the composition of the flora

is consistent with somewhat seasonal precipitation, there is nothing in the megaflores to indicate real aridity at this time (Myers, 1991). This megaflores has been interpreted as paratropical broad-leaved evergreen forest (Myers, 1991).

Southern California evidently was floristically distinct from the Gulf Coast region during the middle Eocene (Frederiksen, 1982, 1989). Eocene paleoclimatic reconstructions for southern California have ranged from wet to dry paratropical to tropical (Novacek and Lillegraven, 1979; Peterson and Abbott, 1979; Frederiksen, 1991). Frederiksen (1991) reports a decline in the diversity of southern California palynofloras that began slightly later than the middle Eocene diversity decline in the Gulf Coast region, but attributes it to the same cause – climatic drying. A palynoflores from northern Baja California that co-occurs with the equid *Hyracotherium* may provide the oldest record of pollen of the sunflower and aster family, along with a variety of wind-pollinated tree types of temperate deciduous groups (Cross and Martinez-Hernandez, 1980).

Eocene Pacific Coast megaflores, particularly those of Washington and Oregon, present the most wet-tropical appearance of any known Eocene North American assemblages. This is probably a result of high rainfall, low temperature range, and low altitudes on the West Coast of the continent, in conjunction with the globally warm temperatures of the Eocene. Evidence exists for a gradient of increasing seasonal dryness from north to south along the West Coast, but more megafossil evidence from southern California and/or Mexico would be helpful in confirming this.

### The Arctic and Alaska

Alaskan Eocene megafossils have for the most part been collected from coal-bearing, fluvio-deltaic sequences in southern Alaska (e.g., Kulthieth Formation and Kushtaka Formation of Wolfe, 1977). Diverse middle Eocene (early Ravenian of Wolfe) assemblages from this area have many large, probably evergreen, leaves, and a fairly high proportion of entire margins and drip tips. The floras also contain palms, and at some localities there are leaves thought to be derived from woody lianas. These characteristics, in addition to the tropical to subtropical Asian affinities of many species, led Wolfe (1972) to reconstruct the vegetation as near tropical to tropical. Although more recently Wolfe (pers. comm., 1990) has interpreted these floras to represent subtropical vegetation, this reconstruction still places broad-leaved evergreen forests as far as 60°N latitude along the West Coast of North America during the early and middle Eocene.

The correlation of middle and late Eocene floras of Alaska with those of the continental United States is somewhat problematic, which introduces considerable uncertainty in trying to infer the latitudinal distribution of paleovegetation. Parts of coastal Alaska have been rifted northward since the early Eocene (Bruns, 1983), but the magnitude of the displacement has been disputed (Plafker, 1984; Wolfe and McCoy, 1984). The resolution of the disagreement may lie in a Tertiary displacement of smaller magnitude, one that still indicates much warmer climate along the Northwest Coast of North America than exists today. Later Eocene floras in southern Alaska contain higher proportions of nonentire, presumably deciduous, leaves, and have been interpreted as indicating warm, although

perhaps not entirely frostless, climates (Wolfe, 1972, 1992). Wolfe (1992) reconstructs the late Eocene Katalla flora (Poul Creek Formation) as having been at the latitude of the northern part of south-east Alaska. This flora contains diverse broad-leaved evergreen laurels and deciduous broad-leaved taxa related to oaks and hickories (Wolfe, 1992). Even in the Alaskan interior, late Eocene floras reflect forest vegetation growing under a relatively warm climate. The probably late Eocene (36–33 Ma) Rex Creek flora from the central Alaska Range contains a diverse group of woody, broad-leaved taxa represented by both pollen and megafossils, and some leaves that are likely to be evergreen broad-leaved taxa, such as holly (Wolfe, 1992).

Eocene megafloras from Axel Heiberg and Ellesmere Islands in the Canadian Arctic are dominated by conifers, especially the deciduous *Metasequoia*, but also pine-family conifers such as larch, fir, and spruce (Basinger, McIver, and LePage, 1988; Greenwood and Basinger, 1994). The diversity of these Arctic assemblages is low, the most common dicots belong to the birch and alder families, and all dicots were deciduous. Physiognomic analysis of the Axel Heiberg assemblage implies a mild but cool climate, and there are no frost-intolerant taxa in the flora (Greenwood and Basinger, 1994). Dicot leaf fossils from Ellesmere Island are extremely large, perhaps a response to the effects of the polar light regime (Hickey, pers. comm.). Although the Arctic Eocene assemblages resemble Paleocene floras of the Rocky Mountain region in the abundance of *Metasequoia* and birch family species, the presence of oaklike dicots and pine-family conifers is more consistent with an Eocene age.

### Summary

Global climate began to warm during the last 1–2 million years of the Paleocene, and this trend continued into the early Eocene, reaching a Cenozoic peak during the late early Eocene (Wolfe, 1978; Wolfe and Poore, 1982; Miller, Fairbanks, and Mountain, 1987). During this time, broad-leaved evergreen forests occurred as far north as 60° (Wolfe, 1985), and forests of bald-cypress relatives and deciduous broad-leaved trees existed on Ellesmere and Axel Heiberg Islands well within the Arctic Circle (Hickey et al., 1983; Greenwood and Basinger, 1994). The early Eocene was the time of maximal interchange between floras of North America, Europe, and Asia; even frost-sensitive plant lineages were able to expand their ranges across the North Atlantic and Beringia (Tiffney, 1985a, 1985b).

However, even as warm climates at middle and high latitudes permitted maximum spread of broad-leaved evergreen forests and frost-sensitive lineages, volcanic activity and uplift in the Rocky Mountains were creating montane regions with cooler climates (Axelrod, 1966, 1968; Wolfe and Wehr, 1987; Gregory, 1994) and casting local or regional rain shadows to the east (Leopold and MacGinitie, 1972; Wing, 1987). The fluctuating withdrawal of the Mississippi Embayment from the northern midwest also may have contributed to increasing seasonal dryness, or even aridity, in the continental interior during the middle and late Eocene.

The slow drying trend in the interior of the continent began to divide North America into separate floristic and vegetational regions. Mesic, broad-leaved evergreen and semideciduous forests remained the dominant vegetation-type along the Pacific Coast, and probably

across Beringia into East Asia. Palynofloras suggest that such vegetation also occurred up the East Coast of North America and across North Atlantic coastlines to Europe (Frederiksen, 1994). Differences in the composition of Eocene megafloras from the Mississippi Embayment and the eastern Rocky Mountains suggest that drying in the interior of North America decreased interchange between the western and eastern areas of mesic forest. Some of the forest taxa that are now disjunct between East Asia and eastern North America originally may have separated at this time. Although global and North American temperatures decreased in a fluctuating manner through most of the Eocene (Wolfe, 1978; Miller, Fairbanks, and Mountain, 1987), latitudinal temperature gradients were still low enough that precipitation was the preeminent force in creating vegetational differences at the continental scale. Highly seasonal light regimes may also have been an important factor in limiting the northward distribution of many evergreen plant lineages (Wolfe, 1985).

