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Origins and Relationships of the Mixed Mesophytic Forest of Oregon–Idaho, China, and Kentucky: Review and Synthesis

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ORIGINS AND RELATIONSHIPS OF THE MIXED MESOPHYTIC FOREST OF OREGON–IDAHO, CHINA, AND KENTUCKY: REVIEW AND SYNTHESIS[1]

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Abstract

The Arcto-Tertiary Geoflora concept of Ralph Chaney, that the Mixed Mesophytic Forest of eastern Asia and eastern North America are relicts of a Northern Hemisphere high-latitude circumglobal deciduous forest of the Late Cretaceous–Early Tertiary that migrated south to the temperate zone as an intact unit, was shown by Wolfe and others to be invalid. To explain the origin and development of these disjunct forests, Wolfe and Tiffney developed the boreotropical hypothesis. Accordingly, a paratropical (near-tropical) rainforest flora containing a mixture of tropical, paratropical, and temperate genera developed at several places in the middle latitudes of the Northern Hemisphere in the Eocene and spread around the globe via the Bering and North Atlantic land bridges and shores of the Tethys Seaway. Further, the Mixed Mesophytic Forest of eastern Asia and eastern North America developed independently after disruption of the boreotropical flora by subsequent changes in climate and geography, thus accounting for differences in the flora and physiognomy of the present-day Mixed Mesophytic Forest in the two areas. The fruit and seed flora of the Middle Eocene Clarno Nut Beds of Oregon are representative of the boreotropical forest. In response to climatic cooling during the Eocene–Oligocene transition, this broad-leaved evergreen rainforest was replaced by a temperate broad-leaved deciduous (Mixed Mesophytic) forest, which remained present in the Pacific Northwest through most of the Miocene. The Early Oligocene Bridge Creek flora of Oregon, the Middle Miocene Succor Creek flora of eastern Oregon and adjacent Idaho, and the Middle Miocene Clarkia and Musselshell Creek floras of northern Idaho are good examples of the Mixed Mesophytic Forest. These Oligocene–Miocene fossil floras include important genera in the present-day Mixed Mesophytic Forest of eastern Asia and eastern North America, as well as those that today occur only in eastern Asia or only in eastern North America. Using Graham as the primary source of, and guide to, information on microfossil and megafossil plant paleoassemblages and paleoclimates in eastern North America, we chart the Late Cretaceous–Tertiary sequence of vegetation and climate for Kentucky. Further, we briefly review the palynofloral provinces in which Kentucky was situated during the Middle and Early Cretaceous. In contrast to the Mixed Mesophytic Forest flora (a component of the boreotropical forest) of the Middle Eocene Clarno Nut Beds, the Middle Eocene Claiborne flora of Tennessee and Kentucky represents a semideciduous tropical dry forest dominated by Leguminosae taxa that have strong phylogenetic and biogeographical relationships with the Old World and tropical South America. Apparently, this dry forest developed from a Paleocene–Early Eocene tropical rainforest following a decrease in amount and an increase in seasonality of rainfall. The Mixed Mesophytic Forest developed from this seasonally dry forest following the Eocene as a result of an increase in the amount of rainfall and a decrease in its seasonality. The hypothesis that closely related disjunct taxa between eastern Asia and eastern and western North America represent relicts of a circumglobal Mixed Mesophytic Forest in the Miocene is supported by fossil and molecular phylogenetic data.

Key words: Arcto-Tertiary Geoflora concept, biogeography, boreotropical hypothesis, China, Mixed Mesophytic Forest, North America.

Ever since Linnaeus (Graham, 1966, 1972; Boufford & Spongberg, 1983; Wen, 1999), botanists have known that there are many similarities at the generic level between the deciduous forest floras of eastern North America and those of eastern Asia (Gray, 1840, 1846, 1859, 1878; Fernald, 1931; Li, 1952, 1972; Graham, 1972; Wood, 1972; Boufford & Spongberg, 1983; Wu, 1983; Boufford, 1992; Hong, 1993; Xiang et al., 1998, 2000; Manchester, 1999; Qian, 1999, 2002; Wen, 1999; Guo & Ricklefs, 2000). Less well known, however, is that there is a high similarity between the Middle to Late Tertiary Mixed Mesophytic Forest of western North America and the modern Mixed Mesophytic Forest of eastern Asia (China, Japan, Korea) and eastern North America (Meyer & Manchester, 1997). The primary purpose of this review is to discuss the origins of, and the floristic and physiognomic relationships between, the Tertiary Mixed Mesophytic Forest of Oregon–Idaho and the present-day Mixed Mesophytic Forest of China and Kentucky.

Arcto-Tertiary Geoflora Concept

According to the Arcto-Tertiary Geoflora concept (e.g., Chaney, 1940, 1944, 1947, 1948, 1959;

Axelrod, 1966, 1983; also see Gray, 1878), the forests of eastern North America, eastern Asia, and western and central Europe are relicts of a temperate, broad-leaved deciduous forest (Arcto-Tertiary forest) of a particular floristic composition (Arcto-Tertiary Geoflora, sensu Chaney, 1959) that evolved (in association with some deciduous gymnosperms such as *Ginkgo* L. and *Metasequoia* Hu & W. C. Cheng) at high northern latitudes during the Late Cretaceous and Early Tertiary, moved southward across North America, Europe, and Asia, as the climate cooled, and became distributed across the Northern Hemisphere by the Miocene. In response to climatic cooling, this climax forest community migrated more or less intact to middle latitudes in the Oligocene.

According to Wolfe (1994: 224), "Chaney's hypothesis differs little from that of Asa Gray (1878), and his usage of 'arcto-tertiary' differs little from that of Engler (1882), who first coined the term." Some assumptions of Chaney's hypothesis are as follows. A temperate climate predominated at northern latitudes, and thus vicariant patterns should be found only in temperate taxa, such as the disjuncts between eastern Asia and eastern North America. As such, the cool temperate climate precluded the migration of tropical taxa between the Old World and the New World. A Neotropical Tertiary Geoflora occurred south of the Arcto-Tertiary Geoflora, and the ultimate source of this tropical flora was South America. Land bridges (Beringian) between Eurasia and North America facilitated exchange (or interchange) of primarily temperate plants between these continents. Climate tolerance of fossil flora was the same as that of modern analogs, i.e., no change in tolerance through geological time. This temperate, broad-leaved deciduous forest (i.e., fossil assemblage) closely resembled the North American Eastern Deciduous Forest (many genera the same), and it was stable over a wide interval of time and space (tens of millions of years and thousands of kilometers). A detailed account of the history and philosophy of the Arcto-Tertiary Geoflora concept is given by Wolfe (1977; see also Graham, 1972; Lavin & Sousa S., 1995).

The major present-day Northern Hemisphere moist-temperate deciduous forest regions left over from fragmentation of this circumglobal forest are in eastern Asia, Europe, and eastern North America. Tree species richness differs considerably among these three regions, with richness greater in eastern Asia than in eastern North America and richness greater in eastern North America than in Europe (Latham & Ricklefs, 1993; Guo et al., 1998; Svenning, 2003). The Mixed Mesophytic Forest of Oregon–Idaho and of western North America in general were extirpated by the Late Miocene by increasing summer-dry conditions caused by the rain shadow resulting from the rise of the Cascades and Coastal Ranges (Chaney, 1936, 1938a, 1938b, 1959; Wolfe, 1969, 1981; Graham, 1972; Axelrod & Schorn, 1994). This drying climate in western North America caused extinction of many taxa of the Mixed Mesophytic Forest in that region, which probably accounts, at least in part, for the considerably fewer disjunctions between eastern North America and western North America than between eastern North America and eastern Asia (Donoghue & Smith, 2004). Extirpation of mixed forest genera in the Oligocene (Meyer & Manchester, 1997) and Miocene (e.g., Smiley & Rember, 1981) has been supported by fossil data (see also Manchester, 1999).

Species richness of the forests of western and central Europe was reduced greatly in the Pliocene/Pleistocene via climatic cooling (Wolfe, 1997; Willis & McElwain, 2002; Svenning, 2003; Willis & Niklas, 2004). The classical explanation for tree species' extinctions in Europe is that the east-west–trending mountains and the Mediterranean Sea prevented migration of plant taxa southward to warmer areas (Gray, 1878; Reid, 1935; Graham, 1972; Tiffney, 1985b; Milne & Abbott, 2002). However, according to Huntley (1993), evidence does not support east-west–trending mountains or the Mediterranean Sea being barriers to movement of tree taxa in Europe in the Quaternary. Instead, the greater extinction of trees at the generic level in Europe than in Asia and North America during the Quaternary was due to the greater reduction in forest area in Europe, i.e., ". . . limited areas available to such taxa on this continent during the glacial stages that have dominated the Quaternary" (Huntley, 1993: 170). Huntley suggests, however, that the increased species:genus ratio of the European tree taxa, due to speciation via long-term isolation during the Pliocene/Pleistocene in localized refugia in southern Europe, goes a long way in compensating for the greater extinction of tree genera in Europe than in Asia and North America. Further, according to Campbell (1982), certain woody plant genera, including *Alnus* Mill., *Corylus* L., *Pyrus* L., and *Taxus* L., are 100% to 1000% taller in Europe than they are in North America and they may be ecological substitutes for trees such as *Liriodendron* L., *Carya* Nutt. (*Tsuga* (Endl.) Carrière–*Thuja* L.), and *Diospyros* L., respectively, which are no longer extant in Europe. However, according to Huntley (1993: 170) the several genera that today are trees in Europe but low-growing trees/shrubs in eastern North America ". . .are too few in number to

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compensate for these genera that have become extinct [in Europe]."

Svenning (2003) presented evidence that the differential extinctions in the cool temperate tree flora of Europe during the Pliocene/Pleistocene are related to differences in cold and drought tolerances among them. The cold tolerance of the genera in the Pliocene tree flora currently widespread in Europe is greater than that of the genera that went extinct during the Pliocene/Pleistocene or that survive today in Europe as relicts. Further, the relictual genera are more drought-tolerant than those that went extinct (Svenning, 2003). Svenning (2003) explained this differential survival of Pliocene tree genera as a deterministic ecological sorting process determined by generic evolutionary conservatism for tolerance to cold and drought. This suggests that tree genera that survived the Pliocene/Pleistocene extinctions in southern Europe did so either in cool, moist mid-elevation refuges (i.e., cold-tolerant genera) or in low-elevation, drought-prone refuges (i.e., drought-tolerant genera). Svenning and Skov (2007: 242) stated that numerous tree genera that today form an important component of the warm-temperature vegetation in eastern Asia and North America went extinct during the Plio-Pleistocene climatic changes because of "[t]he scarcity of warm moist glacial refugia...." Milne (2004) suggested that the survival of three or four lineages (four species) of *Rhododendron* L. subsect. *Pontica* (Tagg) Sleumer, a Tertiary relict group, in the southwestern Eurasian refugium during Quaternary glaciations can be attributed to their cold tolerance.

The traditional paradigm about the geographic location of European trees during the Pliocene–Pleistocene glaciations is that they were restricted to refugia (more accurately to refugia within refugia [Feliner, 2011]) in southern Europe, and in particular to the Balkan, Italian, and Iberian Peninsulas, where they grew in mid-elevation zones (ca. 500–800 m elevation) on mountains between lowland xeric steppe vegetation and high-elevation, tundra-like vegetation (Willis & McElwain, 2002; Willis & Niklas, 2004; Birks & Willis, 2008). However, current plant fossil material (pollen, plant macrofossils, and macroscopic charcoal) (Willis et al., 2000; Willis & Van Andel, 2004; Bhagwat & Willis, 2008; de Lafontaine et al., 2014a, 2014b), genetic evidence (de Lafontaine et al., 2013), and climatic niche modeling (Svenning et al., 2008) have documented the occurrence of at least 34 woody species of gymnosperms and angiosperms, most of them trees, that survived in cryptic refugia in tundra-type vegetation in central and eastern Europe, north of

the southern refugia during the latest glacial advance. Moreover, some taxa of angiosperm trees occurred in both northern and southern refugia.

