3. History of the Vegetation: Cretaceous (Maastrichtian)–Tertiary

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A discussion of the history of the vegetation of North America most logically begins with the events of the late Upper Cretaceous epoch, 70–60 Ma (million years ago). By then, the angiosperms and other major present-day groups were clearly established as dominant in the world's terrestrial flora. The continents were closer together than they are at present, and indeed, Eurasia and North America were still conjoined across the northern Atlantic. The plate tectonic forces that have placed the continents in their present configurations, however, were already in motion.

Our knowledge of the botanical events of the past rests on an interpretation of the fossil record, which for vascular plants occurs in two forms. Macrofossils are structures such as leaves, stems, fruits, seeds, wood, and flowers, whereas plant microfossils representing terrestrial or freshwater aquatic macrophytic vegetation include pollen grains, spores, and phytoliths (crystals formed within living plants). Paleobotany (including specialized approaches such as dendrochronology and analysis of pack-rat middens) has come to imply the study of plant macrofossils, and paleopalynology designates studies concerned with plant microfossils.

Experience has shown that most elements comprising a fossil assemblage are broadly consistent in terms of habitat preference, or they can be sorted into subsets reflecting habitat diversity (viz., elevational gradients). This organization gives rise to the concept of paleocommunities from which it is possible to deduce past climates, paleophysiography, and biogeographic patterns. Such reconstructions are based on a direct comparison and presumed general equivalency of most members of a fossil flora with modern analogs (composition of the flora), on the observation that present-day plants with certain morphological attributes (e.g., leaf physiognomy) are found in certain habitats, and on the assumption that most fossil plants with similar morphological attributes occurred in comparable habitats. For example, modern plant assemblages containing many large-leaved, entire-margined species with drip-tips typically occur in humid tropical habitats; therefore, a fossil flora with many similar leaf types is taken to indicate a humid tropical paleoenvironment. The composition of a fossil flora, based on the combined inventories provided by macro- and microfossil remains, leaf physiognomy, and dendrochronology, are all valuable methods for studying vegetational history and reconstructing the environments that influenced the development of North American vegetation through time.

The following discussion begins with the floras of the Maastrichtian stage of the Upper Cretaceous, 70–65 Ma, and progresses forward in time through the Tertiary to 2 Ma, the end of the Pliocene epoch, i.e., to the advent of the Pleistocene, the "Ice Ages." Within each section, the fossil floras are discussed in a sequence that begins with the southeastern corner of the continent and proceeds westward and around the con-

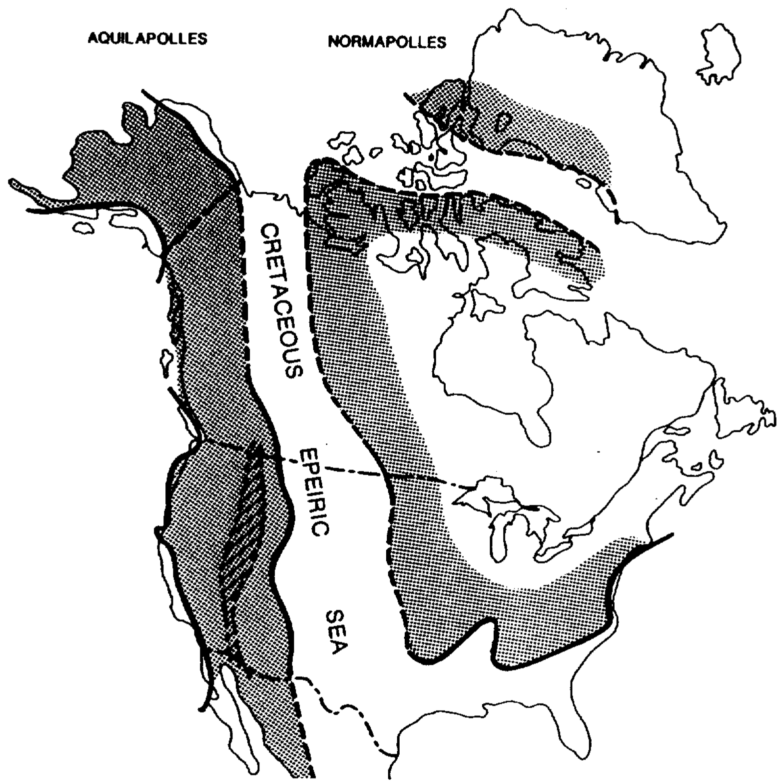

FIGURE 3.1. Map showing extent of Cretaceous epeiric sea in Maastrichtian time and Aquilapolles/Normapolles provinces. Shading shows presumed land areas; hachured area shows highlands during late Cretaceous time. [From E. B. Leopold and H. D. MacGinitie 1972. Reprinted with permission from the authors.]

tinent in a clockwise fashion. Events from the Pleistocene to the present are covered by P. A. Delcourt and H. R. Delcourt (chap. 4).

In describing paleoevents, degrees of latitude and longitude, unless otherwise noted, are given in terms of present-day locations of the poles and continents, even though the North American continent has moved slightly relative to the poles during the Tertiary and to the present.

Late Cretaceous

As the late Cretaceous came to a close (Maastrichtian times, 70–65 Ma), an epeiric (epicontinental) sea extended from the Gulf of Mexico through the western interior lowlands to the Arctic Ocean (fig. 3.1). The Appalachian Mountain system, uplifted at the end of the Paleozoic, had undergone 185 million years of erosion. In the western portion of the continent, the Rocky Mountains were locally of moderate relief, the Sierra Nevada was only a series of low hills until the Mio-Pliocene, and the High Cascades would not appear until the Pliocene. As a consequence of widespread inundation, low physiographic relief, and high temperatures (fig. 3.2), equable subtropical, warm temperate, and temperate climates extended in successive zones along low thermal gradients from the southern present-day United States to the Arctic regions. Across the latitudinal zones of late Cretaceous vegetation in North America, a temperature gradient of only about 0.3° C/1° latitude is inferred from leaf physiognomy of Maastrichtian megafossil floras, compared to just under 1° C/1° latitude at present. As noted in E. M. Friis et al. (1987), the period from the Cretaceous through the middle Eocene (70–35 Ma) included some of the warmest temperatures in all of Phanerozoic time, perhaps 5°–10° C warmer than at present at low midlatitudes (30° N) and 30° C warmer at high latitudes (80° N) (J. T. Parrish 1987).

With the continent physically divided by the epeiric sea into western and eastern regions, two principal floristic provinces characterized the late Cretaceous vegetation of North America (fig. 3.1; D. J. Batten 1984; N. O. Frederiksen 1987). In the west, and extending into Asia, palynofloras are distinguished by the presence of Aquilapolles (*Aquilapollenites* and other *Triprojectacites* types; M. J. Farabee 1990), while in the east, and extending into Europe, the Normapolles group is prominent. Suggested affinities of *Aquilapollenites* include the Loranthaceae and Santalaceae (D. M. Jar-

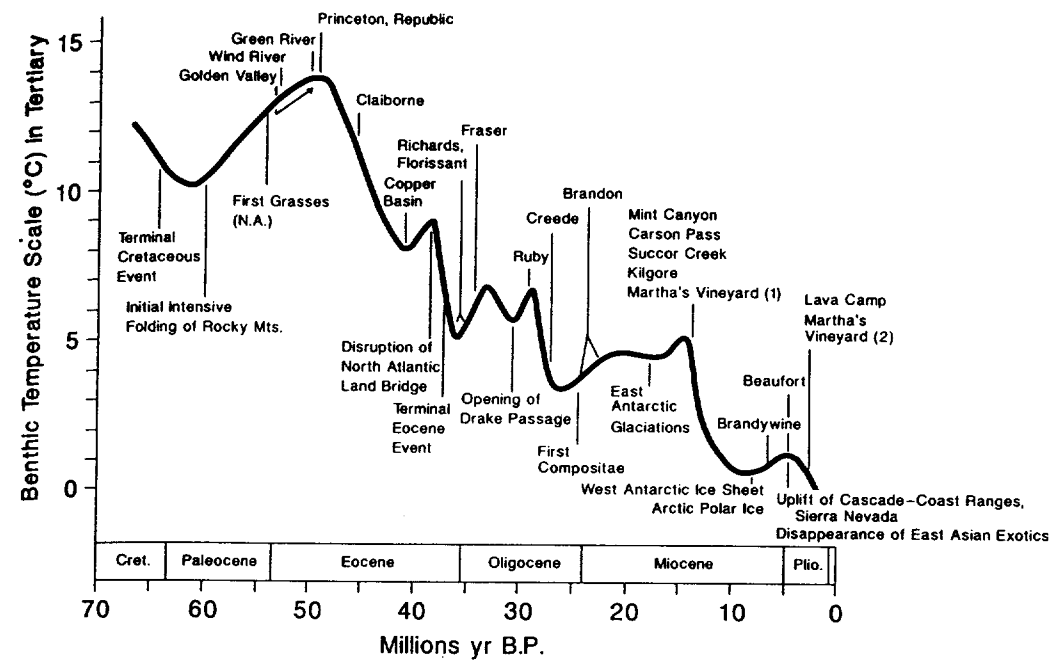

FIGURE 3.2. Tertiary paleotemperature curve of benthic temperatures with principal events and floras cited in text. [Based on fig. 4 in D. I. Axelrod and P. H. Raven 1985, with permission from the Journal of Biogeography.]