## OLIGOCENE (SEE FIG. 2.3)

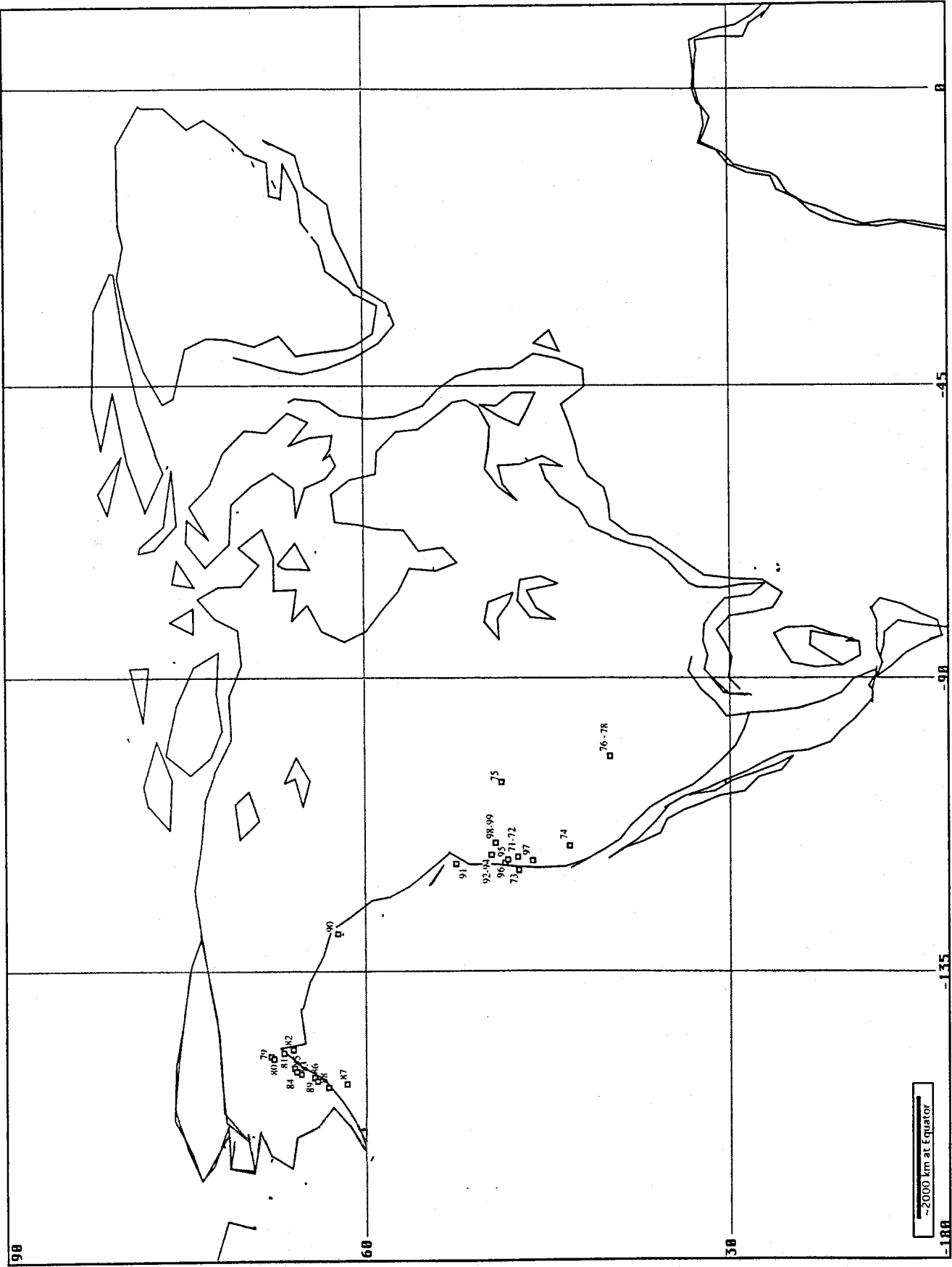
### East Coast

Well-dated early Oligocene megafloras from eastern North America are not known, but the May's Landing core from southeastern New Jersey has produced palynofloras that record the Eocene-Oligocene transition in shallow marine sediments that also contain marine microfossils (Owens et al., 1988). A minor extinction, and an increase in the dominance of oaklike pollen, appear to correlate with the early Oligocene (33 Ma) climatic cooling event that is also seen in floras from the Pacific Northwest and possibly the Gulf Coastal Plain (Wolfe, 1978; Frederiksen, 1980b; Owens et al., 1988; Wolfe, 1992).

There is only one East Coast megafossil assemblage of possible Oligocene age, the Brandon Lignite of Vermont. Although this deposit produces diverse fruits, seeds, wood, and pollen, its age is poorly constrained, most probably being late Oligocene or early Miocene (Tiffney, 1985b, 1994). The composition of the flora is consistent with a subtropical to warm-temperate forest that had a mixture of evergreen and deciduous species, and at least five species of vines. Based on comparisons of fossils with living relatives, Tiffney (1994) argues that evergreen species were dominant and the frosts would have been rare. Similar forests occur today along the Gulf Coast of the United States and in the highlands of northeastern Mexico (Tiffney, 1994).

### Mississippi Embayment and Gulf Coast

The Mississippi Embayment shrank in size during the Tertiary, but early Oligocene floras are still derived largely from low-energy fluvio-deltaic settings, coastal marshes and swamps, or in the case of some palynofloras, from nearshore marine environments (Frederiksen, 1981). Little has been said about the vegetational implications of Oligocene megafloras of this region, but early Oligocene palynofloras have been considered from a paleoecological perspective (Frederiksen, 1980b, 1981, 1985, 1988). Early Oligocene (lower Vicksburgian) palynofloras are distinct from those of the late Eocene in the abundance of oak-family pollen and the greater importance of fern spores and pollen of bald-cypress and related families (Taxodiaceae-Cupressaceae-Taxaceae [Frederiksen, 1981]). This is



**Figure 2.3.** Oligocene vegetation of North America. Numbers indicate the positions of Oligocene floras. Name, age, present coordinates, literature citation, and inferred paleovegetation are given for each number in the chapter appendix. See text for details.

consistent with a significant change in vegetation, and depending on how the strata are correlated with Pacific Coast floras and the marine record, could reflect the early Oligocene (33 Ma) cooling event described by Wolfe (1978, 1992). Palm fossils remain abundant at some Oligocene sites, indicating an absence of severe frost.

#### Great Plains and eastern Rocky Mountains

There are few megafossil assemblages of Oligocene age in the Rocky Mountain region (Wing, 1987). A series of early Oligocene (Orellan) floras from the "Medicine Lodge Beds" of western Montana reported by Becker (1969) do not appear to be substantially different from Eocene floras of the same region. (The Oligocene age of these beds was proposed by Fields et al. [1985], which generally has not been noted or accepted by paleobotanists.) Wolfe (1992) argues that the Orellan Antero flora from central Colorado represents a cool conifer-dominated forest, but notes that the small size of the dicot leaves is also seen in woodland and chaparral vegetation. Although it is only about 1 million years younger than the Florissant flora, the Antero flora already shows similarity to the well-known late Oligocene flora from Creede (Wolfe, 1992).

The late Oligocene (approximately 26 Ma) Creede flora is derived from volcanic caldera lake beds in southern Colorado (Axelrod, 1987). Pinaceous conifers are abundant in the Creede flora, and dicot leaves are typically small and represent deciduous species. Based on Creede, Axelrod and Raven (1985) and Axelrod (1987) argued that many elements of the extant vegetation of the southwestern United States were already native to the area by the end of the Oligocene. The Creede flora records both subalpine coniferous forest and a woodland/scrub vegetation (Axelrod, 1987). Wolfe and Schorn (1990) substantially revised the taxonomy of the flora, but reached broadly similar conclusions about its inferred vegetation (Wolfe and Schorn, 1989). Wolfe and Schorn suggested that moisture was the primary environmental gradient influencing the composition of the vegetation around the Creede caldera, with fir-spruce and pine-fir forest occupying the wettest sites, juniper-pine woodland growing on sites with intermediate moisture levels, and mountain mahogany chaparral covering the driest areas. Estimates of the paleoelevation of the Creede flora have ranged from 1 to more than 2 km (Meyer, 1986; Axelrod, 1987; Wolfe and Schorn, 1989).

A palynoflora approximately the same age as the Creede megaf flora (26–28 Ma) has been described from the Sevier Desert region of western Utah (Lindsey et al., 1980). This low-diversity palynoflora was derived from a sequence of interbedded volcanic sediments and thick evaporites, and is dominated by xeric-adapted plants like *Ephedra* (Mormon tea) and pollen that was probably derived from members of the herbaceous families *Chenopodiaceae*, *Elaeagnaceae*, and *Compositae*. Pine pollen is rare and may have been transported from a distant upland source. Based on both palynofloral and sedimentological evidence, the late Oligocene paleoclimate of the region was inferred to have been very dry. The data are consistent with a low-diversity, largely herbaceous local vegetation,

although higher elevation sites in the same region might have supported forests more like those at Creede.