BOREOTROPICAL HYPOTHESIS

To account for the floristic similarities between eastern North America, Europe, eastern Asia, and western North America, Wolfe and Tiffney proposed the boreotropical hypothesis, in recognition of the northern geography, near-tropical climate, and thermophilic affinities of the flora's many component taxa (Wolfe, 1975, 1977; Tiffney, 1985a, 1985b). They derived this hypothesis on the basis of tropical taxa shared by the Eocene floras of Europe and North America and on the close taxonomic relationship of these floras to those present today in tropical Southeast Asia and, to some extent, Central America and the Greater Antilles (Lavin & Luckow, 1993). Thus, in contrast to the Arcto-Tertiary Geoflora concept, tropical climates and vegetation extended to northern latitudes during the Eocene (e.g., broad-leaved evergreen multistratal rainforest to 65°–70°N paleolatitudes in Alaska [Wolfe, 1985]), which allowed the exchange of tropical taxa via land bridges with the Old World tropical flora. According to this concept, a large number of modern taxa first appeared in the middle latitudes of the Northern Hemisphere in the Early Tertiary (latest Paleocene to Eocene) and spread via the Bering and North Atlantic land bridges and the shores of the Tethys Seaway. The Tethys Seaway was important for the spread of plants across Eurasia (see Wolfe & Leopold, 1967; Tiffney, 1985a, 1985b) and also for the spread of tropical, subtropical, and warm-temperate plants between Southeast Asia and the southeastern United States (Dilcher, 2000). Accordingly, the claim of the Arcto-Tertiary Geoflora concept that many lineages in this flora evolved in the Arctic during the Late Cretaceous is invalid. Thus, according to Spicer et al. (1987), the first appearance of a clade (woody angiosperms) present in Late Cretaceous–Early Tertiary floras is consistently later in Alaska than at middle latitudes. That is, lineages first appeared in low to middle latitudes and then in the Arctic (Spicer et al., 1987). The migration of angiosperms was poleward (Axelrod, 1959; Hickey & Doyle, 1977).

Wolfe (1994: 232) stated that "a few arcto-tertiary lineages (e.g., those of *Ginkgo* and *Metasequoia*) may even have histories as envisioned by Chaney (1938 [1938b])." Thus Wolfe suggested that a few Arcto-Tertiary lineages may have diversified in montane environments at middle latitudes and then moved downslope as the climate cooled. Note, however, that Wolfe restricted his Arcto-Tertiary use in reference to

trees and shrubs of the Arctic Tertiary plant assemblages that now occur in eastern Asia and eastern North America. He did not embrace the Arcto-Tertiary Geoflora concept of Chaney. In fact, Wolfe stated, "... I consider the concept of an 'Arcto-Tertiary Geoflora' to be negated by the fossil record. ..." (1994: 232).

The boreotropical flora is postulated to have had a diffuse origin, i.e., appearing in several locations in the Northern Hemisphere. This flora had its origins from several separate sources and thus did not originate only in Southeast Asia (Tiffney, 1985b). Southeast Asia (Indomalayan area) is a refugium for the boreotropical flora, not its center of origin (Tiffney, 1985a; also see Schuster, 1972, 1976; Thorne, 1999). "Thus, much of the present Indomalayan flora can be thought of as a relict of this Paleogene boreotropical flora" (Wolfe, 1975: 269, 270). Further, this boreotropical flora was not homogeneous; it exhibited spatial and temporal change in taxonomic composition, and its taxa appeared in the fossil record at different times and had different ecologies (Tiffney, 1985a, 1985b). The boreotropical flora existed in a warm, equable (paratropical) climate with a mean annual temperature of 20°C −25°C and a low mean annual range of temperatures. This flora included a mixture of temperate, tropical, and paratropical genera, many of which were retained in/associated with the Mixed Mesophytic Forest of the Middle to Late Tertiary, e.g., *Acer* L., *Alangium* Lam., *Betula* L., *Calycocarpum* (Nutt. ex Torr. & A. Gray) Spach, *Carpinus* L., *Carya*, *Celtis* L., *Cercidiphyllum* Siebold & Zucc., *Cladrastis* Raf., *Cocculus* DC., *Fagus* L., *Gordonia* J. Ellis, *Halesia* J. Ellis ex L., *Hamamelis* L., *Hydrangea* L., *Juglans* L., *Liquidambar* L., *Liriodendron*, *Magnolia* L., *Nyssa* L., *Platanus* L., *Pterocarya* Kunth, *Quercus* L., *Tetracentron* Oliv., *Tilia* L., *Ulmus* L., and *Zelkova* Spach (Wolfe, 1977). These taxa still persist in the Mixed Mesophytic Forest of eastern Asia and/ or eastern North America today.

Unlike the Arcto-Tertiary Geoflora concept, the boreotropical hypothesis views the Mixed Mesophytic Forest of eastern Asia and eastern North America as having developed *independently* (emphasis ours) after the geographical disruption of the boreotropical flora and not as lineal descendants (remnants, relicts) of a broad-leaved deciduous forest that evolved in high latitudes of the Northern Hemisphere and then migrated as an *intact unit* (emphasis ours) to middle latitudes during gradual climatic cooling during the Tertiary (i.e., Arcto-Tertiary Geoflora concept). According to Tiffney (1985b: 244), "Once the early Tertiary boreotropical flora had spread, it was influenced and altered by subsequent geographic and climatic events, giving rise to the modern flora and vegetation of Eurasia and North America." Further, "... plants sharing a common distribution pattern in the modern day need not have attained this distribution in the same way at the same time" (Tiffney, 1985a: 84). Thus, the eastern Asian–eastern North American pattern in the extant flora of these two areas did not arise as a result of a single historical event.

According to Wolfe (1972, 1977, 1985), the vegetation of southern Alaska (ca. 70°N paleolatitude) in the Early Eocene was paratropical rainforest. This implies that the Bering land bridge may have served as a route for tropical evergreen taxa into North America from Asia in the Early Eocene (Tiffney, 2000). However, winter darkness may have presented a physiological barrier to evergreen taxa in crossing the Bridge (ca. 75°N paleolatitude, but see Royer et al., 2003; Beerling, 2007: chapter 6). Further, the evergreen floras studied by Wolfe were located on exotic terrains, in which case plants in this flora may have grown at more southern latitudes and were transported as fossils to their present localities (Tiffney, 2000; Tiffney & Manchester, 2001). Thus, while the North Atlantic land bridge seemed to have served as a migration route for tropical and subtropical plants during the Eocene (Tiffney, 2000; Tiffney & Manchester, 2001), the Bering land bridge may or may not have done so. Dilcher (2000: 18) postulated that the tropical/subtropical elements in the Eocene flora of the southeastern United States are not products of the northern routes proposed by the boreotropical hypothesis, but rather suggested that these high-latitude routes were too cold for the subtropical and tropical plants in the fossil flora of the southeastern United States, which "...must have been distributed under the warm climatic influence of the Tethys Sea."

MIDDLE EOCENE PARATROPICAL RAINFOREST OF OREGON

In North America, the fruit and seed flora of the Middle Eocene (ca. 44 million years ago [Ma]) Clarno Nut Beds of central Oregon is an excellent example of the boreotropical flora that was widespread across the Northern Hemisphere in the Eocene (Manchester, 1981, 1994). Today, the vegetation of this area of Oregon, which is in the rain shadow of the Cascade Mountains, is primarily shrub-steppe with scattered junipers at lower elevations and coniferous forests (*Abies* Mill., *Pinus* L., *Pseudotsuga* Carrière) at higher elevations (Franklin & Dyrness, 1988). Only five extant tree genera (*Celtis*, *Cornus* L., *Pinus*,

Table 1. Present geographical distribution (marked by x) of extant genera represented in the Middle Eocene Clarno Nut Beds flora (from Manchester, 1994), except *Sargentodoxa* Rehder & E. H. Wilson and *Torricellia* DC. (from Manchester, 1999).

Genus	Southeast Asia	Malesia	Western North America	Eastern North America	Central America	South America	Europe	Africa
Actinidia Lindl.	x	x						
Alangium Lam.	x	x						x
Ampelocissus Planch.	x	?			x			?
Ampelopsis Michx.	x	?		x				
Anamirta Colebr.	x	x						
Aphananthe Planch.	x	x			x			x
Calycocarpum Nutt. ex Torr. & A. Gray				x				
Castanopsis (D. Don) Spach	x	x	x					
Celtis L.	x	x	x	x	x	x	x	x
Cleyera Thunb.	x				x			
Cornus L.	x	x	x	x	x	x	x	x
Decodon J. F. Gmel.				x				
Diploclisia Miers	x	x						
Emmenopterys Oliv.	x	x						
Ensete Horan.	x	x						x
Hydrangea L.	x	x		x	x	x		
Iodes Blume	x	x						x
Juglans L.	x		x	x	x	x	x	
Lindera Thunb.	x			x				
Magnolia L.	x	x		x	x			
Mastixia Blume	x	x						
Meliosma Blume	x	x			x	x		
Nyssa L.	x	x		x	x			
Parthenocissus Planch.	x		x	x	x			
Pinus L.	x	x	x	x	x	x	x	x
Platanus L.	x		x	x	x		x	
Prunus L.	x		x	x	x	x	x	x
Pyrenacantha Hook.	x	x						x
Quercus L.	x	x	x	x	x	x	x	
Rhus L.	x	x	x	x	x	x	x	x
Sabal Adans.				x	x	x		
Sabia Colebr.	x	x						
Sargentodoxa Rehder & E. H. Wilson	x							
Schisandra Michx.	x	x		x				
Symplocos Jacq.	x	x	x	x	x	x		
Tapiscia Oliv.	x							
Taxus L.	x	x	x	x	x		x	
Tinospora Miers	x	x						x
Torreya Arn.	x	?	x	x				
Torricellia DC.	x							
Trema Lour.	x	x			x	x		x
Vitis L.	x		x	x	x		x	x
Totals	39	26	14	22	21	12	10	13

Quercus, and *Taxus*) in the Clarno Nut Beds flora are still native to Oregon; most are found in other geographic regions (Table 1). Thirty-nine (92.9%) of the 42 extant genera recorded from the fruit and seed flora of the Clarno Nut Beds are currently native to Southeast Asia, 26 (61.9%) to Malesia, and 22 (52.4%) to eastern North America (Manchester, 1994). Further, 28 of the 42 (66.7%) extant genera in the Clarno Nut Beds flora occur in the Mixed Mesophytic Forest (sensu Wolfe, 1979) of eastern Asia. A smaller number also occurs in other types of deciduous forest in eastern Asia (Manchester, 1994). Thus, the boreotropical flora had a definite Indomalayan affinity, and the present distribution of this flora is in the Indomalayan area (Table 1; Wolfe, 1975). According to Manchester (1994: 27), "The close floristic similarity [of the Nut Beds flora]

with southeastern Asia and Malesia probably reflects the status of this area as a refugium for once-widespread thermophilic genera that could not withstand the effects of climatic cooling and glaciation at the end of the Tertiary in other parts of the northern hemisphere."

