

BIOGEOGRAPHY OF OAKS IN THE ARCTO-TERTIARY PROVINCE¹

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ABSTRACT

Numerous allied trees, shrubs, and herbs inhabit the discontinuous mixed deciduous hardwood and conifer-hardwood forests of Holarctica. Their close ancestors occupied middle and high latitudes into the Middle Miocene (15–16 m.y.a.). As the forests retreated southward and were disrupted by spreading colder and drier climates following Antarctic glaciation (13 m.y.a.), numerous paired or allied species (or sections, series) originated and have survived in the disjunct segregate forests across Holarctica. In addition, all major climatic-topographic provinces served as centers of evolution from which taxa have not ranged widely. It is this latter pattern to which oaks conform most closely. Only species of allied subsects. *Prinoideae* and *Diversipiloeseae* had an Holarctic occurrence, occupying lands above latitude 60°N during the late Cretaceous and Tertiary. Although climate was favorable for numerous deciduous hardwoods and conifers at high latitudes, taxa of most *Quercus* sections and subsections have been confined to one continent or to parts of them where they ranged somewhat more widely during the Tertiary. The rarity of Tertiary oaks linking Eurasia-North America may owe to the light factor (long day) at the north; fully four-fifths of all oak species occur below latitude 30–35°N and only six or seven reach latitude 50°N. Proliferation into 280 to 300 species was chiefly in response to spreading drier and colder climate that commenced in the middle Eocene, to increasing topographic diversity in the later Cenozoic, and to fluctuating Quaternary climate. At times of major climatic shifts or increased relief, oaks responded opportunistically, probably by quantum steps (punctuated equilibria) that account for the numerous series.

Oaks have left a rich fossil record in North America and Eurasia. This is expectable for the numerous species have hard, durable leaves that favor preservation, each large, spreading tree sheds thousands of leaves yearly, of which a few (or many) may contribute to an accumulating record, and they occur in many environments ranging from low to middle-high latitudes. Some 280 to 300 species are present today,³ with their principal areas of concentration in Mexico-Central America and southeastern Asia, and with smaller areas of differentiation in the Mediterranean Basin and southcentral United States. Oaks range from the montane tropics, where evergreen taxa are prominent, to near latitude 50°N, where oaks are deciduous; *Quercus petraea* and *robur* have the most northerly distributions, reaching latitude 60°N in the Baltic region. The trees and shrubs, both evergreen to deciduous, have adapted to climates ranging from the equable montane tropics, with a twelve-month growing season, to near the borders of subalpine and boreal forests, with a growing season of three months. In terms of precipitation, they occur in

most climates from perhumid montane tropical and temperate regions to the borders of deserts and in areas of very diverse seasonal distribution of precipitation. Some oaks are confined to specific edaphic conditions, as serpentine (*Q. durata*), sand barrens (*Q. incana*, *laevis*), limestone rocks (*Q. fusiformis*), and swamps (*Q. palustris*).

OLDER RECORDS OF FAGACEAE

Megafossils that can reasonably be assigned to the three subfamilies were in existence in the later Cretaceous. Fagoideae were then represented by *Fagus* and *Nothofagus*, Castaneoidae by *Castanea* and probably *Castanopsis* and *Lithocarpus*, and Quercoideae by *Quercus*. That Quercoideae were in existence in the Cretaceous is implied also by the occurrence of *Trigonobalanus* in the montane rain forest (elev. 1,500 m) of Colombia (A. Gentry, letter of April 1982), disjunct from Yunnan, Thailand, and Borneo; connections probably were via Africa across a narrower Atlantic on islands and old pre-Cambrian highs that have since been removed by

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³ Although some authorities state that there are 450 oak species, C. H. Mueller (pers. comm. March, 1983) believes that 250 is more nearly an acceptable figure.

erosion (Raven & Axelrod, 1974). The megafossil and distributional data agree generally with the pollen record (Muller, 1981). Pollen of the subfamilies Castaneoideae (*Castanea*, *Castanopsis*, *Lithocarpus*) and Fagoideae (*Fagus*, *Nothofagus*) occur in the Cretaceous [Santonian, 80 million years ago (Ma)]. The first reliable pollen records of Quercoidae are Oligocene, probably because the grains are not especially distinctive; certainly, undoubted oak leaves are in much older rocks.

Most *Quercus* species from older Tertiary rocks can scarcely be referred to modern species, although they foreshadow them in foliar type. Members of sects. *Leucobalanus* and *Erythrobalanus* were present in the Eocene and Paleocene, and members of subsect. *Prinoideae* were also present. Oaks were already diverse in the late Eocene, as shown by nine species in the Florissant flora (MacGinitie, 1969) that reflect adaptation to subhumid climate. Fossil leaves probably assignable to subgenus *Protobalanus* (cf. *chrysolepis*) are in the Florissant flora but are not now known from older horizons. Diversity of oaks increased in the Oligocene and by the Miocene many essentially modern species were present. Records of their past distribution provide reliable clues to the Tertiary history of the genus.

NEOGENE DISTRIBUTION PATTERNS IN HOLARCTICA

To evaluate the historical biogeography of oaks in the temperate forests of the Northern Hemisphere, it is appropriate to review the distribution of taxa associated with them and that still live with their descendants. Neogene floras of middle and higher latitudes are made up of species derived chiefly from mixed deciduous hardwood forests that gave way to conifer-hardwood and then to pure subalpine conifer forests in cooler regions. Many of the fossil floras occur now in areas that support sclerophyll woodland, steppe, grassland, desert, taiga, and tundra vegetation that displaced the rich temperate forests as conditions became drier and colder following the middle Miocene. The general composition of the Neogene floras reviewed here is in terms of the geographic occurrences of modern taxa allied to fossil species, with special note taken of the presence of oaks in floras that are scattered across Holarctica. It is these occurrences that clarify their history.

Numerous fossil species recorded in Neogene floras of the far West are similar to taxa now in the eastern United States (Fig. 1). These species

of *Alnus*, *Acer*, *Carpinus*, *Carya*, *Diospyros*, *Fagus*, *Hamamelis*, *Ilex*, *Juglans*, *Liriodendron*, *Magnolia*, *Nyssa*, *Ostrya*, *Persea*, *Prunus*, *Quercus* (cf. *bicolor*, *borealis*, *coccinea*, *falcata*, *imbricaria*, *muhlenbergii*, *prinus*, *velutina*), *Sassafras*, *Taxodium*, and *Ulmus* occur at many localities. They were associated with forest trees and shrubs similar to those now in the West, distributed in *Abies*, *Alnus*, *Chamaecyparis*, *Cornus*, *Fraxinus*, *Gaultheria*, *Picea*, *Populus*, *Quercus* (*chrysolepis*, *kelloggii*, *gambelii*, *lobata*), *Sequoia*, *Tsuga*, *Vaccinium*, and others.

Associates of the Neogene species in the western United States (Fig. 1) also included taxa whose nearest counterparts are now in eastern Asia (Fig. 2), notably species of *Alnus*, *Betula*, *Cercidiphyllum*, *Exbucklandia*, *Ginkgo*, *Hydrangea*, *Ilex*, *Lindera*, *Paulownia*, *Phoebe*, and *Zelkova*.

Fossil oaks in the Neogene of the West previously reported to have Asian affinities (e.g., *Q. myrsinaefolia*, *Q. stenophylla*) need reexamination; most of the records certainly are not of Asian alliance. Furthermore, the absence of oaks in the Paleogene of Alaska, apart from species of subsects. *Prinoideae*-*Diversipiloseae*, raises a problem as to the identity of Paleogene oaks (e.g., *Q. nevadensis* Lesq.) previously suggested to have southeast Asian affinity. Actually, the nervation of *Q. nevadensis* shows it is more nearly allied to *Lithocarpus densiflorus* than to *Q. glauca*, with which it has been compared; this implies a probable late Cretaceous connection with east Asia, probably via Europe and across a narrower Atlantic. The Paleogene La Porte, Weaverville, and Goshen floras of western California and Oregon have oaks that have been compared with Mexican species, as *Q. durangensis*, *conzattii*, *magnoliaefolia*, and *xalapensis*.

In western Europe, there are fossil records of species similar to those now in the eastern United States (Fig. 3), distributed in *Acer*, *Berchemia*, *Betula*, *Carya*, *Diospyros*, *Fagus*, *Juglans*, *Liquidambar*, *Liriodendron*, *Magnolia*, *Morus*, *Nyssa*, *Ostrya*, *Persea*, *Picea*, *Quercus* (*prinus*), *Sabal*, *Sassafras*, *Taxodium*, and *Ulmus*. Their associates included taxa allied to those now in western Europe, distributed in *Acer*, *Betula*, *Cornus*, *Larix*, *Pinus*, *Populus*, *Quercus* (*petraea*, *pubescens*, *robur*), or in the extended Mediterranean (Tethyan) region, notably *Abies*, *Acer*, *Callitris*, *Carpinus*, *Castanea*, *Cedrus*, *Celtis*, *Cercis*, *Cornus*, *Fraxinus*, *Juglans*, *Parrotia*, *Pinus*, *Platanus*, *Ostrya*, *Quercus* (*castanaefolia*, *cerris*, *coccifera*, *ilex*, *libani*, *mirbeckii*, *sessiflora*, *suber*), and *Zelkova*.

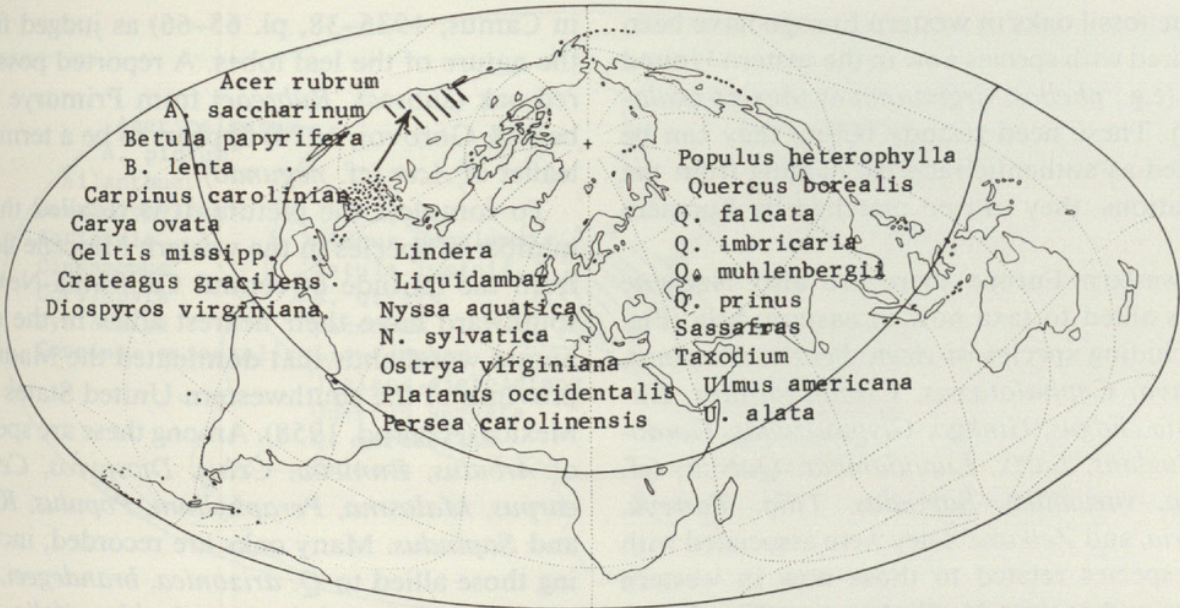


FIGURE 1. Many taxa now in eastern United States are represented by closely similar species in Neogene floras of the Far West.

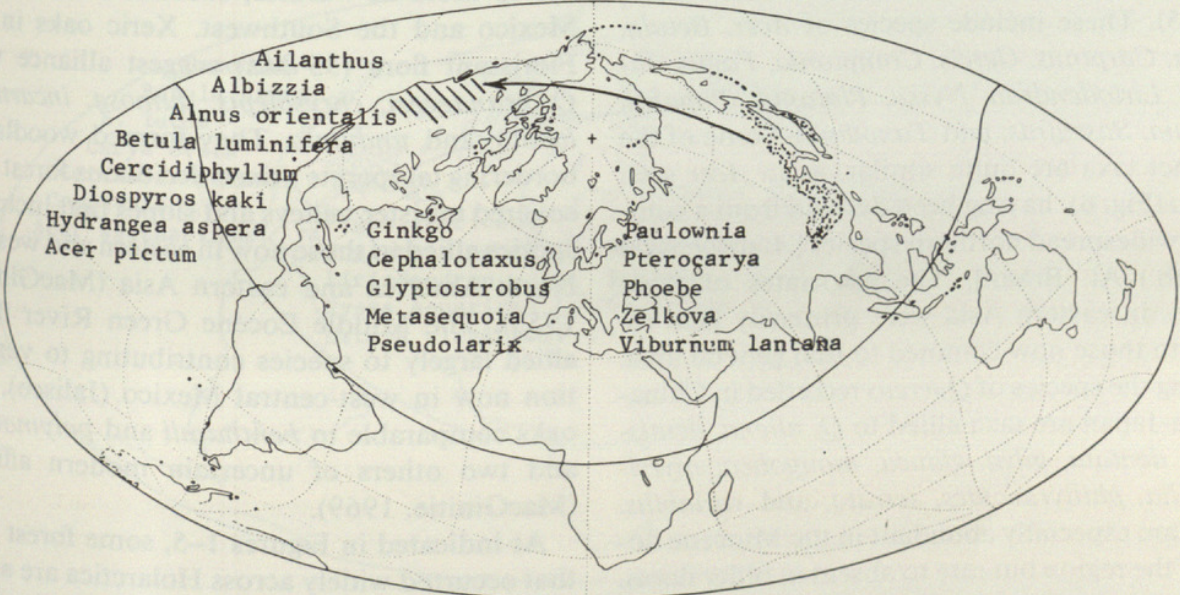


FIGURE 2. Numerous taxa now in eastern Asia have close counterparts in western Miocene floras.

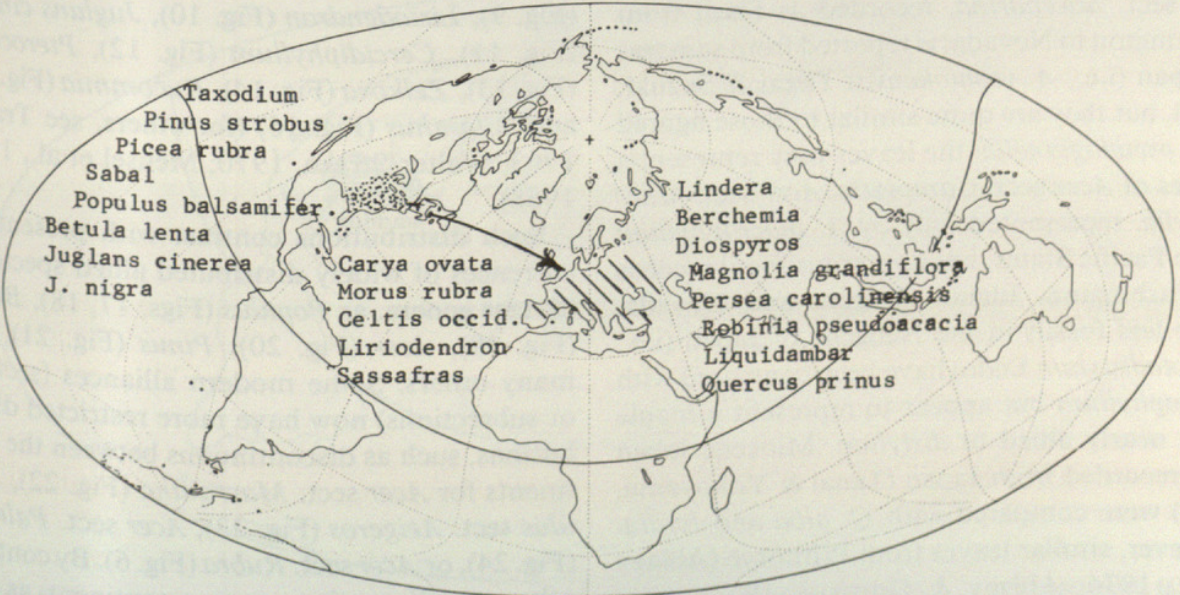


FIGURE 3. Many species now in eastern United States have similar species in the Neogene of western Eurasia.

Some fossil oaks in western Europe have been compared with species now in the eastern United States (e.g., *phellos*, *virginiana*) or Mexico (*xalapensis*). These need restudy before they can be accepted as authentic records; judging from the illustrations, they can be matched by Eurasian taxa.