#### Western Rocky Mountains and Pacific Coast

There are a great many assemblages from Oregon, for example, Lyons (Meyer, 1973), Rujada (Lakhanpal, 1958), John Day of Fossil (Manchester and Meyer, 1987), and many assemblages lumped under the name Bridge Creek (Chaney, 1927). These floras derive from volcanoclastic sediments associated with the Cascade Range, and most are dated radiometrically in the range of 30–32 Ma, just following the early Oligocene climatic cooling event (Wolfe, 1978, 1992). The vegetational and paleoclimatic implications of these floras have been reviewed by Wolfe (1981) and Manchester and Meyer (1987). Vegetation of this region during the early Oligocene was a forest composed of a mixture of deciduous and broad-leaved evergreens and conifers. Differences in the relative dominance and diversity of evergreen versus deciduous taxa probably reflect a fairly strong coastal effect because more easterly floras tend to be less diverse with a higher proportion of toothed, deciduous, small-leaved taxa (Wolfe, 1981). Manchester and Meyer (1987) inferred that the vegetation producing the Fossil, Oregon, assemblage was most similar to the living Mixed Northern Hardwood Forest of Asia, growing under a mean annual temperature (MAT) of perhaps 5°C, and possibly with a cold month mean below –2°C. Wolfe (1981) suggested the more coastal vegetation was a mixed broad-leaved evergreen and coniferous forest of moderate diversity (MAT 12–13°C). In both areas of Oregon several lineages persisted that were extinct in the midcontinent region during or by the end of the Eocene (e.g., dawn redwood [*Metasequoia*], katsura tree [*Cercidiphyllum*], and a walnut relative now restricted to East Asia, *Engelhardia*). Wolfe (1987b) described late Oligocene vegetation of the Columbia Plateau region as Mixed Mesophytic Forest – a rich mixture of broad-leaved evergreen and deciduous species with conifers.

Farther south in California, Oligocene floras are less abundant. Leaves from the early Oligocene Laporte Flora of the western Sierra Nevada appear to represent a mixed evergreen and deciduous broad-leaved forest growing in a climate with a MAT estimated at about 20°C (Potbury, 1935; Wolfe, 1992). Axelrod (1979) suggested that seasonally dry forest was characteristic of much of southern California and the southwestern United States, as well as northwestern Mexico during the Oligocene, although there are few floras of this age from the region.

#### The Arctic and Alaska

A number of early (Kushtaka, Katalla, and Kuthieth Formations) to late (Healy Creek, Stepovak, Tsadaka, Kootznahoo, and lower Kenai Formations) Oligocene assemblages are known from coastal southern Alaska (Wolfe, 1977). The early Oligocene (Kummerian Stage of Wolfe, 1977) vegetation of southern Alaska has been interpreted as a variety of subtropical forest with strong floristic relationships to roughly coeval forests of the Pacific Northwest (Wolfe,

1977). Thick-textured, possibly evergreen, broad-leaved species are a major component of these floras. By the late Oligocene (Angoonian Stage of Wolfe, 1977) low-diversity forests were dominated by broad-leaved deciduous species to the exclusion of broad-leaved evergreens (Wolfe, 1972). Presumably emplacement of the Yakutat Block was complete by late Oligocene time, although displacement of blocks from the Pacific Northwest region to southeastern Alaska has been proposed for times more recent than 40 Ma (Cowan, 1982).

### Summary

Sharp cooling in the early Oligocene shown by floras from the Pacific Coast of North America (Wolfe, 1978), and more gradual cooling during the late Eocene shown by European floras (Collinson, Fowler, and Boulter, 1981), generally coincide with temperature estimates for ocean bottom water derived from benthic foraminifera (Miller, Fairbanks, and Mountain, 1987; Miller, 1992). This implies a global cause for the cooling, probably related to enhanced bipolar production of cold deep-ocean currents, and possibly the growth of continental ice sheets in Antarctica (Miller, 1992).

Although the cause of the climatic cooling may have been global, the effects on North American vegetation do not appear to have been uniform. Wolfe (1978, 1992) has argued for dramatic shifts in the vegetation of the Pacific Northwest and Alaska, from dominantly broad-leaved evergreen vegetation typical of subtropical or warmer climates to forests dominated by deciduous broad-leaved taxa and conifers. This rapid (less than a million years?) vegetational shift is thought to reflect a major increase in temperature seasonality and to have coincided with the continental extinction of a number of warm-climate lineages (Wolfe, 1992). Data from eastern North America are sparse, and although they imply changes in vegetational importance of some taxa, they do not demonstrate major extinctions (Frederiksen, 1980b; Owens et al., 1988). Early Oligocene floras from the interior of North America are also few in number, but seem to show less dramatic change than those from coastal areas (Wing, 1987). There are at least four possible explanations for this difference in response: (1) Continental areas were subject to more seasonal and diurnal temperature fluctuation throughout the Eocene and thus the flora had already lost taxa sensitive to these conditions, (2) seasonality of rainfall during the Eocene had already favored deciduous taxa, (3) local environmental variations (e.g., paleoaltitudinal differences between floras, rain shadow effects) make the global climatic signal harder to pick out, and (4) climatic change driven by shifts in ocean circulation was not as severe in continental interiors. Interpretation of admittedly scant paleobotanical data from around North America suggests that even a major climate change "forced" by shifts in global ocean circulation produced effects of different magnitude in different parts of the continent. Continental ecosystems and climates are so heterogeneous that it is overly simplistic to expect them to react in a uniform manner to even the largest environmental perturbations.

Although paleobotanical and isotopic data support an amelioration of climate during the later Oligocene in coastal regions, it appears that low-biomass vegetation continued to develop in parts of the western interior and southwestern United States. The enhanced vegetational differences between coastal and interior areas are probably attributable to increased continentality (which may have been influenced by the regression of the Mississippi Embayment) and to continued orographic influences on rainfall.