Interestingly, the generic similarity between the Clarno Nut Beds flora and that of the Middle Eocene Claiborne Formation of Kentucky and Tennessee is low, including only *Magnolia*, *Nyssa*, †*Paleocarya*, and *Sabal* Adans. (Manchester, 1994). Manchester (1994) suggested that differences in the Clarno and Claiborne floras may have been caused by geographic barriers to dispersal between eastern and western North America, namely the mid-continental Cretaceous sea and high paleoelevations of the southern Rocky Mountains. However, although more limited than in the western United States, there also is fossil evidence for the occurrence of several other boreotropical genera in eastern North America, i.e., *Alangium*, *Ampelopsis* Michx., †*Conarium*, *Engelhardia* Lesch. ex Blume, *Eucommia* Oliv., *Ficus* L., *Glyptostrobus* Endl., members of Icacinaceae (including *Iodes* Blume), *Nypa* Steck (a mangrove palm), *Platycarya* Siebold & Zucc., *Pterocarya* Kunth, *Pteroceltis* Maxim., *Sargentodoxa* Rehder & E. H. Wilson, *Sciadopitys* Siebold & Zucc., *Sinomenium* Diels, *Symplocos* Jacq., *Tinospora* Miers, *Vitis* L., and †*Wetherellia* (extinct) (Tiffney, 1985b, 1993, 1999; Call & Dilcher, 1997; Manchester et al., 2009; Liu & Jacques, 2010; Stull et al., 2011). Further, molecular phylogenetic data provide evidence that closely related eastern North American–western North American disjunct taxa did not diverge until the Late Miocene or later (Xiang et al., 1998, 2000; see below), indicating that floristic exchange between the two regions continued through the Late Neogene.

The fruit and seed flora of the Early Eocene London Clay of southern England and of the Middle Eocene Messel and Geiseltal floras of continental Europe are other examples of the boreotropical flora. Most of the families and 24% of the Clarno Nut Beds genera occur in these three Early to Middle Eocene floras (Manchester, 1994, and references cited therein). These floristic similarities support other evidence (see Tiffney, 1985a, 1985b, 1994, 1999; Frederiksen, 1988; Manchester et al., 1994; Kvaček et al., 2000; Denk et al., 2010) for the existence of a land connection (most likely across the North Atlantic) between Europe and North America during Early or Middle (and perhaps to the Late, see below) Tertiary. No comparable seed and fruit floras are known from Asia (Manchester, 1994).

EARLY OLIGOCENE MIXED MESOPHYTIC FOREST OF OREGON

ORIGIN

During the Eocene–Oligocene transition (see Prothero, 1994), the global climate changed from warm and equable to cooler, more seasonal (temperate) conditions (Chaney, 1948; Retallack, 1992; Wolfe, 1992; Smith et al., 1998). As a result, the vegetation of central Oregon shifted, through a succession of floristic changes between ca. 39 and 33 Ma, from a paratropical/subtropical rainforest containing many tropical/subtropical elements, e.g., bananas (*Ensete* Horan.), cycads, *Mastixia* Blume, *Meliosma* Blume, palms (*Sabal*), and many lianas in the families Icacinaceae, Menispermaceae, and Vitaceae (Manchester, 1981, 1994, 1995; Wolfe, 1981; Smith et al., 1998) to a temperate broad-leaved deciduous (Mixed Mesophytic) forest (Manchester, 1990, 2000; Meyer & Manchester, 1997). The Early Oligocene Bridge Creek flora (ca. 33 Ma) of Oregon is among the oldest, largest (total minimum taxa of 34 families, 106 genera, and 125 species), and best documented in the middle latitudes of the Northern Hemisphere dominated by broad-leaved deciduous taxa (Manchester & Meyer, 1987; Meyer & Manchester, 1997). This flora differs from that of the Middle Eocene Clarno Nut Beds in its low diversity of both broad-leaved evergreens and lianas. Meyer and Manchester (1997: 51) conclude that this forest "... developed from the congregation of various lineages having origins in older floras of dissimilar character." They envisioned (1997: 51) "... plant species as having had at least five possible responses to climatic cooling of the Eocene-Oligocene transition: (1) local or global extinction, (2) survival through preadaptation, (3) survival through rapid physiological evolution, (4) dispersal from upland regions, and (5) dispersal of particular species (not whole communities) from higher latitudes."

RELATIONSHIPS TO PRESENT-DAY FORESTS

Genera of the Bridge Creek flora include those that had become distributed across the Northern Hemisphere by the Early Miocene and are important components in present-day deciduous forests of eastern Asia and eastern North America (e.g., *Acer*, *Aesculus* L., *Betula*, *Carya*, *Cercis* L., *Cornus*, *Fagus*, *Fraxinus* L., *Juglans*, *Liquidambar*, *Ostrya* Scop., *Quercus*, *Tilia*, and *Ulmus*). Many of these genera also occur in Europe. Noteworthy is the occurrence on the escarpment of eastern Mexico (Sierra Madre Oriental) of identical species and species pairs, including *Acer*, *Carpinus*, *Carya*, *Cercis*, *Cornus*, *Fagus*, *Liquidam-*

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bar, *Magnolia*, *Nyssa*, *Pinus*, and *Platanus*, that are disjunct from the eastern United States (Miranda & Sharp, 1950; Graham, 1973). Arrival of this Mixed Mesophytic Forest element into eastern Mexico began in the Miocene and had become considerably more diverse by the Pliocene (Graham, 1993b, 1999b, 2010; Ruiz-Sanchez & Ornelas, 2014; Manos & Meireles, 2015). Graham (1999b) noted that the appearance of these temperate species in Mexico, which he envisioned to be due to north to south migration from the eastern United States, was coincident with climate cooling in the Late Cenozoic, beginning in the Middle Miocene (see Graham, 2011; Zachos et al., 2001). Neither Milne and Abbott (2002) nor Milne (2006) included eastern Mexico as an area of disjunct Tertiary relicts, whereas Manos and Meireles (2015) included it as an area of endemism for temperate flora in the Northern Hemisphere.

Phytogeographic patterns of the extant members of this flora include eastern Asian–eastern North American disjuncts (*Catalpa* Scop., *Carya*, *Cladrastis*, *Liquidambar*, and *Menispermum* L.); eastern Asian endemics (*Acuba* Link, *Craigia* W. W. Sm. & W. E. Evans, *Cercidiphyllum*, *Cunninghamia* R. Br. ex A. Rich., *Hovenia* Thunb., *Keteleeria* Carrière, *Metasequoia*, and *Pterocarya*); and eastern North American endemics (*Comptonia* L'Hér. ex Aiton, *Decodon* J. F. Gmel., *Fothergilla* L., and *Pinckneya* Michx.). *Metasequoia* was the dominant conifer in the Bridge Creek flora (Meyer & Manchester, 1997). Further, 86% of the extant genera in this flora are native to eastern Asia today and 68% to eastern North America (Meyer & Manchester, 1997). The Bridge Creek flora was floristically and physiognomically similar to the present-day deciduous forests of eastern Asia and eastern North America. Based on various temperature parameters, the Bridge Creek flora is representative of a Mixed Mesophytic Forest (sensu Wolfe, 1979), but it is near the transition with Mixed Northern Hardwood Forest (cf. Meyer & Manchester, 1997). Although the greatest representation of extant taxa in this flora is in the present-day Mixed Mesophytic Forest of eastern Asia, it has fewer evergreen taxa than the Asian Mixed Mesophytic Forest, and in this respect the Bridge Creek forest was more similar to the present-day Mixed Northern Hardwood Forest (sensu Wolfe, 1979; Meyer & Manchester, 1997) of eastern Asia. According to Meyer and Manchester (1997: 43), "Floristically the Bridge Creek flora is most similar to the Mixed Mesophytic forest [of Southeast Asia] in the presence of *Torreya* [Arn.], *Cunninghamia*, *Keteleeria*, *Cedrela* [P. Browne], *Cercidiphyllum*, and *Pterocarya*. Most of the other extant genera of the fossil assemblage occur today in both Mixed Mesophytic and Mixed Northern Hardwood forest types."

MIOCENE MIXED MESOPHYTIC FORESTS OF OREGON–IDAHO

Floristic elements of the Mixed Mesophytic Forest were present in the western United States until the Middle to Late Miocene (Axelrod, 1992). Characteristic Miocene examples of this microfossil/megafossil flora/vegetation include the Succor Creek flora of eastern Oregon–adjacent Idaho (Taggart & Cross, 1980, 1990; Cross & Taggart, 1982), and the Clarkia (Smiley et al., 1975; Smiley & Rember, 1981; Baghai, 1988; Manchester & Chen, 2006) and Musselshell Creek (Baghai & Jorstad, 1995) floras of northern Idaho. Fossils of the mature forests at these sites represent a gradient of plant communities and successional stages. The Mixed Mesophytic Forest was represented by the mature slope-bottomland (floodplain) hardwood forest (Fig. 1). Many genera of woody plants (except *Pachysandra* Michx., an herb) in these floras have become extinct in North America and survive only in the Asiatic region, including the Caucasus, the Himalayas, and Malesia (C = Clarkia, MC = Musselshell Creek, SC = Succor Creek). These include *Ailanthus* Desf. (SC), *Cephalotaxus* Siebold & Zucc. ex Endl. (SC), *Cercidiphyllum* (C), *Cunninghamia* (C), *Exbucklandia* R. W. Br. (MC), *Ginkgo* (MC, SC), *Glyptostrobus* (SC), *Keteleeria* (SC), *Metasequoia* (C, MC), *Paliurus* Mill. (C), *Paulownia* Siebold & Zucc. (C), *Platycarya* (MC), *Pterocarya* (C, MC, SC), *Tetracentron* (C), and *Zelkova* (C, MC, SC). Those that became extinct in western North America and survive in both eastern Asia and eastern North America include *Carya* (C, MC, SC), *Gordonia* (C), *Halesia* (C), *Hamamelis* (C), *Lindera* Thunb. (C, MC), *Liriodendron* (C), *Magnolia* (C, MC, SC), *Nyssa* (C, SC), *Pachysandra* (SC), and *Sassafras* J. Presl (C, SC) (Taggart & Cross, 1980; Smiley & Rember, 1981; Golenberg et al., 1990; Baghai & Jorstad, 1995); all of these latter genera except *Gordonia* occur in Kentucky. However, *Gordonia*, as *G. lasianthus* (L.) J. Ellis, does remain to the southeast of Kentucky, on the Atlantic and Gulf coastal plains of North Carolina to southern Florida and west to southeastern Louisiana (Seiler et al., 2015). *Comptonia* is the only present-day endemic genus in eastern North America that was present in these Miocene forests. Other genera in the Clarkia, Musselshell Creek, and/or Succor Creek floras present in the forests of Kentucky today but that no longer occur in western North America include the vines *Ampelopsis*, *Berchemia* Neck. ex DC., and *Cocculus*; the shrubs *Asimina* Adans. and
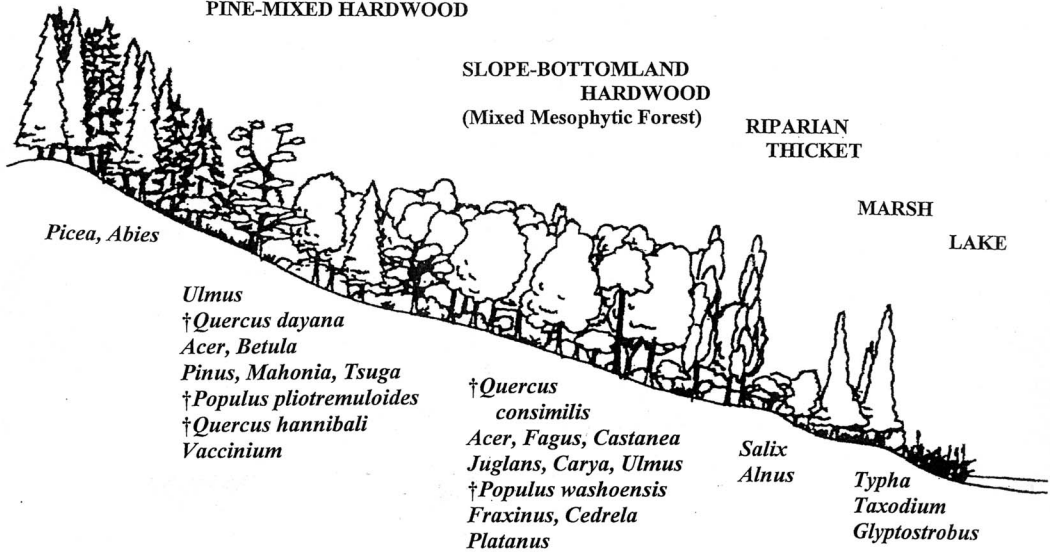
Figure 1. Generalized reconstruction of the Middle Miocene mature closed-canopy (climax) vegetation at Succor Creek, eastern Idaho–adjacent Oregon. Mixed Mesophytic forest is represented by the slope-bottomland hardwood portion of the gradient. Adapted from Cross and Taggart, 1982: 693, with permission for re-use from the Missouri Botanical Garden Press, St. Louis.

