
BIOGEOGRAPHICAL RELATIONSHIPS OF NORTH AMERICAN TERTIARY FLORAS¹

Steven R. Manchester²

ABSTRACT

Comparisons of Tertiary floras of North America with those of Europe and Asia document a long history of floristic interchange. The stratigraphic and geographic ranges of selected conifer and angiosperm genera that are easily recognized in the fossil record provide a basis for discerning patterns in the routes and timings of intercontinental dispersals through the Tertiary.

The origin of the extant flora and vegetation of North America has been the subject of much interest and debate ever since the floristic similarities between North America and Asia were first documented. Many of the woody genera comprising North America's present-day forests have excellent fossil records that can be traced through the Tertiary in North America and other continents of the Northern Hemisphere (Wolfe, 1975; Graham, 1993; Tiffney, 1985a, b; Mai, 1995). In addition, many genera that are no longer native to North America have well-documented Tertiary records. Patterns of geographic disjunction among extinct and extant genera provide important clues to the history of North American flora and the former continuity of Tertiary forests in the Northern Hemisphere. By comparing the stratigraphic records of genera shared among two or more continents it is possible to consider the pathways and timing of plant interchange through the Tertiary.

Many ideas have been published on the paleobotanical origins and development of extant flora and vegetation of the Northern Hemisphere (e.g., Engler, 1879; Chaney, 1940, 1947; Wolfe, 1975; Raven & Axelrod, 1974; Latham & Ricklefs, 1993; Mai, 1995; Akhmetiev, 1996). In the attempt to be as comprehensive as possible, investigators have sometimes relied uncritically upon genera reported in the literature. Closer scrutiny reveals many erroneous generic determinations (Dilcher, 1974).

The purpose of this review is to highlight Tertiary records of selected conifer and angiosperm genera that may be considered soundly identified and which are significant in understanding the biogeographic affinities of North American Tertiary floras. I present a review of about 90 genera with reliable Tertiary records in North America and other continents. Examination of the stratigraphic ranges of different taxa in North America, Europe, and Asia provides the basis for assessing phytogeographic patterns and pathways of biotic dispersal through the Tertiary. South American and African records are mentioned when known, but the emphasis is on affinities within the Northern Hemisphere. For a review of relationships between North and South America, see Burnham and Graham (1999, this issue).

Because of our familiar vantage point of the present day, neobotanists and paleobotanists alike tend to regard the modern flora as an endpoint showing the "true" floristic patterns of extant genera and species. Thus a genus such as *Ginkgo*, with a wide paleogeographic distribution (Tralau, 1968), may be classified as an "East Asian element." Clearly, such "elements" have more to do with extinctions elsewhere than they do to the natural geographic affinity or origin of the genus (Wolfe, 1975). Fossils can document former geographic distribution patterns of both extinct and extant genera and thus provide a means of tracking the changing floristic relation-

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² Florida Museum of Natural History, Gainesville, Florida 32611, U.S.A.

ships among different landmasses through time. Recent studies have emphasized morphological and molecular phylogenetics as a framework to construct phytogeographic history of disjunct taxa (reviewed by Wen, in press). Biogeographic hypotheses developed from phylogenetic and molecular studies can be tested by observations from the fossil record.

It might be argued that the fossil record is too fragmentary to provide a thorough understanding of phytogeographic history; however, the alternative of using only modern distributions or phylogenetic hypotheses to determine phytogeographic history leads to an even more incomplete picture. If forced to rely only on extant generic distributions, we would be unlikely to predict that *Carya* had its greatest diversification in the Tertiary of Europe (Mai, 1981; Manchester, 1987a) despite its absence from the extant European flora, or that *Ensete* and *Pyrenacantha* (both native to Africa and Asia today) would be present in the early Tertiary of North America (Manchester, 1994b).

In this article, I review the North American Tertiary fossil record of selected conifer and angiosperm genera in comparison with their stratigraphic ranges in other parts of the Northern Hemisphere. These case history studies illustrate a variety of biogeographic patterns that may be analyzed to gain insight into the timing of past intercontinental migrations.

METHODS

It is a well-known problem that paleobotanical literature includes a large number of generic assignments of dubious validity. In North America the problem applies to much of the literature prior to the 1970s and actually persists to the present day. This is because different investigators apply different standards of what is necessary to identify a genus. It may also reflect the need for stratigraphic geologists to obtain quick, tentative names for fossils that may not be well preserved or that may not provide sufficient characters for a more secure determination. In many instances assignment to a particular extant genus is justified by discussing a few similarities between the fossil species and the modern genus, but the criteria that distinguish it from all other possible candidates are not considered. For this reason, it is inadvisable to accept reports from the literature as valid without critical evaluation. Databases and surveys that simply take generic names from the literature must be used with considerable caution.

One of the most thorough and critical reviews of

Tertiary genera is that of Kirchheimer (1957), which emphasizes the European fossil record but also reports selected reliable occurrences of genera in North America and Asia. Many of the age assignments in Kirchheimer's catalog have since been revised, but Kirchheimer was careful to give locality information, so that it is possible to determine current age assignments by attention to more recent literature. Helpful, but less comprehensively documented, reviews of taxa reported in the paleobotanical literature are provided by Taylor (1990), Collinson et al. (1993), and Mai (1995). Useful guides to Asian literature on Cenozoic Paleobotany include Tanai (1992a, 1994) and Liu et al. (1996). Published critical reviews of the fossil record of particular phylogenetic groups, for example, that of the magnoliid angiosperms (Friis et al., 1997), and individual families (e.g., Betulaceae, Crane, 1989) or genera (e.g., *Nyssa*, Eyde, 1997) are also very useful.

The decision whether to accept generic records for this summary was based on whether the organ(s) and morphological/anatomical features preserved and described can be considered truly diagnostic of the genus indicated. As in the taxonomy of modern plants, it is often difficult to make reliable generic determinations of fossil material based upon sterile specimens. Rare paleobotanical specimens showing fruits and/or flowers attached to twigs with foliage have revealed "mosaic" plants, in which the leaves closely resemble those of a modern genus, while the fruits or flowers reveal novel characters that indicate they belong to an extinct genus (Manchester, 1989a; Manchester et al., 1998). In the usual case, when interconnected vegetative and reproductive parts are unavailable, studies of fertile material, particularly flowers and fruits, provide the best systematic resolution.

Reports based on fossil foliage are also important, particularly since leaves are more commonly preserved than fruits in many depositional environments, but they require careful scrutiny to determine the likelihood of correct generic determinations. Leaves in some families are so distinctive as to be reliable in diagnosing a genus, as in Platanaceae and Berberidaceae. More commonly there are instances of convergence and parallelism in foliage that cause me to be less confident of generic assignments. In the Betulaceae, Juglandaceae, and Menispermaceae, for example, identification of the family using leaf morphology is relatively easy, but secure generic determinations require fruits. In these families the leaves may provide a good "best estimate" of genera that are present, but identifi-

cations should be viewed with caution if corroborating fruit records are lacking.

I emphasize megafossil reports of fruits, flowers, and leaves, because I am more confident with the evaluation of these organs. Wood and pollen also provide biogeographically important records, but often with coarser systematic resolution. In the case of pollen the decreased systematic resolution is balanced by the relatively high stratigraphic resolution (wind-dispersed pollen may be found throughout a sedimentary sequence, whereas megafossils are confined to specific facies). For critical systematic review of the voluminous literature on fossil pollen, refer to Muller (1981).

In addition, before accepting records for inclusion in this summary, it was necessary that they be fully documented in the literature with convincing photographs or that I had the opportunity to observe the specimens in museum collections. For access to study critical specimens, I am indebted to curators of the following collections: University of California, Berkeley (specimen numbers cited have the prefix UCMP); University of Idaho, Moscow; Denver Museum of Natural History; Peabody Museum of Natural History, Yale University (YPM); United States National Museum, Washington, D.C. (USNM); Burke Museum of Natural History and Culture, Seattle (UWBM); Department of Biological Sciences, University of Alberta; Natural History Museum, London (BM-V); National Museum, Prague; Senckenberg Museum of Natural History, Frankfurt (SM); Botanical Department, Hungarian Natural History Museum, Budapest; Geological Institute and Geological Museum, Moscow; Komarov Botanical Institute, St. Petersburg; National Science Museum, Tokyo; Nanjing Institute of Geology and Paleontology, Academia Sinica, Nanjing; Institute of Botany, Academia Sinica, Beijing. Specimens cited with the prefix UF are from the Florida Museum of Natural History, Gainesville. Extant comparative material was studied at herbaria including A, FLAS, MO, and PE.