## MIocene AND PLIOCENE (SEE FIG. 2.4)

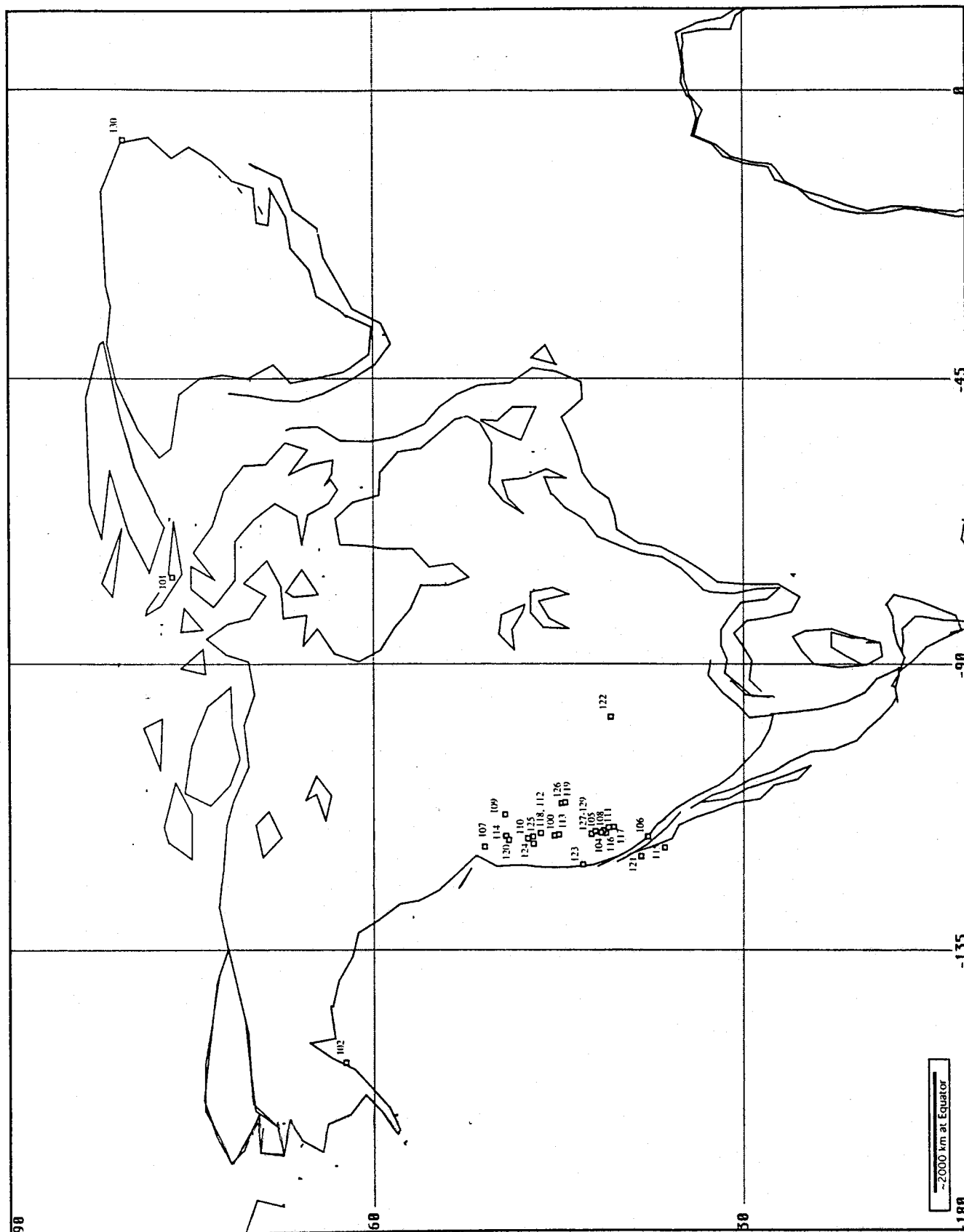
### East Coast

Miocene and Pliocene plant-bearing deposits on the East Coast are rare and consist mostly of isolated lignitic layers, clay lenses, and nearshore marine deposits. The general impression of paleovegetation that emerges from these deposits is of dominantly broad-leaved deciduous forest, perhaps more diverse, but otherwise not too dissimilar from that occupying the southeastern part of North America today. Miocene forests of the East still contained some lineages that are presently confined to East Asia and/or Mexico and Central America. The presence of these warm-climate genera in Miocene floras of the Calvert, Bridgeton, and Pensauken Formations was noted during the late nineteenth and early twentieth centuries, although these identifications are not wholly reliable (Berry, 1916b, 1937; Hollick, 1882). However, recent workers have confirmed the presence of these "exotic" elements. For instance, an early middle Miocene (middle Barstovian to Clarendonian) palynoflora from Massachusetts contains the bald-cypress-family conifer *Sciadopitys* and the East Asian walnut relative *Pterocarya* (Frederiksen, 1979b). The Cohamsey Formation of southern New Jersey, about 11 Ma, produces a palynoflora of which four or five genera are now confined to regions with warmer winters, including *Oreomunnea*, a walnut relative now restricted to Central America, and *Podocarpus*, a warm-climate conifer of a largely Southern Hemisphere family (Rachele, 1976; Grellier and Rachele, 1983). Even a late Miocene to early Pliocene flora from Brandywine, Maryland, still contains a number of lines now extinct in North America (Tiffney et al., 1989; McCartan et al., 1990). In all probability these genera were eliminated from the East Coast during the later Pliocene or early Pleistocene by increasing winter cold. The degree of grassland development in eastern North America during the Miocene is poorly understood, but grass pollen is uncommon in palynofloras. (The meaning of this negative evidence is not clear because grass pollen is not always abundant in western Miocene palynofloras that are believed to come from areas that had substantial grass cover.)

### Mississippi Embayment and Gulf Coast

In contrast to the abundant Paleocene through Oligocene megaflores from this region, Miocene and Pliocene assemblages are few. A small flora reported from Alum Bluff in northern Florida is probably early Barstovian, and it is dominated by palms, laurels, and other

**Figure 2.4.** Miocene-Pliocene vegetation of North America. Numbers indicate the positions of Miocene and Pliocene floras. Name, age, present coordinates, literature citation, and inferred paleovegetation are given for each number in the chapter appendix. See text for details.





plants expected in a frostless climate (Berry, 1916c). One Pliocene assemblage from the region is the Citronelle flora from Alabama, which strongly resembles extant floras in the same region (Berry, 1916d).

### Great Plains and eastern Rocky Mountains

Several reviews of Neogene vegetational change in this region cover the topic in greater detail than is given here (Stebbins, 1981; Axelrod, 1985; Leopold and Denton, 1987; Thompson, 1991). Much of the available paleobotanical information for the Miocene and Pliocene is from pollen floras (e.g., Leopold and MacGinitie, 1972; Barnosky, 1984; Thompson, 1991), although abundant silicified fruits and seeds of herbaceous plants derived from volcanic sediments have been known for some time (Elias, 1932, 1935; Chaney and Elias, 1936) and are currently under study (e.g., Thomasson, 1980, 1982; Thomasson, Nelson, and Zakrzewski, 1986; Thomasson et al., 1990).

The oldest Miocene floras from the region are Hemingfordian equivalents from the Troublesome Formation, Colorado, and the Split Rock Formation, Wyoming (Leopold and Denton, 1987). Next in age are the early Barstovian Sheep Creek, Nebraska, flora and the one major Neogene compression flora from the Great Plains, the Kilgore of Nebraska (MacGinitie, 1962), which is mid-Barstovian. The Saratoga Valley palynoflora from southeastern Wyoming is roughly the same age as Kilgore (Leopold and Denton, 1987). Younger Miocene assemblages include the mid-Clarendonian Ash Hollow flora, the late Clarendonian (9 Ma) Teewinot palynoflora from western Wyoming (Leopold and MacGinitie, 1972; Barnosky, 1984; Leopold and Denton, 1987), and the Barstovian or younger Moonstone palynoflora (Leopold and Denton, 1987). Most or all of these palynofloras are similar in that they are dominated by pine pollen. Pollen of other pinaceous conifers (spruce, fir) and junipers is also common, as is that of a few deciduous hardwoods (walnut family, oaks, elms, birch, willow) and halophytic or xerophytic shrubs such as Mormon tea (*Ephedra*), greasewood (*Sarcobatus*), and herbs of the family Chenopodiaceae. Pollen of sagebrush and other composites is also moderately abundant, but grass pollen generally is rare or absent (Leopold and Denton, 1987).

The Kilgore megafloora records a low-diversity deciduous hardwood riparian forest (MacGinitie, 1962). Based on this record Leopold and Denton (1987) inferred two vegetation types: an open basin or lakeside shrub vegetation dominated by xerophytic or halophytic shrubs, and montane conifer forest, although Leopold, Liu, and Clay-Poole (1992) suggest that this palynoflora indicates the development of grassy savanna. The deciduous hardwoods may well have been restricted to stream courses. Probable Pliocene (>2 Ma) palynofloras from western Wyoming have abundant pine and sagebrush, along with other indicators of steppe and montane conifer forest, indicating that vegetation similar to that of the present day existed in the area at this time (Richmond, Mullenders, and Coremans, 1978).

Summarizing Hemingfordian through Hemphillian floras from Nebraska, Kansas, Oklahoma, and Texas described by Elias (1932, 1935), Axelrod (1985) inferred a steady drying trend from about 16 Ma through the end of the Miocene, with the driest climate period in the early Pliocene providing a major spur to the diversification of

dry-adapted grasses. The sequence of Miocene floras also is thought to reflect the spread of grassland at the expense of woodland and riparian forest, although the development of extensive prairie may not have occurred until as late as the Pleistocene (Axelrod, 1985). Axelrod (1985) argued that frequent fire is a prerequisite for excluding trees from grassland vegetation, and the vast prairies observed by European colonists of the Great Plains may have been in part the result of anthropogenic fire. Stebbins (1981) also argued for a recent origin of prairie vegetation and floras, suggesting that the present communities did not arise until the Pleistocene.