zen 1977), but the Aquilapolles in the broad sense are likely polyphyletic (M. J. Farabee and J. J. Skvarla 1988). The Normapolles are a group of Cretaceous and lower Paleogene colpate and porate (usually triporate) pollen with a complex pore structure of thick protruding ektexine (A. Traverse 1988). Suggested affinities of the polyphyletic Normapolles include various Hamamelidae, the Juglandaceae, the related family Rhoipteleaceae, or an extinct family of the Juglandales.

At the end of the Cretaceous, much of southeastern North America (30°–45° N) was covered by megathermal (mean annual temperature above 20° C) evergreen tropical woodland (estimated mean annual temperature above 25° C), and in the west by broad-leaved evergreen forests of dicotyledons and conifers (paratropical vegetation, estimated mean annual temperature 20°–25° C) (fig. 3.1; G. R. Upchurch and J. A. Wolfe 1987; J. A. Wolfe and G. R. Upchurch 1987). Fossil woods show little evidence of seasonality.

In the west, between latitudes 45° N and 65° N, mesothermal vegetation (estimated mean annual temperature 13°–20° C) was prominent (C. N. Miller Jr. et al. 1987; J. A. Wolfe 1987b). Leaf size was commonly of the notophyll class (maximum size 45 cm^2), intermediate between the microphylls (20 cm^2) indicative of drier and/or colder climates and the macrophylls (1640 cm^2) and megaphylls (no maximum size) indicative of more tropical climates. The canopy was less open in the notophyll forest than in the paratropical woodland. Middle latitude forests contained araucarian, rosid, platanoid, hamamelid (D. L. Dilcher et al. 1986; P. R. Crane and S. Blackmore 1989), and trochodendroid elements, as well as Betulaceae, Ulmoideae, Tiliaceae, Flacourtiaceae, Juglandales (possibly represented by some Normapolles), and Loranthaceae-Santalaceae (some *Aquilapollenites-Triprojectacites*). At the southern limits of this western zone (ca. 45° N), growth rings in fossil woods are absent or poorly developed, whereas at the northern limits (56°–60° N) they are clearly defined. Evergreen conifers were common, and woody dicots were represented mostly by small trees and shrubs.

Deciduous angiosperm vegetation is first recorded in high northern latitudes in the Cenomanian. Above 55° N latitude, late Cretaceous macrofossil floras occur in central Alberta (W. A. Bell 1949; C. G. K. Ramanujam and W. N. Stewart 1969; J. A. Wolfe and G. R. Upchurch 1987b), and slightly older ones (Campanian to Maastrichtian, 82–65 Ma) are known from Alaska (R. A. Spicer et al. 1987). The vegetation was a mosaic of deciduous angiosperm and gymnosperm forests in a climate where temperatures ranged from mesothermal to microthermal (estimated mean annual temperature at or below 13° C). Macrofossil remains include platanoids, trochodendroids, hamamelids, and *Viburnum*-like leaves representing vegetation from middle latitudes and extending into these northern regions primarily along streams. Away from the streams the vegetation included *Fagopsis,* a genus of the Fagaceae that became extinct at the end of the Eocene (S. R. Manchester and P. R. Crane 1983; W. L. Stern et al. 1973), Flacourtiaceae, Aceraceae, *Alnus,* and possibly *Betula.* Fossil woods show well-defined growth rings, an indication of contrasting seasons.

The estimated 1° C mean temperature isotherm for the coldest month separated the zone of predominantly broad-leaved, evergreen, subtropical vegetation from the more northern broad-leaved deciduous vegetation. Regions with coldest month means between −2° C and 1° C had notophyll broad-leaved evergreens as understory vegetation. In modern climates with coldest month means lower than −2° C, notophyll broad-leaved evergreens are lacking (J. A. Wolfe 1978).

At the close of the Cretaceous two events occurred that influenced subsequent development of the North American flora. The first, regression of the western interior sea, reduced the principal physical barrier to dispersal between the eastern and western portions of the continent. In geological strata of this age, diversity in Normapolles increased in California and the Canadian Arctic; *Aquilapollenites* has been reported from the Atlantic Coastal Plain.

The second event marks the end of the Cretaceous. Major extinctions are noted for marine plankton and certain large terrestrial animals and lesser ones for terrestrial vegetation. These extinctions may have resulted from climatic changes immediately following the impact of a large asteroid. A relatively brief lowering of temperatures (winter effect), followed by a rise in temperature (greenhouse effect), is plausible.

Such an event also may have set into motion, or intensified, selection favoring the deciduous habit at the expense of evergreens. J. A. Wolfe (1987) described a change from dominantly broad-leaved evergreen megathermal forest to dominantly broad-leaved deciduous mesothermal forest in the high middle latitudes of North America. Soon afterward temperatures and vegetation resumed the trends of pre-impact times under primarily climatic and physiographic influences.

Tertiary: Paleocene through Middle Eocene (65–35 Ma)

Generally warm temperatures, and possibly increased but seasonal (winter-dry) rainfall regimes, characterized the Paleocene and early and middle Eocene (J. A. Wolfe and G. R. Upchurch 1987b).

Several events important to the history of North American vegetation occurred during the period from late Cretaceous through middle Eocene times. Tropical dry-season vegetation first appeared; the Betulaceae, Fabaceae, Fagaceae, Juglandaceae, and Ulmoideae diversified in the middle and higher latitudes. Araucarian conifers became extinct in the Northern Hemisphere at the end of the Cretaceous. *Glyptostrobus* and *Metasequoia* became abundant, the latter the most frequent and widespread member of the Taxodiaceae (Cupressaceae in the flora) in North America from Cretaceous to Miocene times. *Momipites* (*Alfaroa-Engelhardia-Oreomunnea* type), *Carya, Platycarya* (first appearing in the early Eocene), *Cyclocarya-Pterocarya* of the Junglandaceae, lianas (Vitaceae), Anacardiaceae, and Rutaceae became abundant. *Acer, Ailanthus, Celtis, Chaetoptelea, Comptonia, Eucommia, Hydrangea, Liquidambar, Populus,* and *Rhus* made their first appearance. The family Poaceae was present in North America by the Paleocene/Eocene (W. L. Crepet and G. D. Feldman 1991). The midlatitude mesothermal, broad-leaved deciduous vegetation also extended across the midcontinent region that now supports prairie vegetation. At high elevations in the higher latitudes in western North America, coniferous forests of Pinaceae and Cupressaceae first appeared. In the middle and late Eocene, the Rosaceae, Juglandaceae, and Aceraceae underwent rapid adaptive radiation. By the end of the Paleocene, the epeiric seaway had retreated to a position some 300–500 km inland from the present Gulf and Atlantic coasts.

Interpretations based on fossil pollen (N. O. Frederiksen 1980) and macrofossils (D. L. Dilcher 1973; J. A. Wolfe 1985) suggest that the climates of southeastern North America during the lower and middle Eocene varied between seasonally dry tropical and humid subtropical. In all probability, the flood plain at the northern end of the Mississippi Embayment in Kentucky and Tennessee experienced occasional frosts, but the climate near the sea was frost-free, winter-dry tropical (N. O. Frederiksen 1980).