The authorities for extant genera mentioned in the paper may be found in Mabberley (1997). The authors of fossil genera not presented by Mabberley are specified at their first mention in the text.

Stratigraphic charts presented in this paper are simplistic in that they condense diverse records from different parts of each northern continent into a single column. However, this enables a quick visual summary that provides some constraints on the timing of intercontinental exchange events for each taxon. More details for each genus are provided in the family narratives of the following section, leading to the more informative literature for the genera

considered. Another weakness of this overview is that the southern continents are not included in the stratigraphic charts. The Tertiary record for South America and Africa is still poorly known relative to that for the northern continents, and evidence for direct exchange of plant species between North and South America during the early to late Tertiary remains weak. For more detailed accounts of relationships inferred between the fossil record of North America and the living genera of Africa and South America, see Raven and Axelrod (1974), Taylor (1990), and Burnham and Graham (1999).

The million-year chronology of Tertiary epochs follows Berggren et al. (1995). The Brandon Lignite flora of Vermont is significant as one of the few informative Tertiary megafossil floras in the northeastern United States. Unfortunately, there are no associated datable rocks or animal fossils to provide an independent means of determining the age. Although for many years considered likely to be Oligocene, the current consensus is that it may be early Miocene (Tiffney, 1994a; Traverse, 1994). I adopt this age for the discussions involving Brandon fossils. There are also problems with the precise age of many floras in eastern Asia. I have usually accepted the assignments given by the most recent authors, but in some cases there continue to be disagreements among different investigators and it may be expected that the ages of many sites will continue to be revised in the future.

I have attempted to be conservative in the positioning of stratigraphic ranges. Thus the ranges presented here are often shorter (begin later) than those indicated by other authors, e.g., Mai (1995). For example, it is possible to find reports of *Engelhardia* based on pollen from the Paleocene. However, the fruits diagnostic of this tribe do not occur until the Eocene, and *Engelhardia*-like pollen (usually called *Momipites* Wodehouse) is known to have been produced by other genera of Juglandaceae in the Tertiary (Manchester, 1989b). Likewise, there are reports of *Alnus* from the Cretaceous, but without convincing infructescences. Because the scope of this treatment is limited to genera known from the Tertiary and/or Recent flora of North America, I have omitted some interesting examples of taxa shared only between Europe and Asia, many of which are reviewed by Mai (1995).

CASE HISTORIES

The following section highlights records that I consider useful in evaluating the biogeographic affinities of North American Tertiary floras. These paragraphs cite the references upon which the

stratigraphic ranges plotted in the summary chart (Fig. 19) and in Figures 21–25 are based. This section is arranged alphabetically by families under the headings Gymnosperms and Angiosperms, with angiosperms of uncertain affinities treated last, under the heading *Incertae Sedis*. Common patterns are reviewed in the subsequent section.

GYMNOSPERMS

Cupressaceae. Distinctive leaves of the extinct *Fokieniopsis* McIver & Basinger and associated cones occur in the Paleocene of Wyoming, Saskatchewan, Alberta (McIver & Basinger, 1990; McIver, 1992) and in the Paleocene of Altai, Xinjiang, China (Guo et al., 1984, as *Ditaxocladus* Guo), indicating a transboringial distribution.

Tetraclinis, with one species living in the western Mediterranean today, has a good Tertiary record in Europe (Kvaček, 1989; Mai, 1995). In addition, one species is known from the early Oligocene to Miocene of western North America based upon cones, seeds, and foliage (Meyer & Manchester, 1997). As it has not been observed in the east Asian Tertiary, it appears likely that this genus traversed the North Atlantic in the late Eocene.

Ginkgoaceae. The record of *Ginkgo* in the Northern Hemisphere extends back to the Jurassic, but its record in the Tertiary is of biogeographic interest, documenting the relatively late confinement to Asia. The Tertiary records in North America extend from the Paleocene of the Rocky Mountains (Brown, 1962) to the Miocene of Oregon (Chaney, 1920). A worldwide review of the distribution of this genus through space and time was presented by Tralau (1968).

Pinaceae. Various genera of the Pinaceae are well represented in the Cretaceous and Tertiary of the Northern Hemisphere, including, for example, *Abies* (Schorn & Wehr, 1986), *Keteleeria* (Meyer & Manchester, 1997), *Larix* (LePage & Basinger, 1991; Schorn, 1994), *Picea* (Crabtree, 1983), *Pinus* (Miller & Malinky, 1986), and *Pseudolarix* (LePage & Basinger, 1995). Most of these genera are widespread in the Northern Hemisphere today, but *Keteleeria* and *Pseudolarix* are limited to eastern Asia in their modern distribution. LePage and Basinger (1991) provided a comprehensive analysis of the phytogeographic history of *Pseudolarix* in the Northern Hemisphere based on its distinctive seeds, cones, and foliage, with earliest records in the Cretaceous of Asia and North America followed by Oligocene establishment in Europe. They concluded that the genus became extinct in North America by the middle to late early Miocene, and

in Europe after the Pliocene. *Keteleeria*, found today only in the broad-leaved evergreen forests of China and Taiwan, is known based on distinctive seeds from the Eocene of the Quilchena flora of British Columbia (R. Mathewes, unpublished data), and Oligocene of Oregon (Meyer & Manchester, 1997).

Taxaceae. *Amentotaxus*, with four extant species in China and southeast Asia, has an excellent fossil record in North America and Europe. It is readily recognized by its broad needle-like leaves with a pair of prominent stomatal bands and distinctive epidermal anatomy (Ferguson et al., 1978). *Amentotaxus* extends from the Upper Cretaceous (Santonian) to Miocene of North America and from the Paleocene to Upper Miocene of Europe (Ferguson et al., 1978; Jähnichen, 1990). Other genera of the Taxaceae, including *Taxus* and *Torreya*, and at least one extinct genus, are well represented in the Tertiary of western North America (Manchester, 1994b; Meyer & Manchester, 1997) and central Europe (Kvaček, 1982), but their history is best explored through attention to Mesozoic floras.

Taxodiaceae. This family includes several genera with relictual extant distribution. *Metasequoia* has become famous as an example of a genus once widespread in the Northern Hemisphere that is now native only to China. I do not see the need to review this again here as there are already many accounts (most recently in Meyer & Manchester, 1997).

Cunninghamia grows today in mixed mesophytic and broad-leaved evergreen forests of China and Taiwan. Its fossil record includes cones, seeds, and foliage from the Eocene to Miocene of western North America (reviewed in Meyer & Manchester, 1997), the Tertiary of Europe (Mai, 1995), and the Eocene to Miocene of Japan (Matsuo, 1967; Horiuchi, 1996).

Glyptostrobus is native today only in southeastern China, but, like *Metasequoia* and *Cunninghamia*, was widespread in the Tertiary. It extends from the Paleocene (Boulter & Kvaček, 1989) to the Pliocene in Europe (Mai, 1995; Martinetto, 1998). *Glyptostrobus europaeus* twigs with attached cones occur in the Eocene to Pliocene of Japan (Tanai, 1961; Matsumoto et al., 1997b). In North America, *Glyptostrobus* is well represented in the Paleocene to Eocene of the Rocky Mountain region (Brown, 1962; Hoffman, 1996), and in the Miocene of Idaho, Oregon, and Washington (Brown, 1936; Chaney & Axelrod, 1959; Fields, 1996).

Sequoia and *Taxodium*, although restricted in their modern distribution to Pacific Coastal North America and eastern North America, respectively, were widespread in the Northern Hemisphere in the

Tertiary. Cones of *Sequoia* occur as late as the Pliocene in Italy (Martinetto, 1994).

ANGIOSPERMS

Actinidiaceae. *Actinidia* is distributed in Indomalaysia and eastern Asia today, but was present in North America and Europe during the Tertiary. In North America, it is known based on seeds from the Eocene Clarno Formation of Oregon (Manchester, 1994b). In Europe, fossil seeds occur from the Eocene to the Pliocene (Tralau, 1963; Friis, 1985; Martinetto, 1998).

Anacardiaceae. *Pentoperculum* Manchester is an extinct genus of fruits belonging to the Spondiaceae shared between the middle Eocene of Oregon (Manchester, 1994b) and the lower Eocene of England (Reid & Chandler, 1933, as *Dracontomelon*). The calyces called *Astronium truncatum* by MacGinitie (1953) from the Eocene and Oligocene of the western United States are very different in venation and fruit morphology from the extant genus and are no longer believed to represent Anacardiaceae (Manchester & Wang, 1998). The leaves that MacGinitie placed in the same species may in fact represent Anacardiaceae, but they are at least as similar to *Rhus* as they are to *Astronium*. *Rhus* is known from anatomically preserved fruits from the Eocene of Oregon (Manchester, 1994b).