Studies of the stable carbon isotope values of soil nodules and mammalian tooth enamel for the Miocene to Pliocene interval indicate a shift from C3- to C4-dominated vegetation at about 7 Ma (Cerling, Wang, and Quade, 1993; Wang, Cerling, and MacFadden, 1994). This probably reflects the spread of grasses that grow during the hot summer months at the expense of cool season grasses and all shrubs and trees. In modern vegetation the relative importance of C4 grasses decreases with increasing latitude, and C4 grasses are not important north of about the U.S./Canadian border. Most of the carbon isotope data for the Mio-Pliocene are from the southern Great Plains and indicate C4-dominated vegetation; carbon isotope values from the northern United States and southern Canada are consistent with mixed C3/C4 vegetation after about 7 Ma (Wang, Cerling, and MacFadden, 1994).

Although the bulk of the paleobotanical and palynological sources cited here do not offer evidence for grassland vegetation, the 7 Ma (later early Hemphillian) Minium's Quarry Flora from Kansas clearly represents both grassland and riparian woodland (Thomasson et al., 1990), and fragments of grass demonstrating C4 anatomy have been recovered from the Miocene of Kansas (Thomasson, Nelson, and Zakrzewski, 1986). The carbon isotopic evidence for widespread C4 plants contrasts with rare fossils of C4 plants. The discrepancy probably reflects the tendency for fossil floras of all types (even palynofloras) to be dominated by local wetland plants, whereas the soil nodule data are constrained to come from well-drained soils with strong development of a calcic B horizon (Cerling, Wang, and Quade, 1993). If both sets of data reflect local conditions accurately, the implication is a regional vegetation with a strongly mosaic pattern of domination by C3 herbs, shrubs, or trees in wetter areas, and open C4 grasslands on the drier interfluvies.

Pliocene palynofloras from the Western Interior are relatively rare, but 2-million-year-old assemblages from the Jackson Hole area in Wyoming suggest essentially modern vegetation (Barnosky, 1984; Thompson, 1991). The distribution of large, terrestrial tortoises and other temperature-sensitive animals implies that Pliocene winters in the Western Interior were much warmer than at present even though rainfall regimes clearly favored grassland and other low-biomass vegetation (evidence summarized in Thompson, 1991).

### Western Rocky Mountains and Pacific Coast

A very large number of Neogene megaflooras and palynofloras have been collected and described from the Columbia Plateau region. Many of these are derived from volcanoclastic lacustrine or fluvial settings. The climatic and vegetational history of the region during the Neogene have been discussed by authors including Wolfe (1981, 1987b), Leopold and Denton (1987), Smiley (1985),

Taggart, Cross, and Satchell (1982), and Thompson (1991), who have provided lists of known floras as well as more detailed interpretations of the important assemblages. The plant record is relatively sparse during much of late Arikarean and Hemingfordian time, but quite dense throughout the Barstovian and Clarendonian and into the Pliocene (e.g., Mascall, Clarkia, Succor Creek, Trout Creek, Payette, Ellensburg, The Dalles, Troutdale, Poison Creek). Wolfe (1981) interpreted many of the earlier Miocene Columbia Plateau floras as representing Mixed Mesophytic forest, a diverse mixture of broad-leaved deciduous, broad-leaved evergreen, and coniferous species that lived under a mild, summer-wet climate. He argued that this forest type gave way in some areas to a less diverse Mixed Coniferous forest during the late Barstovian (13–14 Ma), possibly as a result of drier summers.

Leopold and Denton (1987) place the shift to drier climates in post-Clarendonian time on the basis of the composition of the Ellensburg and Hanford floras in eastern Washington State. For instance, swamp settings in eastern Washington continued to harbor *Taxodium* (bald cypress) and *Metasequoia* (dawn redwood) until 12–8 Ma. The Deschutes flora (about 4.5 Ma) has been interpreted as riparian vegetation in a region where interfluvial areas had few trees, and taken as an indication of decreased summer precipitation (Leopold and Denton, 1987). However, Leopold and Denton (1987) place the spread of steppe vegetation on the Columbia Plateau as a post-Hemphillian phenomenon, and state that steppe and palouse grassland did not come to dominate the Snake River Plain until the Quaternary.

Taggart, Cross, and Satchell (1982) argued for a much earlier, although areally and successional limited occurrence of xerophytic vegetation. Many palynofloras from the Succor Creek area (late Barstovian?, about 14 Ma) document fairly diverse, angiosperm-dominated or mixed conifer-angiosperm vegetation, but samples from intervals immediately following volcanic episodes show much less diversity and are dominated by pine pollen and other palynomorphs thought to have been derived from forbs and grasses (Taggart, Cross, and Satchell, 1982). The frequency, intensity, and regional extent of volcanic events may have created a major habitat for more xeric, open vegetation, even under climatic conditions that tended to produce a diverse forest “climax” vegetation (Taggart, Cross, and Satchell, 1982). These authors argued that vertebrate faunas occupying this open, successional vegetation would have had a better chance of preservation than those of the “climax” forests because of the deposition and redeposition of large quantities of ash in the intervals immediately following major volcanic eruptions. In contrast, megafossil assemblages are mostly found in lake basins and represent more mature forest vegetation because herbaceous plants are seldom transported to or preserved in such settings. This would explain why vertebrate faunas containing mammals with grazing adaptations would be approximately coeval with floras indicating diverse, closed-forest vegetation.

Many Miocene floras also are known from California and Nevada, although as in the Pacific Northwest, the Barstovian and later intervals are better represented than the earlier Miocene. Generally, early to mid-Miocene floras from northern California are similar in composition to those of the Columbia Plateau and are thought to be derived from a similar type of vegetation, a diverse broad-leaved

deciduous, broad-leaved evergreen and coniferous forest, growing under a mild moist climate (e.g., Axelrod, 1979). Furthermore, mid-Miocene floras as far east as Nevada are compositionally similar to those of the Pacific Northwest. For instance, Wolfe (1964) placed the late Hemingfordian flora from Fingerrock, in southwestern Nevada, in the same province as the Columbia Plateau assemblages. All of the pre-15 Ma floras from Nevada contain many genera that are now found in summer-wet climates in eastern North America and East Asia, but later in the Miocene (Barstovian-Clarendonian) floras from this area indicate drier conditions (Axelrod and Schorn, 1994). The floral shift was apparently caused by decreasing summer precipitation, which was in turn a consequence of increased upwelling of cold water along the Pacific Coast. Although the decrease in summer precipitation is thought to have been time transgressive (15 Ma in Nevada to as late as 11 Ma in the Pacific Northwest), it appears to have been very rapid in certain local areas (Axelrod and Schorn, 1994).

Pliocene pollen assemblages from cores and outcrops in California, Oregon, Washington, and Idaho provide a fairly detailed record of climatic and vegetational fluctuations from 5 to 2 Ma (Thompson, 1991). During the earlier part of this interval, mixed conifer forest predominated in northern California, and climates were probably warmer and more equable than they are today along much of the Pacific Coast and even in areas far inland. Summer drought remained a feature of climate along the Pacific slope as it had been in the late Miocene. On the Snake River Plain in southeastern Idaho, pollen assemblages from about 3 Ma have high proportions of sagebrush and other steppe taxa (Thompson, 1991). Between 2.4 and 2 Ma, climates in western North America generally became colder and drier, followed by a moister phase between 2 and 1.8 Ma (Thompson, 1991). A core from Tule Lake in northern California provides evidence for Milankovitch-scale fluctuations in climate, but these were of lower amplitude than Pleistocene glacial/interglacial cycles (Adam et al., 1990; Thompson, 1991).

The Tehachapi Flora of southern California (late Hemingfordian, about 17 Ma) is thought to represent dry woodland, or even semi-desert, although in a climate without freezing temperatures (Axelrod, 1939, 1979). A vegetation of dry woodland or scrubland has also been inferred for the Mint Canyon flora (12–13 Ma), although the assemblage is quite diverse (Axelrod, 1940, 1979). The oldest known fossil grass that demonstrates the anatomical and carbon isotope characteristics of the C<sub>4</sub> photosynthetic pathway was recovered from roughly 12-million-year-old sediments in California, although it was originally described as Pliocene (Nambudiri et al., 1978; Thomasson, 1986). The undescribed Topanga and Modelo floras were cited by Axelrod (1979) as evidence for a wetter coastal strip of vegetation during the Miocene in southern California. Axelrod (1979) states that in southern California, as in the Pacific Northwest and the Western Interior, the early Pliocene was the driest phase of the Cenozoic.