In western Europe there are also Neogene species allied to taxa now in eastern Asia (Fig. 4), including species of *Acer*, *Betula*, *Carpinus*, *Cathaya*, *Cephalotaxus*, *Cinnamomum*, *Eucommia*, *Fagus*, *Ginkgo*, *Glyptostrobus*, *Gordonia*, *Juglans*, *Larix*, *Liquidambar*, *Quercus* (cf. *serrata*, *variabilis*), *Sapindus*, *Tilia*, *Torreya*, *Wisteria*, and *Zelkova*. They were associated with fossil species related to those now in western Europe and eastern North America (Fig. 3).

There also are Neogene fossils in Japan that are allied to taxa now in the eastern United States (Fig. 5). These include species of *Acer*, *Betula*, *Carya*, *Carpinus*, *Cercis*, *Comptonia*, *Fagus*, *Juglans*, *Liriodendron*, *Nyssa*, *Platanus*, *Populus*, *Robinia*, *Sassafras*, and *Taxodium*. Some of the disjunct taxa are quite similar, as in *Acer* sect. *Rubra* (Fig. 6), having been derived from a common, widespread northern species [*A. trilobatum* (Sternb.) Al. Braun]. The associates of these species in eastern Asia were primarily taxa related to those now confined to that general area. Among the species of *Quercus* recorded in China-Korea-Japan are taxa allied to *Q. aliena*, *acutissima*, *dentata*, *gilva*, *glauca*, *mongolica*, *myrsinaefolia*, *phillyraeoides*, *serrata*, and *variabilis*. They are especially abundant in the Miocene floras of the region but rare to absent in older floras.

Some reports of otherwise wholly temperate American taxa in Japan probably are not valid. *Acer* sect. *Saccharina*, recorded as fossil from Washington to Nevada, is reported from samaras in Japan (i.e., *A. yoshiokensis*, Tanai & Suzuki, 1960), but they are quite similar to those figured as *A. pseudogianella*; the leaves may represent a species of *Acer* sect. *Campestre*. *Acer* sect. *Macrophylla*, represented only by *A. macrophyllum* of the Pacific States, has numerous fossil records in Washington, Idaho, Oregon, and Nevada. Some leaf fossils in the Neogene of Japan (i.e., *A. protodistylum* Endo) have been compared with *macrophyllum* but appear to represent a maple more nearly allied to *distylum*. Miocene lobed oaks recorded from Japan (Tanai & Yokoyama, 1975) were compared with *Q. alba* and *lyrata*. However, similar leaves from Primorye (Ablaev et al., 1974; Ablaev & Gorovoi, 1974) more probably represent sect. *Cerris* (cf. *Q. cerris* L.,

in Camus, 1936–38, pl. 65–66) as judged from the nature of the leaf lobes. A reported possible red oak (subject. *Rubrae*) from Primorye (Ablaev & Gorovoi, 1974) appears to be a terminal leaflet of *Acer* (cf. *negundo*).

To complete the picture, it is recalled that a number of species in the western Miocene floras from the latitude of central California-Nevada southward have their nearest allies in the subhumid woodlands that dominated the Madrean province of the southwestern United States and Mexico (Axelrod, 1958). Among these are species of *Arbutus*, *Bumelia*, *Celtis*, *Diospyros*, *Cercocarpus*, *Malosma*, *Peraphyllum*, *Populus*, *Rhus*, and *Sapindus*. Many oaks are recorded, including those allied to *Q. arizonica*, *brandegeei*, *dumosa*, *emoryi*, *mohriana*, and *oblongifolia*. The Paleogene floras in the interior include taxa similar to those in warmer, subhumid climates of Mexico and the Southwest. Xeric oaks in the Florissant flora (35 Ma) suggest alliance with *Q. brandegeei*, *chrysolepis*, *dumosa*, *incarnata*, *lobata*, and *undulata*. They formed woodlands bordering temperate mixed deciduous forest that covered moister valleys and slopes that included species allied to those now in eastern and western North America and eastern Asia (MacGinitie, 1953). The Middle Eocene Green River flora, allied largely to species contributing to vegetation now in west-central Mexico (Jalisco), has oaks comparable to *benthamii* and *polymorpha* and two others of uncertain modern affinity (MacGinitie, 1969).

As indicated in Figures 1–5, some forest taxa that occurred widely across Holarctica are allied to species now in relict or restricted areas, such as *Ginkgo* (Fig. 7), *Pseudotsuga* (Fig. 8), *Sequoia* (Fig. 9), *Liriodendron* (Fig. 10), *Juglans cinerea* (Fig. 11), *Cercidiphyllum* (Fig. 12), *Pterocarya* (Fig. 13), *Zelkova* (Fig. 14), *Eucommia* (Fig. 15), and *Ailanthus* (Fig. 16) (for others, see Tralau, 1963; Walter/Straka, 1970; Meusel et al., 1965, 1968).

Such distributions contrast with present occurrences of widely distributed allied species of diverse genera, as *Populus* (Figs. 17, 18), *Betula* (Fig. 19), *Acer* (Fig. 20), *Pinus* (Fig. 21), and many others. Some modern alliances (sections or subsections) now have more restricted distributions, such as discontinuous between the continents for *Acer* sect. *Macrantha* (Fig. 22), *Populus* sect. *Aeigeros* (Fig. 23), *Acer* sect. *Palmata* (Fig. 24), or *Acer* sect. *Rubra* (Fig. 6). By contrast, others are discontinuous on a continent, as *Acer* sect. *Saccharina* (Fig. 25). Some sections or sub-

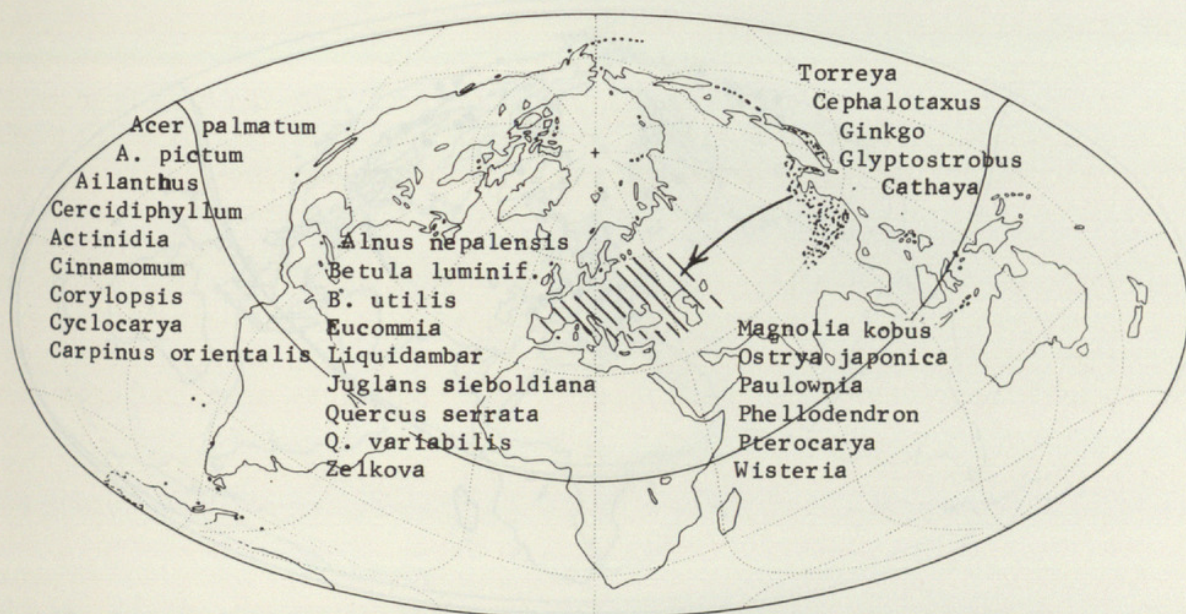


FIGURE 4. Many taxa now in the Far East occur in fossil floras of Europe and border areas.

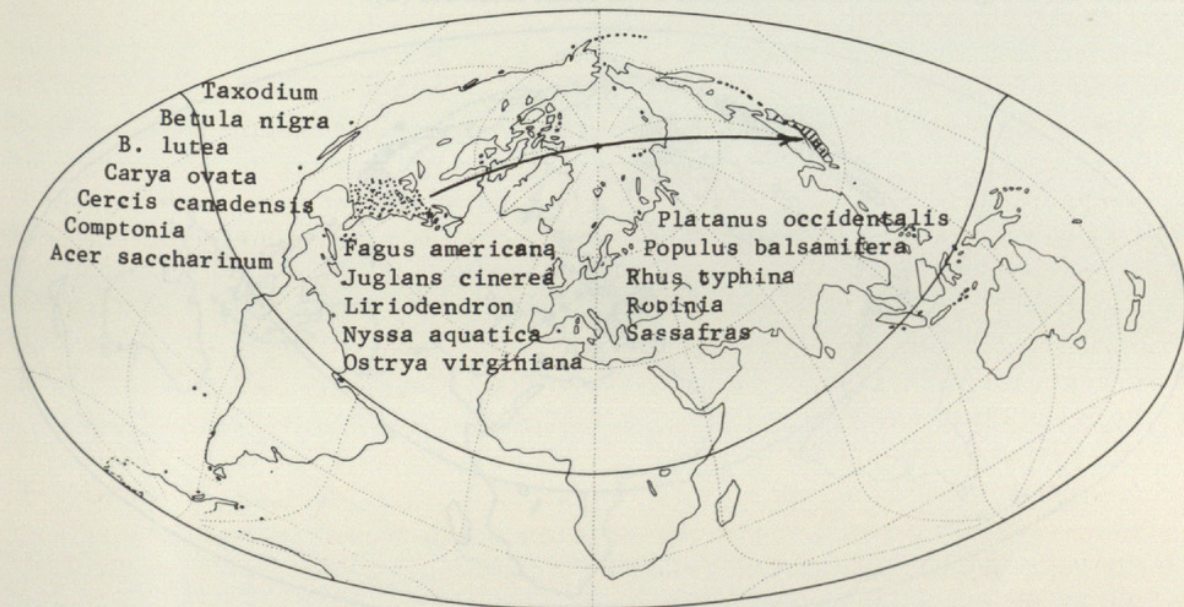


FIGURE 5. A number of species now in eastern United States have close counterparts in Neogene floras of Japan.

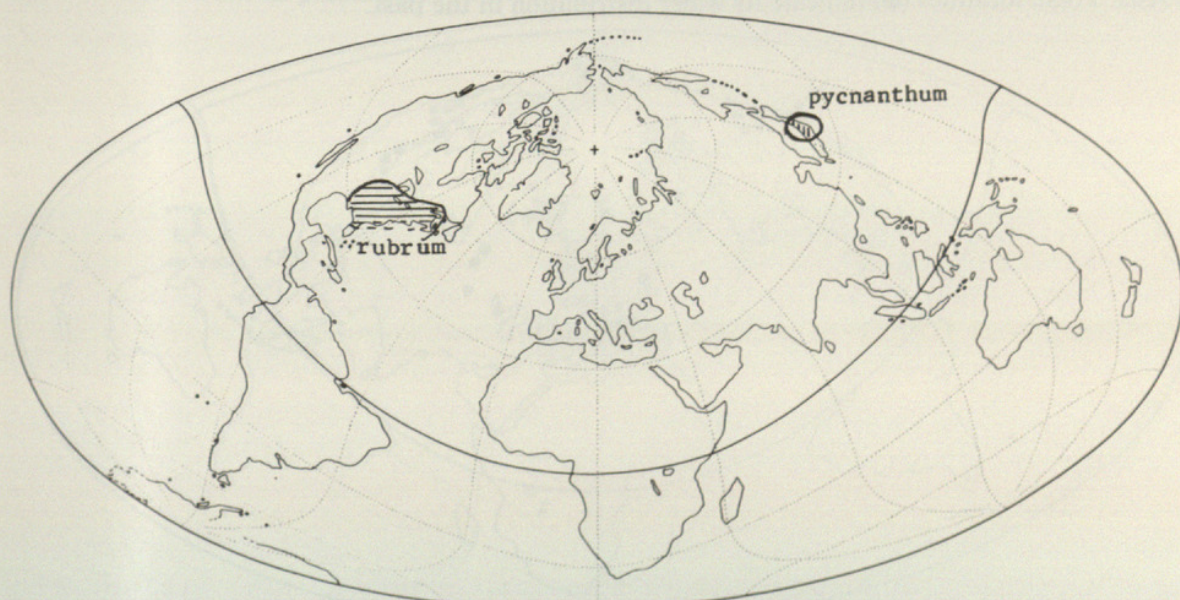


FIGURE 6. Disjunct maples of *Acer* sect. *Rubra* ser. *Rubra* imply a wider distribution for the ancestral taxon, a relation confirmed by the wide distribution of red maple in Eocene and later floras.

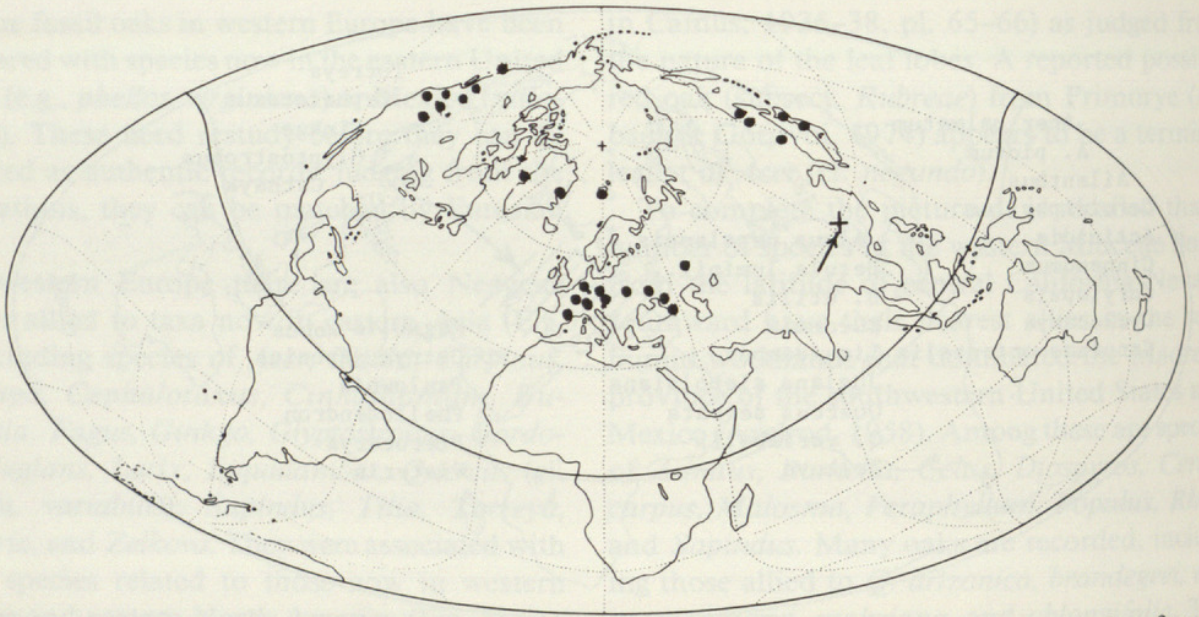


FIGURE 7. *Ginkgo*, now confined to eastcentral China (+), had a wide Holarctic distribution from the Paleocene into the Neogene as indicated by some of its fossil localities (●).