Apocynaceae. Elongate seeds with a terminal streamer-like tuft of hairs two to four times the length of the seed body are found in many extant genera of Apocynaceae, e.g., *Anodendron*, *Cleghornia*, *Echites*, *Forsteronia*, *Holarrhena*, *Kibatalia*, *Odontadenia*, *Pottsia*, *Prestonia*, *Strophanthus*, and *Wrightia*. Apocynaceous seeds can be recognized with ease, but the distinction of genera based only on seed characters is a difficult challenge. Thus, the fossil generic name *Echitonium* Unger 1850 (= *Cypselites* Heer = *Apocynospermum* Reid & Chandler, 1926) is applied to fossil remains. In the North American Tertiary, such seeds occur in the middle Eocene Green River Formation (*Apocynospermum coloradensis* Brown in MacGinitie, 1969: pl. 18, fig. 4), the Clarno shales of Oregon (Manchester, unpublished), and the late Eocene of Florissant, Colorado (Manchester, unpublished). They are not known in North America after the Eocene, but in Europe they extend from the Middle Eocene (Messel, Germany: Senckenberg Collection-ME 7624), the Late Eocene of England (Reid & Chandler, 1926), Early Oligocene of Budapest-Obuda, Hungary (Botanical Department, Hungarian Natural History Museum Collection, BP 63.1039), and the České středohoří Mountains (Kvaček & Walther,

1995: pl. 9, fig. 2) to the Middle Miocene of Switzerland.

Araliaceae. *Toricellia* of western and eastern Asia, sometimes placed in its own family, was considered by some taxonomists to be allied to the Cornaceae, but recent molecular work indicates a position within the Araliaceae (Plunkett et al., 1996). *Toricellia* has distinctive fruits (Fig. 1A, B) with three locules: a single-seeded central locule with a terminal germination valve and two enlarged, bladder-like lateral chambers that are infertile. The endocarp tissue is composed of isodiametric sclereids. These same characters occur in Eocene fruits (Fig. 1D, G) that I had previously described as the fossil genus *Tripartisemen* Manchester (1994b). Therefore, I now offer the new combination, *Toricellia bonesii* (Manchester) Manchester comb. nov. (see Appendix 1). *Toricellia bonesii* occurs in the middle Eocene of the Clarno Formation, Oregon (Fig. 1C–F), Roslyn Formation, Washington (Fig. 1G), and Messel, Germany (Collinson, 1988: pl. 1, fig. 11). Fruits are also present in the lower Miocene Obendorf locality of Austria (Meller, 1996, and pers. comm. 1998). These occurrences indicate that *Toricellia* was shared between Europe and North America during the Eocene, although it is still unknown from the Asian Tertiary. The timing of its arrival in Asia, where it occurs today, remains a mystery.

Bignoniaceae. *Catalpa* lives today in eastern Asia, eastern North America, and the Caribbean region. Small biwinged seeds of *Catalpa* have been recognized from the Early Oligocene of Oregon (Meyer & Manchester, 1997). Similarly small *Catalpa* seeds (*Catalpa microsperma* Saporta) occur in the late Oligocene of France and Germany (Saporta, 1889; Weyland, 1937), suggesting a possible North Atlantic linkage during or prior to the Oligocene.

Berberidaceae. *Mahonia* is distributed in Asia, Malesia, and North and Central America today. Although sometimes subsumed within *Berberis* (Whittemore, 1997), *Mahonia* is easily distinguished by its compound foliage. This genus is readily recognized by the distinctive architecture of its imparipinnately compound leaves and spiny leaflets, without the need for associated flowers or fruits, and thus is a good candidate for recognition in the fossil record. *Mahonia* is well represented in western North American Tertiary floras, extending from the Eocene to Pleistocene (Schorn, 1966). Although not native in Europe today, it occurs in the Oligocene of France (Saporta, 1865) and North Bohemia (Bůžek et al., 1990), in the Neogene of Hungary (Andreánszky, 1959), and in the late Miocene of Abkhasia (see Takhtajan, 1974). *Mahonia bil-*

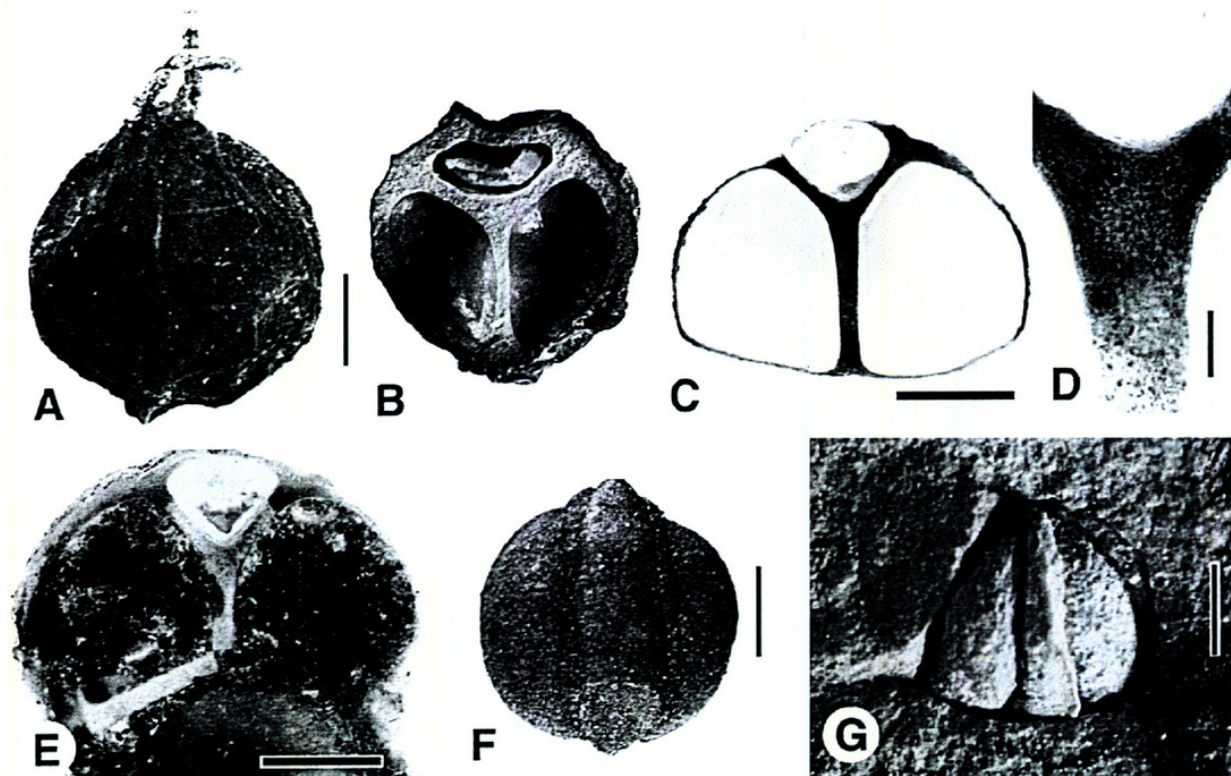


Figure 1. Extant and fossil *Toricellia* (Araliaceae) fruits from Asia and North America. —A. Fruit of *Toricellia tiliacifolia*, Yunnan, China, MO 52556: A Henri 11907. —B. Transverse section of the same fruit, showing three chambers: two large and empty, one smaller and containing a seed. C–F. *Toricellia bonesii* (Manchester) comb. nov. from the Eocene Clarno Nut Beds, Oregon. —C. Transverse section showing small central chamber and large laterals, UF 9578. —D. Detail of the septum of specimen in C, enlarged to show isodiametric sclereids. —E. Transversely sectioned specimen showing a small chamber containing a seed, and two larger lateral chambers filled with sediment, UF 9577. —F. Dorsal surface of a silicified fruit with the pericarp partially stripped away showing two symmetrically placed lateral chambers, and the median chamber with a small facet corresponding to the germination valve, holotype, UF 9288. —G. Sedimentary cast of *Toricellia bonesii* from the Eocene of Ronald, Washington, showing the small fertile chamber and larger lateral chambers, UWBM 95238-B4738. Scale bars = 1 mm in A–C, E–G, 0.1 mm in D.

inica (Unger) Kvaček & Bůžek from early Miocene of Bilina, western Czech Republic, is similar to *M. simplex* Arnold from the Oligocene of western North America (Kvaček & Bůžek, 1994).