Tropical forests (Annonaceae, Lauraceae, Menispermaceae) in the Southeast reached their maximum northern expansion (to ca. 50°–60° N). The middle Eocene Claiborne flora of western Kentucky and Tennessee (fig. 3.3) is regarded as preserved in oxbow lake sediments several miles inland from the embayment.

These paleocommunities were a complex assemblage that have no exact modern analog. In addition to neotropical elements, they had at least several paleosubtropical taxa introduced into North America from the Old World tropics over the North Atlantic land

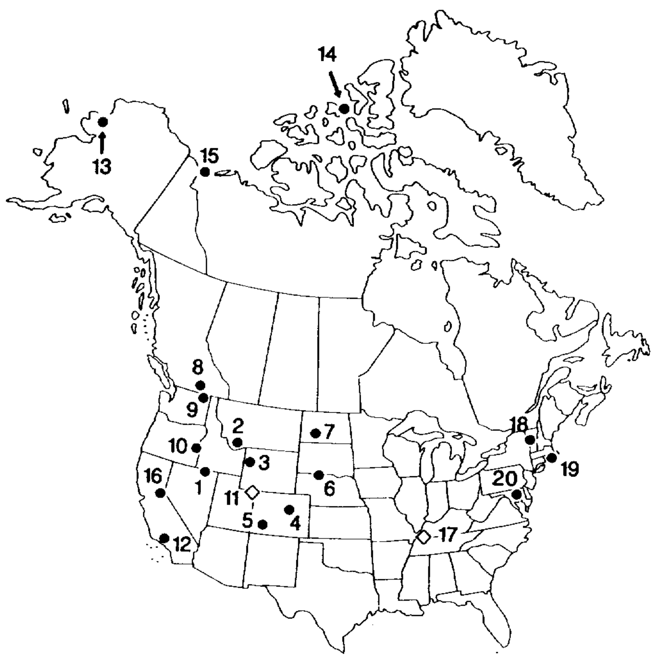

FIGURE 3.3. Location of Tertiary plant fossil formations in North America. 1 = Copper Basin, 2 = Ruby, 3 = Wind River, 4 = Florissant, 5 = Creede, 6 = Kilgore, 7 = Golden Valley, 8 = Princeton, 9 = Republic, 10 = Succor Creek, 11 = Green River, 12 = Mint Canyon, 13 = Lava Camp, 14 = Beaufort, 15 = Richards, 16 = Carson Pass, 17 = Claiborne, 18 = Brandon, 19 = Martha's Vineyard, 20 = Brandywine. ◇ = several sites in close proximity.

bridge during the late Paleocene and early Eocene (N. O. Frederiksen 1988; M. C. McKenna 1983; D. W. Taylor 1990; B. H. Tiffney 1985b). The macrofossil components of the lowland flora have primarily tropical affinities. The nearby Appalachian and Ozark highlands, however, added a substantial temperate pollen component to this lowland paleoflora. Pollen types include *Pinus, Alnus, Betula, Castanea, Corylus, Nyssa* (also present in Eocene megathermal assemblages), and *Tilia,* as well as the tropical Annonaceae (*Annona,* possibly *Cymbopetalum*), Bombacaceae (oldest records are in the eastern United States [J. A. Wolfe 1975]), *Engelhardia* (also winged fruits and catkins of *Engelhardia* and *Oreomunnea-Alfaroa* [W. L. Crepet et al. 1980]), Euphorbiaceae (*Retitricolporites* = ? *Amanoa* group), and Sapindaceae (*Cupanieidites, Duplopollis*). Macrofossils include *Nypa* (from the Laredo formation of the Claiborne group in South Texas [J. W. Westgate and C. T. Gee 1990]), *Podocarpus, Ceratophyllum* (P. S. Herendeen et al. 1990), *Dendropanax,* Fagaceae (Castaneoideae), *Ficus,* Euphorbiaceae (*Hippomaneoidea*), Gentianaceae (flowers with *Pistillipollenites* pollen), *Hura,* Lauraceae (*Androglandula* flowers with *Ocotea-Cinnamomum* affinities), Fabaceae (flowers *Eomimosoidea, Protomimosoidea*; *Crudia* [P. S. Herendeen and D. L. Dilcher 1990]), Malpighiaceae (pollen, flowers—*Eoglandulosa,* affinities possibly with subfamily Byrsonimoideae [D. W. Taylor and W. L. Crepet 1987]), *Philodendron* and *Acorites* of the Araceae, *Sabal,* Ulmaceae (*Eoceltis*), and Zingiberaceae (D. W. Taylor 1988).

The Golden Valley formation of North Dakota is of late Paleocene and early Eocene age (L. J. Hickey 1977). The macrofossils in it include *Lygodium, Hemitelia, Onoclea, Salvinia, Glyptostrobus, Metasequoia, Pinus, Acer, Betula, Carya, Cercidiphyllum, Cornus, Corylus, Dombeya, Meliosma, Palmae, Platanus, Platycarya, Pterocarya, Salix, Stillingia,* and Zingiberaceae. The flora and associated fauna are interpreted to indicate a warm temperate climate (mean annual temperature near 15° C) in the late Paleocene, and warmer subtropical conditions in the early Eocene (ca. 18.5° C). The different composition of the sequential florulas suggests the region may have been within a broad ecotonal belt between a predominantly deciduous forest to the north and a broad-leaved evergreen forest to the south (L. J. Hickey 1977, p. 72).

Another Paleocene flora from the Sentinel Butte formation near Almont, North Dakota, is under study (P. R. Crane et al. 1990), and when completed, the results will provide additional information on the Paleocene vegetation and environments of the region. In general, the tropical to warm temperate component of Paleocene and early Eocene floras from the eastern Rocky Mountain region shows affinity with eastern Asia, while by the middle Eocene the affinity is with seasonally dry vegetation of northern Latin America (E. B. Leopold and H. D. MacGinitie 1972; C. N. Miller Jr. et al. 1987; S. L. Wing 1987; J. A. Wolfe 1987b).

In western North America, lower to middle Eocene floras include the Republic flora of eastern Washington (J. A. Wolfe and W. Wehr 1987), the Princeton flora of British Columbia (S. R. S. Cevallos-Ferriz and R. A. Stockey 1989, 1990, 1990b; R. A. Stockey 1984, 1987), the Wind River flora of northwestern Wyoming (H. D. MacGinitie 1974), and the Green River flora of Colorado and Wyoming (H. D. MacGinitie 1969). The paleolatitudes of the locations and the proposed stratigraphic relationships of these and other Eocene floras in the region are summarized by D. I. Axelrod and P. H. Raven (1985, p. 23), S. L. Wing (1987, pp. 752–753), and J. A. Wolfe and W. Wehr (1987, pp. 5, 7). Collectively they reflect a seasonally dry, subtropical to warm temperate megathermal vegetation at the lower elevations, a deciduous broad-leaved mesothermal vegetation in the uplands, and locally at higher elevations a dominant coniferous element (D. I. Axelrod 1990), suggesting microthermal climates.

The Wind River flora includes *Acrostichum, Lygodium, Acalypha, Aleurites, Apeiba, Canavalia, Cedrela, Dendropanax, Eugenia, Ilex, Luehea, Machilus-Persea, Platanus, Populus, Sabalites, Saurauia, Schefflera, Sterculia,* and *Symplocos*. The Green River flora includes a more prominent coniferous element with *Picea, Pinus,* and *Tsuga*. The Princeton flora includes *Equisetum, Azolla, Glyptostrobus, Metasequoia, Pinus, Alnus,* Araceae (tribe Lasioideae), *Betula* (also from the nearby middle Eocene Allenby formation [P. R. Crane and R. A. Stockey 1987]), *Cercidiphyllum, Comptonia, Platanus, Sassafras,* and Sapindaceae (Allenby formation [D. M. Erwin and R. A. Stockey 1990]).

The Republic flora was a low montane mixed coniferous forest with the coniferous element dominant, with some lakeside or streamside broad-leaved deciduous and deciduous gymnospermous trees, plus a minor forest element of broad-leaved evergreen and broad-leaved deciduous small trees and shrubs (J. A. Wolfe and W. Wehr 1987). Among the plants were *Abies, Chamaecyparis, Ginkgo, Metasequoia, Picea, Pinus, Pseudolarix, Thuja, Acer, Cornus, Crataegus, Itea, Phoebe, Photinia,* aff. *Potentilla, Prunus, Pterocarya, Rhus, Tilia,* and *Ulmus*. The estimated elevation of the Republic flora is 700–900 m, and at that level the mean annual temperature was below 13° C, the mean of the warmest month was below 20° C, the coldest month mean was between 1° C and 2° C, and the warmest month mean was more than 15° C.