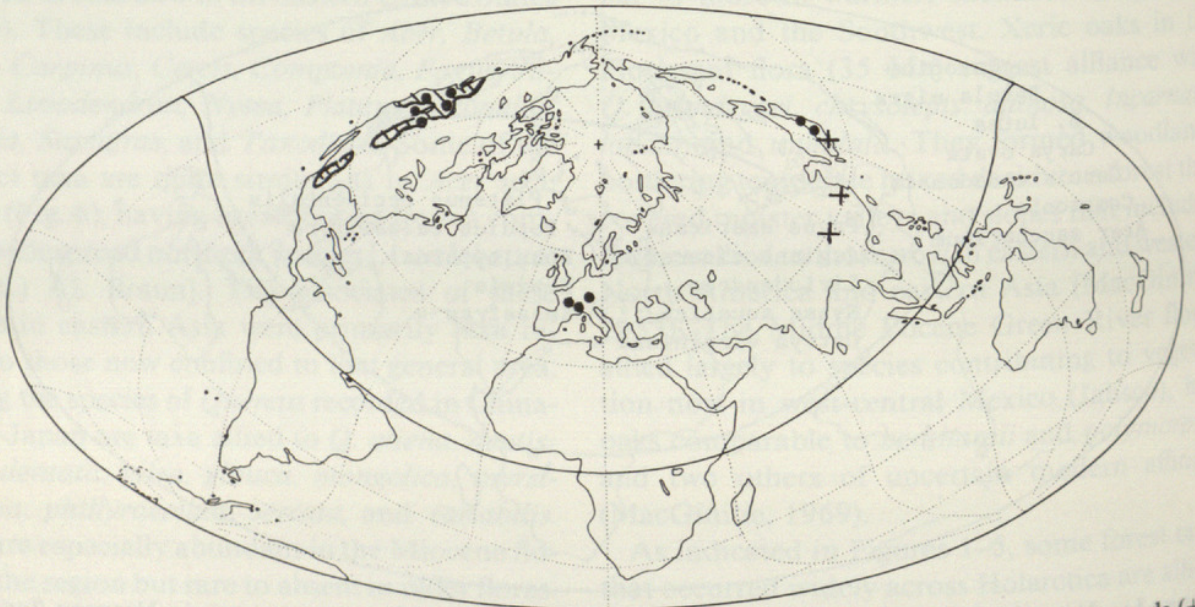


FIGURE 8. *Pseudotsuga* is widespread today in western North America but has only relictual stands (+) in eastern Asia. Fossil localities (●) indicate its wider distribution in the past.



FIGURE 9. *Sequoia*, confined now to coastal California and adjacent Oregon, had an Holarctic Tertiary distribution as indicated by some of its fossil sites (●).



FIGURE 10. *Liriodendron* is disjunct between the eastern United States and China. Some of its fossil localities (●) shown here attest to its former Holarctic occurrence.

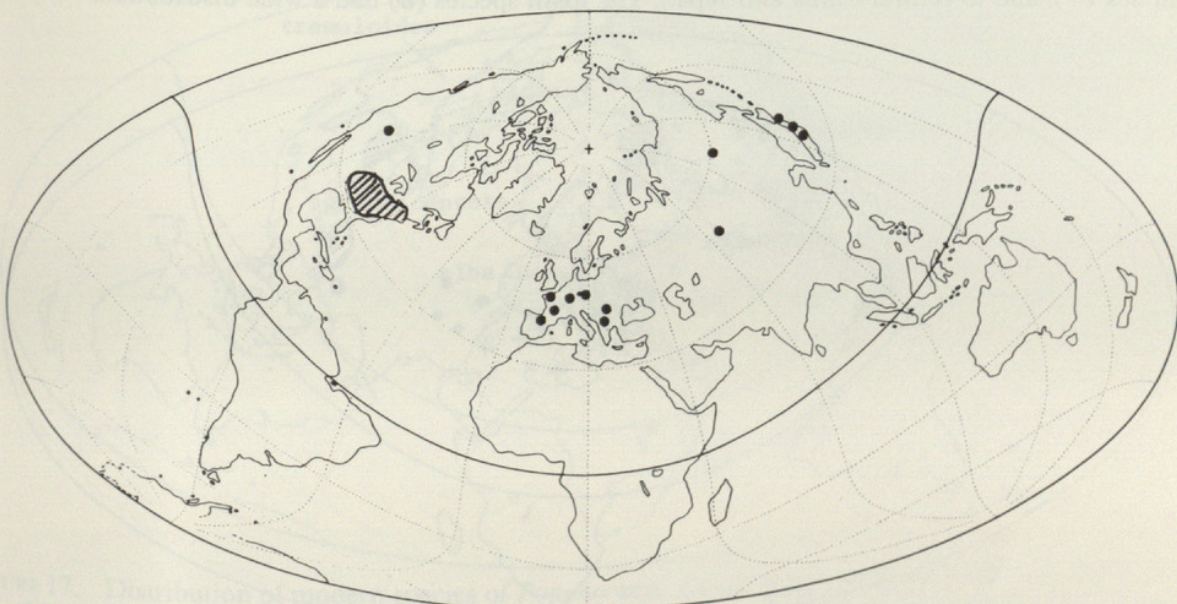


FIGURE 11. The distinctive fruits of butternut, *Juglans cinerea*, have been recovered at a number of Neogene sites (●) far removed from its present area in the eastern United States.



FIGURE 12. *Cercidiphyllum*, confined now to central China (+) and Japan, has been recorded at numerous sites across Holarctica, some of which are indicated (●).



FIGURE 13. *Pterocarya* species are confined now to eastern Black Sea region (+), the south shore of the Caspian Sea (+), and to central China and Japan. The fossil species (●) had a wide distribution.



FIGURE 14. Species of *Zelkova* had a wide distribution into the later Neogene (●) but are restricted now to the eastern Mediterranean-Caspian Sea region (+) and to China, Japan-Korea.



FIGURE 15. Neogene fossil localities (●) for *Eucommia*, a relictual genus confined now to central China.

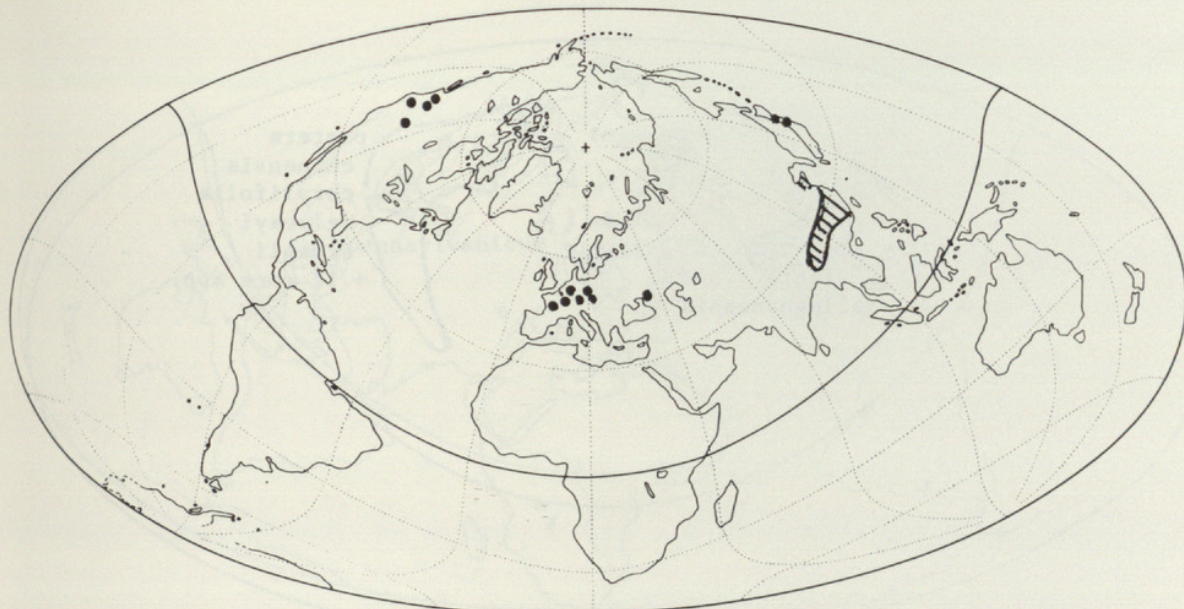


FIGURE 16. *Ailanthus*, now native to China, has been recovered at a number of Neogene sites (●).

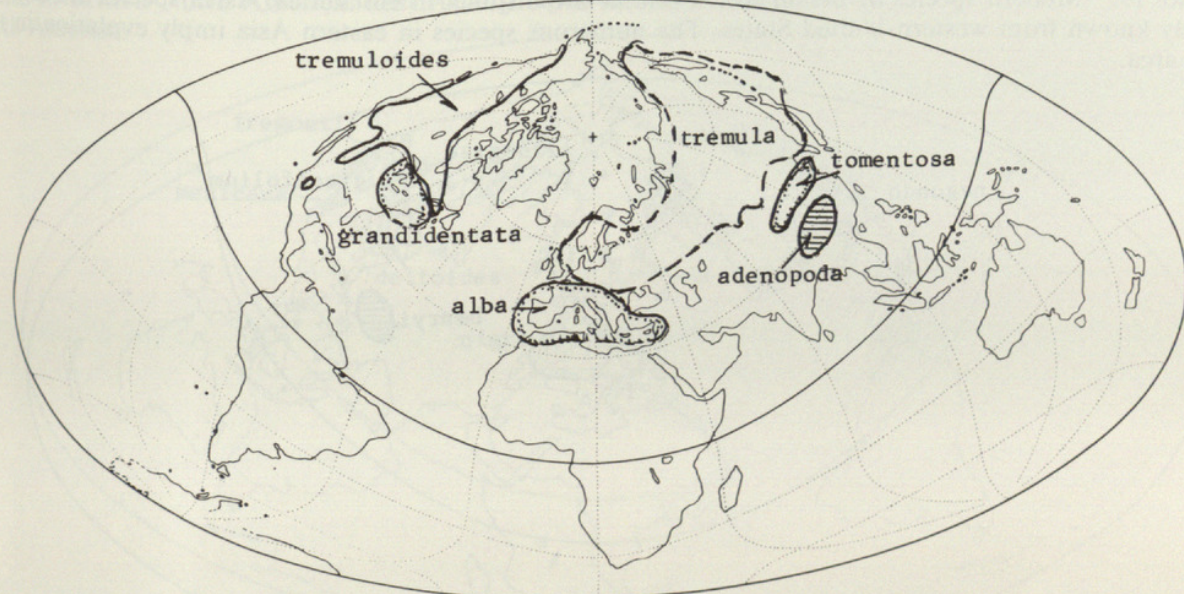


FIGURE 17. Distribution of modern species of *Populus* sect. *Leuce*, most of which are represented by similar taxa in Miocene floras of Asia and North America. The fossil record suggests that these diverged from an ancestral taxon in the Eocene, or possibly earlier.

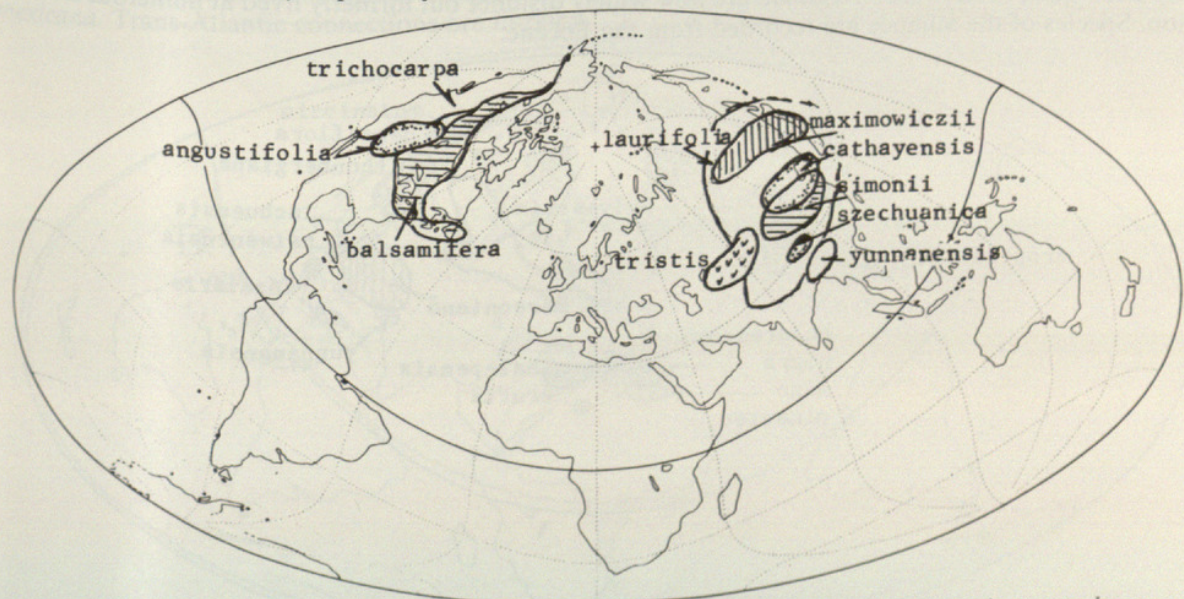


FIGURE 18. General distribution of species of *Populus* sect. *Tacamahaca*. The American species are represented by similar fossils over a wide area in western North America. Asian poplars of this group are not now certainly known from North America.

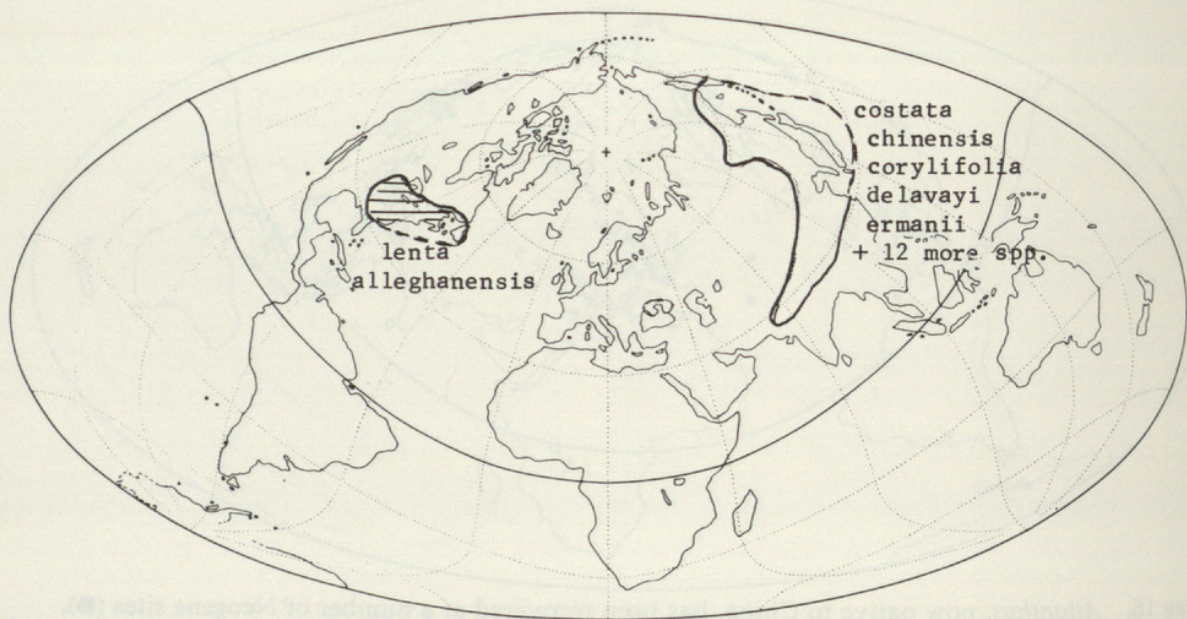


FIGURE 19. Modern species of *Betula* sect. *Costatae* are disjunct in Holarctica. Asian species are not now definitely known from western United States. The numerous species in eastern Asia imply evolution in that general area.

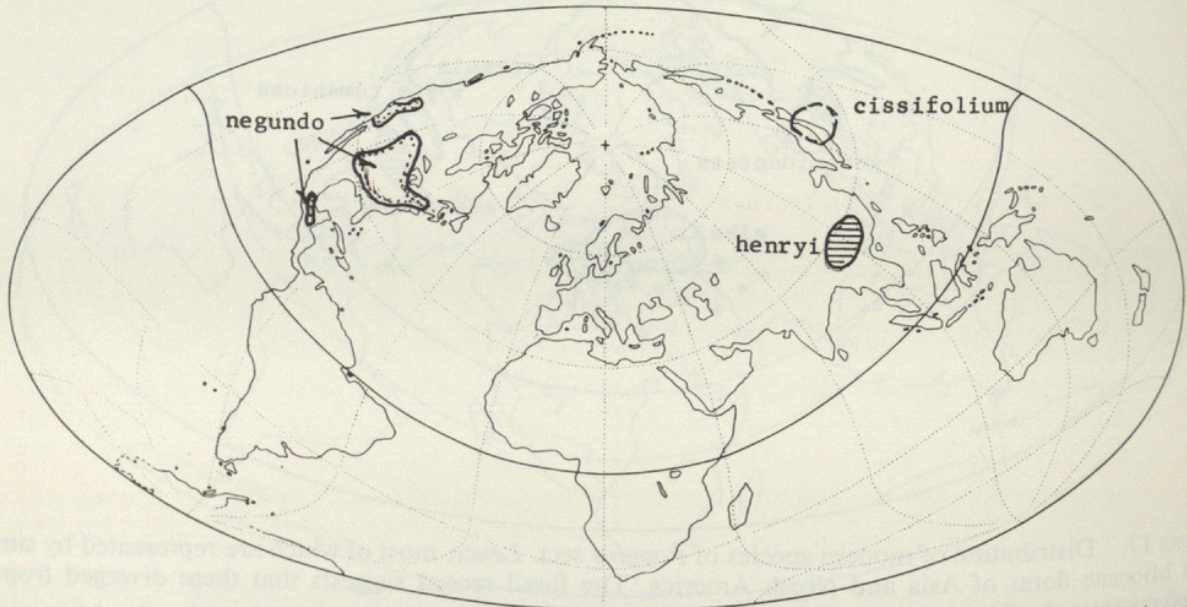


FIGURE 20. Taxa of *Acer* sect. *Negundo* are now widely disjunct but formerly lived at numerous sites across the region. Species of the alliance are recorded from the Eocene.