Although most diverse in Asia today, *Mahonia* is poorly represented in the Asian fossil record. Tanai and Suzuki (1963) described *Mahonia lanceifolia* from the Miocene of southwestern Hokkaido, but the single known leaflet lacks spinose teeth and its affinity to *Mahonia* may be questioned. Based on the available fossil record, it appears that *Mahonia* spread from North America to Europe in the early Tertiary and to Asia in the late Tertiary. Its arrival in Asia may have been either from Europe or North America.

Betulaceae. The birch family has an excellent fossil record in the Northern Hemisphere (Crane, 1989). *Alnus*, which is distributed today around the Northern Hemisphere and south into the Andes, is confirmed on the basis of infructescences and associated leaves in the early Eocene in Wyoming and in the middle Eocene of Oregon (Crane,

1989). It continues to be a common element of subsequent Tertiary flora in North America. In Asia, *Alnus* is confirmed from infructescences by the Middle Eocene (Ube coal field in southwestern Honshu; Huzioka & Takahashi, 1970), and from strata in Kamchatka that Budantsev (1997) considers to be late Paleocene. In Europe, it is first recorded from the Eocene Bournemouth Beds of England (Chandler, 1963).

Betula, which is widespread in the Northern Hemisphere today, has commonly been reported in the fossil record on the basis of leaves, but because of overlap in venation patterns between *Betula* and other genera of the Betulaceae, such reports remain speculative unless accompanied by the diagnostic trilobed infructescence bracts. In North America the earliest *Betula* documented by such bracts is *B. leopoldae* Wolfe & Wehr from the middle Eocene of One Mile Creek, British Columbia (Crane & Stockey, 1987). Subsequently, another species with broader bracts, *B. angustifolia* Newberry, is documented in the Bridge Creek flora of Oregon (Meyer

& Manchester, 1997). In Asia *Betula* is already confirmed by bracts in the Paleocene of the Sikhote-Alin (Akhmetiev, pers. comm. 1997). In Europe, the earliest example confirmed by bracts is in the early Oligocene of Markvartice, Czech Republic (Bůžek et al., 1978).

Carpinus occurs in North Temperate areas today, and is easily identified by the enlarged asymmetrical leaflike bract attached to the ribbed nutlet. The genus is common in the Tertiary of Asia beginning in the late Eocene (Tanai, 1972; Uemura & Tanai, 1993). In Europe the genus is confirmed by two kinds of bracts from the Middle Eocene Eckfeld flora (Wilde & Frankenhäuser, 1998) and continues as a common element in Oligocene and later floras (Berger, 1953; Roiron & Vernet, 1978; Mai, 1995). It is much more rare in the North American Tertiary. Possibly the oldest record is an undescribed species from the middle Eocene of Republic, Washington (Wehr, 1995: pl. 3, fig. 3). It conforms to *Carpinus* in the size and morphology of the nutlet, and the venation, asymmetry, and serration of the bract, but the bract differs from modern species in the obovate, rather than ovate, outline. Curiously, *Carpinus* appears to be lacking from the subsequent Tertiary record of North America. Its presence in the forests of eastern North America today indicates either that the genus persisted on this continent after the Eocene without leaving a record, or that the Eocene populations perished, followed by a later Tertiary or Quaternary recolonization from Europe or Asia. Leaves formerly referred to *Carpinus* from the late Eocene and Oligocene of western North America are now placed in *Paracarpinus*, and are considered the probable candidate for the foliage of the extinct fruit *Asterocarpinus* (Manchester & Crane, 1987; Crane, 1989; Meyer & Manchester, 1997).

Corylus, which occurs in North America, Europe, and Asia today, is first confirmed on the basis of nuts with multilobed, both foliar and spiny bracts in the Middle Eocene of Republic, Washington (Wehr, 1995). *Corylus*-like leaves are known from many Paleocene and Eocene sites around the Northern Hemisphere, but it is virtually impossible to determine whether they are the leaves of *Corylus*, or *Palaeocarpinus*. Hence, they are best placed in the fossil leaf genus *Corylites* Gardner (Boulter & Kvaček, 1989; Kvaček et al., 1994; Manchester & Chen, 1996). Silicified nuts of *Coryloides* Manchester from the Eocene of Oregon resemble *Corylus* in morphology and anatomy, but differ from modern species by being perfectly spherical (Manchester, 1994b).

Cranea Manchester & Chen (1998) is an extinct

betulaceous genus common in the Paleocene of Wyoming with elongate, cone-like infructescences bearing small wingless nuts. As this genus has not been recovered from regions outside North America, it may have been endemic to North America.

Ostrya, which occurs in North Temperate areas today, is readily recognized by the persistent bladderlike involucre which surrounds the nutlet. It is first observed in the early Oligocene of central Europe (Engelhardt, 1885: 320; Kvaček & Walther, 1998, pl. 12, figs. 6, 7) and western North America (Meyer & Manchester, 1997) and in the Miocene of China (WGCP, 1978) and Japan (Tanai, 1972). Although absent from northwestern North America today, the genus occurred as late as the middle Miocene in Oregon and Idaho (Chaney & Axelrod, 1959; Fields, 1996). In Asia, *Ostrya* fruits occur in the fossil record by the middle Miocene (Huzioka, 1963; WGCP, 1978; Tanai, 1961).

Palaeocarpinus Crane is an extinct genus of fruit with bract characters similar to *Corylus* and nutlet characters similar to *Carpinus*. It was circumboreal during the Paleocene, with occurrences in England (Crane, 1981), France (Crane, 1989), China (Manchester & Guo, 1996), and North America (Crane et al., 1990; Sun & Stockey, 1992; Manchester & Chen, 1996). *Palaeocarpinus* persisted into the Eocene in western North America (Republic flora; Wehr, 1995: pl. 3, fig. 4) and eastern Asia (Buoy flora, Sikhote Alin; Akhmetiev & Manchester, in progress).

Caprifoliaceae. *Diplodipelta* from the Eocene to Miocene of the western United States is an extinct genus of fruits related to extant *Dipelta* of Asia (Manchester & Donoghue, 1995). Both genera have elongate fruits with persistent epigynous sepals, but the dispersal units differ. Dispersal units of *Dipelta* consist of a single fruit subtended by three wings developed from the inflorescence bracts. *Diplodipelta* dispersal units also have three bract-derived wings, but the involucre subtends a pair of fruits rather than just one. The occurrence of *Dipelta* based upon fruits in the late Eocene of England (Reid & Chandler, 1926) indicates that the genus was not always confined to Asia and apparently crossed directly between Europe and Asia. In addition, the morphologic similarity between *Diplodipelta* and *Dipelta* suggests early Tertiary geographic continuity.

Cercidiphyllaceae. Cercidiphyllaceae are represented by one living genus with two species native to eastern Asia. The family has an excellent fossil record, with leaves and fruits extending back to the late Cretaceous. Cretaceous and early Tertiary leaves are usually placed in the fossil genus *Troch-*

odendroides Berry (Crane, 1984). Fruits of *Nyssidium* Heer (syn. *Trochodendrocarpus* Kryštofovich), commonly found in the same localities as *Trochodendroides* leaves, are pod-like follicles similar to those of *Cercidiphyllum*, but they are obliquely striated, and are borne in elongate racemes rather than clusters (Crane, 1984). *Nyssidium* is common in the late Cretaceous, Paleocene, and Eocene of North America, the late Cretaceous to Paleocene of Asia, and the Paleocene to Eocene of Europe, Greenland, and Spitsbergen. The southernmost occurrence in North America is from Hope, Arkansas (UF loc. UF 18607).

At one locality in the Paleocene of Alberta, Canada, *Nyssidium* fruits, *Trochodendroides* leaves, and associated seeds and seedlings were placed together as a single species in a separate genus, *Joffrea* Crane & Stockey (1985a). Elsewhere, the more conservative practice of providing separate names to the fruits and leaves continues.

Detailed multiple organ investigations on *Nyssidium*-related plants from Paleocene localities in Canada, England, and Far Eastern Russia reveal that these plants were diverse in phyllotaxy, shoot growth, and inflorescence position (Crane & Stockey, 1985b). *Joffrea speirsii* from Alberta had opposite phyllotaxy (possibly also alternate) on long and short shoots with inflorescences in the leaf axils of monopodial short shoots. *Nyssidium arcticum* from the Paleocene of England had long shoots with whorled, or pseudowhorled, leaves and terminal inflorescences. The plant referred to as *Trochodendrocarpus arcticus* (Krassilov, 1976; Crane & Stockey, 1985b) has alternate phyllotaxy and bears inflorescences in the leaf axils of long shoots. Although it is clear that infructescences and fruits corresponding to *Nyssidium* were widespread in the Northern Hemisphere, more work is needed to determine the geographic ranges of the different species. For example, it remains uncertain whether plants with the *Joffrea speirsii* type of growth architecture occurred outside North America.