Hydrangea; and the trees *Carpinus*, *Castanea* Mill., *Diospyros*, *Fagus*, *Gleditsia* J. Clayton, *Gymnocladus* Lam., *Ilex* L., *Liquidambar*, *Ostrya*, *Taxodium* Rich., *Tilia*, and *Ulmus*.

LATE CRETACEOUS AND TERTIARY VEGETATION OF THE
EASTERN UNITED STATES

Compared to the Pacific Northwest, macrofossil data from which to reconstruct the Tertiary history of the Mixed Mesophytic Forest in eastern North America are meager (Graham, 1964, 1993a, 1999a; Wallace & Wang, 2004). Only a few relatively diverse fossil macrofloral assemblages are known in which a high percentage of the taxa have been identified accurately (see Dilcher, 1971). Macrofloral assemblages relevant to reconstruction of the Tertiary vegetation of the eastern United States include the Middle Eocene Claiborne flora of the upper portion of the Mississippi Embayment of Kentucky and Tennessee (Table 2); the Late Oligocene or Early Miocene Brandon lignite flora of Vermont (Tiffney, 1994; the middle Early Miocene, sensu Traverse, 1994); the Late Miocene Brandywine flora of the southern Maryland Coastal Plain (McCartan et al., 1990); the Early Eocene fruit and seed flora from the Fisher/Sullivan site in coastal eastern Virginia (Tiffney, 1999); and the Late Miocene/Early Pliocene Gray Fossil Site in northeastern Tennessee (Gong et al., 2010; Liu & Jacques, 2010).

Frederiksen (1989) used a combination of microfossils (pollen) and macrofossils (fruits, seeds, leaves, and wood) to reconstruct what he thought was probably the Late Cretaceous–Tertiary vegetation of New England, but there are many gaps in the fossil record on which this reconstruction is based. The Mixed Mesophytic Forest has been shown to be present in New England from the Middle Oligocene to the Late Miocene (Frederiksen, 1989). This fossil flora included genera that occur in present-day temperate deciduous forests of eastern North America (e.g., *Betula*, *Carya*, *Castanea*, *Fagus*, *Gordonia*, *Juglans*, *Liquidambar*, *Nyssa*, *Platanus*, *Quercus*, and *Tilia*) as well as Asian exotics that have been extirpated from North America and survive only in eastern Asia (i.e., *Alangium*, *Glyptostrobus*, *Pterocarya*, *Sargentodoxa*, and *Sciadopitys*). Frederiksen's study contains the only diagram we are aware of that heretofore illustrates the sequence of Late Cretaceous–Tertiary vegetation in eastern North America.

LATE CRETACEOUS AND TERTIARY VEGETATION OF KENTUCKY

Although Late Cretaceous (Maestrichtian) strata occur in western Kentucky (Olive, 1980; McDowell, 1986), and many representatives of the †Normapolles palynoflora have been collected from them, no megafloral assemblage has been found in these sediments. However, two studies in the adjacent states of Illinois and Tennessee provide information

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Table 2.   Some Tertiary megafossils from western Kentucky–Tennessee. Most of the taxa were collected only from the Middle Eocene Claiborne Formation. Fossil species names (and occasional genus names if no extant species) indicated by a dagger.

Family	Taxon	References
GYMNOSPERMS		
Podocarpaceae	*Podocarpus* Labill. sect. *Stachycarpus* Endl.	Dilcher, 1969
	Podocarpus sect. *Podocarpus*, sp. indet.	Moore et al., 2003
ANGIOSPERMS, MONOCOTS		
Araceae	†*Acorites heeri*	Crepet, 1978
	Philodendron limnestis	Dilcher & Daghlian, 1977
Palmae	†*Amesoneuron*, sp. indet.	Daghlian, 1978
	†*Costapalma philipii*	Daghlian, 1978
	†*Eopalma fibrosa*	Grote, 1989
	†*Palmacites eocenica*	Daghlian, 1978
	†*Palustrapalma agathae*	Daghlian, 1978
	†*Sabal dortchii*	Daghlian, 1978
	†*Sabalites grayanus*	Daghlian, 1978
	Palm	Moore et al., 2003
Poaceae	Grass	Crepet & Feldman, 1991
Smilacaceae	*Smilax* L., two sp. indet.	Dilcher & Lott, 2005
	Smilax	Moore et al., 2003
ANGIOSPERMS, DICOTS		
Altingiaceae	*Liquidambar* L., sp. indet.	Dilcher & Lott, 2005
Anacardiaceae (tribe Spondideae) or Humeriaceae (?)	†*Campanurbia lenticularis*	Grote, 1989
Annonaceae	†*Duguetia leei*	Roth, 1981
	Duguetia A. St.-Hil., sp. indet.	Dilcher & Lott, 2005
	Duguetia, two sp. indet.	Moore et al., 2003
Apocynaceae	†*Apocynophyllum*, sp. indet.	Dilcher & Lott, 2005
	†*Apocynophyllum mississippiens*	Moore et al., 2003
Araliaceae	†*Dendropanax eocenensis*	Dilcher & Dolph, 1970; Dilcher & Lott, 2005
	Dendropanax Decne. & Planch., two sp. indet.	Moore et al., 2003
Cannabaceae (including Celtidaceae)	†*Pteroceltis knowtonii*	Manchester et al., 2009
Ceratophyllaceae	*Ceratophyllum muricatum* Cham. subsp. †*incertum*	Herendeen et al., 1990
Eucommiaceae	†*Eucommia eocenica*	Call & Dilcher, 1997
	Eucommia Oliv., sp. indet.	Moore et al., 2003
Euphorbiaceae, Euphorbioideae	†*Crepetocarpon perkinsii*	Dilcher & Manchester, 1988
	†*Hippomaneoidea warmanensis*	Crepet & Daghlian, 1982
Fagaceae, Castaneoideae	†*Castaneoidea puryearensis*	Crepet & Daghlian, 1980
	†*Castaneophyllum tennesseensis*	Jones & Dilcher, 1988
	†*Castaneophyllum moorii*	Jones & Dilcher, 1988
	†*Castanopsoidea columbiana*	Crepet & Nixon, 1989
Fagaceae, Fagoideae	†*Paleojulacea laxa*	Crepet & Nixon, 1989
	†*Trigonobalanoidea americana*	Crepet & Nixon, 1989
Fagaceae, Quercoideae	†*Berryophyllum warmanense*	Jones & Dilcher, 1988
	†*Berryophyllum saffordii*	Jones & Dilcher, 1988
	†*Berryophyllum tenuifolium*	Jones & Dilcher, 1988; Dilcher & Lott, 2005
	†*Berryophyllum*, sp. indet.	Dilcher & Lott, 2005
	†*Knightiophyllum wilcoxianum*	Dilcher & Mehrotra, 1969; Moore et al., 2003; Dilcher & Lott, 2005
Hamamelidaceae	†*Corylopsis americana*	Grote, 1989

Table 2.   Continued.

Family	Taxon	References
Icacinaceae	†*Natsiatum wilcoxiana*	Stull et al., 2011
	†*Phytocrene densipunctata*	Stull et al., 2011
Juglandaceae	†*Eokachyra aeolius*	Crepet et al., 1975
	†*Eoengelhardia puryearensis*	Crepet et al., 1980
	†*Oreoroa claibornensis*	Dilcher & Manchester, 1986
	†*Oreoroa*, sp. indet.	Moore et al., 2003
	†*Paleocarya puryearensis*	Manchester, 1987
	†*Paleooreomuunnea stoneana*	Dilcher et al., 1976
	†*Paraengelhardia eocenica*	Berry, 1916; Manchester, 1987
	†*Paraengelhardia*, sp. indet.	Moore et al., 2003
Lauraceae	†*Androglandula tennesseensis*	Taylor, 1988b
	Ocotea obtusifolia Kunth	Dilcher, 1963a
	Ocotea Aubl., sp. indet.	Dilcher & Lott, 2005
	Persea Mill., two spp. indet.	Moore et al., 2003
Leguminosae, Caesalpinioideae	cf. *Acrocarpus* Wight ex Arn., sp. indet.	Herendeen, 1992
	Caesalpinia L. subg. *Caesalpinia*	Herendeen, 1992
	Caesalpinia subg. *Mezoneuron* (Desf.) Vidal ex Herend. & Zarucchi	Herendeen & Dilcher, 1991
	†*Caesalpinia claibornensis* Herend. & Dilcher	
	cf. Caesalpinioideae	Herendeen, 1992
	Caesalpinia, sp. indet.	Moore et al., 2003
	†*Leguminosites prefoliatus*	Herendeen, 1992
	cf. †*Leguminosites ingafructoides*	Herendeen, 1992
	cf. †*Leguminosites phyllocarpoides*	Herendeen, 1992
	cf. *Erythrophleum* Afzel. ex R. Br., sp. indet.	Herendeen, 1992
	†*Crudia grahamiana*	Herendeen & Dilcher, 1990a
	Senna Mill., sp. indet.	Herendeen, 1992
	cf. *Stemonocoleus* Harms/*Aubrevillea* Pellegr.	Herendeen, 1992
Leguminosae, Mimosoideae	†*Eomimosoidea plumose*	Crepet & Dilcher, 1977
	†*Duckeophyllum eocenicum*	Herendeen & Dilcher, 1990b
	†*Eliasofructus catahoulensis*	Herendeen & Dilcher, 1990b
	†*Eliasofructus claibornensis*	Herendeen & Dilcher, 1990b
	†*Parvileguminophyllum georgianum*	Herendeen & Dilcher, 1990b
	†*Protomimosoidea buchanensis*	Crepet & Taylor, 1986
Leguminosae, Papilionoideae	†*Barnebyanthus buchananensis*	Crepet & Herendeen, 1992
	cf. *Cladrastis* Raf., sp. indet.	Herendeen, 1992
	cf. *Cladrastis*	Dilcher & Lott, 2005
	†*Diplotropis claibornensis*	Herendeen & Dilcher, 1990c
	cf. †*Gleditsia? mississippiensis*	Herendeen, 1992
	†*Gleditsiophyllum eocenicum*	Herendeen, 1992
	cf. *Machaerium* Pers., sp. indet.	Herendeen, 1992
	cf. *Ormosia* Jacks., two or three sp. indet.	Herendeen, 1992
	cf. *Ormosia*, sp. indet.	Dilcher & Lott, 2005
	Ormosia, sp. indet.	Moore et al., 2003
	cf. *Sophora* L. subg. S*typhenolobium*	Herendeen, 1992
	cf. Sophoreae	Herendeen, 1992
	cf. *Swartzia* Schreb., two or three sp. indet.	Herendeen, 1992
	Swartzia, sp. indet.	Dilcher & Lott, 2005
	Swartzia, sp. indet.	Moore et al., 2003
Magnoliaceae	†*Magnolia tiffneyi*	Grote, 1989
	†*Magnolia kentuckyensis*	Grote, 1989

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Table 2.   Continued.