#### The Arctic and Alaska

An early Miocene flora from the Houghton Astrobleme (Devon Island, Canada, at about 75°N latitude) shows cool-temperate, deciduous, broad-leaved, and coniferous forest at about 22 Ma (Hickey, Johnson, and Dawson, 1988). The low diversity of the megaflo-

may in part reflect its recovery from a single locality in a restricted lake basin, but the associated palynoflora indicates low regional diversity as well. Based on overlap in the climatic preferences of living relatives of the common genera in the flora (e.g., pine, spruce, larch, birch, and pollen of the heath family), these authors inferred a mean annual temperature of 8 to 12°C with a cold month mean of -7 to -4°C. The closest modern analogue of the vegetation is the mixed conifer and northern hardwood forest that today occurs south of boreal forests; grass pollen is absent from the assemblage (Hickey, Johnson, and Dawson, 1988).

The Seldovia Point Flora of southern Alaska is a late early to middle Miocene assemblage from southern Alaska that contains 40–50 species of plants, and is thought to have been derived from a diverse, but totally deciduous, broad-leaved vegetation growing under a mean annual temperature of about 12°C and a warm month mean temperature around 20°C (Wolfe and Tanai, 1980; Wolfe, 1994b). The latitude of this area during the Miocene was presumably close to its present-day position of 60°N. Similar assemblages have been recovered from Nenana Coal Fields south of Fairbanks and suggest the presence of deciduous forest well inland (Wolfe and Tanai, 1980). On the basis of palynological and some supporting megafossil data, however, Wolfe and Tanai (1980, Figure 7) inferred the presence of dominantly coniferous vegetation along a coastal strip in southern Alaska extending from Kodiak Island at least as far as the present border with Canada. Mid-Miocene palynofloras from the Seward Peninsula and the North Slope are also dominated by conifers (Wolfe and Tanai, 1980).

Later Miocene floras from southern Alaska are the basis of the Homerian Stage (roughly 8–13 Ma; Wolfe et al., 1966, Wolfe, 1994b), the upper part of which is now thought to be approximately correlative with the Clarendonian or early Hemphillian Land Mammal ages (8–11 Ma; Wolfe, 1994b). Generally, Homerian floras are much less diverse than the earlier Miocene floras such as Seldovia Point and are more heavily dominated by pines and hardy deciduous groups like the birch family (Wolfe, Hopkins, and Leopold, 1966). These floral changes have been attributed to an approximately 7°C decline in mean annual temperature and a 9°C decrease in the mean temperature of the warmest month from the Seldovian to the Homerian (Wolfe, 1972; Wolfe and Tanai, 1980; Wolfe, 1994b). A number of genera of broad-leaved deciduous trees have their last Alaskan records during the middle and late Homerian (Wolfe, 1994b).

Pliocene floras from southern Alaska are even less diverse than those of the late Miocene, being dominated largely by pines, willows, and birches (Wolfe, 1972). Palynofloras of this age demonstrate the increasing abundance and diversity of herbaceous or shrubby angiosperms such as composites, grasses, and sedges, but there is no evidence for tundra vegetation in southern Alaska during the Pliocene (Wolfe, 1972).

Repenning and Brouwers (1992) identified two major cycles of climatic cooling between 3 and 0.85 Ma in the area bordering the Arctic Ocean. About 3 million years ago mixed coniferous forests with a small component of deciduous broad-leaved trees extended essentially to the shores of the Arctic Ocean (80°N), but during the succeeding 600,000 years the vegetation shifted toward tundra as permafrost developed at high latitudes. Following this cold pe-

riod, high-latitude climates warmed again rapidly, and boreal coniferous forest/tundra vegetation is recorded at the northernmost tip of Greenland about 2 million years ago (Kap København flora; Bennike, 1989). Following this shorter period of warmth, Arctic climates began to oscillate between colder and warmer periods between 1.7 and 1.2 Ma, finally sliding into full glacial/interglacial cycles in the last million years (Repenning and Brouwers, 1992).

### Summary

Long-term decreases in temperature and precipitation caused changes in the vegetation of North America during the Miocene. The early part of the epoch was relatively warm, but was followed by a mid- to late Miocene cooling that was probably one cause of a shift to more deciduous broad-leaved forests in Alaska and the Pacific Northwest, and perhaps a greater importance of montane coniferous forest and steppe vegetation in the northern Rocky Mountains. It is probable that increasing seasonal dryness, in part due to orographic and edaphic effects caused by Cascade volcanism, was also a major factor in the spread of the steppes and grasslands in the Pacific Northwest. More open, dry-tolerant vegetation was widespread by Barstovian time, but probably was much more extensive in the Western Interior, the eastern Rockies, and the Southwest than it was in other parts of the continent. However, even in areas that today have an extreme continental climate (e.g., northern Nebraska), fossil floras indicate the existence of riparian forest with eastern North American affinities growing under a warm climate (MacGinitie, 1962). This may indicate that fingers of broad-leaved forest extended along river courses much farther into the continent from the East Coast than presently. Floristic and vegetational connections between eastern and central North America may have been stronger than between the interior and the West Coast, based both on the composition of Miocene floras and on the floristic affinities of modern vegetation. The steppe and montane conifer forest of the Rockies evidently formed a major barrier to floral migration between developing grasslands on either side of the mountains (Leopold and Denton, 1987). The Rockies may have formed a barrier to faunal interchange as well. For instance, differences between the (coevolved?) herbivore faunas of the Great Plains as opposed to the western palouse prairie are suggested by the greater tolerance of eastern grasses to intense grazing (Mack and Thompson, 1982).

Even as late as the Pliocene, when forests in eastern North America were compositionally modern, except for a few "exotic" genera now confined to East Asia, the range of forest was probably much greater than it is now, both to the north and perhaps into the continental interior. Although high-latitude vegetation generally became less diverse, lower statured, and more cold tolerant during the late Miocene and Pliocene, the shift took place through a series of fluctuations rather than as a unidirectional trend. Boreal forest existed on the shores of the Arctic Ocean as recently as about 3 Ma, indicating that boreal forest taxa could have moved across Beringia as late as the Pliocene. Interpretations of late Pliocene vegetation in the continental interior of North America are based on slim evidence, but in the early Pliocene it appears that climate was warmer and forest or woodland vegetation was substantially more prevalent than in Holocene times.

## ANIMAL-PLANT INTERACTIONS

This has been a climate-centered description of vegetational history, which is appropriate because climate plays the primary role in dictating vegetational structure and floristic composition. However, evolutionary changes in plant lineages and changes in the ecological interactions of animals and plants should not be disregarded, even when dealing with only the last 65 Ma. The most obvious ecological relationship between mammals and plants is herbivory. Most considerations of the evolutionary interactions between mammals and plants implicitly assume that the major direction of influence is from producer to consumer: Changes in plants ("fodder") require changes in herbivores. No doubt this does occur, but the numerous mechanisms in plants that deter herbivores testify that the interaction is bidirectional, raising the possibility of a series of responses and counter-responses. Seed dispersal and pollination are also significant ecological interactions between mammals and plants, and vegetation is also important as the substrate for mammalian locomotion. In each of these interactions there is the potential for reciprocal effects both on ecological and evolutionary time scales.

Although climate, particularly rainfall, is the "first-order" predictor of vegetational characteristics and distributions, the effect of mammalian herbivores should not be discounted. The effect of large herbivores on vegetation may be particularly important in regions where cold or drought reduce levels of primary productivity (Oksanen, 1988), conditions that became increasingly common in the interior of North America during the Neogene and Pleistocene.