Cercidiphyllum, native today in China and Japan, is first recognized on the basis of clustered fruits and associated leaves like those of the extant species in the lower Oligocene both in Oregon and central Europe (Meyer & Manchester, 1997). In North America it continues through the Middle Miocene of Idaho (Smiley & Rember, 1985). In Europe, *Cercidiphyllum* fruits and leaves are known from the Early Oligocene to Pliocene (Jähnichen et al., 1980; Kovar-Eder et al., 1998). Staminate flowers found with the fruits and leaves in the Miocene of Bohemia differ from extant species by the development of a perianth (Kvaček & Konzalová,

1996). In the Asian Tertiary, the genus is confirmed by clustered fruits and associated foliage in the Miocene of Zaliv Korfa, eastern Kamchatka (Chelebaeva, 1978).

Cornaceae. The Cornaceae sensu lato (including Nyssaceae, Mastixioideae; Alangiaceae) have an excellent fossil record in the Northern Hemisphere that includes both extant and extinct genera.

Alangium is distributed today from China to eastern Australia and in tropical Africa. *Alangium* leaves are strikingly convergent in shape and the primary, secondary, and tertiary venation to the leaves of some genera in the Malvales, and there are many cases of mistaken identity in the literature. However, the endocarps are very diagnostic. *Alangium* has unequivocal fossil fruit remains in the Tertiary of North America, Europe, and Asia (Eyde et al., 1969). In North America species are known from the Eocene of Oregon (Manchester, 1994b) and Miocene of Vermont (Eyde et al., 1969). In Europe, it ranges from the Eocene of England (Chandler, 1961) and Germany (Mai, 1970) to the Pliocene in Alsace, France (Geissert & Gregor, 1981). In Asia, fruits are known from the Pliocene and Pleistocene of Japan (Miki, 1956; Miki & Kokawa, 1962; Eyde et al., 1969). The fossil fruits all correspond to section *Marlea*, which occurs in eastern Asia and Indonesia today (Eyde et al., 1969).

Infructescences and fruits of the extinct genus *Amersinia* Manchester, Crane & Golovneva (1999), related to the extant Chinese endemics *Davidia* and *Camptotheca*, occur in association with leaves formerly called "*Viburnum*" *cupanioides* both in North America and Asia. The infructescences are heads of tricarpetate fruits with four or five prominent bract scars on the peduncle below the head. Permineralized fruits have been sectioned to show trilocular endocarps composed of fibers, lacking an axial bundle, and having single-seeded locules with apical-dorsal germination valves. These fruits, and the associated foliage, *Beringiaphyllum* Manchester, Crane & Golovneva (1999), occur together at eight localities in the Rocky Mountains of the U.S. and Canada, in northeastern China, and in southern Primorye, Koryak Highland, and western Kamchatka, Russia. The apparent absence of *Amersinia* from the Tertiary of Europe, Greenland, and Spitsbergen suggests that the genus dispersed across Beringia but did not populate the North Atlantic or Turgai region.

Cornus occurs in North Temperate regions, and extends into South America and Africa today. The genus is known in the Paleocene of North America both from leaves (e.g., *Cornus hyperborea* Heer, in Hickey, 1977: 144, pl. 47, fig. 1) and fruits (Crane

et al., 1990: fig. 31G–I) in the Paleocene of North Dakota. Leaves are readily identified to the genus (*sensu lato*) because of the smoothly curving acrodromous secondaries, thin, widely spaced, percurrent tertiary veins, and entire margin, but discrimination of subgenera or sections requires reproductive material. Paleocene *Cornus* fruits from North Dakota, and those described from the Early Eocene of England (Reid & Chandler, 1933, as *Dunstanea*) are anatomically preserved, showing resin cavities in the wall that indicate affinities with the Cornelian Cherry group of dogwoods. Thus, the Cornelian Cherry group seems to have traversed the North Atlantic during the early Tertiary. Evidence of the big-bracted dogwoods is provided by the fruit of *Cornus clarnensis* from the Eocene of Oregon, which resembles extant *C. florida* (Manchester, 1994b).

Nyssa, with a disjunct distribution in eastern Asia, eastern North America, and Central America, has an excellent fossil record in the Northern Hemisphere (Eyde, 1997). *Nyssa* fruits have woody stones composed of fibers and have one to three locules with apical-dorsal germination valves. Transverse sections of permineralized specimens reveal that the endocarps are composed of tortuous fibers, lack an axial bundle, and possess apical dorsal germination valves—a syndrome diagnostic of *Nyssa*. The genus is well represented in the Eocene and later Tertiary of North America (Manchester, 1994b) and Europe (Mai, 1995). In Asia, it extends from the Oligocene to Recent (Eyde, 1997).

Mastixia, which occurs in Asia today, is well known for its excellent representation by fruits in the European Tertiary, extending from the Eocene (Reid & Chandler, 1933) to the Miocene (Kirchheimer, 1957; Mai, 1993). *Mastixia* endocarps are anatomically similar to *Nyssa*, but the endocarps have more pronounced dorsal infolds, resulting in locules that are u-shaped in cross section, and the germination valves extend the entire length of the endocarp, rather than being confined to the apical end. *Mastixia* also occurs in the Eocene of Oregon and California (Manchester, 1994b; Tiffney & Haggard, 1996). In addition to *Mastixia* itself, there is a complex of closely related extinct genera of mastixioids in the Tertiary of Europe (Kirchheimer, 1936, 1957; Mai, 1993) distinguished by differences in size, surface sculpture and presence or absence of gum/resin cavities, with some members extending back to the late Cretaceous (Maastrichtian; Knobloch & Mai, 1986). The living mastixioid genus *Diplopanax* is a native of Asia today, but has fossil occurrences in North America (Stockey et al., 1998) and Europe (Eyde & Xiang, 1990). The tax-

onomic levels to be accorded different taxa within the mastixioids are still not agreed upon. Murrell (1993) recommended that *Diplopanax* be treated as a section within *Mastixia*. If this proposal were to be accepted, then most of the taxa now treated as extinct mastixioid genera (Mai, 1993) would need to be subsumed within the extant genus *Mastixia*. Whichever approach might be taken in the future, it is clear that the fruit morphological diversity of this complex was much greater in the Tertiary than it is today.

Langtonia is one of the most distinctive of the extinct mastixioids. These bilocular ellipsoid fruits conform to the Mastixioideae by having an endocarp composed of tortuous fibers, single-seeded locules, and elongate germination valves. The fruit differs from other modern and fossil mastixioids by the occurrence of paired dorsal infolds in each locule, giving a W-shaped cross section of the locule and seed in contrast to the usual U- or V-shape. This genus was first described based on specimens from the Early Eocene of England (Reid & Chandler, 1933) and was subsequently recognized in the middle Eocene of Oregon (Manchester, 1994b) and Paleocene of Wyoming (Tiffney & Haggard, 1996).

Elaeocarpaceae. *Sloanea* occurs today in tropical and subtropical America, Asia, and Australia. Fruits of four to five spiny valves corresponding to those of extant *Sloanea* occur in the Paleocene of North America, where they have gone under the name *Carpolithes spinosus* (Fig. 2A–C; Newberry, 1898: 138, pl. 68, figs. 2, 3), and in the Paleocene of Greenland (Fig. 2D, E; “*Castanea ungeri*” in Heer, 1869: 470, pl. 45, fig. 2). These remains occur at numerous sites in the Paleocene and into the Eocene of the Rocky Mountain region. *Sloaneaecarpum* is a genus based on a similar spiny valve from the lower Oligocene of Hungary (Rásky, 1962).