Family	Taxon	References
Malpighiaceae	†*Eoglandulosa warmanensis*	Taylor & Crepet, 1987
Moraceae	†*Cornerocarpon copiosum*	Grote, 1989
	†*Cornerocarpon crassibracteatum*	Grote, 1989
	cf. *Ficus* L., sp. indet.	Dilcher & Lott, 2005
	†*Pseudomedia*, sp. indet.	Dilcher & Lott, 2005
Myricaceae	*Myrica* L., sp. indet.	Dilcher & Lott, 2005
Myrtaceae	†*Syzygiodes*, sp. indet.	Moore et al., 2003
Nyssaceae	†*Nyssa eolignitica*	Dilcher & McQuade, 1967
	Nyssa L., sp. indet.	Moore et al., 2003
Oleaceae	†*Fraxinus wilcoxiana*	Call & Dilcher, 1992
	Oleaceae leaf morphotype	Dilcher & Lott, 2005
Platanaceae	*Platanus* L., sp. indet.	Dilcher & Lott, 2005
Rhamnaceae	†*Berhamniphyllum claibornense*	Jones & Dilcher, 1980; Dilcher & Lott, 2005
	†*Berhamniphyllum*, sp. indet.	Dilcher & Lott, 2005
Rosaceae	—	Moore et al., 2003
Rubiaceae	†*Paleorubiaceophyllum eocenicum* var. *eocenicum*	Roth & Dilcher, 1979
	†*Paleorubiaceophyllum eocenicum* var. *amplum*	Roth & Dilcher, 1979
	†*Paleorubiaceophyllum eocenicum* var. *lawrensis*	Roth & Dilcher, 1979
	cf. †*Paleorubiaceophyllum*, sp. indet.	Dilcher & Lott, 2005
Salicaceae	*Populus* L., sp. indet.	Dilcher & Lott, 2005
Sapindaceae	†*Cupanites*, sp. indet.	Dilcher & Lott, 2005
	Sapindus L., sp. indet.	Moore et al., 2003
Sapotaceae	†*Platyulota kentuckyensis*	Grote, 1989
	†*Sapotispermum cucullatum*	Grote, 1989
Theaceae	†*Ternstroemites*, sp. indet.	Dilcher & Lott, 2005
Theaceae, Camelloideae, Gordonieae	†*Andrewsiocarpon henryense*	Grote, 1989
	†*Gordonia lamkinensis*	Grote & Dilcher, 1992
	†*Gordonia warmanensis*	Grote & Dilcher, 1992
	Gordonia J. Ellis, sp. indet.	Grote, 1989
	cf. *Gordonia*, sp. indet.	Dilcher & Lott, 2005
	Gordonia, sp. indet.	Moore et al., 2003
	†*Gordoniopsis polysperma*	Grote & Dilcher, 1992
Ulmaceae, Celtidoideae	†*Eoceltis dilcheri*	Zavada & Crepet, 1981

relevant to a description of the Late Cretaceous vegetation of Kentucky. Wheeler et al. (1987) described five species of fossil dicotyledonous woods from the McNairy Formation (Maestrichtian) in southern Illinois, which also occurs in Kentucky: †*Paraquercinum cretaceum* (similar to the evergreen oak *Lithocarpus* Blume, Fagaceae), †*Paraphyllanthoxylon illinoenense* (most likely a phyllanthoid Euphorbiaceae s.l.), †*Icacinoxylon alternipunctata* (affinity appears to be with Icacinaceae); †*Parabombacaceoxylon magniporosum* (likely Bombacaceae); and †*Parapocynaceoxylon barghoorni* (likely Apocynaceae). None of these five species had growth rings, which infers a non-seasonal climate. Further, all five would have had a high vulnerability (to air embolisms, caused by drought or freezing tempera-

tures) index (V), where $V = d/D$, d is mean vessel diameter, and $D =$ mean number of vessels/mm^2 (Carlquist, 1977), indicating these taxa did not experience water stress and had low-density wood, a characteristic of fast-growing woody plants. Thus, it seems likely that these were colonizing species in a lowland to middle-elevation tropical rainforest (Wheeler et al., 1987).

In another study of fossil plant material from the McNairy Formation, Wolfe and Upchurch (1987) analyzed leaf physiognomy and wood structure of specimens collected by E. W. Berry (1916) in Tennessee, as part of their effort to describe climate and vegetation of the Late Cretaceous in North America. They concluded that the climate was subhumid megathermal (mean annual temperature

> 20°C) with a mean annual rainfall < 1650 mm and little seasonality in either temperature or precipitation. The vegetation was described as open-canopy, broad-leaved, evergreen woodland without lianas and not multistratal. The leaves were small (i.e., low size index), generally lacked drip-tips, and 62%–69% of them had entire margins. The wood had a high vulnerability index and a high water-conducting capability, and lacked growth rings.

Horrell (1991) used preserved climatic indicators, including paleofloras, evaporite deposits, and coal deposits, to reconstruct world climates and terrestrial biomes in the latest Cretaceous (Maestrichtian). He recognized seven biomes. Kentucky is located in Biome 4, (winter-wet), a winter-wet, summer-dry climate with sclerophyllous-leaved vegetation consisting of shrubs and small trees and with conifers common. In their study of world terrestrial vegetation and its effects on climate during the Maestrichtian, Otto-Bliesner and Upchurch (1997) and Upchurch et al. (1998, 1999) also recognized seven biomes. Kentucky is located in their Biome 3, subtropical broad-leaved evergreen forest and woodland, an angiosperm-dominated vegetation with palms and gingers, in addition to cold-sensitive fungal taxa.

The only Tertiary macrofossil floral assemblage in Kentucky is that of the Middle Eocene Claiborne Group of the Mississippi Embayment of the Gulf Coastal Plain in western Kentucky and adjacent portions of western Tennessee. Thus, the Tertiary vegetation of Kentucky is somewhat speculative. Although the Middle Eocene boreotropical flora of the Clarno Nut Beds of Oregon contains many genera from the Mixed Mesophytic Forest (Manchester, 1994), the Claiborne flora of Tennessee and Kentucky represents a semideciduous tropical dry forest with a high number of Leguminosae (Herendeen, 1992; Graham & Dilcher, 1995; Graham, 1999a; cf. Table 2). According to Graham (1999a), the Paleocene to Early Eocene tropical rainforest in the southeastern United States was replaced by tropical dry forest in response to a decrease in amount and an increase in seasonality of rainfall.

Based on the distribution of closely related extant taxa, Herendeen (1992) recognized four biogeographic patterns among Leguminosae in the Claiborne flora: (1) tropical South America, e.g., *Diplotropis* Benth., (2) tropical Asia and Africa, e.g., *Caesalpinia* L. subg. *Mezoneuron* (Desf.) Vidal ex Herend. & Zarucchi, (3) pantropical, e.g., *Crudia* Schreb. (Herendeen & Dilcher, 1990a), and (4) temperate North America–temperate Asia, e.g., *Cladrastis*. *Cladrastis* (Herendeen, 1992) and *Diplotropis* (Herendeen & Dilcher, 1990b) are extant genera, and

Caesalpinia subg. *Mezoneuron* (Herendeen & Dilcher, 1991) is an extant subgenus, all of which date back to the Middle Eocene. Herendeen (1992: 150) stated that "When [the Leguminosae are] taken together with the fossil record of other families from the Mississippi Embayment, it is evident that many of the fossils are related to taxa restricted to South America today." He suggested that the high representation of South American taxa in this fossil flora is due to their dispersal from tropical South America during the Late Cretaceous and Paleogene (Herendeen, 1992; Herendeen et al., 1992).

Taylor (1988a; also see Taylor, 1990) analyzed reports of Early Tertiary plant fossils from the southeastern United States in relation to the phylogeny and present-day geographic distribution of extant relatives and fossil records outside North America. He concluded that (1) the Paleogene tropical flora of the southeastern United States contained both boreotropical and West Gondwanaland elements, and (2) there was bidirectional, perhaps more so to the north, interchange of taxa between North and South America in the Late Cretaceous–Early Tertiary via the proto-Caribbean sea. South America was isolated from other land masses from the Late Cretaceous to the Middle Pliocene. Undoubtedly, there were Gondwanan elements in the southeastern United States in the Early Tertiary. For example, macrofossils of *Podocarpus* sect. *Stachycarpus* Endl. (a gymnosperm) and of *Duguetia* A. St.-Hil. (Annonaceae) have been collected from the Claiborne Formation (Dilcher, 2000).

Following the Eocene, rainfall in the southeastern United States increased as a result of continued uplift of the Rocky Mountains, which in turn caused changes in atmospheric circulation that brought warm, moist winds from the Gulf of Mexico. Consequently, the gradual disappearance of the tropical dry forest favored the development of the Eastern Deciduous Forest. Graham (1999a: 232) characterized the vegetation of the southeastern United States during the Oligocene as "Tropical" on the coast, "Tropical toward deciduous (mixed mesophytic)" inland, and "Deciduous (mixed mesophytic)" in uplands; and that of the Early Miocene was "Warm-temperate to subtropical?" Graham also noted that by the Middle and Late Eocene floristic elements already were available for vegetation associations found today in the southeastern United States.

Graham (1999a: 266) summarized the development of the vegetation of this region from Middle Miocene (apparently) through the Pliocene as follows.

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Ma	EPOCH OR AGE	VEGETATION	CLIMATE
2.6	Pliocene	Temperate Deciduous Forest (apparently with Asian exotics)	Warm-Cool Temperate
5.3	Miocene — MMCO —	Mixed Mesophytic Forest (with Asian exotics)	Warm-Temperate (ample year-round rainfall)
15			
23	Oligocene	Mixed Broad-Leaved Deciduous/Mixed Mesophytic Forest (with Asian exotics)	Warm-Temperate (ample year-round rainfall)
33.6	Eocene	Semideciduous Dry Tropical Forest (many Leguminosae taxa) (†*Cupuliferoidaepollenites*/ †*Cupuliferoipollenites* Pollen Flora)	Subtropical (seasonally-dry)
50	— EECO —	Tropical Rainforest (closed canopy, multistratal)	Tropical Wet
55	— PETM —		
	Paleocene	Tropical or Paratropical Rainforest (temperate plants in Appalachian Highlands?)	Tropical or Paratropical Wet
65.5	— K/T —		
	Maastrichtian	Evergreen Broad-Leaved Tropical or Paratropical Woodland (open canopy)	Subhumid Tropical or Paratropical
74			