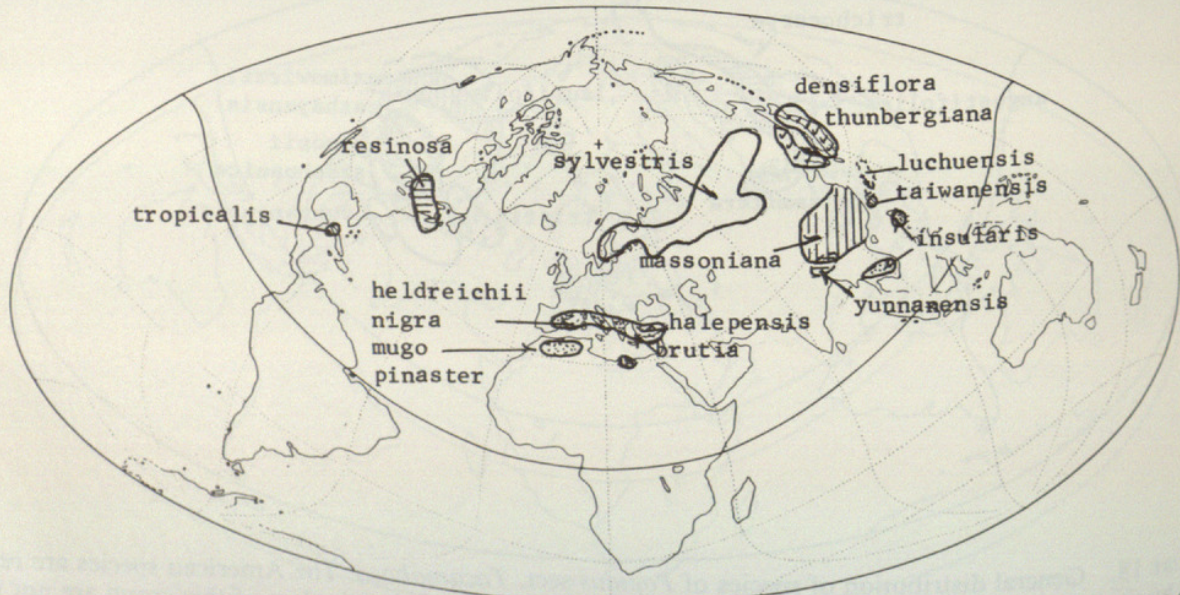


FIGURE 21. The wide distribution of species of *Pinus* subsect. *Sylvestres* implies an ancient dispersal for an ancestral group, probably in the Late Cretaceous.

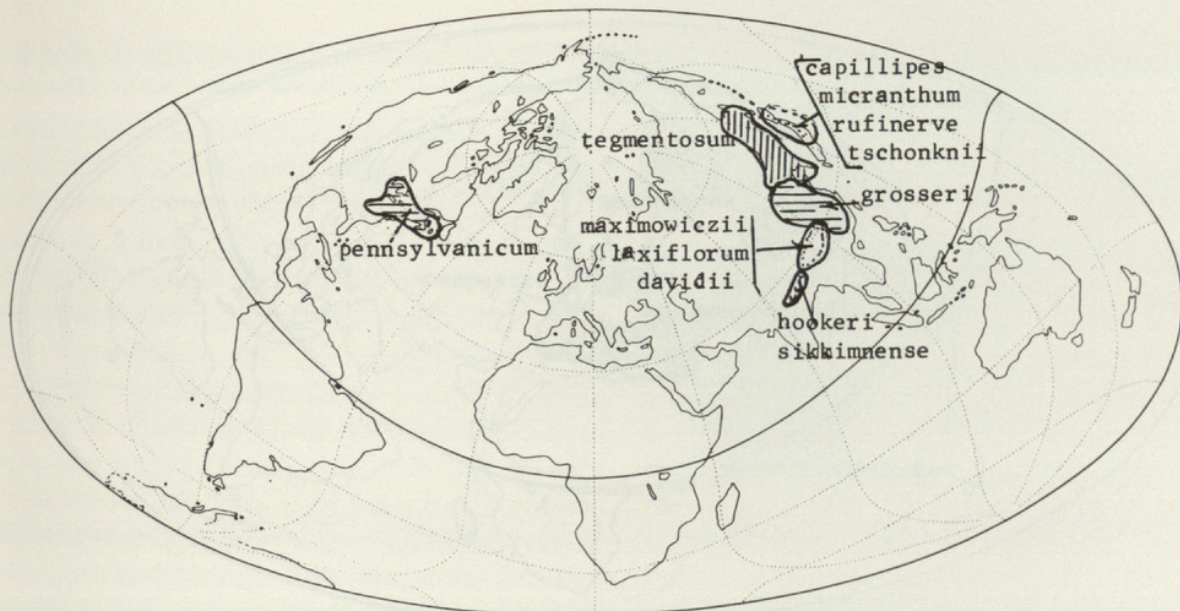


FIGURE 22. Species of *Acer* sect. *Macrantha* ser. *Macrantha* are concentrated in eastern Asia, with a single species in eastern North America. East Asian maples of this alliance are not presently known from western North America.

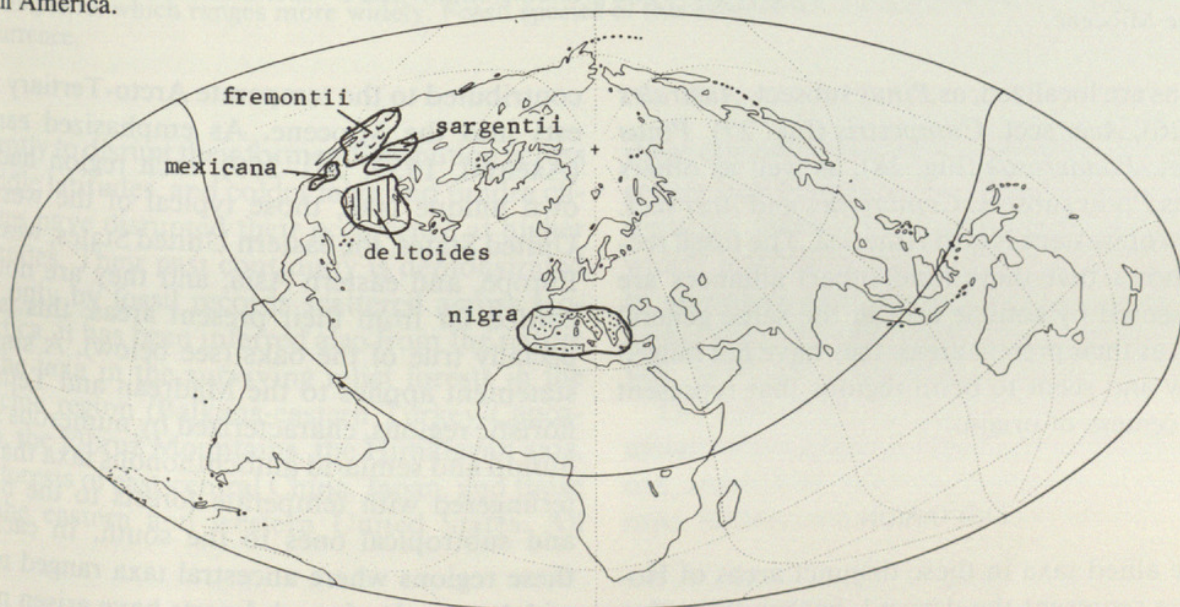


FIGURE 23. Species of *Populus* sect. *Aigeros* are disjunct across the Atlantic. Taxa of both alliances have been recorded as fossil in their respective regions and some have ranged more widely, as fossil species allied to *P. mexicana*. Trans-Atlantic connections are implied.

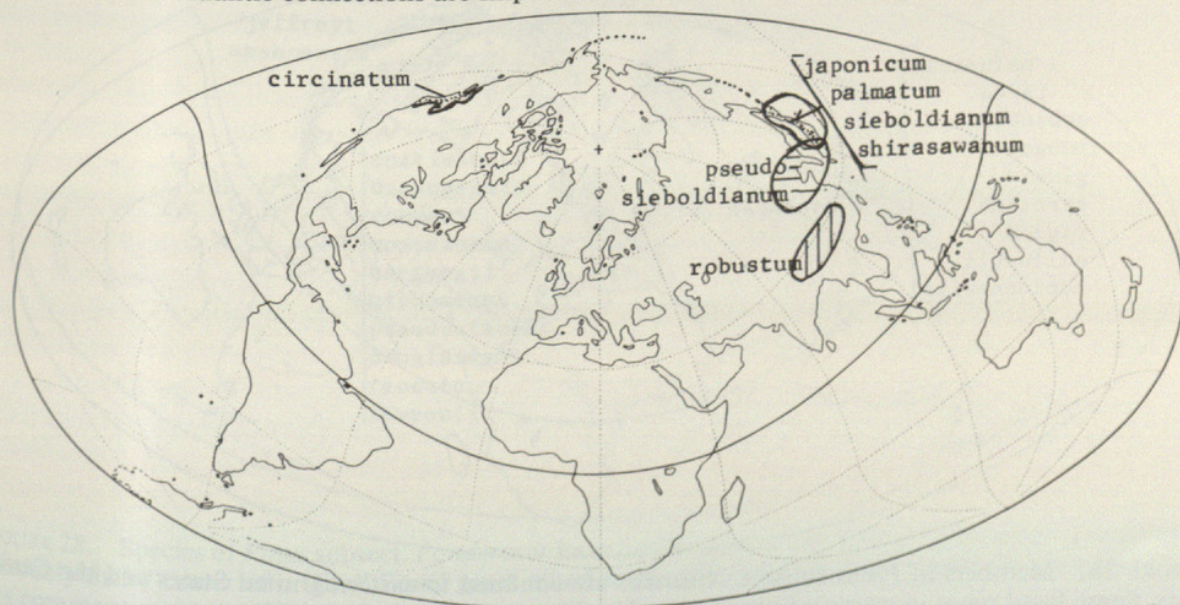


FIGURE 24. Species of *Acer* sect. *Palmata* ser. *Palmata* are concentrated in eastern Asia, with one along the Pacific Coast of North America. A species of this series occurs in the Eocene of Nevada.

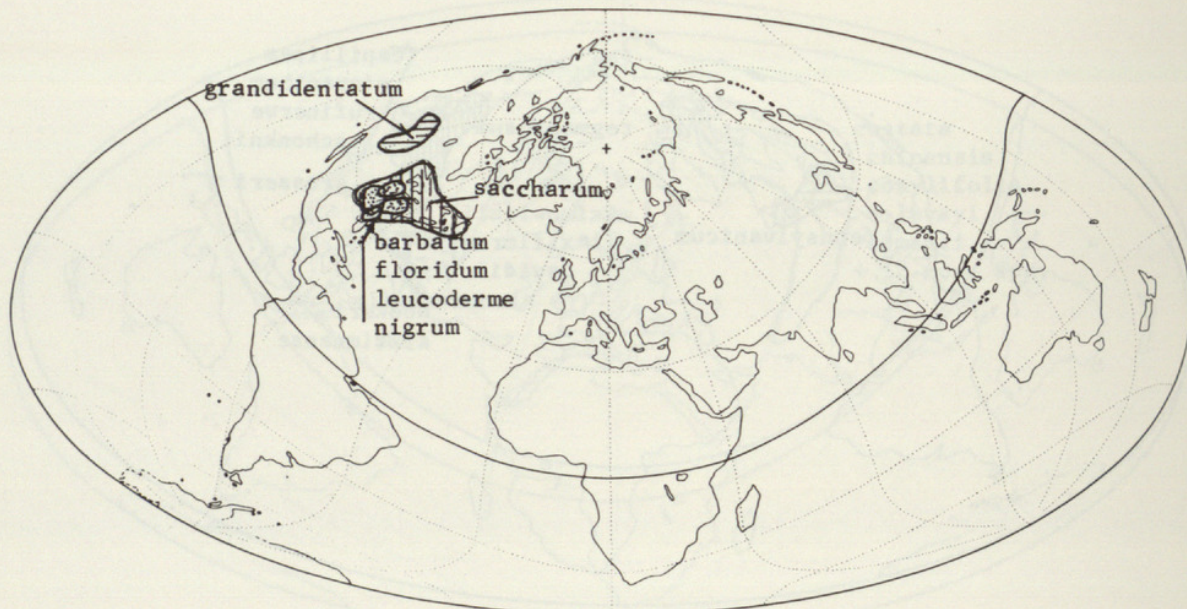


FIGURE 25. *Acer* sect. *Saccharina* is represented by disjunct taxa now in the Cordilleran region and eastern North America. Fossil species allied to *saccharum* and *grandidentatum* had a wider distribution in the far West into the Miocene.

sections are localized, as *Pinus* subsect. *Australes* (Fig. 26), *Acer* sect. *Campestris* (Fig. 27), *Pinus* subsect. *Ponderosae* (Fig. 28), as well as others such as *Pinus* subsect. *Cembroides* and *Acer* sect. *Glabra* of western North America. The fossil record shows that these (and other) alliances are represented by similar taxa in the same general region as their present areas: they have not ranged widely and seem to be in regions that represent their centers of origin.

DISCUSSION

The allied taxa in these disjunct areas of Holarctica represent the derived, broken links that

contributed to the temperate Arcto-Tertiary forests into the Miocene. As emphasized earlier (Axelrod, 1959: 261–269), each region had its own unique taxa, those typical of the western United States, the eastern United States, western Europe, and eastern Asia, and they are not recorded far from their present areas: this is especially true of the oaks (see below). A similar statement applies to the Madrean and Tethyan floristic regions, characterized by numerous sub-humid and semiarid autochthonous taxa that interfingered with temperate forests to the north and subtropical ones to the south. In each of these regions where ancestral taxa ranged more widely, grasslands and deserts have arisen more

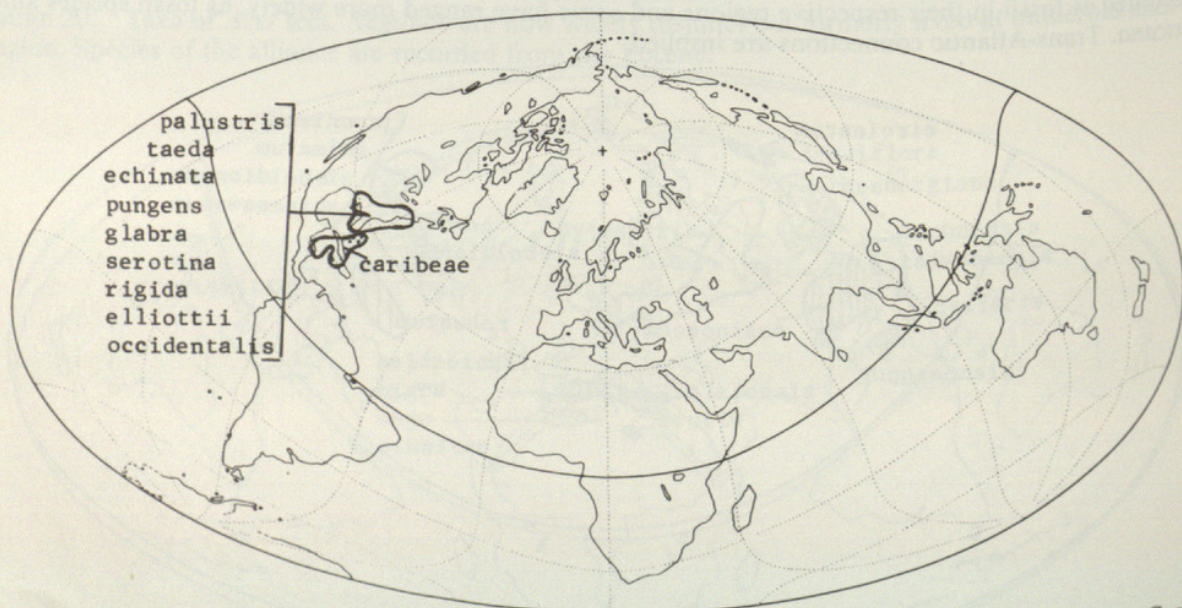


FIGURE 26. Members of *Pinus* subsect. *Australes* are confined to eastern United States and the Caribbean Islands. Some fossil pines in western Europe resemble this group.