The short-term effect of large grazers and browsers on vegetational structure is well documented: Generally, they tend to reduce the cover of woody plants and maintain a physically more open habitat (e.g., Laws, 1970; Merton, Bourn, and Hnatiuk, 1976). Several authors have suggested that these effects are also important at longer time scales (e.g., Stebbins, 1981; Janzen and Martin, 1982; Mack and Thompson, 1982; Janzen, 1986; Owen-Smith, 1987). If mammalian herbivores do have long-term effects on vegetation, then the possibility arises that they may have played an important role in the success of certain vegetation types.

Considering the entire Tertiary in North America, the overall pattern has been the restriction of forests and the concomitant spread of open, herbaceous vegetation. It may well be that the limited areas of open vegetation during the early Tertiary precluded the radiation of large browsing or grazing herbivores and favored the evolution of small, frugivorous, terrestrial, arboreal, and volant types. These small frugivores may in turn have favored the success of the animal-dispersed plants characteristic of closed forest. This kind of ecosystem appears to have been dominant over much of the continent during the first 10–20 Ma of the Tertiary. Under the combined influence of drying and cooling in the mid-Tertiary and Neogene, these closed-forest ecosystems were fragmented. Plants with shorter life cycles and less woody tissue diversified in this climatic regime, and larger grazing and browsing herbivores evolved to take advantage of this expanded resource. These large herbivores in turn probably favored the success of such herbaceous or grassland vegetation by physically disturbing it through feeding. Positive feedback loops like these may play a role in the long-term persistence of particular asso-

ciations of plants and animals and may retard climatically induced change. Although the ultimate importance of climate in controlling plant distributions is not disputed, it is possible that many of the second-order patterns of floral and faunal change and stasis during the Tertiary are mediated through the reciprocal effect of plants and mammalian herbivores on one another.

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Appendix Partial list of Tertiary plant fossil localities in North America

#	Locality/Flora	m/p*	NALMA**	Epoch or Ma	Inferred vegetation	Paleoclimate	Lat	Long	Reference
1	POLICE IS	p		~64	conifer swamp forest	warm temperate	65	-125.2	Sweet & Braman, 1992
2	CASTLE RIV	p		~64	conifer swamp forest	warm temperate	49.5	-114	Sweet & Braman, 1992
3	JUDY CRK NORTH	p		~64	conifer swamp forest	warm temperate	54.5	-115.4	Sweet & Braman, 1992
4	LUSCAR STERCO	p		~64	conifer swamp forest	warm temperate	53	-116.7	Sweet & Braman, 1992
5	RED DEER V KNUDSN	p		~64	conifer swamp forest	warm temperate	51.9	-113	Sweet & Braman, 1992
6	CYPRESS MAP FV	p		~64	conifer swamp forest	warm temperate	49.4	-108.4	Sweet & Braman, 1992
7	WOOD MTN CRK	p		~64	conifer swamp forest	warm temperate	49.4	-106.3	Sweet & Braman, 1992
8	ROCK CRK EAST	p		~64	conifer swamp forest	warm temperate	49	-105.5	Sweet & Braman, 1992
9	MARMATH	m		~64	mixed conifer/broadleaved deciduous forest	subtropical	46.5	-103.8	Johnson, 1992
10	SMOKY TOWER	m		~63	conifer swamp forest	warm temperate	54.3	-118.7	Christophel, 1976
11	UPPER ATANIKERDLUK	m		PAL	broadleaved deciduous forest	warm temperate	70.3	-53	Koch, 1963
12	CHICKALOON	m		L_PAL	broadleaved deciduous forest	warm temperate	61.8	-148.8	Wolfe et al., 1966
13	ELSINORE	m		L_PAL	savanna forest	tropical	33.7	-117.3	Axelrod, 1979
14	STENKUL FIORD	m/p		L_PAL	polar broadleaved deciduous & conifer swamp forest	temperate	79	-82.5	Hickey et al., 1983;
15	SILVERADO	p/m		L_PAL	mixed evergreen & deciduous broadleaved forest	subtropical	33.5	-117.6	McIntyre et al., 1994 Gaponoff, 1984
16	GENESEE	m		PAL	conifer swamp forest	warm temperate	53.4	-114.4	Chandrasekharam, 1974
17	BEAR DEN	m	CF	L_PAL	mixed evergreen & deciduous broadleaved forest	warm temperate	47.3	-102.1	Hickey, 1977
18	ALMONT	m	CF	L_PAL	broadleaved deciduous forest	warm temperate	46.9	-101.4	Crane et al., 1990
19	MONTGOMERY CRK	m	CF-WA	PAL-EO	mixed evergreen & deciduous broadleaved forest	warm temperate	40.8	-121.9	
20	LOWER WILLWOOD	m	WA	E_EO	conifer swamp forest	subtropical	44.3	-108.1	Bown et al., 1994;
21	MIDDLE WILLWOOD	m	WA	E_EO	mixed evergreen & deciduous broadleaved forest	subtropical	44.3	-108.4	Wing et al., 1995 Bown et al., 1994;
22	UPPER WILLWOOD	m	WA	~52.8	broadleaved forest	subtropical	44.2	-108.5	Wing et al., 1995 Bown et al., 1994;
23	WIND RIVER FLORA	m	WA	E_EO	broadleaved evergreen forest	paratropical	43.7	-110	MacGinitie, 1969
24	CAMELS BUTTE	m/p	WA	E_EO	mixed evergreen & deciduous broadleaved forest	subtropical	46.8	-103	Hickey, 1977; Bebout, 1978
25	YELLOWSTONE	m/p	WA	E_EO	mixed evergreen & deciduous broadleaved forest	subtropical	44.9	-110.5	Knowlton, 1899;
26	MEGANOS "C"	p	WA	E_EO	mixed evergreen & deciduous broadleaved forest	paratropical	37.9	-121.8	Wheeler et al., 1977, 1978 Lucas-Clark & Lampley, 1988
27	CHALK BLUFFS	m	WA	E_EO	mixed evergreen & deciduous broadleaved forest	paratropical	39.17	-120.85	MacGinitie, 1941

(cont.)

Appendix (cont.)

#	Locality/Flora	m/p*	NALMA**	Epoch or Ma	Inferred vegetation	Paleoclimate	Lat	Long	Reference
28	FRANKLIN BLUFFS	p	WA	E_EO	broadleaved deciduous forest	warm temperate	69.8	-148.7	
29	SEWARD PEN DV	p	WA	E_EO	broadleaved deciduous forest	warm temperate	65.1	-162.3	Ager & Kaufman, 1987; Dickinson et al., 1987
30	NANJEMOY	p/m	WA	E_EO	mangrove	subtropical	38.4	-77	Mazer & Tiffney, 1982
31	TUFF LAKE BEDS	m	WA-BR	E/M_EO	mixed evergreen & deciduous broadleaved forest	subtropical	44	-109	
32	COAL MINE CANY	p	WA-BR	E/M_EO	broadleaved deciduous forest	warm temperate	41	-115.5	Wingate, 1983
33	BOYSEN	m	BR	M_EO	palm swamp forest	paratropical	43.4	-108.1	Wing, 1987
34	TORREY	p	BR	M_EO	mixed evergreen & deciduous broadleaved forest	paratropical	33	-117.3	Myers, 1991
35	KISINGER LAKES	m/p	BR	M_EO	mixed evergreen & deciduous broadleaved forest	subtropical	43.8	-110	MacGinitie, 1974
36	REPUBLIC	m	BR	~49	broadleaved forest mixed conifer/broadleaved deciduous forest	temperate	48.71	-118.91	Wolfe & Wehr, 1987
37	BEARPAW MTNS	m	BR	M_EO	mixed evergreen & deciduous broadleaved forest	subtropical	48.5	-109.9	Brown & Pecora, 1949
38	SMITHERS		BR-UI	M_EO			53.66	-125.27	Wolfe, 1987
39	CHU CHUA CRK	m	BR-UI	M_EO			51.22	-119.79	Wolfe, 1987
40	KAMLOOPS	m	BR-UI	M_EO			50.51	-119.93	Wolfe, 1987
41	PRINCETON	m	BR-UI	M_EO			49.21	-120.07	Wolfe, 1987
42	PURYEAR	m	BR-UI	M_EO	mixed evergreen & deciduous broadleaved forest	subtropical	36.4	-88.4	Dilcher, 1973; Crepet & Taylor, 1986
43	WARDELL RANCH	m/p	BR-UI	M_EO	woodland	subtropical	39.8	-107.9	MacGinitie, 1969
44	AXEL HEIBERG	m/p	BR-UI	M_EO	mixed conifer/broadleaved deciduous forest	temperate	80	-88	Basinger et al., 1988; McIntyre, 1990
45	CLARNO NUT BEDS	m	UI	~43.7	broadleaved evergreen forest	subtropical	44.8	-120.4	Manchester, 1990
46	THUNDER MT DEWEY	m	UI	~45	evergreen coniferous forest	cold temperate	44.44	-114.32	Axelrod, 1990
47	THUNDER MT ROAD	m	UI	~45	mixed conifer/broadleaved deciduous forest	temperate	44.44	-114.32	Axelrod, 1990
48	RATE HOMESTEAD	m	UI	M_EO	mixed evergreen & deciduous broadleaved forest	subtropical	43.8	-107.5	MacGinitie, 1969
49	CHUMSTICK I	m	UI	~43	mixed evergreen & deciduous broadleaved forest	subtropical	47.6	-120.5	Evans, 1991
50	COPPER BASIN	m	UI	~41	mixed conifer/broadleaved deciduous forest	cold temperate	41.8	-114.1	Axelrod, 1966
51	CHUMSTICK II	m	UI	~41	broadleaved deciduous forest	warm temperate	47.6	-120.5	Evans, 1991