(†Normapolles Pollen Flora spans Maastrichtian through Eocene)
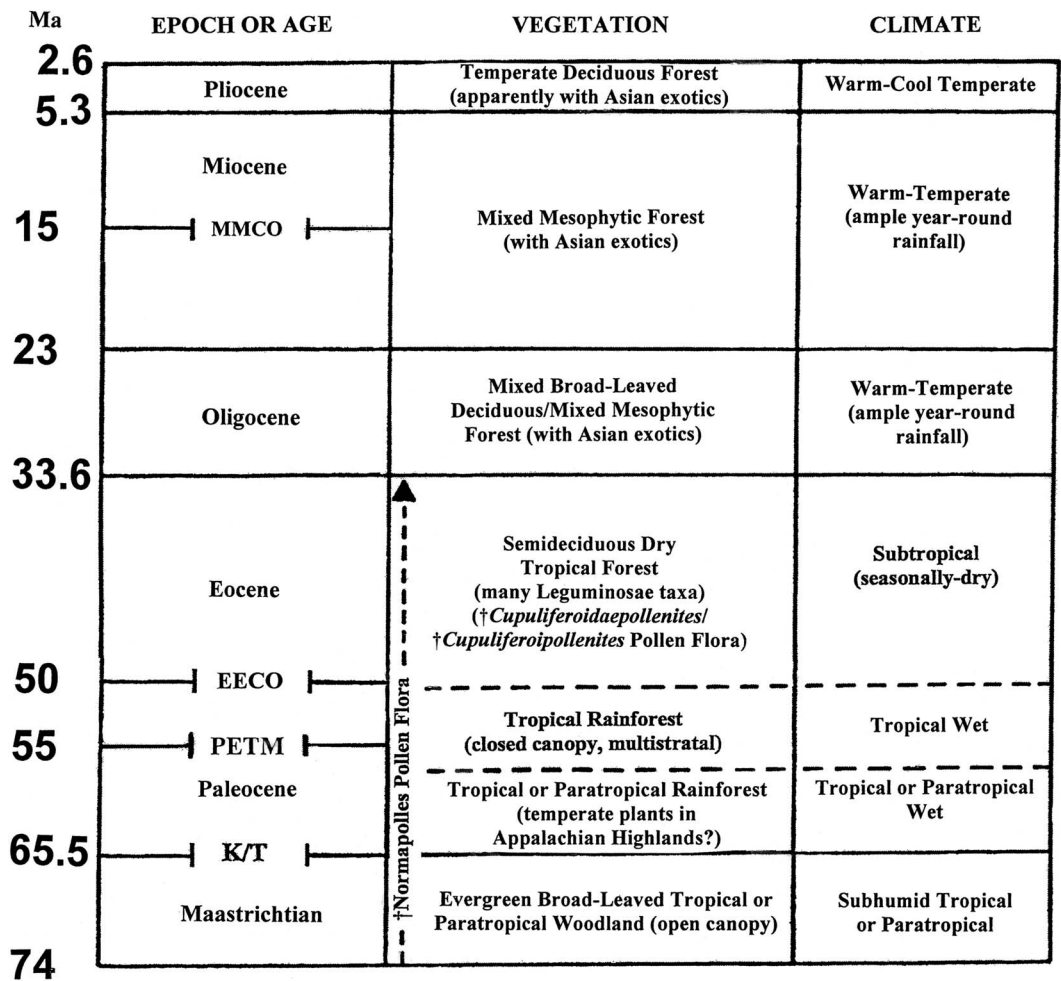
Figure 2. Inferred Late Cretaceous and Tertiary climax vegetation and climate of Kentucky constructed from numerous sources, including Graham (1999a). K/T refers to the Cretaceous–Tertiary boundary, PETM to the Paleocene–Eocene Thermal Maximum, EECO to the Early Eocene Climatic Optimum, and MMCO to the Middle Miocene Climatic Optimum.

"Although published information of vegetational history is surprisingly meager for the Middle Miocene through the Pliocene of the southeastern United States [see Wallace & Wang, 2004; Ochoa et al., 2012], it is likely that modernization of the vegetation [of the southeastern United States] accelerated with the Middle to Late Miocene cooling event.[...] The principal effects were the disappearance of most Asian and neotropical exotics by the Pliocene [see Liu & Jacques (2010) and Ochoa et al. (2012), who report *Pterocarya*, *Sargentodoxa*, and *Sinomenium* from the Miocene-earliest Pliocene (7–4.5 Ma) Gray Fossil Site in northeastern Tennessee, for which the palynoflora is dominated by *Carya*, *Quercus*, and *Pinus*], modernization and expansion of the mixed mesophytic forest, the temporal association of different forest genera to constitute various other deciduous forest associations, and development of the Appalachian coniferous forest. In Chapter 6, it was noted that by Claiborne (Middle Eocene)–Jackson (Late Eocene) time, elements [taxa; e.g., see Gray, 1960; Graham, 1972] were available for assemblage into the mixed mesophytic, southern mixed hardwood, oak–hickory, oak–chestnut, sandpine scrub (*Pinus*, *Sabal*, other rosette palms), flood-plain (*Taxodium*, *Nyssa*), and mangrove (*Acrostichum* [a fern], *Nipa* [*Nypa*, a palm]) associations."

Thus, by the Early Tertiary many elements of today's Mixed Mesophytic Forest were present (but not dominant) in the warm temperate to tropical broad-leaved evergreen forests of the southeastern United States (Gray, 1960; Graham, 1972). As such, the origin of the mixed mesophytic forests can be traced to the Early Eocene (Graham, 1972).

Using information in the literature, we have made an attempt to reconstruct the Late Cretaceous and Tertiary vegetation of Kentucky (Fig. 2). Except for the †Normapolles (Tschudy, 1970, 1981) and †*Cupuliferoidaepollenites*/†*Cupuliferoipollenites* pollen

floras (Potter, 1976, 1977; Hower et al., 1990), the main sources of this information were Graham (1999a) and the many references cited in this book. Thus, the open-canopy tropical or paratropical woodland of the latest Cretaceous changed to a tropical or paratropical rainforest (perhaps with temperate plants in the Appalachian Uplands) in the earliest Tertiary (Paleocene); to a closed canopy wet tropical rainforest with multiple strata in the Late Paleocene; to a semideciduous dry tropical forest with many Leguminosae in the Middle Eocene (Claiborne Flora); to a broadleaved deciduous forest with several Asian exotics following the Eocene–Oligocene climatic cooling period; to a Mixed Mesophytic Forest by the Miocene; to a cooler-climate temperate deciduous forest in the Pliocene following further climatic cooling, with which Asian exotics persisted until at least the Late Miocene–Early Pliocene (Liu & Jacques, 2010; Ochoa et al., 2012).

Angiosperm pollen of the †Normapolles complex/type has been found in Late Cretaceous and Paleogene sediments of the Mississippi Embayment portion of Kentucky and adjacent parts of Tennessee (Tschudy, 1970, 1981, 1984). This pollen type, which appears to belong to a core Fagales clade comprising the extant families Betulaceae, Casuarinaceae, Ticodendraceae, Myricaceae, Rhoipeteleaceae, and Juglandaceae (Wolfe, 1974; Friis, 1983; Batten, 1989; Sims et al., 1999; Schönenberger et al., 2001; Friis et al., 2003, 2006; Hermanova et al., 2011), first appeared in the Cenomanian, reached peak abundance in the Late Campanian–Maestrichtian, and then declined to extinction by the latest Eocene or Early Oligocene. Thus, during the latest Cretaceous, Kentucky was in the Normapolles Palynofloral Province (Fig. 3), which included eastern North America and western-central Europe (e.g., Srivastava, 1978; Herngreen & Chlonova, 1981; Batten, 1984; Krutzsch & Pacltova, 1987–1988; Herngreen et al., 1996). Two other names used for this region are the North Atlantic–European Province (Muller, 1970) and Euramerian-Turonian Region (Samoylovich, 1977).

In addition to the †Normapolles pollen type, pollen of other angiosperms and of gymnosperms and spores of pteridophytes, bryophytes, and fungi have been found in the latest Cretaceous–Paleogene of the northern portion of the Mississippi Embayment (Jackson Purchase physiographic region) in Kentucky and Tennessee (Dilcher, 1963b, 1965; Elsik & Dilcher, 1974; Potter, 1976; Hower et al., 1990). Elsik and Dilcher (1974) identified palynomorphs of various fungi, ferns, gymnosperms, and dicotyledonous and monocotyledonous angiosperms from uppermost Claiborne sediments (sensu Potter, 1976) in Lawrence clay pit in Henry County, Tennessee, which adjoins Calloway County, Kentucky. An interesting aspect of their study was the presence of the boreotropical genera (Asian exotics) *Sciadopitys*, *Engelhardia*, and *Platycarya*. Pollen assemblages of both the clay and lignite zones of the Claiborne Formation in the Miller clay pit in Henry County, Tennessee, were dominated by species of †*Cupuliferoidaepollenites* and †*Cupuliferoipollenites* (Potter, 1976), non-magnoliid eudicots, perhaps with affinity to the Fagaceae (Hower et al., 1990). These two pollen genera also were found to be quite abundant in lignite deposits of the Claiborne Formation at several sites in the Jackson Purchase of Kentucky (Hower et al., 1990). However, a considerable number of other pollen morphs were present in the Claiborne Formation, and thus the diversity of this angiosperm-dominated floral assemblage that grew in a warm-temperate to subtropical environment are represented (Potter, 1976; Hower et al., 1990). Based on foliar physiognomy and the temperature limits of palms, Greenwood and Wing (1995) inferred a mean annual, a mean annual range, and a cold-month mean Middle Eocene temperature of 23.9°C, 10.2°C, and 16.1°C, respectively, at a Claiborne site in Henry County, Tennessee. †*Cupuliferoidaepollenites* and †*Cupuliferoipollenites* also were present in notable abundance in lignites of the uppermost Cretaceous–Paleocene McNairy Formation in Kentucky.

Middle and Early Cretaceous Palynofloral Provinces That Included Kentucky

In the Middle Cretaceous, Kentucky was located in the Southern Laurasian Palynofloral Province (Brenner, 1976; Srivastava, 1981; Batten, 1984; see also Crane, 1987) or Palynofloral Realm (Batten & Wenben, 1987) (Fig. 4). In both North America and Europe, this province was characterized by a high diversity of Pteridophyta, especially ferns in the Schizaeaceae and Gleicheniaceae, and of bisaccate pollen-producing gymnosperms in the Pinaceae and Podocarpaceae. Further, "*Classopollis* [pollen of Cheirolepidaceae, an extinct family of conifers] occurs regularly and may be numerous, and *Araucariacites* is consistently recorded" (Batten, 1984: 136). Land-plant dominance by this pteridophyte/gymnosperm complex of the Middle Cretaceous (Albian–Cenomanian) gave way to the angiosperms by the Late Cretaceous (Brenner, 1976). In terms of both taxonomic diversity and abundance, angiosperms dominate the megafossil flora by the Cenomanian (earliest Late Cretaceous) and also the microfossil

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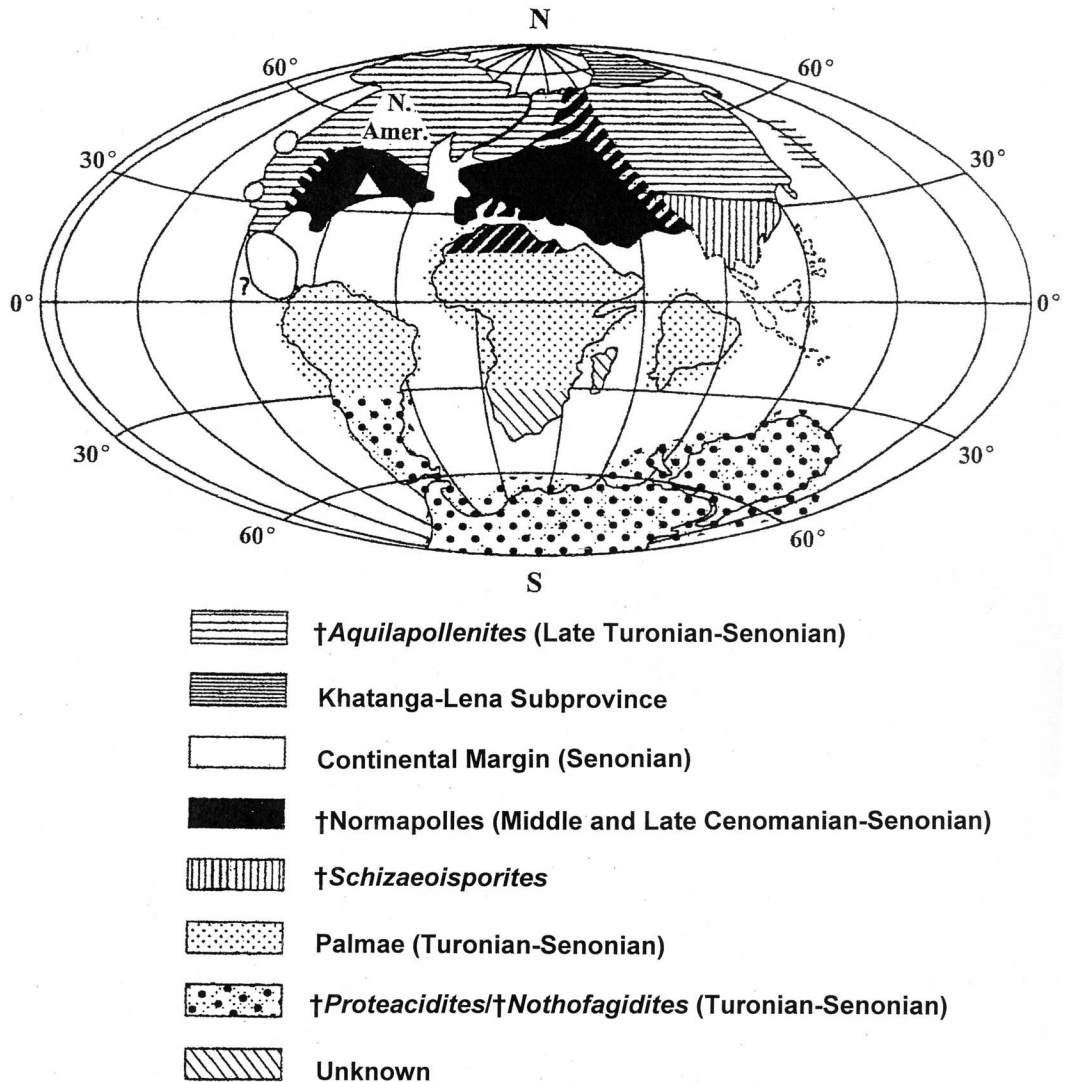Mixed Mesophytic Forest of Oregon–Idaho,
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Figure 3. Late Cretaceous palynofloral provinces of the world. Open triangle shows approximate location of Kentucky in the †Normapolles Palynofloral Province (from Herngreen et al., 1996: 1162, with permission for re-use from the American Association of Stratigraphic Palynologists Foundation, Dallas, Texas, <www.schweizerbart.de>).