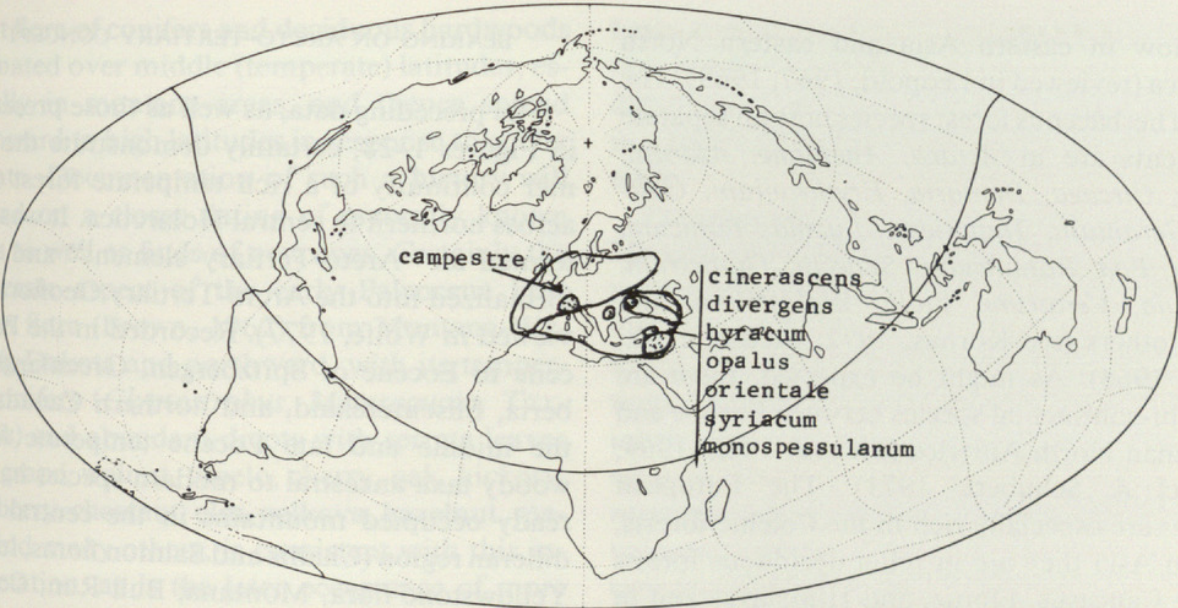


FIGURE 27. Members of *Acer* sect. *Campestris* are confined chiefly to the Mediterranean basin apart from *A. campestre*, which ranges more widely. Fossil species of this alliance are common in the area of their present occurrence.

recently to disrupt their former distribution across middle latitudes, and colder taiga and tundra climates have disrupted their occurrence at higher latitudes. Their past continuity is demonstrated not only by fossil records scattered across Holarctica, it has been inferred also from the nature of the taxa in the surviving relict forests in the Colchic region (Balkans-eastern Turkey-Caucasus), the Elbruz Mountains, the Himalayan axis, the forests of east-central China, Japan, and those of the eastern and western United States. All

these disjunct areas have allied taxa in numerous genera (see Meusel et al., 1965, 1968), including sensitive mesic forest herbs that still link the widely separated relict forests that were isolated by spreading drought and cold over middle and higher latitudes following 13 Ma (Axelrod & Raven, 1972: 227; Axelrod, 1979).

The associated herbaceous understory of the mixed forest is largely unknown in the fossil record, apart from a few seed floras in western Europe, Siberia, and Japan. The former do contain

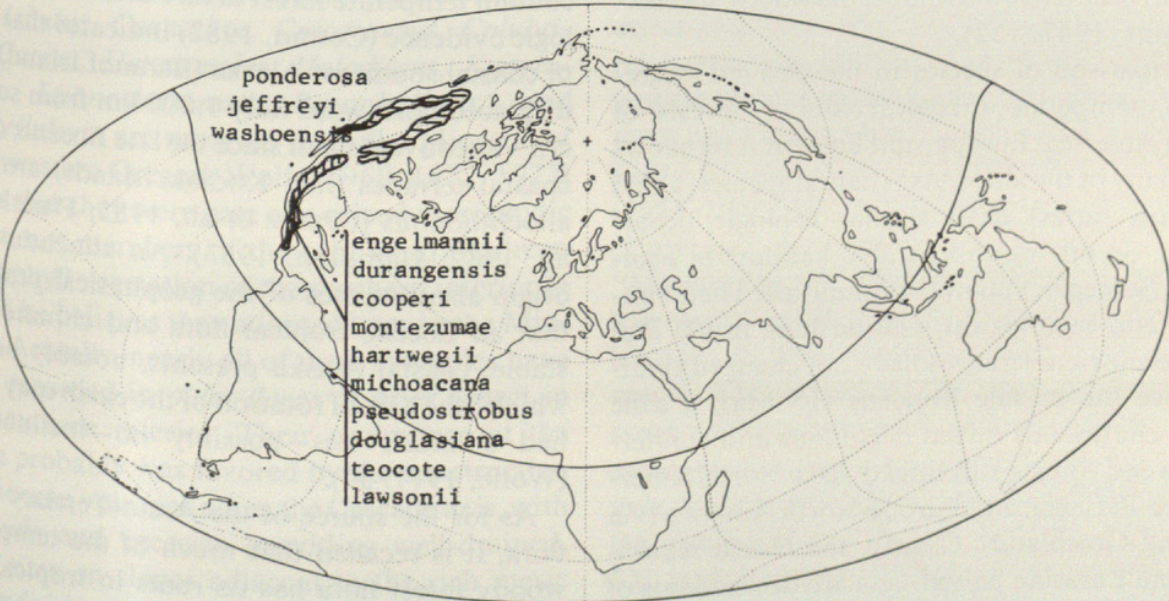


FIGURE 28. Species of *Pinus* subject. *Ponderosae* have proliferated in the uplands of Mexico-Central America, presumably their "center of origin." Fossil pines allied to the group are recorded widely in the western United States commencing in the Oligocene.

taxa now in eastern Asia and eastern North America (reviewed in Leopold, 1967, 1969). The related herbaceous forest species now on separate continents are in *Actaea*, *Anemone*, *Asarum*, *Carex*, *Circaea*, *Dentaria*, *Erythronium*, *Galium*, *Geranium*, *Impatiens*, *Luzula*, *Panicum*, *Oxalis*, *Poa*, *Ranunculus*, *Senecio*, *Thalictrum*, *Sanicula*, *Veratrum*, *Viola*, *Waldsteinia*, and many others (see Kornas, 1972; Meusel et al., 1965, 1968). As might be expected, there are more bi-continental species between Europe and Asia than North America (Meusel, 1968, 1969; Meusel & Schubert, 1971). The European species are especially rich in the Colchic forests, and in Asia they are in relict deciduous forests of the Caucasus, Elbruz, and Himalayas and in the scattered higher mountains of arid central Asia that link the European and east Asiatic centers. The present arid central Asian region supported broadleaved mixed deciduous forests into the middle Miocene (reviewed in Axelrod, 1979). Stebbins noted that there are similar herbaceous groups confined to eastern Asia and eastern America, not only in families regarded as generally "primitive" (Berberidaceae, Liliaceae, Ranunculaceae) but in advanced families (Orchidaceae, Poaceae, Polygonaceae). The disjunct species, as in *Antenoron* (= *Tovara*), *Brachyelytrum*, *Cypripedium*, and *Polygonum*, are scarcely different and at most are only varietally or sub-specifically distinct; these herbs are not only ancient, they have changed but little over the past 15 million years. Clearly, "the evolution of herbaceous elements (in the mixed deciduous forests) has been as slow as that of the woody species" (Stebbins, 1947: 152).

Comparison of species in the derived (segregated), temperate mixed-deciduous forests of North America, Europe, and Eastern Asia shows that many of the allied taxa (paired species, allied sections, series) have similar ecologic occurrences, occupying comparable habitats in analogous (segregate) plant communities. Their similar phyto-sociological relationships imply that their ecologic tolerances have not changed greatly since the middle Miocene (15 Ma), a time when continuous mixed deciduous and conifer-hardwood forests still linked Asia-North America (via Beringia) and Europe-North America (via Iceland-Greenland). Clearly, the North American and Eurasian paired-taxa are descendants of common ancestral forms that contributed to the Arcto-Tertiary forests (Medwecka-Kornas, 1961; Kornas, 1972).

BEARING ON ARCTO-TERTIARY CONCEPT

The preceding data, as well as those presented in Figures 1–28, certainly demonstrate the former continuity of a rich temperate forest flora across northern to central Holarctica. It was first termed an "Arcto-Tertiary element" and then formalized into the Arcto-Tertiary Geoflora (reviewed in Wolfe, 1977). Recorded in the Paleocene to Eocene of Spitzbergen, Greenland, Siberia, Ellsemereiland, and northern Canada, by the middle and late Eocene temperate forest woody taxa ancestral to modern species had already occupied mountains in the central Cordilleran region (Challis and Salmon floras, Idaho; Yellowstone flora, Montana; Bull Run, Copper Basin, Elko floras, Nevada). As climate progressively cooled following the late Eocene, evolving taxa in the temperate forest flora shifted into lowland basins, first in the interior and then the coastal strip. By the Miocene many woody taxa were scarcely separable from living species.

Reports of the demise of the Arcto-Tertiary Geoflora "have been greatly exaggerated." The basis for that belief stems partly from the description of a late Middle and Upper Eocene tropical flora from coastal Alaska (Wolfe, 1972, 1977), which was then at a latitude near 70°N (Smith et al., 1981). It has been evident to me for a decade (unpubl. manuscript) that the flora, which occurs in the marine Kushtaka Formation, is allochthonous. This agrees with the fact that later Eocene floras from middle and high latitudes in Eurasia and North America regularly contain temperate forest taxa. Furthermore, geologic evidence (Cowan, 1982) indicates that part of coastal southeast Alaska (Baranof Island) was displaced northward fully 1,000 km from southern Vancouver Island since the late Eocene; other coastal terranes (i.e., Kodiak Islands) are also allochthonous (Grantz et al., 1982; Plumley et al., 1982; Hamilton, 1983). An allochthonous origin also disposes of the geophysical problem that an Eocene tropical flora and climate in a stable, coastal Alaska presents, notably one in which "the axis of rotation of the earth may have had a much less—possibly no—inclination" (Wolfe, 1977: 37).

As for the source of the Arcto-Tertiary Geoflora, it is recalled that much of the temperate woody forest flora has its roots in tropical and subtropical alliances (Axelrod, 1952; see Wu, this symposium). It is probable that the early Arcto-Tertiary and late Cretaceous temperate

forest flora of conifers and deciduous hardwoods originated over middle (temperate) latitudes, especially in montane areas, and thence spread northward to high latitudes in response to cooler climate. Documentation of such a history will depend on a closer dating of presently known floras as well as finds of new ones. Certainly the temperate aspect of the early Paleocene Fort Union flora (Brown, 1962) from Montana-Wyoming-Dakota and northward, with its temperate conifers (*Glyptostrobus*, *Metasequoia*, *Taxodium*) and abundant dicots with serrate leaves as in grape, walnut, tupelo, cherry, oak, hickory, hackberry, chestnut, elm, zelkova, hazelnut, maple, and many others, is consistent with this interpretation, as is the later occurrence of more modern temperate dicots at higher latitudes. It is supported also by the more archaic character of taxa in the high arctic late Cretaceous-Paleocene floras, paralleling the persistence of a flora of "Late Jurassic-Aptian" aspect at high latitudes when early angiosperms were already in the lowlands at lower latitudes and spreading polewards (Axelrod, 1959).

The preceding distributional and phyto-sociological evidence show that in spite of slight to moderate morphological differences, the ecologic tolerances of scores of temperate taxa have not changed greatly. This statement conflicts with the notion (Mason, 1947; Wolfe, 1969: 197, 1972: 230, 1977: 47) that numerous Tertiary forest taxa have changed their physiology and have shifted to new vegetation zones. The examples purported to support this notion can be interpreted in other ways. For instance, species of *Arctostaphylos*, *Arbutus*, *Ceanothus*, *Cercocarpus*, *Colubrina*, *Garrya*, *Heteromeles*, *Holodiscus*, *Karwinskia*, *Lyonothamnus*, *Peraphyllum*, and *Umbellularia* are reported from the Miocene of northwestern Oregon. Wolfe (1969, 1972, 1977) states that they were part of a mixed mesophytic forest, not members of the subhumid Madrean sclerophyll vegetation of the southern interior to which he believes they adapted later in the Miocene. Actually, nearly all of these examples have been recorded in older floras of drier aspect in the southern interior. Their occurrence at the north probably was favored by the construction of Miocene volcanos along the Cascade axis, with the tuffs and breccias providing well-drained, drier sites on slopes adjacent to the rich mesic valley forests. Significantly, these taxa are essentially absent from large Miocene floras of the nearby region (Mascall, Blue Mountains, Spo-

kane, Grand Coulee, 49 Camp, Succor Creek) that bordered local ponds and lakes formed by damming by the Columbia River plateau basalts in a region of generally low relief and high water-table.

The suggestion that the Madrean taxa from the Miocene of northwest Oregon had only a temporary, seral relation on drier volcanic slopes in that area is paralleled by distributions that resulted from the late Quaternary climatic fluctuations. Some Californian taxa that range far north inhabit the warmest, driest available sites that were invaded only since the last glacial. *Arbutus menziesii* occurs on dark (heat-retaining) meta-volcanic rocks on Vancouver Island, rocks that were covered by ice only 12,000 years ago. *Quercus garryana* is confined to drier slopes in west-central Oregon and southern Washington, an area it invaded in post-glacial time (Hansen, 1942, 1947). The oak groves in the Puget Sound area are being actively invaded by *Pseudotsuga* forest and have only a seral relation (Franklin & Dryness, 1973: 89). The same relationship is implied by *Vaccinium ovatum*, a common member of the closed-cone pine forest of California that ranges northward into Washington, and was cited by Mason (1947) as an example of floristic instability. Its nearest ally, *V. confertum*, occurs in the closed-cone pine forests (*Pinus* sect. *Oocarpeae*) of Mexico where there are many related species that also make up the Californian coastal pine forests (Axelrod, 1977: 171, 1980). Ecologic studies (Franklin & Dryness, 1973: 85-86) show that *V. ovatum* borders the coastal forests to the north and has only a seral relation, occupying open, drier sites that presumably are relict from the warmer Xerothermic and more recently from logging and fire. The occurrence of these and many other typically Californian taxa far to the north has been discussed by Detling (1953, 1958, 1961) for Oregon and by Schofield (1969) who reviewed the floristic makeup of the "Mediterranean" climatic portion of southern Vancouver Island and southwestern British Columbia. As they emphasize, the "Californian" species are not an integral part of the climax conifer forests but occur in open, sunnier, drier areas for the most part, and entered this region only since the last glacial, most probably during the Xerothermic (also in Axelrod, 1966: 42-55). It thus seems unlikely that forest taxa have greatly changed their physiologic requirements, shifting to wholly new associations. Furthermore, since rapid, severe environmental shifts

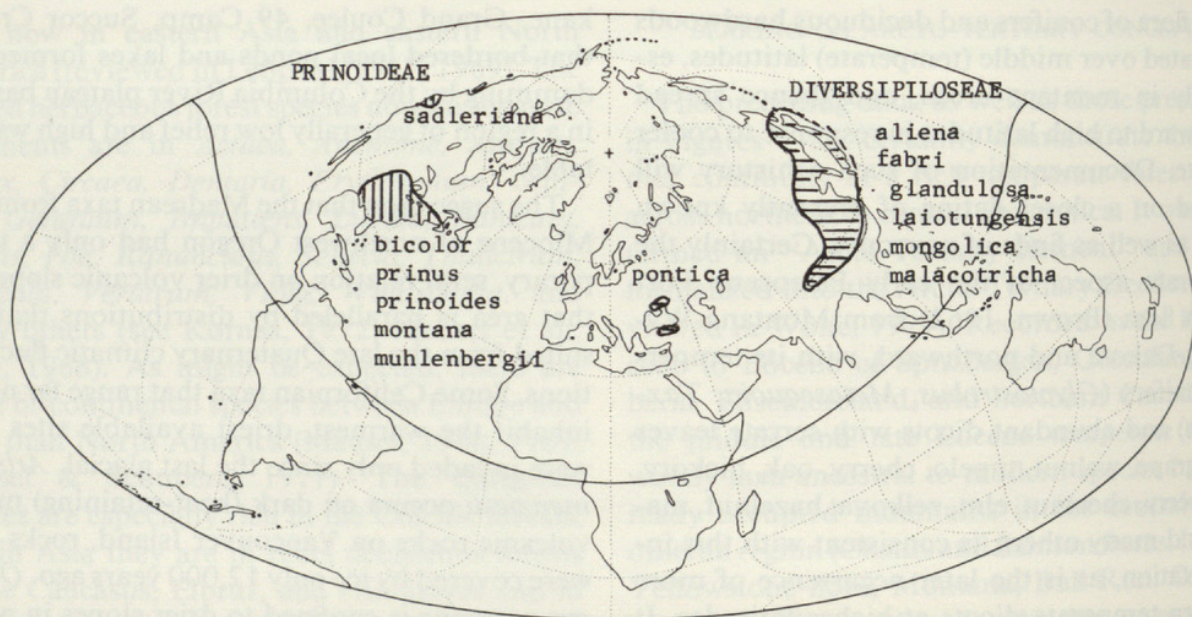


FIGURE 29. Oaks of the allied subjects. *Prinoideae* and *Diversipiloideae* are confined now to separate continents. Fossil species of these alliances were widespread across middle and high latitudes into the Miocene.

like those of the Quaternary are not documented for the Tertiary, there probably was little interchange between North America and Eurasia of taxa that represent sections of genera that originated in restricted parts of one continent or the other.