Late Paleocene macrofossil floras from Alaska are stratigraphically complex (J. A. Wolfe 1972, 1977) and include leaves similar to *Anemia, Dioön, Zamia, Glyptostrobus, Metasequoia, Pseudolarix, Acer, Carya, Corylus, Cercidiphyllum, Cocculus, Comptonia, Hypserpa, Macaranga, Palmacites, Planera, Pterocarya,* and *Sabalites*. The varied biogeographic affinities suggested by these assemblages include the Sino-Japanese region, Atlantic North America, to a lesser degree the Neotropics, and possibly Malaysia and continental Southeast Asia. The leaves are mostly evergreen and of the mesophyll size class. About 50% have entire margins, suggesting a subtropical climate. Later Paleocene floras suggest a slight cooling.

Lowland Malaysian genera are prominent in some Alaskan strata of early Eocene age, and the floras include *Alangium, Alnus, Anamirta, Barringtonia* (a tropical Pacific beach plant), *Cananga, Clerodendrum, Kandelia* (a mangrove), Lauraceae (five species), *Luvunga, Limacia, Melanorrhoea, Meliosma,* Menispermaceae (five paleotropical genera), *Myristica,* the dipterocarp *Parashorea, Phytocrene, Platycarya, Pyrenacantha, Sageretia, Saurauia, Stemonurus,* and *Tetracentron*. None are exclusively neotropical. The leaves are mostly broad-leaved evergreen. The most similar modern analogs of these floras occur in tropical or near-tropical frost-free climates with a mean annual temperature of ca. 18° C (warm mesothermal). J. A. Wolfe (1972, p. 212) applied the name Paratropical Rain Forest to the distinctive lowland vegetation. It apparently had two (rarely three) tree stories, abundant and diverse woody lianas, buttressed trees, and leaves of notophyll to mesophyll size classes and with drip-tips. Approximately 60–75% of the species had entire-margined leaves.

According to the summary by M. C. McKenna (1983, p. 469), most of the terranes south of the Denali Fault in Alaska were formed at sites far to the south and have been accreted to the North American Plate. By this view, fossil floras of Malaysian affinities on these terranes do not tell about ancient Alaska but about some other place (M. C. McKenna 1983). Indeed, the Eocene Beringian land bridge was primarily occupied by a broad-leaved deciduous forest (J. A. Wolfe 1985, cited in B. H. Tiffney 1985b) and may not have been a major route of migration for megathermal elements. A comparable situation exists with the Miocene Mint Canyon flora of southern California and the Carmel flora near Monterey, California, both of which have been displaced 200–300 km from the south (D. I. Axelrod 1986), and late Cretaceous floras from western California and British Columbia that were transported at least 2000 km (N. O. Frederiksen 1987). Paleomagnetic data cited in R. A. Spicer et al. (1987), however, suggest that the Yakutat terrane containing the plant fossils was located

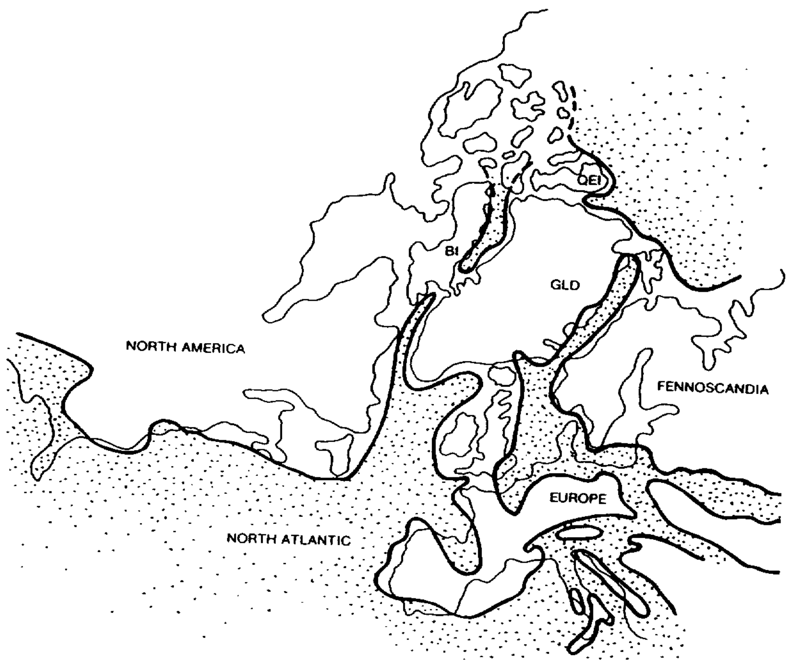

FIGURE 3.4. Paleogeography of eastern North America in the early Eocene. Stippled area = sea, heavy lines = paleocoastlines, light lines = present coastlines, BI = Baffin Island, GLD = Greenland, QEI = Queen Elizabeth Islands. [From B. H. Tiffney 1985b. Reprinted with permission from Journal of the Arnold Arboretum.]

off what is now central British Columbia and southeastern Alaska (as shown in J. A. Wolfe 1985).

From farther east, between latitudes 65° and 81° N, early Tertiary floras have been described from Ellesmere Island (R. L. Christie and G. E. Rouse 1976; S. Manum 1962), then located at about latitude 65°–70° N (J. A. Wolfe, pers. comm., 1989; 75.9° N fide M. C. McKenna 1983, p. 463), the Mackenzie River Delta (F. L. Staplin 1976; G. Norris 1982), Peel River (G. E. Rouse and S. K. Srivastava 1972), and eastern Greenland (B. E. Koch 1963; S. Manum 1962). The plants include *Abies, Glyptostrobus, Larix, Picea, Pinus, Metasequoia, Taxodium, Alnus, Betula, Castanea, Cercidiphyllum, Fagus, Liriodendron, Nyssa, Platanus, Populus, Pterocarya, Quercus, Ulmus,* and *Zelkova.* Surface marine water temperature bordering east Greenland was about 17° C in the late Cretaceous, and about 15° C bordering Ellesmere Island during the middle Eocene.

Land connection between North America and Asia existed for much of the early Tertiary via the Bering land bridge (D. M. Hopkins 1967), and perhaps until later in the Tertiary (J. T. Parrish 1987, p. 61). The latitude of the bridge, however, was ca. 75° N, some 7° farther north than the present Bering platform. It was also intermittent. Unfavorable climate and marine transgression formed a barrier in the Paleocene and middle Eocene, and the bridge was available for migration in the early and the late Eocene. Some filtering of Old World tropical to subtropical species must have occurred.

To the northeast, North America was connected to Europe by the now sundered landmass of Euramerica (fig. 3.4), which existed at the end of the Paleocene but was beginning to fragment by the early Eocene. Two routes for migration existed. There was a southern one along the Greenland-Scotland Ridge (the Thulean route, ca. 45°–50° N paleolatitude), disrupted in the early Eocene, but possibly providing land surfaces from North America east to Iceland until the Miocene. There was also a more northern route (the DeGeer route, ca. 10°–15° farther north, but still at a lower paleolatitude than Beringia), resulting from compression between Spitsbergen (Svalbard) and Greenland during the Eocene and from volcanic activities over the Iceland hotspot (M. C. McKenna 1983; B. H. Tiffney 1985b; P. A. Ziegler 1988). Migrants along this route were mostly deciduous elements through the early Oligocene, at which time the Greenland-Norwegian Sea connected with the Arctic Ocean. Prevailing climatic conditions of the two land bridges, rather than physical barriers, limited free exchange of floral elements between North America and Europe or Asia during the Tertiary. The early Eocene was the warmest interval of the Tertiary, and this was a time of rapid migration from Europe to North America over the North Atlantic land bridge (N. O. Frederiksen 1988).

Late Eocene to Late Miocene (35–10 Ma)

Analyses of Deep Sea Drilling Project cores record a significant drop in temperature in North America and elsewhere during the mid-Tertiary. The drop was particularly notable for winter minimum temperatures near the end of the Eocene, ca. 33 Ma. The lower temperature had an influence on the flora.