(palynomorph) flora by the Maestrichtian (latest Cretaceous). The increase in diversity and abundance of angiosperms through the Cretaceous was accompanied by decreases in these measures for gymnosperms and free-sporing plants, especially a decrease in abundance of the former and a decrease in diversity of the latter (Crane, 1987; Lidgard & Crane, 1988, 1990; Lupia et al., 1999, 2000; Peralta-Medina & Falcon-Lang, 2012). Boulter et al. (1998) identified major radiations of the angiosperms at around the Cenomanian/Turonian boundary (90 Ma) and at the Cretaceous/Tertiary boundary (65.5 Ma).

On a world map of the Middle Cretaceous (Barremian–Aptian), Srivastava (1994) recognized three palynoflora provinces: Boreal (most of Northern Hemisphere); Equatorial (elater-bearing pollen of unknown affinity, but possibly with Ephedraceae) (Herngreen et al., 1996); and Austral (post-Gondwanaland southern South America, Antarctica, and Australia). Kentucky was located on or near the boundary of the Boreal and Equatorial Provinces. The Elater-Bearing Palynoflora Province replaced the †Dicheiropollis Province of the Early Cretaceous. The Elater-Bearing Pollen Province includes the southern part of Brenner's (1976) South Laurasian
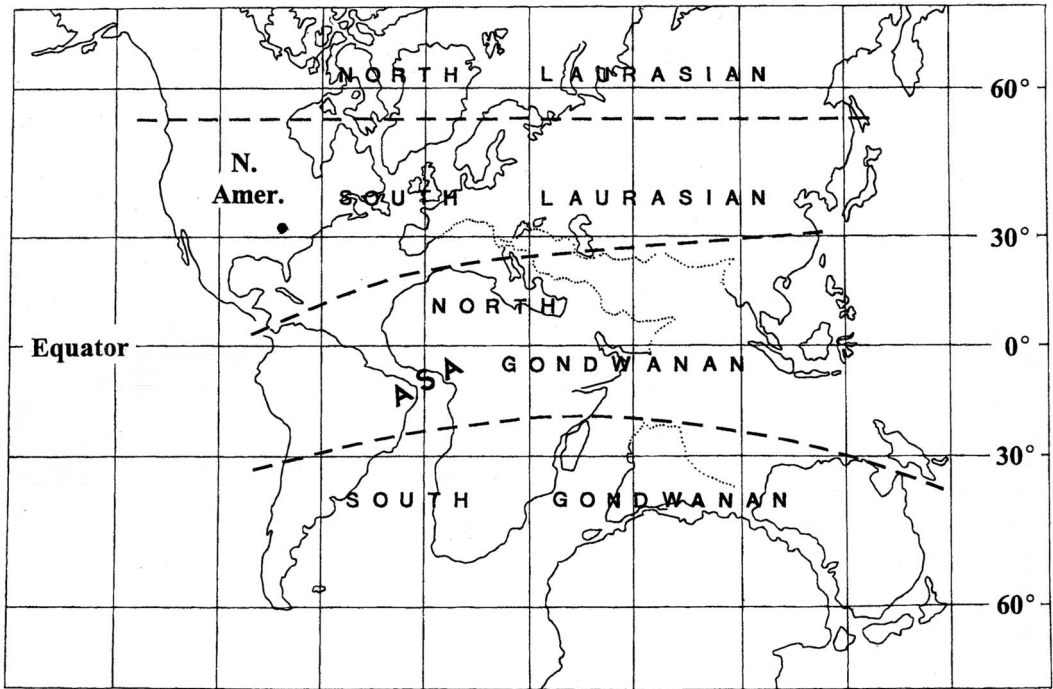
Figure 4. Middle Cretaceous Palynofloral Realms of the world. Longitudinal lines are at 30° intervals. ASA refers to the African/South American Province within the North Gondwanan Realm. Solid circle in North America shows approximate location of Kentucky. From Batten and Wenben, 1987: 223, with permission for re-use from Schweizerbart Scientific Publishers Permissions, Stuttgart, Germany).

Palynofloral Province and most of his North Gond-wana Province (Fig. 4).

Finally, in the Early Cretaceous, when angiosperms first appeared in the fossil record (Hickey & Doyle, 1977; Wing & Boucher, 1998; Lupia et al., 1999), Kentucky was located in the southern portion of the Boreal or †*Cerebropollenites* Province (Herngreen & Chlonova, 1981; Herngreen et al., 1996). This province included most of the Northern Hemisphere: North America, Europe, and Asia; it did not include Italy, India, or the Indonesian-Philippine Archipelago. The †*Cerebropollenites* Province was characterized by high diversity of pteridophyte spores, together with spores of bryophytes and bisaccate and other gymnosperm pollen. Nonbisaccate pollen included †*Araucariacites*, †*Cerebropollenites* ("a common and distinctive element in the province") (Herngreen et al., 1996: 1158), †*Classopollis*, and other gymnospermous pollen types. Angiosperm pollen made up only a small percentage of the assemblage (Herngreen & Chlonova, 1981; Srivastava, 1981, 1994; Herngreen et al., 1996).

However, Srivastava (1994) recognized an Early Cretaceous (Neocomian) Equatorial Province (a pre-Albian Early Cretaceous †*Dicheiropollis etruscus/*

†*Afropollis* Province in part), which was characterized by the gymnosperm †*Dicheiropollis*. According to Srivastava (1994), this province became differentiated from the southern and northern portions of the Boreal (†*Cerebropollenites*) and Austral (†*Microcachyridites*, a podocarp) Provinces, respectively, that represented continuities of these two phytoprovinces from the Jurassic. The southeastern United States was included in Srivastava's (1994) Equatorial Province, and from his map it appears that Kentucky would be near the border between the Equatorial and Boreal Provinces. However, the southeastern United States was not included in the Equatorial Province as delineated by Herngreen et al. (1996), in which case Kentucky clearly is included in the Boreal (†*Cerebropollenites*) Province in the Early Cretaceous.

MIXED MESOPHYTIC FORESTS OF KENTUCKY AND CHINA

There are differences in both species composition and physiognomy between the eastern Asian and eastern North American Mixed Mesophytic Forest (Braun, 1950; Li, 1953; Wang, 1961; Wolfe, 1979). Thus, compared to the Mixed Mesophytic Forest of eastern North America, the Mixed Mesophytic Forest of eastern Asia has a higher woody species richness,

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a higher number of primitive families of woody plants, a higher proportion of broad-leaved evergreen trees and shrubs, a higher percentage of woody taxa with entire-margined leaves, and a higher number of gymnosperm taxa. Based on Wolfe's (1979) classification system of humid to mesic forests of eastern Asia, the potential natural vegetation of most sites in Kentucky would be a Notophyllous (leaf sizes 20.25–45.00 cm²; see Dilcher, 1973) Broad-leaved Evergreen forest, as pointed out by Wolfe (1979: 27), for the deciduous forest of eastern North America in general. Wolfe states that, "...the bulk of the broad-leaved deciduous forests of eastern North America live under a mean annual temperature and a mean annual range of temperatures typical for broad-leaved evergreen forest regions and that fundamentally much of the broad-leaved deciduous forest of North America is an analog of the *secondary vegetation* [italics ours] of the Asian Notophyllous Broad-leaved Evergreen forest region."

Wolfe (1979) suggested that the lack of broad-leaved evergreen trees in the Eastern Deciduous Forest is due to intense cold waves from the Arctic (e.g., the polar vortex of January 2014), which penetrate this region unobstructed by the north-south–trending Appalachian Mountains. In China, on the other hand, cold waves originating in Siberia are blocked from reaching the Mixed Mesophytic Forest by east-west–trending mountains, which, however, have passes (gaps) that allowed migration of Mixed Mesophytic Forest taxa southward as the climate cooled. Thus, although mean annual temperature and mean annual range of temperatures in some parts of Kentucky are within the ranges of those that support Mixed Mesophytic Forest in China, absolute lows in Kentucky (and other parts of eastern North America) are lower than those in this similar forested region of Asia (Wolfe, 1975). According to Wolfe, differences in temperature parameters between the Mixed Mesophytic Forest regions of eastern North America and eastern Asia explain why broad-leaved evergreens are a significant part of this forest type in eastern Asia but are not an important component of the Mixed Mesophytic Forest in eastern North America. Wolfe's contention that there is a greater proportion of broad-leaved evergreen trees in the eastern Asian Mixed Mesophytic Forest than in the eastern North American Mixed Mesophytic Forest because of the extreme lower minimum temperatures in eastern North America is in agreement with the hypothesis of plant geographers/vegetation ecologists that "evergreeness versus deciduousness in extra-tropical forest climates is controlled by extreme minimum temperatures" (Box, 1995, 2002: 148).

Wolfe (1979, 1985) suggested that the broad-leaved deciduous forest of the southeastern United States developed in the Late Cenozoic (Miocene, ca. 13 Ma) from a broad-leaved evergreen forest with a subdominant deciduous component (e.g., *Carya*, *Fagus*, *Liquidambar*) that was dominant in the region in the mid-Cenozoic following the Eocene terminal event. Thus, the dominant broad-leaved evergreens were eliminated gradually from the region by the intense Arctic cold fronts that apparently developed in the Neogene. This scenario does not agree with the vegetation sequence outlined in Figure 2, which shows that a broad-leaved deciduous forest was present by the Oligocene.

Other factors that contribute to the greater species richness in the Mixed Mesophytic Forest of eastern Asia than in eastern North America are that this forest type in Asia (1) has been enriched progressively via migration of tropical and subtropical elements from south of it (whereas for geographical reasons this is not the case for the Mixed Mesophytic Forest of eastern North America), (2) was less extensively glaciated during the Quaternary, (3) is topographically (including elevation) more diverse, and (4) has been progressively enriched via diversification of lineages that already were present (Wolfe, 1977, 1979; Hsü, 1983; Latham & Ricklefs, 1993; Axelrod et al., 1996; Guo, 1999; Qian & Ricklefs, 2000; Ricklefs et al., 2004; Xiang et al., 2004; Renner et al., 2008). The ultimate source of some taxa in the rich woody flora of southern and eastern China may have been via infiltration of Gondwanlandic elements into it in the Tertiary/Pleistocene, as a result of the Australian plate moving north and coming into contact with the Eurasian plate (Florin, 1963; Schuster, 1972, 1976).