This is not to deny that taxa may have shifted to new associations, but these were between the same general forest types, as in the shift of a taxon from the American to the Asian sector of the mixed deciduous or conifer-hardwood forest. Examples of such shifts are not readily demon-

strable today because the record is still too incompletely known to determine whether a fossil species in western North America moved to eastern Asia or *vice versa*. An ancestral species may have moved southward and changed more in one area ("derived") than the other, thus giving rise to the impression that the "primitive" form migrated to give rise to the "derived" taxon. Clearly, the notion that taxa have commonly moved into associations widely different from those in the ancestral community is not demonstrated. Some taxa have been restricted upward, out of

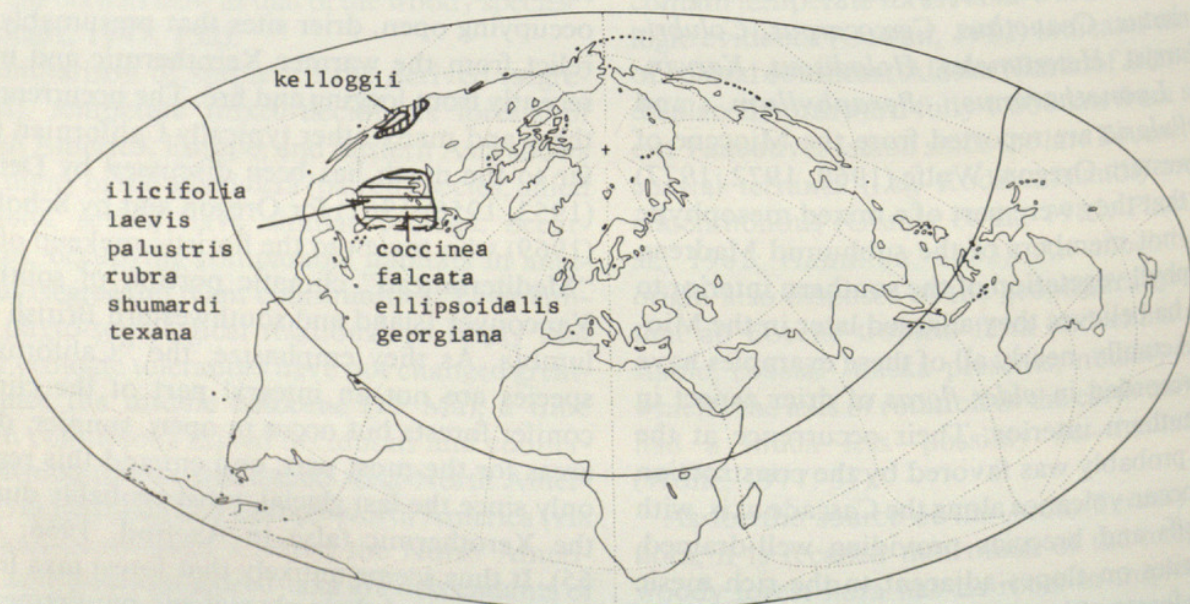


FIGURE 30. Distribution of species of *Erythrobalanus* subject. *Rubrae*. Taxa similar to *coccinea* and *palustris* occur in the Miocene of Oregon. Oaks of this group have also been divided into subjects. *Laeves*, *Ilicifoliae*, *Palustres*, *Coccineae*, *Pagodaefoliae*, and *Californicae*.

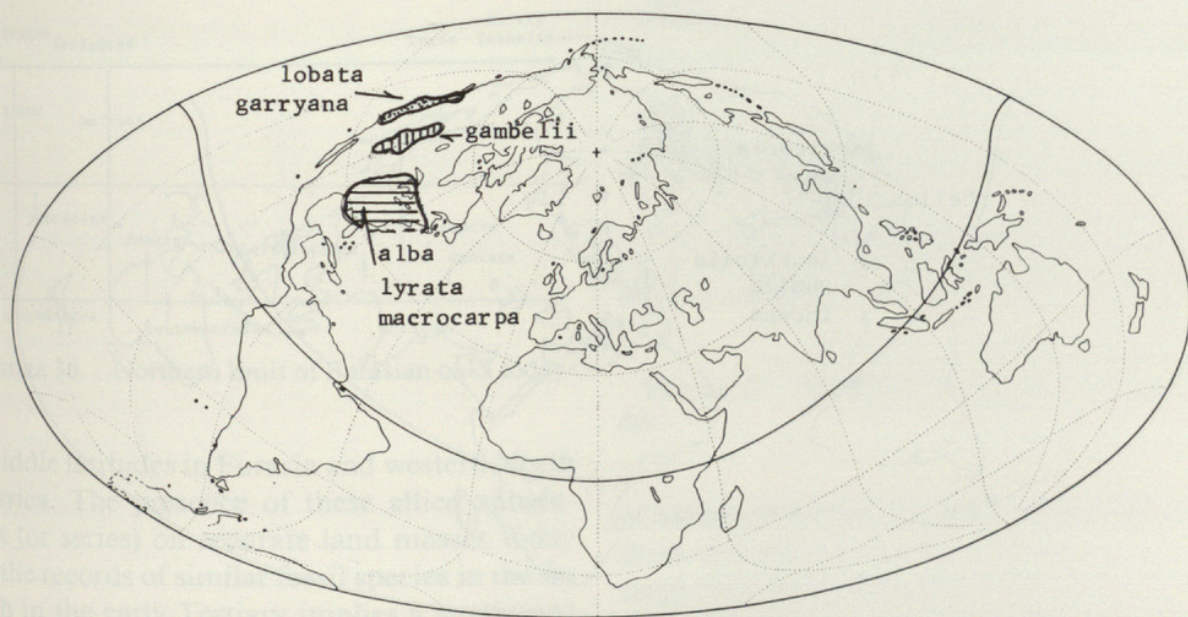


FIGURE 31. Lobed white oaks have been divided into subjects. *Lobateae*, *Gambelieae*, *Albeae*. Those of the former two occur as fossils in the far West during the Miocene. Members of *Albeae* have not yet been certainly recorded there.

associations now too xeric for them, and others have moved to lower elevations where climates are warmer, but in such cases they are still components of associations in which they were present formerly. That is, upland taxa forest earlier reached to lower levels and sclerophyll taxa to higher ones under a climate of ample summer rain and milder winters (Axelrod, 1976, fig. 4).

PAST AND PRESENT DISTRIBUTION OF OAKS

The preceding data provide a basis for interpreting the Tertiary history of oaks in the Arcto-

Tertiary province. Figures 29 to 37 illustrate the present concentrations of some representative species of several *Quercus* sections (from Trelease, 1924; Camus, 1936-54) and Tables 1 to 3 indicate the present distribution of oaks in the temperate regions chiefly. It is apparent that whereas species of many sections or subsections of dicots have ranged widely across Holarctica (see above, Figs. 1-16), only members of the allied subjects. *Prinoideae* and *Diversipiloideae* occurred throughout temperate Holarctica during the Tertiary and earlier, having been recorded in Spitzbergen, Iceland, Alaska, Siberia, and also

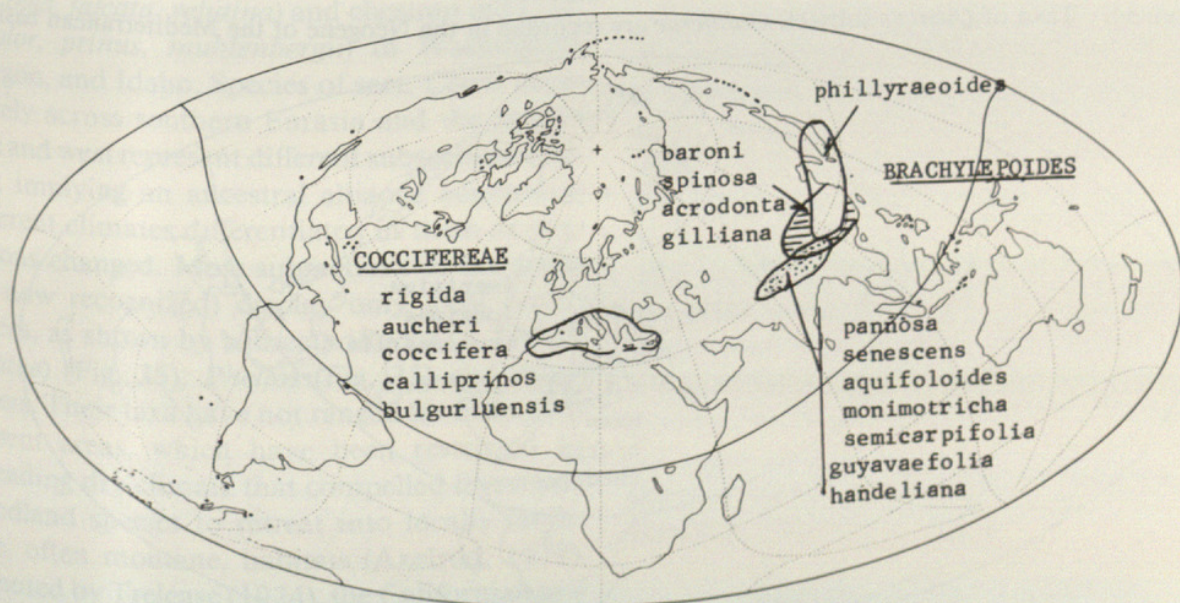


FIGURE 32. Oaks of sect. *Cerris* represent two subsections that imply former trans-Eurasian distribution. Fossils of each subsection have been recorded in their respective areas during the Neogene.

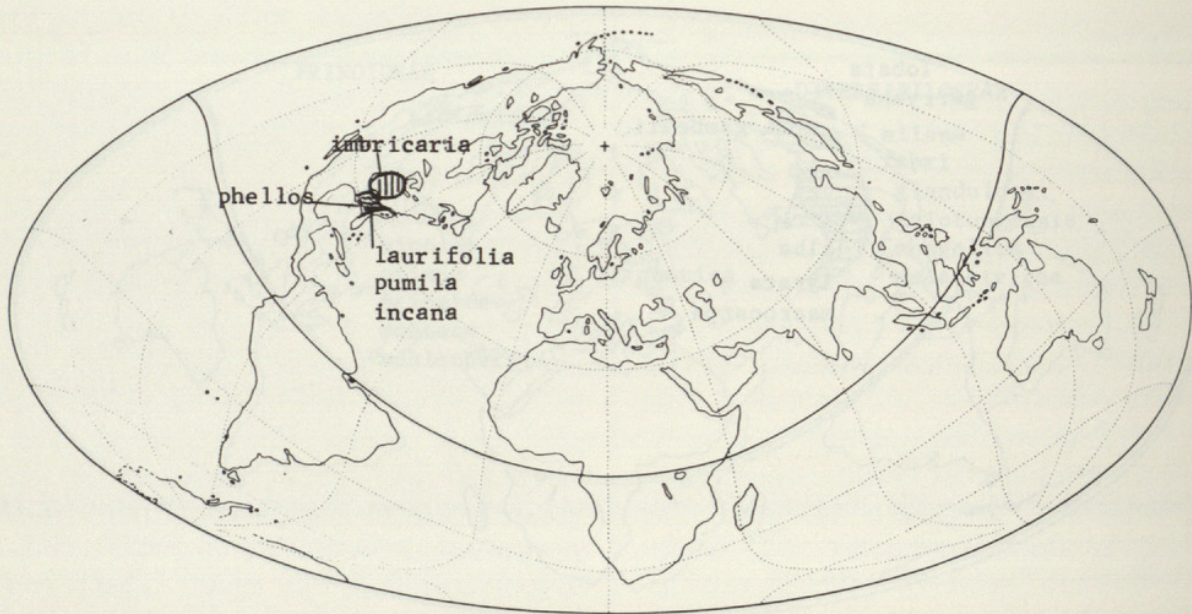


FIGURE 33. Taxa of subgenus *Phellos*, confined now to the southeastern United States, were represented by species allied to *phellos* and *imbricaria* in the Miocene of Oregon.

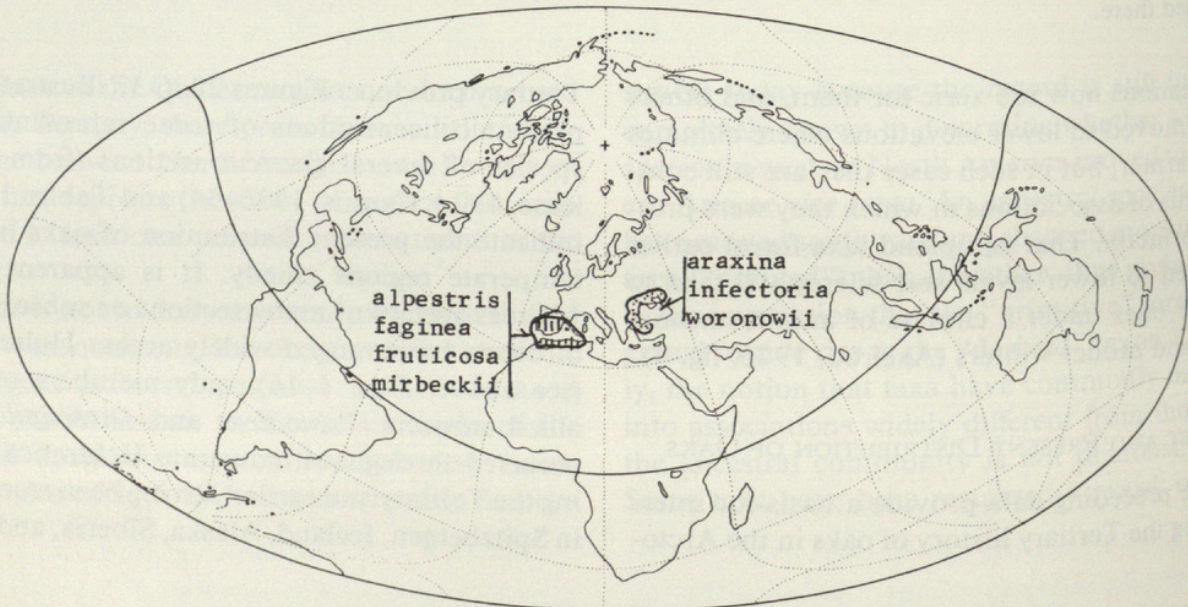


FIGURE 34. Taxa of *Quercus* subgenus *Galliferae* are recorded in the Neogene of the Mediterranean basin.