In the southeastern United States, the period from the middle Eocene to the early Oligocene is marked by two changes in vegetation. Fossil pollen floras record an increase in an oaklike form *(Quercoidites inamoenus)* and, more significantly, a decline in overall diversity (N. O. Frederiksen 1988). Climates fluctuated during this period (J. A. Wolfe 1978; J. A. Wolfe and R. Z. Poore 1982), but a significant cooling at the Upper Eocene–Lower Oligocene boundary (ca. 33–34 Ma) is evident.

There are several floras near the Eocene-Oligocene boundary at midlatitudes (40°–45° N) in western North America. These do not all preserve clear evidence of late Eocene cooling, because some are from localities with an insufficient number of closely spaced, sequential floras for critical comparison.

The Florissant flora of central Colorado (39° N latitude, ca. 34 Ma; H. D. MacGinitie 1953) is assigned to the latest Eocene by J. A. Wolfe and W. Wehr (1987, p. 7) and to the early Oligocene by D. I. Axelrod and P. H. Raven (1985, p. 23; S. L. Wing 1987), predating the period of climatic deterioration. It preserves an extensive flora of *Abies, Picea, Pinus, Chamaecyparis, Acer, Ailanthus, Amelanchier, Bursera, Cardiospermum, Carpinus, Carya, Castanea, Cedrela, Celastris, Celtis, Cercis, Cercocarpus, Colubrina, Crataegus, Daphne, Eugenia, Hydrangea, Lindera, Mahonia, Persea, Philadelphus, Platanus, Populus, Prosopis, Ptelea, Quercus, Ribes, Salix, Sambucus, Sapindus, Sassafras, Tilia, Trichilia, Ulmus, Vitis, Zelkova, Ziziphus,* and others. The basin of deposition was at an elevation of about 900–1000 m, with volcanic highlands to 2700 m to the immediate west. The climate at the lower elevations was warm temperate (average annual temperature 24° C), grading into cooler climates in the adjacent highlands. Annual rainfall was an estimated 525 mm. Mesic deciduous hardwoods grew along the streams and lakes, while more open vegetation occurred on the adjacent slopes. Affinities of the flora are with the temperate broad-leaved deciduous vegetation extending across into Asia and Europe north of latitude 45° N and southward where higher elevations existed, and with more subtropical vegetation farther to the south.

The Ruby Basin flora in southwestern Montana (latitude 45° N [H. F. Becker 1961]) is considered to be of middle Oligocene age (30.8–29.2 Ma [S. L. Wing 1987, p. 763]; it is approximately equivalent in age to the Florissant [J. A. Wolfe, pers. comm., 1989]) and includes many of the same elements as the Florissant flora, in addition to *Pseudotsuga, Glyptostrobus, Metasequoia, Alnus, Betula, Cornus, Fagus, Fraxinus, Myrica, Nyssa,* and others.

A last example of Eocene-Oligocene midlatitude western floras is the Copper Basin flora (ca. 40 Ma) of northeastern Nevada (ca. 42° N latitude). It contains a lake and streamside community of *Alnus, Acer, Amelanchier, Crataegus, Mahonia, Prunus,* and *Salix,* and a conifer–deciduous hardwood forest of *Sequoia, Chamaecyparis, Pseudotsuga, Cephalotaxus, Acer, Aesculus, Prunus, Sassafras,* and *Ulmus.* Montane conifers in the flora include *Abies, Picea, Pinus,* and *Tsuga.* The flora grew at an elevation of 1200 m; the climate was cool temperate (mean annual temperature ca. 11° C), and annual rainfall was between 1200 and 1500 mm.

The sequence of floras from western North America suggests the following general elevational zonation: lowlands (below ca. 300 m)—warm temperate, broad-leaved evergreen forest; 300–1000 m—temperate, mixed deciduous hardwood forest; 1000–1300 m—cool temperate, conifer–deciduous hardwood forest; and above 1300 m—cold temperate montane conifer forest with few deciduous hardwoods. Floras characteristic of the late Tertiary were in the cooler uplands during the Eocene, and they migrated into the lowland basins with the cooler climate later in the Cenozoic (D. I. Axelrod 1966).

In the Pacific Northwest (latitude 45° N), mean annual temperature is estimated to have been 12°–13° C, and in Alaska (latitude 60° N) at about 10°–11° C (J. A. Wolfe 1978).

Palynofloras from the MacKenzie Delta region of the Northwest Territories (latitude 69° N [J. C. Ritchie 1984, chap. 5]) preserve a clear record of lowering temperatures in the late Eocene. The Richards formation in this area encompasses the Eocene-Oligocene boundary. The middle Upper Eocene part of the Richards formation (G. Norris 1982) contains pollen of *Metasequoia, Picea, Pinus, Sequoia, Tsuga, Alnus, Betula, Castanea, Pterocarya, Quercus, Tilia,* and *Ulmus.* By the early Oligocene, diversity decreased sharply, and several thermophilous taxa—*Sequoia, Castanea, Quercus, Tilia,* and *Ulmus*—disappeared from this formation, only to reappear in the late Oligocene. A number of the North

American components of the Richards flora presently have their northern pollen rain limits in the Great Lakes region, reflecting the warmer climates of the late Oligocene.

A pollen flora from central British Columbia (K. M. Piel 1971) of late Oligocene age reflects a warming trend, as does the later portion of the Richards formation (fig. 3.2). The central British Columbia flora contains *Alnus, Carya, Engelhardia* type, *Juglans, Liquidambar, Pterocarya, Quercus,* and *Ulmus-Zelkova.*

The overall effect of the Eocene/Oligocene event was a southward shift of elements of the megathermal tropical vegetation, expansion of the high montane mixed coniferous forest at high latitudes and at high elevations further south, and at midlatitudes expansion of mesothermal broad-leaved temperate deciduous vegetation that would reach its maximum extent in the middle and late Miocene. The Rocky Mountains underwent intensive deformation and uplift in the Paleocene and, by the end of the Eocene, provided local highlands of significant relief (S. L. Wing 1987). The Sierra Nevada was not yet uplifted, and the volcanic pile representing the Cascade Ranges started to accumulate in the late Eocene. Their mean elevation was 700 m by the early Miocene.

Mid-Tertiary floras are rare in northeastern North America where Paleozoic and Mesozoic strata predominate. A notable exception is the Brandon lignite flora from Vermont that is of Oligocene to possibly early Miocene age (latitude 43°50' N [B. H. Tiffney 1985b; B. H. Tiffney and E. S. Barghoorn 1976; A. Traverse 1955]). The flora includes *Glyptostrobus, Pinus, Alangium, Carya, Castanea, Cyrilla, Engelhardia* type, Ericaceae, *Fagus, Gordonia, Ilex, Illicium, Juglans, Jussiaea, Liquidambar, Magnolia, Manilkara, Minusops, Morus, Nyssa, Parthenocissus, Planera, Pterocarya, Quercus, Rhamnus, Rhus, Symplocos, Tilia, Ulmus,* and *Vitis.* A warm temperate climate is inferred from this flora, in contrast to more subtropical conditions to the south. Affinities are with the broad belt of mesophyllous vegetation extending across Europe, Asia, and North America during the mid-Tertiary.

In western North America, late Oligocene plants are known from the Creede flora (27.2 Ma) of southwestern Colorado (D. I. Axelrod 1987). The flora is of interest because it provides insight into local communities of drier aspect within a region generally characterized by more humid vegetation. The flora apparently was deposited in an ecotone between a mixed conifer forest and a pinyon-juniper woodland scrub at 1200–1400 m elevation. Annual precipitation was an estimated 460–635 mm, and mean annual temperature was less than 2.5° C. J. A. Wolfe and H. E. Schorn (1989) revised this flora and state that it included *Abies, Juniperus, Picea, Pinus, Berberis, Cercis, Cercocarpus, Holodiscus, Mahonia, Populus, Prunus, Ribes, Salix, Sorbus,* and others. Affinities are mostly with the southern Rocky Mountain region, but a few elements of the flora have relationships to plants from temperate eastern Asia, eastern North America, and the Sierra Madre Occidental of Mexico. Just as the Eocene Copper Basin flora of Nevada contained cool temperate elements in the uplands that would spread during the late Tertiary period of lowering temperatures, the Oligocene Creede flora of southwestern Colorado contained elements that were able to thrive in the drier habitats that prevailed in the area during Pliocene and later times.