TIMES OF DISJUNCTIONS BETWEEN EASTERN ASIAN–EASTERN NORTH AMERICAN TAXA

The floristic similarities between eastern Asia and eastern North America involve tropical evergreen, temperate deciduous, and boreal and alpine taxa, and thus they could not be the result of a single historical event (Tiffney, 1985a; Xiang et al., 1998; Wen, 1999; Donoghue & Smith, 2004; Pennington & Dick, 2004). Instead, according to Tiffney, the disjunctions were established at several different times in the geologic past. Following is a summary of five historical patterns Tiffney suggests contributed to the floristic similarity between eastern North America and eastern Asia.

1. Late Cretaceous. Some of the disjunct taxa may have originated from the †*Aquilapollenites*–†Normapolles pollen provinces (see Muller, 1970; Meyen, 1987), e.g.,

Juglandales (Friis, 1983; Sims et al., 1999). Other groups that may have become established during this time include bryophytes, ferns, Pinaceae (but not *Pinus*), aquatics, and monocots.

2. Early and Middle Eocene. Basic components of the boreotropical flora evolved in the Paleogene, when a warm climate and land bridges between continents of the Northern Hemisphere allowed its spread (also see Tiffney & Manchester, 2001). Evergreen disjuncts such as Magnoliaceae, Theaceae, and Lauraceae may be accounted for here. Deciduous woody taxa and herbs of the forest floor as well as colonizers of disturbed sites may have accompanied the evergreens. However, some of the deciduous taxa may have moved later in the Tertiary (cooler climate) or evolved in parallel from ancestors inhabiting both areas. Winter darkness, not low temperatures, may have prevented broad-leaved evergreens from crossing the Bering land bridge, which was located at about 75°N paleolatitude. In which case, only deciduous taxa could have crossed it. On the other hand, both deciduous and evergreen taxa could have crossed the North Atlantic land bridge, which lay at a considerably lower latitude (ca. 55°N paleolatitude) than the Bering land bridge. As such, the North Atlantic land bridge was within the same climatic zone as that of Eocene floras, such as the London Clay (Chandler, 1964), with a tropical/subtropical floristic composition, and "... well south of the zone of extensive winter darkness" (Tiffney, 2000; Tiffney & Manchester, 2001: S9).

3. Late Eocene–Oligocene. Deciduous taxa of polar regions spread south. The North Atlantic land bridge was broken up in the Eocene (but see below). Taxa adapted to cooler climates may have moved via the Bering land bridge.

4. Miocene. The Bering land bridge was still present, but cool climate allowed passage of temperate plants only. The North Atlantic land bridge may have existed as a series of stepping stones (see below) and thus permitted passage of some temperate taxa. Some extant temperate taxa may have evolved in parallel from common ancestors in these two areas. Many disjunct herbaceous angiosperm groups evolved during this time, and these may have moved via the Bering land bridge by colonization of disturbed sites in existing forests and as components of open communities. Recent studies on the paleoflora and on the phylogeny and biogeography of several plant groups represented in the Miocene flora of Iceland offer strong support that the North Atlantic land bridge served as a physical link for migration of temperate woody plants between the Old World and the New World through the latest Miocene (Denk et al., 2005, 2010; Grimsson et al., 2007). In contrast to his earlier thinking, Tiffney (2008: 140) now believed that, "[t]he NALB [North Atlantic land bridge] may still have been functional in the later Neogene."

5. Late Tertiary–Quaternary. Arctic and alpine plants evolved and migrated across the Bering land bridge (also see Qian, 1993, 1999). Both molecular phylogenetic (Xiang et al., 1998, 2000; Wen, 1999; Xiang & Soltis, 2001) and fossil (Manchester, 1999) data support the hypothesis that eastern Asian and eastern North American disjunctions (1) represent relicts of a Mixed Mesophytic Forest that was distributed across the mid-latitudes of the Northern Hemisphere in the Miocene and, (2) as postulated by Tiffney (1985a), have multiple origins, i.e., movement of taxa occurred at different times and via different geographical routes. Most of the disjunct taxa appear to have diverged in the Neogene (Miocene–

Pliocene) (Wen, 1999; Xiang et al., 2000; Chanderbali et al., 2001; Donoghue et al., 2001; Liu et al., 2002; Donoghue & Smith, 2004; Nie et al., 2006, 2007, 2010; Jiao & Li, 2009). Manchester's (1999) finding that the circumboreal pattern of distribution of Asian, European, and North American genera was strongest in the Miocene offers strong support for hypothesis number one.

Further, although there are exceptions (e.g., Li, 2008; Jiao & Li, 2009; González et al., 2014), phylogenetic data have shown that most disjunctions involve closely related taxa, but not sister species, when more than two taxa are analyzed (Xiang et al., 1998, 2000; Wen, 1999; Fu et al., 2005; Zhou et al., 2006). Thus, phylogenetic analysis of closely related species with an eastern Asian–eastern North American–western North American disjunct pattern (e.g., *Trautvetteria caroliniensis* (Walter) Vail [Ranunculaceae] in eastern North America, *T. grandis* Nutt. in western North America, and *T. japonica* Siebold & Zucc. in eastern Asia; and *Calycanthus floridus* L. [Calycanthaceae] in eastern North America, *C. occidentalis* Hook. & Arn. in western North America, and *C. chinensis* W. C. Cheng & S. Y. Chang in eastern Asia) shows that the eastern and western North American species are more closely related to each other than either is to the eastern Asian species. That is, eastern and western North American species are sister groups, and the Asian species are the sister groups to the North American species (Xiang et al., 1998; also see Xiang & Soltis, 2001). This indicates that further divergence (geographical isolation) of taxa occurred after the initial disjunction in the Miocene–Pliocene. Thus, in contrast to fossil data, both the present-day disjunction pattern of sister taxa between eastern and western North America (Hong, 1993) and molecular phylogenetic data (Xiang et al., 1998; Wen, 1999; Fu et al., 2005; Harris & Xiang, 2009; Harris et al., 2009) support a strong biogeographic relationship between these two areas (Wen, 1999).

But did all Eurasian–North American disjunctions within genera originate via land bridges? What about long-distance dispersal via water, wind, birds, and floating islands? Although Milne (2006: 465) believes that land bridges are the more likely cause of these disjunctions, he does not rule out long-distance dispersal for "... explanations for disjunctions in any individual genus." Lavin and Luckow (1993) embraced the boreotropical hypothesis as explaining the occurrence of paleotropical taxa in North America during the Early Cenozoic and the subsequent migration of this tropical element to a refugium in seasonally dry tropical forests in the Caribbean Basin and to South America via the Panamanian Land Bridge during the Pliocene.

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Based on several subsequent studies of Fabaceae, Lavin and colleagues continued to embellish the boreotropical hypothesis (Lavin, 1995; Luckow, 1995; Lavin & Sousa S., 1995; Lavin et al., 2000, 2001), and in the meantime they implicated Africa as a refugium for boreotropical flora (Lavin et al., 2000). However, their later studies showed that (1) legume diversity and endemism in the Caribbean Basin is of geologically recent origin and thus much younger than the tectonic events that were thought to be responsible for a relictual boreotropical flora in the Antilles, (2) some lineages in Central and South America are older than the closure of the Panamanian Isthmus (ca. 3 Ma), and (3) the ancestral area of some taxa in the Antilles is South America. In sum, through many studies, most of which were with legumes, they have concluded that the estimated age of divergence of legume clades that occur between continents separated by an ocean are younger than the tectonic events that supposedly were responsible for their vicariance (Lavin et al., 2004; Pennington et al., 2004; Lavin & Beyra Matos, 2008; Ireland et al., 2010).

Many studies, especially those based on molecular phylogenetics and age estimates, have concluded that long-distance dispersal (by water and wind currents, rather than by tectonic history/vicariance) would be the most likely explanation for many transcontinental taxa (e.g., Baum et al., 1998 [*Adansonia* L., Malvaceae]; Renner et al., 2000 [Atherospermataceae], 2001 [Melastomataceae], 2010 [Monimiaceae]; Renner & Meyer, 2001 [Melastomataceae, tribe Melastomeae]; Winkworth et al., 2002 [transoceanic dispersal to and from New Zealand of various families/genera/one tribe]; Schnabel et al., 2003 [*Gleditsia*, Fabaceae]; Givnish et al., 2004 [Bromeliaceae, Rapateaceae]; Pennington & Dick, 2004 [palaeotropical rainforest → Amazon lowland rainforest (20% of species immigrant lineages; most taxonomic similarity derived from transoceanic dispersal)]; Renner, 2004a [eight families, 10 genera; Melastomataceae, tribe Melastomeae], 2004b [Melastomataceae]; de Queiroz, 2005 [oceanic long-distance dispersal of many plant taxa]; Knapp et al., 2005 [*Nothofagus* Blume, Nothofagaceae]; Yuan et al., 2005 [*Exacum* L., Gentianaceae]; Crisp et al., 2009 [transoceanic colonizations contributed to biome (phylogenetic) stasis in the Southern Hemisphere]; Ickert-Bond et al., 2009 [*Ephedra* L., Ephedraceae]; Li et al., 2009 [*Bridelia* Willd., Phyllanthaceae]; Schaefer et al., 2009 [Cucurbitaceae]; Duchen & Renner, 2010 [*Cayaponia* Silva Manso, Cucurbitaceae]; Ireland et al., 2010 [*Ateleia* (DC.) Benth., Fabaceae]; Michalak et al., 2010 [Hernandiaceae]; Bartish et al., 2011 [Sapotaceae,

subfamily Chrysophylloideae]; Li et al., 2011 [*Persea* Mill. group, Lauraceae]; Kadereit & Baldwin, 2012 [long-dispersal may account for 10 (or 11, including *Anemone* L.) of 25 cases of disjunct distribution of plant taxa between western Eurasia and western North America]; Lambertini et al., 2012 [*Phragmites* Adans., Poaceae]; Rivadavia et al., 2012 [*Drosera* L., Droseraceae]; Crisp & Cook, 2013 [48% of 85 Australian vascular plant clades arrived to that continent by transoceanic dispersal]; Nie et al., 2013 [*Paederia* L., Rubiaceae]; Iles et al., 2014 [*Trithuria* Hook. f. (monogeneric family Hydatellaceae)]; Conran et al., 2014 [*Luzuriaga* Ruiz & Pav., Alstroemeriaceae, several transoceanic events across the Southern Ocean]; and Thomas et al., 2014 [Winteraceae]).

Li et al. (2011) explained the biogeography of the *Persea* group (Lauraceae) by a combination of vicariance (boreotropical hypothesis) and long-distance dispersal. The case for long-distance dispersal seems to be especially strong for trans-Atlantic dispersal of tropical genera between Africa and South America. Arrival of immigrants from Africa to South America and from South America to Africa occurred millions of years after the separation of the African and South American plates (ca. 105 Ma) and after land bridges were available for passage of plants across the tropical Atlantic (Morley, 2003; Renner, 2004a; Duchen & Renner, 2010). According to Raven and Axelrod (1974), exchange of plants between South America and Africa would not have occurred after about 84 Ma except by long-distance dispersal.

In any case, however, migration via the North Atlantic land bridge (boreotropical hypothesis) has been used in a number of recent studies to explain the disjunction of various tropical plant taxa between the Old World and the New World (Davis et al., 2002, 2004; Weeks et al., 2005; Zerega et al., 2005; Muellner et al., 2006; Smedmark & Anderberg, 2007; Merckx et al., 2008; Erkens et al., 2009). Interestingly, the study by Davis et al. (2004) also supported Chaney's claim that the source of the tropical element in the flora of North America was South America. According to Davis et al. (2004), the Malpighiaceae originated in South America in the latest Cretaceous (ca. 68 Ma), migrated via the Caribbean Basin to North America, and then to the Old World via the North Atlantic land bridge. Furthermore, flowering material of †*Eoglandulosa warmanensis* (Malpighiaceae), which has distinctive features of the New World members of this family, has been collected from the Middle Eocene Claiborne Formation (ca. 43 Ma) in the southeastern United States (Table 2).

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