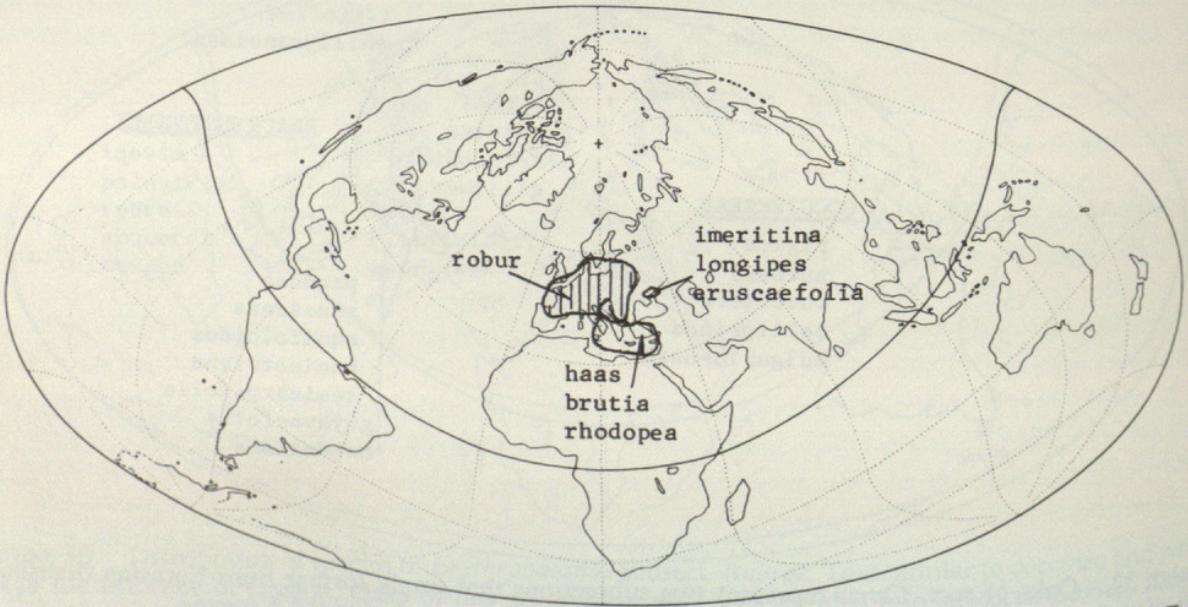


FIGURE 35. Taxa of *Quercus* subgenus *Pedunculatae* are recorded as fossil in the Neogene of western Europe. Three endemics are in the Caucasus Mts.

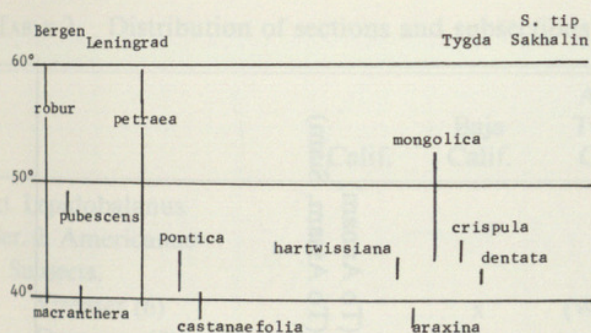


FIGURE 36. Northern limit of Eurasian oaks today.

at middle latitudes in Eurasia and western North America. The presence of these allied subsections (or series) on separate land masses today and the records of similar fossil species in the far north in the early Tertiary implies a southward shift in response to cooling climate and the resultant divergence of two closely allied groups. The alliance was already at middle latitudes by the Paleocene (Brown, 1962, pl. 19) and a fossil species of *Prinoideae* is in the Bull Run flora (40 m.y.a.) of northern Nevada, where it contributed to conifer-deciduous hardwood forest at an elevation close to pure subalpine conifer forest.

Species of most sections and subsections of *Quercus* are restricted to one continent or to specific parts of it, paralleling those discussed for other dicots (see above). Their close fossil allies occurred more widely in the Neogene but most did not range far from their present areas, as judged from the record in Europe, Asia Minor, Japan, China, and western United States (Figs. 1-5). Examples of wider distribution in the far West are provided by the records of red oaks (aff. *coccinea*, *falcata*, *velutina*) and chestnut oaks (aff. *bicolor*, *prinus*, *muhlenbergii*) in Washington, Oregon, and Idaho. Species of sect. *Cerris* occur widely across southern Eurasia and the species east and west represent different subsections (Fig. 32), implying an ancestral alliance adapted to different climates differentiated in them as conditions changed. Most subsections in the genus (as now recognized) display only local occurrences, as shown by subjects. *Robur* (= *Pedunculatae*) (Fig. 35), *Phellos* (Fig. 33) and many others. Their taxa have not ranged far from their present areas, which have been restricted by spreading dry climate that compelled forest and woodland species to retreat into locally favorable, often montane, habitats (Axelrod, 1979). As noted by Trelease (1924), the Californian and Rocky Mountain white oaks are unlike those of the Atlantic region, and the black oaks of the California province are distantly related to those

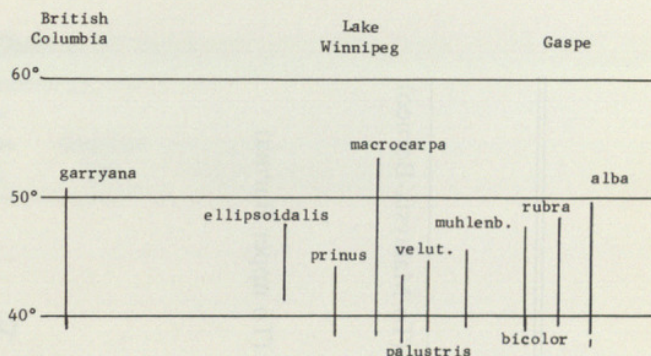


FIGURE 37. Northern limit of American oaks today.

of eastern North America and are remote from those of Mexico-Central America. The relations imply that these oaks originated in relatively local provinces.

Fossil evidence for restriction of species of most subsections (series) to comparatively local regions and with little or no continental interchange during the middle and later Tertiary is consistent with systematic evidence (Tables 1-3). Furthermore, the restriction of most sections to their present continental areas, or to parts of them, is clearly shown by illustrations of the numerous fossil oaks from across the USSR which are of Eurasian affinity (Takhtajan, 1982). As Trelease noted (1924), "the existing oaks of temperate regions have developed since the breaking of the circumpolar land connection of Tertiary time: that the genus may have penetrated Europe by way of the Orient in *Cerris* and *Ilex* types; and that it may have reached America originally over one or more now vanished land connections"

Cretaceous links are implied by the occurrence of *Lithocarpus* and *Castanopsis* (= *Chrysolepis*) in California, which are allied to Asian taxa in warm temperate climates. Furthermore, *Lithocarpus* (as *Q. nevadensis* Lesq. and a distinctive acorn cup) was already present in California in the late Early Eocene Chalk Bluffs flora. Together with the disjunct occurrence of *Trigonobalanus* (Yunnan-Thailand-Borneo to Colombia), connections are implied across the Atlantic (1) when it was narrower than at present and prior to the counter-clockwise rotation of North America, and (2) when more numerous, now-sunken islands linked these regions (Axelrod, 1972, fig. 25, 1979; Raven & Axelrod, 1974).

NORTHERN LIMIT OF *QUERCUS*

Available evidence indicates that most oak species have not followed many widespread taxa

TABLE 1. Distribution of sections and subsections of *Quercus* in Holarctica (from Camus, 1936-54).

	Europe	Mediterr. Basin	Asia Minor & Persia	Himalayas (to Afghan- istan)	S. China (Yunnan)
Subgenus <i>Cyclobalanopsis</i>				x	x
Subgenus <i>Euquercus</i>					
Sect. <i>Cerris</i>					
Subsects.					
<i>Brachylepides</i> (15 sp.)				x	x
<i>Echinolepides</i> (3 sp.)				x	x
<i>Cypriotes</i> (1 sp.)		(Cyprus)			
<i>Cocciferae</i> (4 sp.)		x	x		
<i>Suber</i> (1)		x			
<i>Macrolepides</i> (9)		x	x		
<i>Campylolepides</i> (2)					x
<i>Eucerris</i> (1)	x	x			
Sect. <i>Mesobalanus</i>					
Subsects.					
<i>Malacolepides</i> (1)					
<i>Macrantherae</i> (3) (excl. <i>Ponticae</i>)	x	x	x		
Sect. <i>Lepidobalanus</i>					
Ser. 1. <i>Gerontogaeae</i>					
Subsects.					
<i>Floribundae</i> (6)				x	x
<i>Pachyphyllae</i> (5)				x	x
<i>Englerianae</i> (1)					x
<i>Ilex</i> (1)	x	x	x		
<i>Diversipilosae</i> (9)			x		x
<i>Galliferae</i> (5)		x	x		
<i>Hartwissianae</i> (1)			x		
<i>Sessiliflorae</i> (6)	x	x	x		
<i>Lanuginosae</i> (2)	x	x	x		
<i>Pedunculatae</i> (7)	x	x	x		

TABLE 2. Distribution of sections and subsections of *Quercus* in North America (from Camus, 1936–54).

	Calif.	Baja Calif.	Ariz.- Texas- Colo.	Central US	Southern US	E US- (Canada)
Sect. <i>Lepidobalanus</i>						
Ser. 2. <i>Americanae</i> ^a						
Subjects.						
Virentes (6)		x	(W. Tx)		x	(To E. Mexico)
Dumosae (2)	x	x	x			
Griseae (1)			x			
Oblongifoliae (2)	x	x	x			
Undulatae (3)			x			
Arizonicae (3)			x			
Douglasiae (1)	x					
Confusae (4)			x			
Lobatae (2)	x		x			
Gambelieae (3)			x			
Prinoideae (7)	x			x	x	x
Stellatae (3)				x	x	
Lyratae (1)				x	x	x
Albae (1)				x	x	x
Macrocarpae (1)			(relict)	x	x	x

^a Excluding subjects. in Mexico–Central America; also sect. *Macrobalanus*, first ten subjects. are Madrean in origin.

in terms of a broad Holarctic occurrence during the Tertiary; most species and subsections (or series) have had relatively restricted distributions. Fossil oak remains are not common in Tertiary floras from higher latitudes, as Greenland, Spitzbergen, Ellesmereland, Alaska, or Sakhalin. Those that have been illustrated readily fall into subjects. *Prinoideae* and *Diversipiloseae*, the leaves resembling those of *Q. prinus*, *aliena*, *muhlenbergii*, *mongolica*, and their allies. This raises the problem as to why other fossil oaks are rare (or absent) in floras from latitudes generally above latitude 50°N. Oaks now reach their northern limit near latitude 50°N (Figs. 36, 37) and only *Q. robur* and *petraea* extend to latitude 60°N in the Baltic region, an area they no doubt invaded during the Altithermal. Temperature is not the chief factor that accounts for their rarity at high latitudes in the Tertiary. Those areas supported rich deciduous forests (Figs. 1–16) into the Middle Neogene (15–16 Ma), yet the only oaks encountered there are those of *Prinoideae-Diversipiloseae*. Most oaks occupy latitudes well below 40°N and the highest concentrations are in latitudes 15–30°N, in Mexico–Central America (with some 150 species), and southeastern China. Judging from Figure 38, light may be the principal factor that limits, and has limited, the northern distribution of most oaks.

In this regard, it seems significant that of the 18 species that now reach latitude 45–50° (Figs. 36, 37), five are members of the *Prinoideae-Diversipiloseae*, which had a wider distribution in the Paleocene and later, reaching above latitude 60°N into the middle Miocene.

EVOLUTION

Oaks comprise one of the more active groups of woody plants in terms of evolution during the Tertiary. There are now about 280 to 300 species and scores of hybrids are recognized. The great plasticity of the group is apparent in the convergence in similar leaf form and acorn type among species belonging to different sections of the genus. Oaks proliferated in generally restricted regions, chiefly in response to increasing topographic, climatic and edaphic diversity during the middle and later Tertiary. In addition, there were certain times when climatic extremes increased sharply, as at 35, 13, and 5 Ma (refs. in Axelrod, 1981; Kennett, 1981), as well as during Quaternary fluctuations. These major climatic shifts may have corresponded with times of especially rapid speciation in oaks (and other taxa) as older alliances disappeared and more open communities became available.

An example of such a radiation is suggested by the history of *Quercus wislizenii* and its close

TABLE 3. Distribution of sections and subsections of *Quercus* in North America (from Camus, 1936—

	California	Arizona	N. Baja Calif.	N. Mexico	South US
Sect. Protobalanus (6)	x	x	x		
Sect. Erythrobalanus ^a					
Subjects.					
Durifoliae (1)		x		x	
Agrifoliae (2)					
Vimineae (1)				x	
Hypoleucae (1)		x		x	
Saltillenses (3)				x	
Myrtifoliae (1)					x
Phellos (5)					x
Marylandicae (3)					x
Laeves (1)					x
Pagodaefoliae (2)					x
Ilicifoliae (1)					
Palustres (2)					
Velutinae (1)					x
Coccineae (4)				x	
Californicae (1)	x				x
	(to S. Oregon & Baja Calif.)				

^a Excluded are all subjects. in subtropical Mexico—Central America.

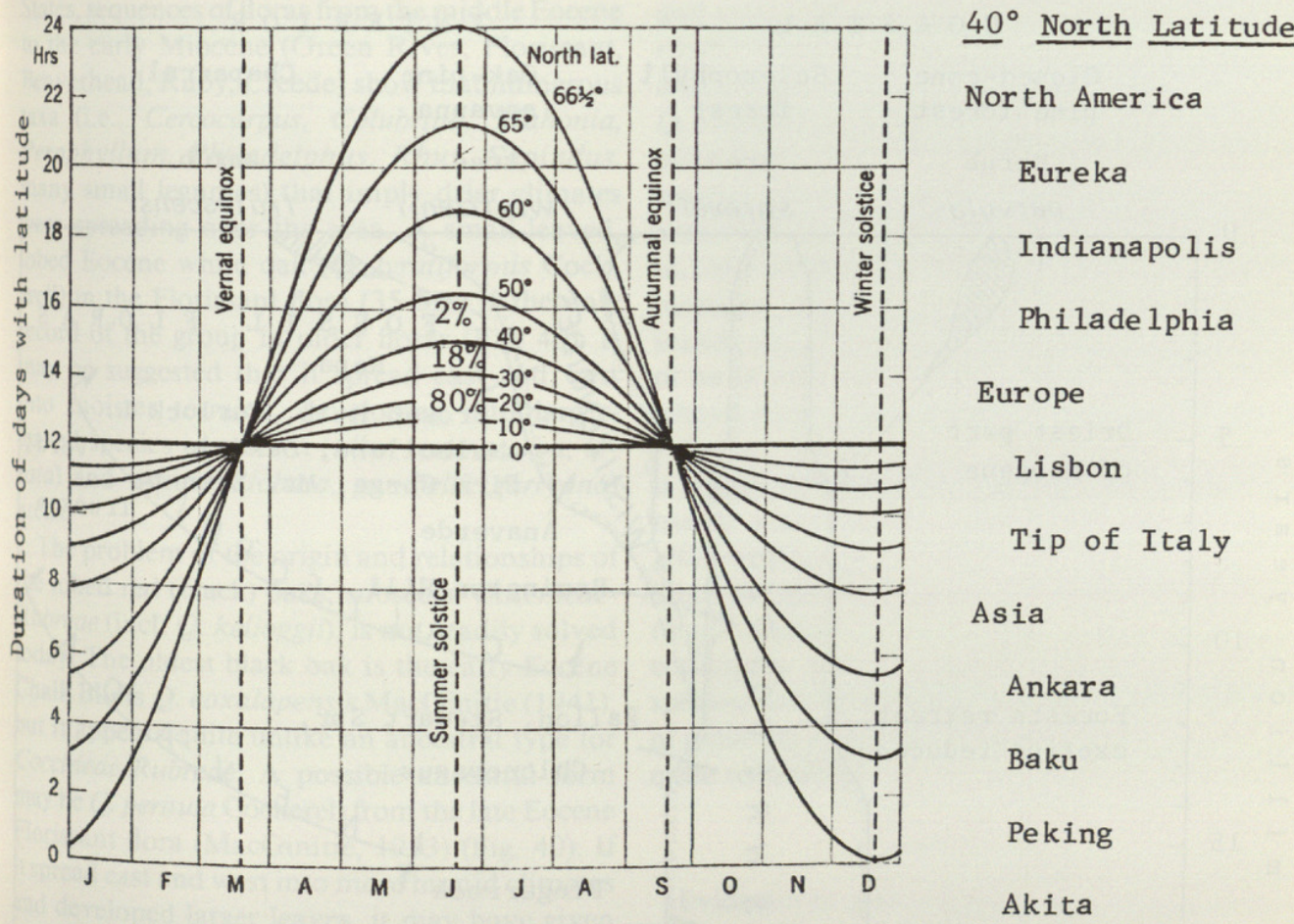


FIGURE 38. Most oaks are adapted to short days at lower latitudes. Percentage figures indicate the approximate representation of oaks in the indicated latitudinal belts. (Figure from Strahler & Strahler, 1977, with permission of J. Wiley & Sons.)

allies, *Q. shrevei*, *parvula*, and *frutescens* (Fig. 39). In California and Nevada there are large suites of fossil leaves of two members of the complex, *Q. wislizenoides* and *Q. shrevoides* ined., that are similar to those produced by the living *Q. wislizenii* and *Q. shrevei*. The fossils commonly form the dominants to subdominants of the floras in which they occur. Figure 39 shows that the alliance appears first as *shrevoides* in west-central Nevada and shifts westward to Sierra Nevada (Remington Hill flora) and is now (as *Q. shrevei*) in the outer south Coast Ranges of California. As climate became drier, *wislizenoides* replaced *shrevoides* in western Nevada (Verdi, Truckee floras) and then in the lower Sierra Nevada and the inner Coast Ranges. The shifts in adaptive type seem related to major environmental changes in the upper Miocene (13–12 Ma) and in the latest Miocene (5–6 Ma). There has clearly been a coastward restriction from the present Nevada desert of the presumed ancestral *Q. shrevoides-shrevei* line which has contributed to mesic broadleaved sclerophyll forest for fully

18.5 million years. *Quercus wislizenoides-wislizenii* have typified semiarid oak-grassland woodland vegetation since the later Miocene, shifting from Nevada into California as conditions became drier and cooler to the east as the Sierran block was elevated. Fossil records of the shrubs are not now known, but their ecologic relations suggest that *parvula* is older than *frutescens*.