Eucommiaceae. *Eucommia*, native only to central China today, has distinctive samaroid fruits (Fig. 3A). Such fruits have an excellent record in the Eocene of the western and southeastern United States (Fig. 3B; Call & Dilcher, 1997), and extending into the Oligocene or Miocene of southern Mexico (Fig. 3C; Magallón-Puebla & Cevallos-Ferriz, 1994a). The generic determination of these fruits is unquestionable because of the unique morphology and venation, and the presence of latex strands observable in the fossils that correspond in position to the laticifers of extant fruits (Szafer, 1954; Tralau, 1963; Call & Dilcher, 1997). In Asia, *Eucommia* is well documented by fruits in the Eocene of Yubari, Hokkaido, Japan (Huzioka, 1961), the lower Oligocene of Kiin Kerish, Kazakhstan (Akhme-

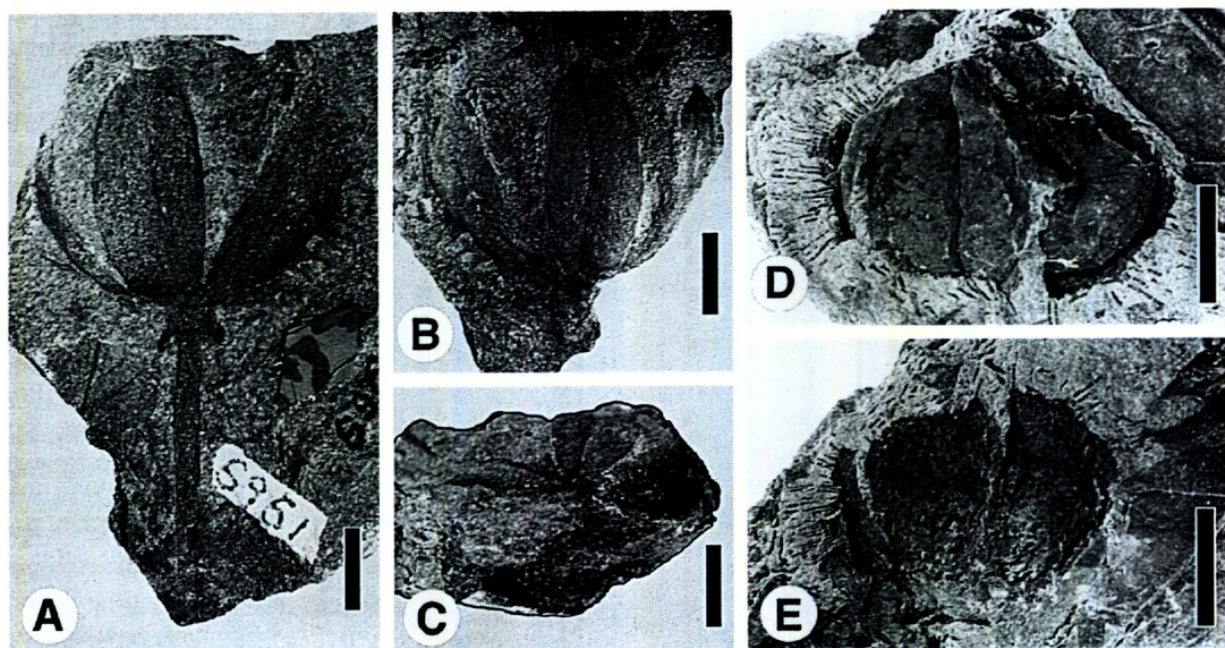


Figure 2. Fruits of *Sloanea* (Elaeocarpaceae) from the Paleocene of North America and Greenland. A–C. *Carpolithus spinosus* Newberry, 1898, USNM 6960, 6961, North Fork of Purgatoire River. —A. Lateral view showing the opened fruit valves, hypogynous perianth scar, and stout peduncle. Note the needle-like spines preserved on the external surface of the valve on the right. —B. Counterpart internal cast, showing the impressions left by internal keels on the fruit valves. —C. Apical view of the same, showing three locules; two more can be inferred from the symmetry and are observed in other specimens. —D, E. Specimen illustrated as *Castanea ungeri* Heer from Paleocene of Atanekrdluk, Greenland, by Heer (1869; *Philos. Trans.*, p. 470, pl. 45, fig. 2), Natural History Museum, London, V/11326. Scale bars = 1 cm.

tiev, 1991), and the Miocene Kraskino flora of Khasan Basin, south Primorye, Russia (Ablaev et al., 1993). The numerous fruit records in Europe extend from the Oligocene to the Pleistocene (Tra-

lau, 1963; Mai, 1995). The North American fruits are about half as large as fruits of the extant species and are slightly more asymmetrical in the placement of stigma at the fruit apex (Call & Dilcher,

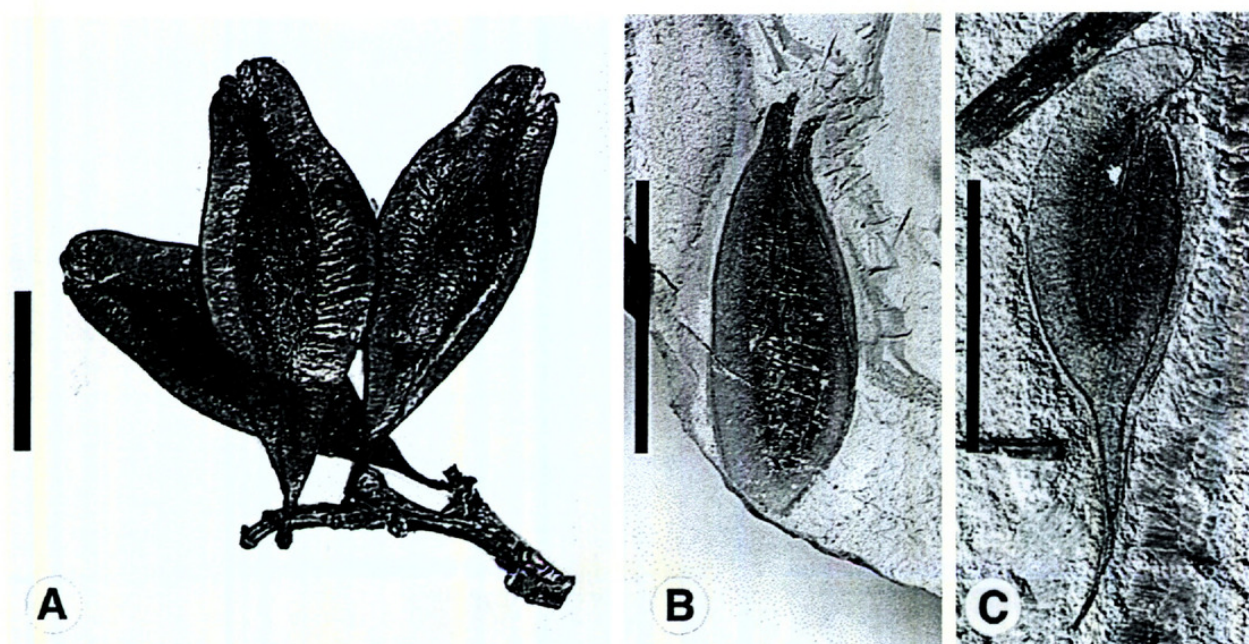


Figure 3. *Eucommia* (Eucommiaceae) fruits from Asia and North America. —A. Extant *Eucommia ulmoides*, Hupeh, China, A: P. C. Silvestri 7378. —B. *Eucommia eocenica* (Berry) Brown from the Bovay Clay Pit, Mississippi, UF 15737–8218. —C. *Eucommia constans* Magallón-Puebla & Cevallos-Ferriz from the Oligocene or Miocene Pie de Vaca Formation, Puebla, Mexico. IGM-PB 2573–632. Scale bars = 1 cm.

1997). The Japanese Eocene species is intermediate in size between the North American fossils and the living species, but it resembles the American fossils in the asymmetry of stigma position.

Fagaceae. Fagaceous flowers are now known to date back to the Santonian stage of the Late Cretaceous in North America (Herendeen et al., 1995; Sims et al., 1998), but the focus here is on Tertiary occurrences.

Castanea, which occurs in North Temperate areas today, has often been reported in literature on Tertiary leaves, but many of these reports are questionable. *Castanea* leaves lack a fimbrial vein, which is present on the leaves of otherwise similar-leaved species of *Quercus*. According to this criterion, many, if not all, of the *Castanea* leaves reported from western North America may represent *Quercus*. No *Castanea* cupules are known from western North America prior to the Miocene (Chaney, 1920). *Castanea* is present, however, in the Eocene of Tennessee based on spiny cupules and associated leaves and staminate inflorescences (Crepet & Daghljan, 1980). This assemblage of organs was given different fossil generic names due to the differences in systematic resolution afforded by isolated organs.

Castanopsis, which occurs today in tropical and warm temperate eastern Asia, occurs in the Eocene Clarno Nut Beds of Oregon based upon fruits with identical anatomy of cupule and nut to that of extant *Castanopsis piriformis* of Vietnam (Manchester, 1994b). Younger records have not been discovered. In Europe, the genus has also been recognized by fruits (Kirchheimer, 1957), but they are most similar to those of different extant species, and are morphologically distinct from the Clarno fossil. No fruit records are known to me from Asia, although the genus grows there today.