The final separation of continents in the Southern Hemisphere profoundly influenced the climate of the Northern Hemisphere. Sustained glaciations are evident in East Antarctica (middle Miocene). Australia separated further from Antarctica, and the Drake Passage between Antarctica and South America opened (middle Oligocene). As a result, cold water flowed northward into the southern oceans and circulated into equatorial latitudes, in turn strengthening high pressure systems and the drier climates associated with them in North America.

Drier climates and colder winters initiated the decline of tropical elements from the North American flora. The expansion of the mesothermal broad-leaved temperate forests occurred at midlatitudes. The early appearance of taxa adapting to these drier habitats was particularly evident in southwestern North America (D. I. Axelrod and P. H. Raven 1985). As the Rocky Mountains uplifted, coniferous forests characteristic of higher elevations expanded. The area of the southern Rocky Mountains and the Sierra Madre Occidental was an important center for the evolution of the Madro-Tertiary geoflora (D. I. Axelrod 1958) and for pines (D. I. Axelrod 1986b). Pollen of the Asteraceae first appeared in abundance at the Oligo-Miocene boundary (ca. 25 Ma), although some argue for an older origin (B. L. Turner 1977).

During the mid-Tertiary, a significant lowering of sea level was evident at about 30 Ma. Major volcanic activity occurred in western North America, the Andes, and the Philippines. The Mississippi Embayment, a remnant of the epeiric sea, was rapidly retreating southward. Temperate conditions continued to prevail across the North Atlantic and Beringia. Tectonic events, however, caused the further disruption of the North Atlantic land bridge. The cooling that occurred near the end of the Eocene (C. Pomerol and I. Premoli-Silva 1986) is reflected in the terrestrial vegetation of the Northern Hemisphere.

Late Miocene through Pliocene (10–2 Ma)

All through this period, a general cooling occurred. The geographic extent of the temperate deciduous hardwood forests declined from their former extensive ranges across the medium and high latitudes. Extensive grasslands appeared during this time, and at high latitudes and elevations coniferous forests continued to expand. Polar ice formed in the Arctic, and tundra elements appeared. The Sierra-Cascades reached substantial heights, and a rain shadow developed in the Great Basin. There was additional uplift in the Rocky Mountains and, at their southern end, the further development of a sclerophyllous element occurred.

The change in vegetation near the Miocene-Pliocene boundary is documented in the east by palynofloras from eastern Massachusetts (N. O. Frederiksen 1984). A middle Miocene assemblage from Martha's Vineyard represents a rich, warm temperate flora of *Abies, Picea, Pinus, Podocarpus, Tsuga, Alnus, Betula, Carya, Castanea, Fagus, Ilex, Liquidambar, Nyssa, Quercus,* and *Ulmus-Zelkova.* A Pliocene flora from the same area is depauperate and cool temperate in aspect. A similar change is evident in Miocene-Pliocene plant and animal communities across the midlatitudes of the Northern Hemisphere.

In the area that is now the plains states and provinces, colder winter temperatures were accompanied by reduced summer rains. The middle Miocene Kilgore flora from Nebraska (H. D. MacGinitie 1962) contains a valley element (*Carya, Liquidambar, Nyssa, Platanus, Populus, Tilia*), with open pine-oak grassy woodlands on the uplands. Other plants included *Acer, Celtis, Fraxinus, Prunus, Pterocarya, Ulmus,* and a more southern element of *Cedrela, Cordia, Diospyros,* and *Meliosma.* The composition suggests reduced rainfall but no well-developed prairie. Associated fossil faunas suggest frost-free climate. The affinities of this flora are with modern taxa growing east of the Rocky Mountains. Only six species of this flora are found also in Miocene floras of the Columbia Plateau, indicating that by the middle Miocene the cordillera was an effective barrier to biotic interchange between eastern and western North America.

Late Miocene to early Pliocene floras from Kansas, Nebraska, and Colorado (R. W. Chaney and M. K. Elias 1936; M. K. Elias 1942; J. R. Thomasson 1979, 1987) are not sufficiently diverse or extensive to reconstruct the vegetation in detail. The floras and associated faunas indicate the presence of savannas or savanna parklands, and temperatures that seldom, if ever, dropped to 0° C. There is no evidence to confirm the presence of treeless grasslands, semiarid conditions, and extremes of temperature that are currently characteristic of the region (J. R. Thomasson 1979).

Miocene pollen floras from the eastern foothills of the Rocky Mountains reflect an impoverished flora of *Artemisia, Sarcobatus, Ephedra, Eriogonum* (steppe, halophytic vegetation), *Salix,* Betulaceae, and riparian plants, and *Abies, Juniperus,* and *Pinus* on mountain slopes (E. B. Leopold and M. F. Denton 1987). D. I. Axelrod's (1985) summary of the grassland biome depicts a trend of gradually decreasing rainfall beginning about 16 Ma. E. B. Leopold and M. F. Denton (1987) noted that the Columbia Plateaus west of the Continental Divide consistently maintained deciduous hardwood and montane coniferous forests, both rich in woody genera. Evidence from the Great Plains east of the Rocky Mountains clearly indicates that deciduous forests with grassland elements existed in the valleys. Floristically these Great Plains floras bear little relation to those west of the Rocky Mountains.

Middle to late Miocene floras from western North America are extensive, particularly in the vicinity of the Columbia Plateau of central Oregon and adjacent regions (R. W. Chaney 1959; R. W. Chaney and D. I. Axelrod 1959). The western American, eastern Asian, and western European floras, as well as the few floras from mid- and eastern North America, record an extensive, temperate, mixed deciduous hardwood forest across the middle and high latitudes. This is the much debated Arcto-Tertiary geoflora (R. W. Chaney 1967; J. A. Wolfe 1972).

The Succor Creek flora (A. T. Cross and R. E. Taggart 1982; A. Graham 1965; R. E. Taggart and A. T. Cross 1980) of southeastern Oregon is typical of middle to late Miocene assemblages in the vicinity of the Columbia Plateau. It includes *Abies, Ginkgo, Glyptostrobus, Picea, Pinus, Tsuga, Acer, Ailanthus, Alnus, Amelanchier, Betula, Carya, Castanea, Cedrela, Celtis, Crataegus, Diospyros, Fagus, Fraxinus, Ilex, Juglans, Liquidambar, Magnolia, Mahonia, Nyssa, Ostrya, Platanus, Populus, Pterocarya, Quercus, Salix, Sassafras, Tilia, Ulmus,* and others (figs. 3.5, 3.6). Other Miocene floras east of the Cascade–Sierra Nevada ranges, and extending to British Columbia, add *Chamaecyparis, Metasequoia, Sequoia, Taxodium, Cercidiphyllum, Cinnamomum, Rosa,* and *Sorbus* (D. I. Axelrod 1986).

In the late Miocene, frost-sensitive plants such as *Cedrela* disappeared from the northern Rocky Mountains. The generic constituents of the flora on the Columbia Plateaus did not take on a modern character until at least late Pliocene (Blancan) or possibly Pleistocene times. Grassland and steppe elements (e.g., *Artemisia, Sarcobatus*) present in the region throughout the Miocene were numerically unimportant during that period. Data from the Snake River Plain indicate that grasses became sporadically abundant in the Pliocene 10 Ma after grasslands presumably developed in the Great Plains (E. B. Leopold and M. F. Denton 1987).