As for their origin, oaks of the *wislizenii* alliance are related to the series *Peninsulares* Trelease (*Q. peninsularis*, *Q. devia*) of Baja California. *Peninsulares* are allied to *Durifoliae* (*Q. emoryi*, *durifolia*) of the southwestern United States and northwestern Mexico, and to the *Vimineae* (*Q. bolanyosensis*, *duranzillo*, *balsequillana*, *viminea*) of the northern Sierra Madre Occidental. The *Peninsulares*, *Durifoliae*, and *Vimineae* represent taxa adapted to subhumid to semiarid areas with summer rain; whereas *Q. shrevoides* and *wislizenoides*, which lived earlier under biseasonal rainfall, have adapted to the dominant winter-rain climate of California. *Peninsulares* were restricted to their present area

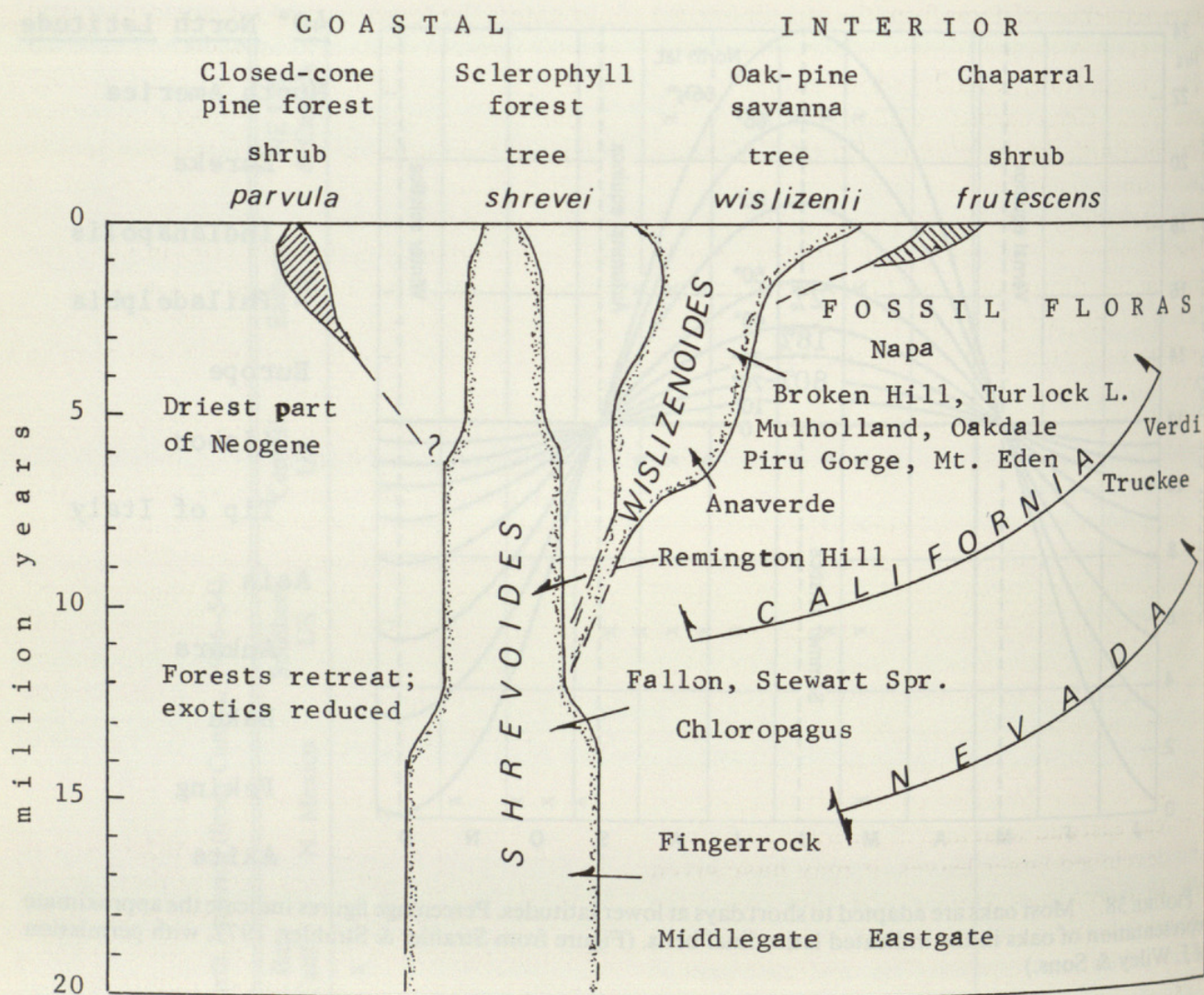


FIGURE 39. Inferred relations of oaks of the *Quercus wislizenii* complex (see text).

as the lowlands became drier; they live in a young mountainous region, one elevated only in the last two to three million years (Gastil et al., 1975). The *Durifoliae* ranged more widely in the past, as shown by records of fossil oaks allied to *Q. emoryi* in the Tehachapi (17 Ma) and Mint Canyon (12 Ma) floras, southern California. The preceding data imply that these series probably are ancient and survived in favorable environments as drier climates spread more widely in the late Cenozoic. To judge from the modern aspect of oaks of subhumid requirements in the Florissant flora (34 Ma), the *wislizenii* complex and its allied series may have diverged from an ancestral alliance in Oligocene time.

The present disjunct subsections of sect. *Cerris* and *Suber* across Eurasia and of the *Albeae* (incl. *Lobateae*) and *Rubrae* (incl. *Coccineae*) across the United States also reflect restriction following the spread of drier climate and of a shift in sea-

sonal rainfall distribution in the far West. Marked aridity had developed over southwestern Asia and North America by the middle Eocene. This may have been the time of origin of some of the major subsections (or series) of the genus. Dry climates commenced to spread rapidly in the middle Miocene as the Tethys Sea was destroyed and as ice spread on Antarctica (13 Ma). Forest taxa now retreated into rapidly rising mountains and differentiated east and west into new subsections (series) and many species. The presence of new upland terrains and their accompanying local climatic differences may well have provided a basis for the origin of numerous distinctive taxa as founder populations exploited these novel environments. With rapid shifts in climate and instability in populations, the effect would have been the rapid origin of distinct taxa, thus simulating the phenomena of punctuated equilibria.

In the central Cordilleran region of the United

States, sequences of floras from the middle Eocene to the early Miocene (Green River, Florissant, Beaverhead, Ruby, Creede) show that numerous taxa (i.e., *Cercocarpus*, *Colubrina*, *Mahonia*, *Peraphyllum*, *Philadelphus*, *Rhus*, *Sapindus*, many small legumes) that imply drier climates were spreading over the area. A small-leaved, lobed Eocene white oak (*Q. lyratiformis* Cockerell) in the Florissant flora (35 Ma) is the only record of the group in older floras (Fig. 40). It may be suggested that it spread east and west into moister terrains, developing into larger-leaved species in eastern (*alba*, *macrocarpa*, *lyrata*) and western (*lobata*, *gambelii*, *garryana*) areas.

The problem of the origin and relationships of the lobed red (black) oaks, subsects. *Coccineae-Rubrae* (incl. *Q. kelloggii*), is not readily solved today. The oldest black oak is the early Eocene Chalk Bluffs *Q. eoxalapensis* MacGinitie (1941), but it appears quite unlike an ancestral type for *Coccineae-Rubrae*. A possible ancestral form may be *Q. peritula* Cockerell from the late Eocene Florissant flora (MacGinitie, 1953) (Fig. 40). If it spread east and west into more humid climates and developed larger leaves, it may have given rise to *Coccineae-Rubrae*. On this basis, the species east and west of the Cordillera would have differed in some respects. The western Miocene fossil species, some undescribed, show relationship to *Q. falcata*, *coccinea* and *velutina* of the eastern United States and to *Q. kelloggii* of the west. The moderate differences east and west may express no more than foliar plasticity in the group. It is also evident that in some floras (Mascall, Stinking Water) there appears to have been hybridization among the lobed oaks.

RADIATION

Some natural subsections have radiated into very diverse environments. For instance, species of sect. *Chrysolepideae* occur in several vegetation zones. *Quercus tomentella* is a woodland tree endemic to islands off southern California and to Guadalupe Island; it occurs with closed-cone pine forest on Santa Cruz and Guadalupe Islands. *Quercus cedrosensis* is a shrub in coastal sage, chaparral, and closed-cone pine vegetation zones on the coastward slopes of northern Baja California. *Quercus dunni* is a co-dominant of the chaparral of southern California and southern Arizona. *Quercus chrysolepis* is a large, widespread evergreen tree that dominates the mixed evergreen forest (sclerophyll forest) of California

and enters the lower part of the adjacent mixed conifer forest in rocky canyon walls and exposed areas. *Quercus vaccinifolia*, clearly derived from *Q. chrysolepis*, ranges from the upper mixed conifer forest into fir-subalpine forest and locally reaches close to tree-line. These taxa occur in areas with precipitation as low as 300 mm (12 in.) and as high as 2,500 mm (100 in.) and the montane sites have heavy snow. The growing season may last fully seven months (Ensenada) or be as brief as two to two and a half months (above Twin Lakes, California).

In sect. *Cerris* subsect. *Brachylepides*, which is largely in the area from central China to Yunnan, *Q. semicarpifolia*, *aquifoloides*, *pannosa*, and *gilliana* range up to 3,000 to 4,000 m in Yunnan. Since the age of the mountains is established, the rate of adaptation of these taxa to high montane conditions, and their derivation from ancestral species, can be estimated. Clearly, field studies of radiation of natural cohorts in *Quercus* can be quite rewarding.

DOMINANCE

Evidence in northeastern Asia suggests that although *Q. mongolica* was present there (as *Q. protodentata*) as a regular member of the Miocene rich deciduous forest, pollen studies indicate that the present oak forests dominated by *Q. mongolica* are late Quaternary (in Ablaev & Gorovoi, 1974). A similar relationship is indicated for the dominant lowland oak communities in California and Arizona as judged from late Pleistocene fossil floras and from evidence provided by wood-rat middens. Fossil species allied to *Q. agrifolia*, *douglasii*, *engelmannii*, and *wislizenii* are recorded in Miocene and Pliocene floras as members of rich sclerophyllous woodland. The living species that form pure stands at low elevations adjacent to grassland have adapted to these drier areas more recently and represent new monoclinal communities. A similar relationship is indicated for *Q. emoryi* and *Q. oblongifolia*, which dominate as pure communities at the edge of grassland and above the desert which supported rich woodlands into the latest Pleistocene.

SUMMARY

The preceding review of the present distribution of oaks and areas of their fossil occurrence leads to the following tentative conclusions.

1. The Fagaceae, which probably originated in



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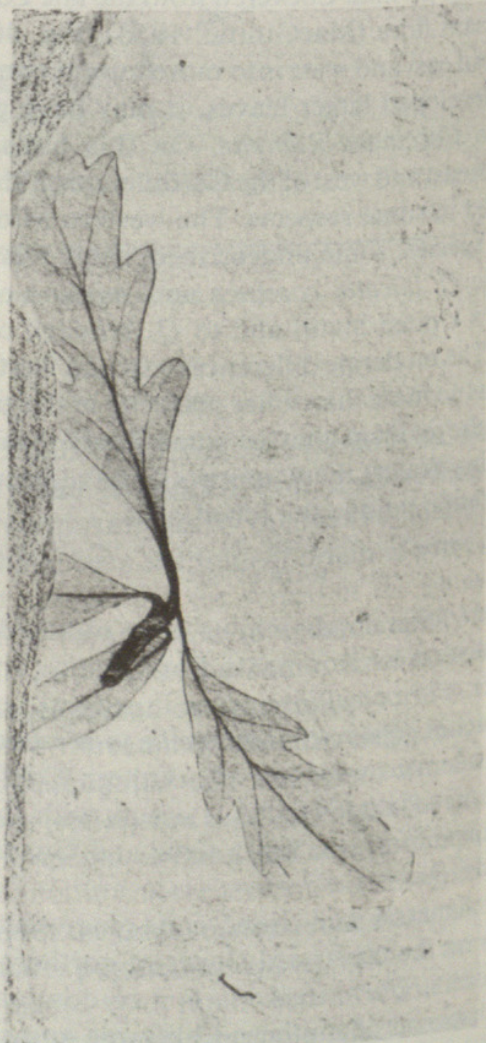
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the montane tropics, had migrated across the tropics via the Atlantic and had diverged into the principal living genera by the later Cretaceous.

2. Following the Eocene, oaks underwent rapid evolution chiefly in regions of mild to warm temperate climate as cooler and drier conditions spread and especially in areas where terrain diversity was increasing rapidly, as in Mexico-Central America, the southwestern United States, the Mediterranean basin and southeastern Asia.

3. Oaks were rare at higher latitudes during the Tertiary even though temperature was mild and well suited for numerous deciduous hardwoods and conifers. Northward distribution of most oaks evidently was controlled primarily by light (long day) north of latitude 50°.

4. Many sections and subsections (or series) are confined to local sectors of the continents and for the most part their antecedents have inhabited the same general areas, although they ranged more widely prior to the spread of grassland and desert climates. This is paralleled by sections of other genera (i.e., *Acer*, *Alnus*, *Betula*, *Pinus*) that occur locally on the continents, although other sections of these and many other genera have been and are still widespread on the continents. Also linking the present disjunct forests are numerous allied forest herbs, many of which have changed only slightly since the Miocene. Together with the trees and shrubs they form the broken floristic threads that make up the surviving matrix of the temperate Arcto-Tertiary Geoflora, whose demise has been certainly misrepresented.

5. Few oaks have linked North America-Eurasia, consistent with their evolution in generally restricted parts of the continents. Only the allied subsects. *Diversipiloseae* and *Prinoideae* have occupied higher latitudes and their derived species still occur on all the northern continents. Taxa of only a few sections have ranged across North America or Eurasia, notably *Albeae*, *Coccineae*, and *Virentes* in the former, *Cerris*, *Suber*, and *Cyclobalanopsis* (probably) in Eurasia.

6. The rise of oaks to dominate temperate forests and woodlands appears to be a phenomenon

of the later Cenozoic, one afforded by selection for greater drought and higher temperature at lower levels (California-Arizona, Spain-Turkey) and by cold in the interior (Manchuria-Primorye, central U.S.).

7. Species of subsections (series) of *Quercus* radiated from subtropical and warm temperate into subalpine environments as mountains were elevated in the late Tertiary; ecologic studies of these cohorts should prove illuminating.

8. Further progress in understanding oak evolution will depend not only on obtaining additional fossil plants and re-evaluating those in older collections, but also on taxonomists providing a more realistic grouping of taxa into natural alliances.

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FIGURE 40. Small-leaved sclerophyllous oaks had appeared over the central Cordilleran region by the close of the Eocene. These are from the Florissant flora (MacGinitie, 1953).—1, 4. *Q. scudleri* Knowlton;—2, 3. *Q. predayana* MacG.;—5, 6. *Q. mohavensis* Axelrod;—7, 8. *Q. peritula* Cockerell;—9. *Q. lyratiformis* Cockerell (natural size).

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