Fagopsiphyllum groenlandicum (Heer) Manchester comb. nov. (see Appendix 1 for generic diagnosis) is a taxon based on leaves of possible fagaceous affinities from the Paleocene of North America, Greenland, Scotland, and with similar species in the Eocene of Far East Russia and Japan. The leaves have simple, triangular to rounded teeth, pinnate, craspedodromous secondaries, and percurrent tertiaries. These leaves have commonly been placed in *Fagopsis* Hollick, a genus with very similar foliage (Wolfe, 1977; Boulter & Kvaček, 1989; Tanai, 1995). However, *Fagopsis* was diagnosed on the basis of twigs with attached leaves and infructescences (Hollick, 1909; Manchester & Crane, 1983) from the late Eocene of Colorado with fruits that are unlike any found in association with the Paleocene leaves. Despite a careful search for

the distinctive fruits of *Fagopsis* where the leaves of *Fagopsiphyllum groenlandicum* occur, both in the field and at museum collections, I have never seen them. This also applies to the localities producing the leaves identified as *Fagopsis nipponica* Tanai from the Eocene of Hokkaido (Tanai, 1995). Therefore, despite the foliar similarity, these fossils lack diagnostic characters of *Fagopsis* (namely, those of the infructescence) and should not be placed in that genus. *Fagopsiphyllum* has an interesting pattern of distribution that indicates communication across the North Atlantic during the Paleocene exemplified by its occurrences in the Rocky Mountains (Brown, 1962), Greenland (Koch, 1963), and Scotland (Boulter & Kvaček, 1989), followed by arrival in Asia during the Eocene exemplified by the occurrences in eastern Russia and Japan. True *Fagopsis* is known on the basis of leaves and infructescences from the Eocene of Washington (Wehr, 1995), Montana (Becker, 1961), and Colorado (MacGinitie, 1953; Manchester & Crane, 1983). So far, it is not known outside North America.

Fagus is distributed at temperate latitudes of the Northern Hemisphere but is not native to western North America today. Nevertheless, the genus is documented by beech nuts and associated foliage in the lower Oligocene of Oregon (Meyer & Manchester, 1997). The fossil record and evolution of *Fagus* foliage has been reviewed by Tanai (1974, 1995), Zetter (1984), and Kvaček and Walther (1991, 1992). The genus extends through the Miocene in western North America and from the upper Oligocene through the Pliocene in Europe and Asia.

Pseudofagus, a North American endemic extinct genus, makes its appearance in the Miocene of Idaho (Smiley & Huggins, 1981; type material at UCMP). Although the leaves are virtually indistinguishable from those of *Fagus*, the attached fruits have a single trikeeled nut (unlike the paired trikeeled nuts of *Fagus*), and a highly dissected cupule that covers only the basal part of the nut (Smiley & Huggins, 1981).

Quercus is widespread in the Northern Hemisphere and extends into Malesia and Colombia. It is first recognized on the basis of silicified nuts with cupules from the Middle Eocene Clarno Nut Beds, Oregon (Manchester, 1994b). Lobed oak leaves are described along with acorns and staminate catkins from the Oligocene of Huntsville, Texas (Daghljan & Crepet, 1983). Reports of unlobed leaf impressions attributed to *Quercus* should be viewed with caution if not accompanied by acorns because of the difficulty in distinguishing from other genera

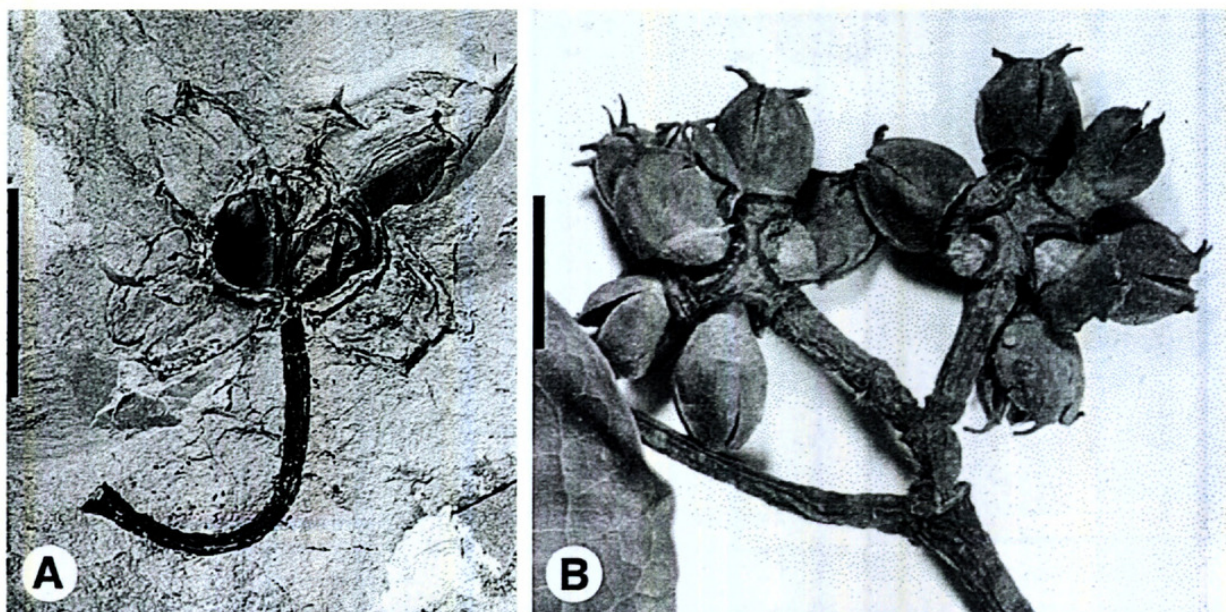


Figure 4. *Exbucklandia* (Hamamelidaceae). —A. *Exbucklandia oregonensis* Brown, 1946, Miocene Spokane flora, Washington, USNM 42366. —B. Extant *Exbucklandia populnea* (R. Br.) R. W. Brown from Yunnan, China, A: T. T. Yu 17269. Scale bars = 1 cm.

such as *Lithocarpus* and *Castanopsis*. *Quercus* species with lobed leaves became widespread in the Northern Hemisphere in the early Oligocene (Tanai & Uemura, 1994). The North American fossil record of *Quercus* was reviewed by Borgardt and Pigg (1999) with special attention to anatomically preserved acorns.

The *Trigonobalanoids* include three extant species that were formerly placed together in the single genus *Trigonobalanus*, but now segregated by Nixon and Crepet (1989) into separate monotypic genera: *Trigonobalanus verticillata* (Borneo and the Malay Peninsula), *Formanodendron doichangensis* (Thailand and southern China), and *Colombobalanus excelsa* (Colombia). Fossils of the extinct genus *Trigonobalanoidea* from the Eocene of Buchanan, Tennessee, resemble *Formanodendron* and *Colombobalanus* on the basis of alternate cupule arrangement and winged fruits (Crepet & Nixon, 1989).

Hamamelidaceae. *Corylopsis* ranges from the Himalayas to Japan today, but was formerly distributed in Europe and North America. The fossil record of the genus, with many European Tertiary seed occurrences, was reviewed by Tralau (1963). Grote (1989) recognized *Corylopsis* on the basis of seeds from the Eocene of Tennessee. He noted that the large, narrow, very asymmetrical, hilar scar facilitates the distinction of *Corylopsis* seeds from other extant genera of the Hamamelidaceae. Infructescences of *Fortunearites* from the Eocene of Oregon bear seeds with a combination of characters found today only in the Chinese genera *Fortunearea* and *Sinowilsonia* (Manchester, 1994b).

Exbucklandia, a genus endemic to China today, was identified on the basis of leaves and associated globose infructescences from the Miocene of Idaho (Brown, 1946a; Lakhanpal, 1958). *Exbucklandia* has a globose infructescence of bilocular woody capsules (Fig. 4B) that are closely similar to the specimens identified to this genus from the North American Tertiary (Fig. 4A). The fossil infructescences are clearly hamamelidaceous, but the enlarged persistent stipules diagnostic of extant *Exbucklandia* have not been observed at these fossil localities, and further work on these fossil occurrences would be desirable to confirm the identification.