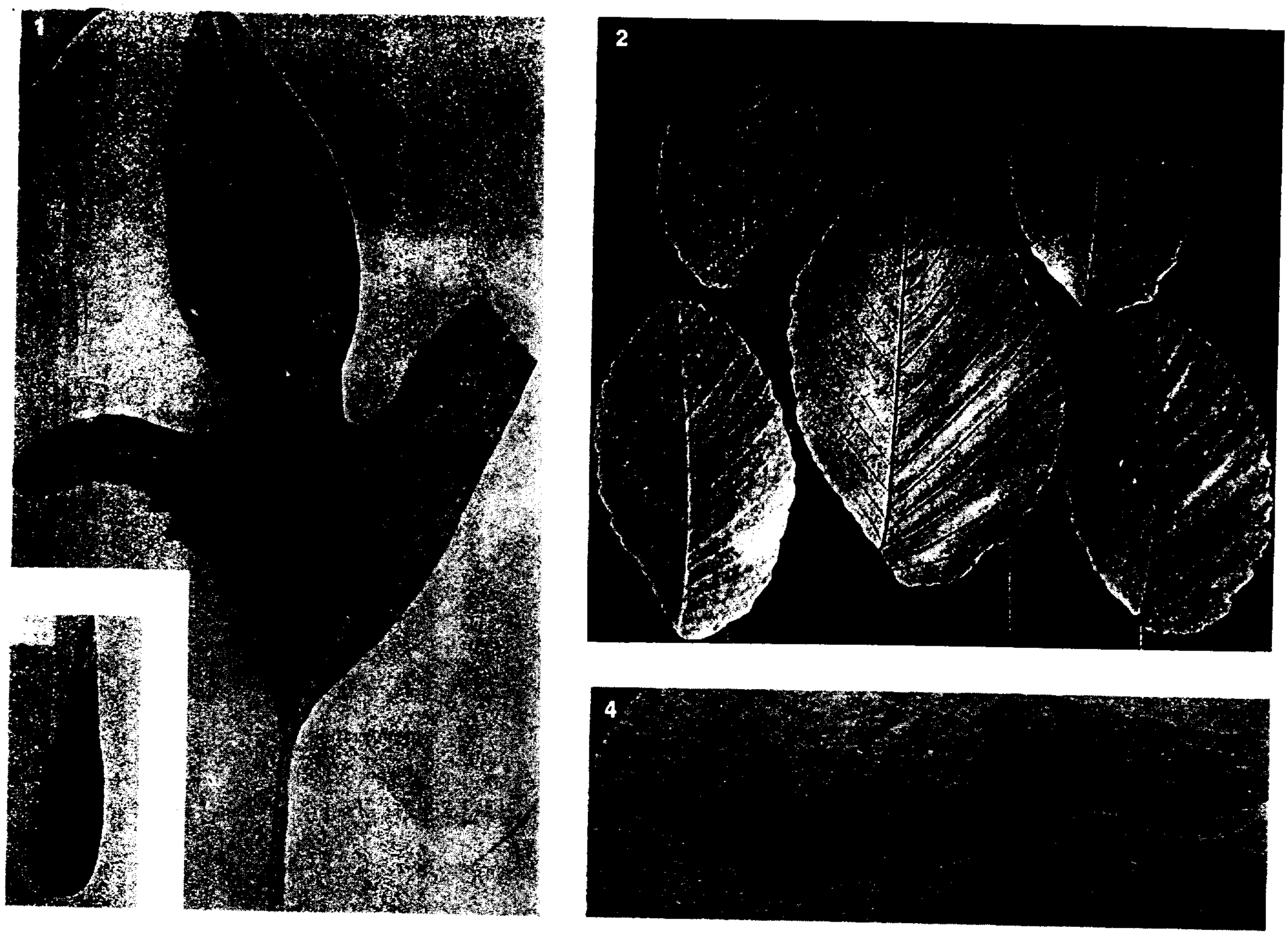

FIGURE 3.5(A). Representative specimens of plant macrofossils from the Succor Creek flora, southeastern Oregon, middle to late Miocene age. 1—*Sassafras columbiana,* 2—*Ulmus speciosa,* 3—*Fraxinus coulteri,* 4—*Acer bendirei* (=*A. chaneyi*).

In the southern Rocky Mountains, further development of the drier sclerophyllous vegetation was favored by a combination of lower minimum winter temperatures, reduced summer rainfall, and the effects of slope exposure, edaphic conditions, volcanism, and tectonic uplift. A tendency toward sclerophyllous vegetation is evident in the late Oligocene Creede flora of south central Colorado (D. I. Axelrod 1987; D. I. Axelrod and P. H. Raven 1985). The transition between the sclerophyllous vegetation to the south and the broad-leaved deciduous vegetation to the north was in central Nevada during the Miocene. Evergreen coniferous forests were prominent at high latitudes, and at high elevations further south.

With the late middle Miocene cooling, the west Antarctic Ice Sheet developed, and polar ice first appeared in the Arctic. Precursors to future tundra vegetation were evolving, and other elements coalesced into early versions of the boreal coniferous forest. Elements of the broad-leaved deciduous forest reached their maximum southern expansion in eastern Mexico.

By the beginning of the late Miocene (7–5 Ma), many Asian, neotropical, and paleotropical elements had disappeared from eastern North America. Nevertheless, the Brandywine flora of Maryland, questionably of late Miocene age, contained *Alangium, Pterocarya, Trapa,* and an *Ilex* similar to the Asian *I. cornuta* (L. McCartan et al. 1990).

In the midcontinental rain shadow to the east of the Rocky Mountains, reduced rainfall and lowered minimum winter temperatures further restricted arborescent vegetation to valley habitats. This favored continued

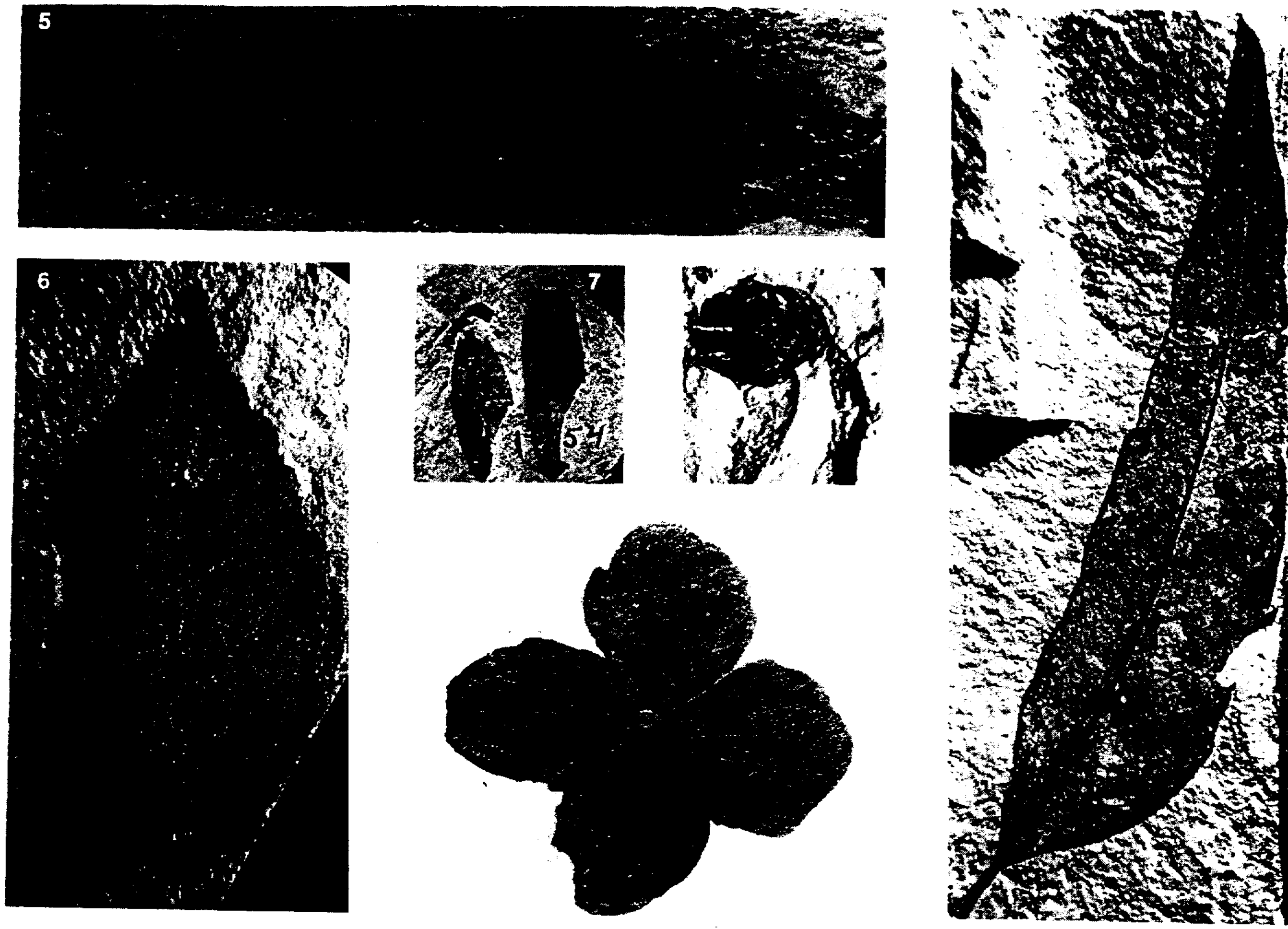

FIGURE 3.5(B). 5—*Quercus consimilis,* 6—*Betula thor,* 7—*Cedrela pteraformis* (with modern *Cedrela* seed), 8—*Glyptostrobus oregonensis,* 9—*Cedrela pteraformis,* 10—*Hydrangea bendirei.* [Photographs by author.]

development of herbaceous vegetation, but true prairie did not develop extensively until Quaternary time. Extensive grasslands probably began at the Miocene-Pliocene transition (7–5 Ma). This was the driest part of the Tertiary. Forests and woodlands were restricted, and grasses and forbs rapidly radiated (D. I. Axelrod 1985).