52	SILICA BAR	m	DU	~40	mixed evergreen & deciduous broadleaved forest	47.7	-122	Burnham, 1990
53	BARILLA	m	DU	~38.2	mixed evergreen & deciduous broadleaved forest	30.7	-103.8	Berry, 1919; Axelrod & Bailey, 1976
54	SHEEP ROCK CRK	m	DU-CH	M-L_EO		43.91	-120.59	
55	ALVORD CRK	m	DU-CH	M-L_EO		42.47	-118.46	Axelrod, 1944
56	ELKO	m/p	DU-CH	M-L_EO		40.76	-115.77	
57	WARMAN	m	DU-CH	L_EO	mixed evergreen & deciduous broadleaved forest	36.3	-88.5	Dilcher, 1973; Crepet & Taylor, 1986
58	UPPER BULL RUN	m	CH	~36	evergreen coniferous forest	41.8	-116.2	Axelrod, 1966
59	FLORISSANT	m/p	CH	~35	mixed evergreen & deciduous broadleaved forest	39.2	-104.4	MacGinitie, 1953
60	BEAVER CRK		CH	L_EO		46.03	-112.88	
61	DRUMMOND		CH	L_EO		46.41	-113.09	Pearson, 1972
62	SALMON	m	CH	L_EO		45.32	-113.96	Brown, 1937
63	COW CRK	m	CH	L_EO		44.91	-113.58	
64	BEAVERHEAD	m		?		45.15	-113.35	
65	METZEL RANCH	m		?		44.65	-112.8	
66	SUSANVILLE	m		EO	broadleaved evergreen forest	40.3	-120.6	Wolfe-USGS Collections
67	ELLESMERE	m/p		EO	polar broadleaved deciduous forest	79	-85	Hickey et al., 1983
68	GOSHEN			EO		43.9	-123	
69	COMSTOCK			EO		43.8	-123.1	
70	LWR CEDARVILLE			EO		41.4	-120.2	
71	RUJADA	m		OLI		43.67	-122.56	Lakhanpal, 1958
72	LYONS	m		OLI		43.82	-121.43	Meyer, 1973
73	YAQUINA	m		OLI		43.44	-124.18	McClammer, 1978
74	LA PORTE	m	OR-WH	E_OLI	mixed evergreen & deciduous broadleaved forest	39.4	-120	Pothbury, 1935
75	UPPER RUBY RIVER	m	WH	OLI	mixed conifer/broadleaved deciduous forest	45.4	-112.1	Becker, 1961
76	CREEDE 5-MILE	m	AR	~27.2	woodland	36.9	-106.9	Wolfe & Schorn, 1990
77	CREEDE WASON	m	AR	~27.2	chaparral	36.9	-106.9	Wolfe & Schorn, 1990
78	CREEDE BIRDSEY	m	AR	~27.2	coniferous forest	36.9	-106.9	Wolfe & Schorn, 1990
79	CHEENEETNUK R	m		OLI		63.15	-151.61	Wolfe-USGS Collections
80	CHEENEETNUK R	m		OLI		63.39	-151.35	Wolfe-USGS Collections
81	COLORADO CRK			OLI		61.91	-150.19	Wolfe-USGS Collections
82	EAGLE RIVER			OLI		61.12	-149.83	Wolfe et al., 1966

(cont.)

## Appendix (cont.)

#	Locality/Flora	m/p*	NALMA**	Epoch or Ma	Inferred vegetation	Paleoclimate	Lat	Long	Reference
83	HARRIER POINT			OLI			59.94	-152.74	Wolfe-USGS Collections
84	HARRIER CRK			OLI			60.06	-152.61	Wolfe-USGS Collections
85	REDOUBT PT			OLI			60.38	-152.32	Wolfe-USGS Collections
86	DOUGLAS MTN			OLI			58.88	-153.39	Wolfe-USGS Collections
87	SITKINAK IS			OLI			56.55	-154.1	Wolfe-USGS Collections
88	KUKAK BAY			OLI			58.11	-154.62	Knowlton, 1904
89	KUKAK BAY			OLI			58.88	-153.39	Knowlton, 1904
90	KOOTZNAHOO			OLI			57.94	-134.71	Lathram et al., 1965
91	SOOKE			OLI			48.42	-123.53	Lamotte, 1935
92	GUMBOOT MTN			OLI			45.82	-122.3	
93	CASCADE LOCKS			OLI			45.59	-121.95	
94	SANDSTONE CRK			OLI			45.44	-122.43	
95	CASCADIA	m		OLI			44.09	-122.33	
96	WILLAMETTE			OLI			44.2	-123.11	
97	SHALE CITY			OLI			42.35	-122.46	
98	BRIDGE CRK	m		OLI			45.35	-120.39	Chaney, 1927
99	BRIDGE CRK	m		OLI			45.35	-120.2	Chaney, 1927
100	ALVORD CRK	m	AR	~23.8			42.6	-118.6	Axelrod, 1944; Barnett & Fisk, 1984
101	HAUGHTON ASTROBLEME	m/p	AR	~22.4	mixed conifer/broadleaved deciduous forest	cold temperate	75.4	-89.8	Hickey et al., 1988
102	SELDOVIA POINT	m	AR-HE	E_MIO	broadleaved deciduous forest	temperate	59.5	-151.8	Wolfe & Tanai, 1980
103	EASTGATE	m	HE	~18	woodland	temperate	39.4	-117.8	Axelrod, 1989
104	MIDDLEGATE	m	HE	~18	mixed conifer/broadleaved deciduous forest	temperate	39	-118.3	Axelrod, 1989
105	BUFFALO CANYON		HE	~18	mixed conifer/broadleaved deciduous forest	temperate	39.2	-118.1	Axelrod, 1991
106	TEHACHAPI	m	HE	~17	woodland	subtropical	35.3	-118.7	Axelrod, 1939
107	GRAND COULEE	m	HE	M_MIO	mixed evergreen & deciduous broadleaved forest	warm temperate	48.2	-120.1	Wolfe & Tanai, 1980
108	FINGERROCK	m	HE-BA	~16.5			38.7	-117.9	
109	CLARKIA	m/p	BA	~15.5			47.2	-116.3	
110	MASCALL	m	BA	~15			44.7	-119.7	
111	STEWART SPRING	m	BA	~14	conifer swamp forest	temperate	38.5	-117.9	Chaney, 1959
112	SUCCOR CRK	m/p	BA	~13.5			43.5	-117.2	
113	TROUT CRK	m	BA	~13.5			42.4	-118.4	
114	VANTAGE	m	BA	~13			47	-120.3	