A middle Miocene flora from Carson Pass in the central Sierra Nevada suggests uplift of about 2300 m since that time (D. I. Axelrod 1986). In the Pliocene, the Cascade-Sierra Nevada and the Coast Ranges reached sufficient heights to create an effective rain shadow over the Basin and Range Province, resulting in a trend from mesic and summer-wet to xeric and summer-dry conditions. This trend strengthened in late Pliocene and Quaternary times. Sclerophyllous vegetation, containing elements adapted to local arid habitats since the early Tertiary, coalesced and spread across the drier low-elevation regions of southwestern North America.

Modern grassland and steppe vegetation in the Columbia Plateau region became widespread during late Pliocene (ca. 4.5 Ma) to Quaternary times (E. B. Leopold and M. F. Denton 1987). Elements of these vegetation types included *Sarcobatus* and other Chenopodiaceae, *Artemisia* and other Asteraceae, and grasses. Faunas were dominated by browsers and grazers.

As temperatures continued to decrease and rainfall became more seasonal, high elevation and high latitude coniferous evergreen forests expanded. This occurred at the expense of the broad-leaved deciduous forests,

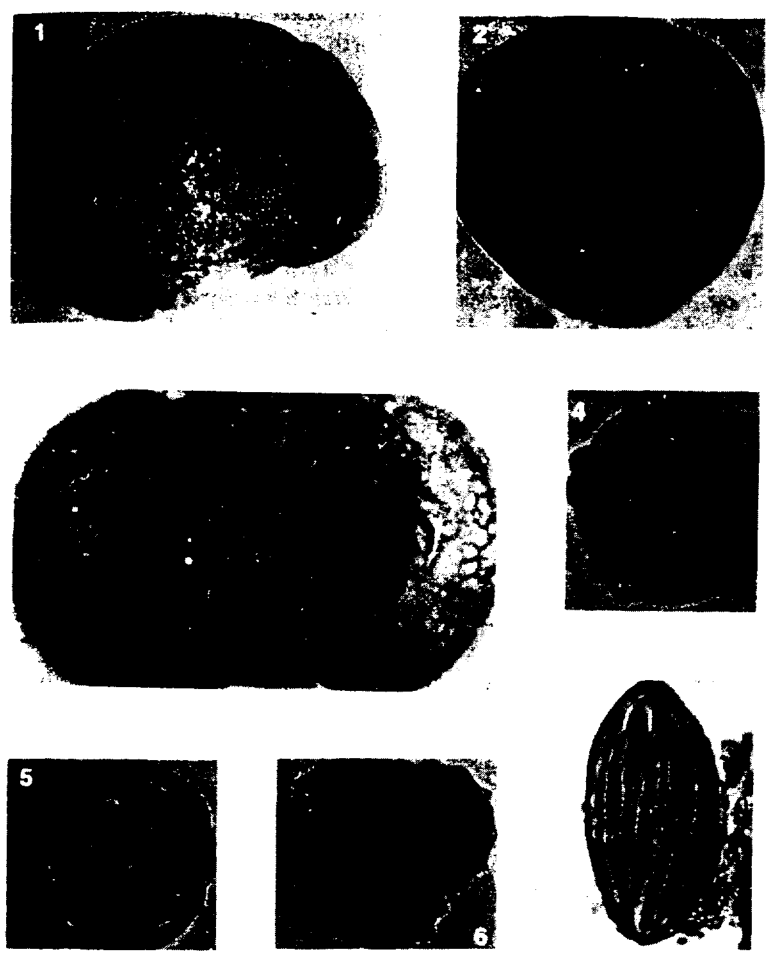

FIGURE 3.6. Representative specimens of fossil pollen grains from the Succor Creek flora, southeastern Oregon, middle to late Miocene Age. 1—*Picea*, 2—*Carya*, 3—*Pinus*, 4—*Alnus*, 5—Chenopodiaceae/Amaranthaceae, 6—*Ambrosia*, 7—*Ephedra*. [Photographs by author.]

which were eliminated from many areas of western North America during the Pliocene.

The Pliocene Lava Camp site in Alaska borders on the Arctic Ocean (D. M. Hopkins et al. 1971) and contains *Picea* and *Pinus* as the dominants, along with *Abies*, *Larix* or *Pseudotsuga*, *Tsuga*, and Cupressaceae-Taxodiaceae. Deciduous gymnosperms (*Ginkgo*, *Glyptostrobus*, *Metasequoia*) and angiosperms (*Pterocarya*), now restricted to East Asia, disappeared in the Pliocene. A narrow fringing zone of adapted tundra elements likely persisted along the expanding Arctic Ice Sheet from its initial appearance in the late Miocene, and perhaps locally along the North Slope region of Alaska, but no true tundra was evident.

The Pliocene vegetation of Alaska was largely coniferous forest. The climate was apparently cooler than that of the late Miocene. The coniferous forest disappeared from the Bering Sea area in the late Pliocene. It was replaced by an herbaceous and shrubby vegetation apparently dominated by Cyperaceae, Poaceae, Salicaceae, and Rosaceae. Typical tundra plants have not been recorded from this vegetation (J. A. Wolfe 1972). Miocene-Pliocene mosses from the Beaufort formation of Meighen Island near latitude 80° N (M. Kuc 1974) are typical of the boreal forest and not characteristic of arctic tundra.

The appearance of widespread prairie vegetation in midcontinental North America, plus sclerophyllous and coniferous vegetation in western and northern North America, was the first major disruption of the broad-leaved deciduous forest, the Arcto-Tertiary geoflora, that had extended across temperate latitudes of the Northern Hemisphere since late Eocene times. The deciduous forests of the Columbia Plateaus and those of eastern North America had been isolated geographically since at least the early Miocene by the montane coniferous forest and steppes of the Rocky Mountains and adjacent plains (E. B. Leopold and M. F. Denton 1987).

Prairie, sclerophyllous, and coniferous communities in western and southwestern North America spread during the Pliocene, and elements of the broad-leaved deciduous forest and associated fauna (particularly amphibians) that had extended into eastern Mexico during the middle to late Miocene became isolated in climatically comparable zones along the eastern escarpment of the Mexican Plateau at elevations of 1000–2000 m. In the Quaternary, versions of the modern broad-leaved deciduous forest persisted in the southeastern United States and in eastern Mexico. Thus the continuity of temperate elements of the biota, established during the middle to late Miocene cooling (A. Graham 1973b), was disrupted during Pliocene and later times, resulting in the present floristic and faunal relationship between eastern North America and eastern Mexico (A. Graham 1973; F. Miranda and A. J. Sharp 1950).

It is well known that the broad-leaved deciduous forests of eastern North America and eastern Asia are floristically related (A. Graham 1972, 1972b; A. Gray 1840, 1846; Li H. L. 1952; G. Davidse et al. 1983; B. H. Tiffney 1985; for patterns derived from molecular [isozyme] data, see M. T. Hoey and C. R. Parks 1991). This relationship was first recorded in 1750 by Linnaeus in the dissertation of his student Halenius (A. Graham 1966). It results from the maximum extension of the temperate deciduous forest in the mid-Tertiary and its disruption in western North America during the Pliocene and in western Europe during the Quaternary. The final events in the modernization of the North American flora were the climatic changes, anthropogenic influences, and vegetation responses during Pleistocene and Holocene times (see P. A. Delcourt and H. R. Delcourt, chap. 4).

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