Liquidambar, which is well known for its disjunct distribution between eastern North America, Mexico, the eastern Mediterranean, and eastern Asia, is first recognizable by leaves from the middle Eocene of California (MacGinitie, 1941), but the infructescences attributed to the same species by MacGinitie were later determined to be platana-ceous (Manchester, 1986). The genus persists through the Oligocene (Meyer & Manchester, 1997) and is common in the Miocene of western North America (Chaney & Axelrod, 1959; Rember, 1991). *Liquidambar* leaves occur in the late Eocene of Kamchatka (Budantsev, 1997) and are common in the Miocene of Japan (Huzioka & Uemura, 1979) and early Oligocene to Pliocene in Europe (Mai & Walther, 1978). Some reports of the genus based on leaves, including that from the Eocene Green River Formation (MacGinitie, 1969), are equivocal because the teeth are absent from the basal part of

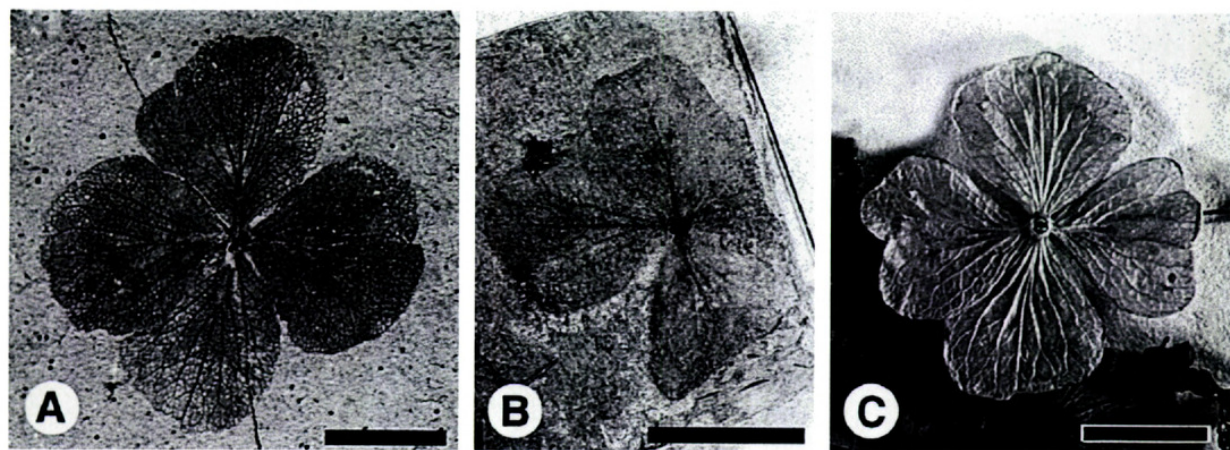


Figure 5. *Hydrangea* (Hydrangeaceae). Sterile calyces of the infructescence. —A. *Hydrangea* sp. from the Gosner Road locality of the Eocene Clarno Formation, Oregon, UF 238–9962. —B. "*Getonia oeningensis* Unger," originally figured by Weber (1852: 24, fig. 2), Oligocene of Rott, Germany. —C. Extant *Hydrangea oerstedii*, Utley 3844 (MO 2592036), epiphytic habit, Costa Rica. Scale bars = 1 cm.

the lamina next to the petiole in contrast to the teeth in extant species, which are uniformly distributed over the entire lamina.

Hydrangeaceae. This family is now considered to be a close relative of Cornaceae (Soltis et al., 1995; Xiang et al., 1993). *Hydrangea*, which occurs in Asia, Atlantic North America, and to Chile today, is readily recognized by the large persistent calyces of its sterile flowers (Fig. 5C), also occasionally by infructescences of capsular fruits (Mai, 1985a; Manchester, 1994b; Meyer & Manchester, 1997). In North America the calyces range from middle Eocene (Fig. 5A; Manchester, 1994b) to middle Miocene (Knowlton, 1902; Fields, 1996). Permineralized fruits of *H. knowltonii* from the Eocene of Oregon were found to contain winged seeds diagnostic of *Hydrangea* sect. *Hydrangea*, subsection *Calypttranthe*, which has a single extant species *H. anomala*, extending from the eastern Himalayas to Japan (Manchester, 1994b). In Europe calyces of *Hydrangea* range from the late Eocene of Kučlin, Czech Republic (Sieber, 1881), and late Oligocene of Rott, Germany (Fig. 5B; *Getonia oeningensis* Unger of Weber, 1852), to the Pliocene (Mai, 1995). Asian examples of these calyces include *Hydrangea* sp. from Miocene Kraskino flora of Khasan Basin, south Primorye, Russia (Ablaev et al., 1993: pl. 20, fig. 7) and *H. sendaiensis* from the Late Miocene flora near Sendai, Japan (Okutsu, 1940).

Icacinaceae. The tribes Phytocreneae and Iodeae of the Icacinaceae are presently paleotropical in distribution, but both are well represented by unilocular endocarps in the early Tertiary of North America and Europe. In the Iodeae, the fruits of modern *Iodes* (Asia, Africa), *Natsiatum* (Asia), and *Hosiea* (Asia) are similar in the possession of reticulately ridged endocarp surfaces, and papillate loc-

ule lining. These genera are distinguished by phyllotaxy, which is opposite in *Iodes*, and alternate in the others, but the distinction of these genera based on their fruits requires details of internal morphology and endocarp sculpture (Manchester, 1994b; Kvaček & Bůžek, 1995). *Iodes* has a funicular canal within the endocarp, whereas *Hosiea* and *Natsiatum* lack this canal, and have the funicle to the outside of the endocarp. Endocarps and locule casts consistent in morphology and anatomy with *Iodes* occur in the Eocene London Clay (Reid & Chandler, 1933) and Clarno (Manchester, 1994b) floras. A new genus, *Palaeohosiea* Kvaček & Bůžek (1995), was recognized on the basis of endocarp fossils from the Eocene and Oligocene of central and western Europe. It is not clear whether the fossils assigned to this fossil genus are truly an extinct genus, or whether they simply lack sufficient characters to specify the correct extant genus to which they belong. The species assigned to *Palaeohosiea* would be difficult to distinguish from those ascribed to *Iodes* in England and western North America. In the distribution chart (Fig. 19), I have lumped the occurrences of *Palaeohosiea* with those of *Iodes*. It is clear that the Iodeae were widely distributed both in western North America and Europe during the early Tertiary. The extinct genus *Iodicarpa* Manchester includes fruits that are morphologically similar to *Iodes*, but three or more times larger than those of extant *Iodes* species (Manchester, 1994b). I am not aware of any Neogene fruits of Iodeae nor of any paleobotanical record of the fruits in Asia.

Fruits of the Phytocreneae are ellipsoidal, with lignified endocarps characterized by conspicuous cylindrical, conical, or laterally elongate invaginations that may appear as pits on the endocarp sur-

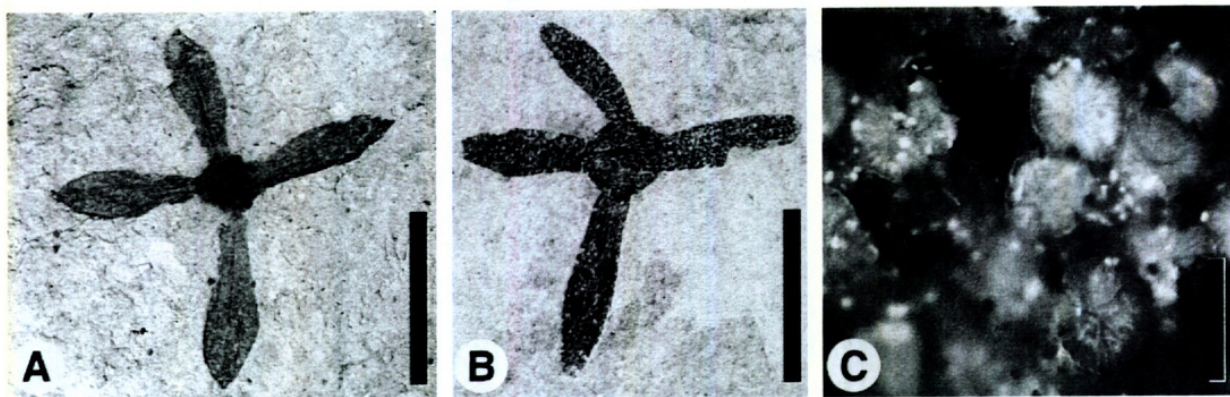


Figure 6. *Cruciptera* (Juglandaceae) from the Eocene of North America and Europe. —A. Samara of *Cruciptera simsonii* with four wings attached to a central globose nut that shows the impression of primary and secondary septa. Middle Eocene, Clarno Gosner Road, Oregon, UF238-9486. —B. Holotype of *C. schaarschmidtii* from the Middle Eocene of Messel, Germany, SM.B. Me 7152. —C. Peltate scales typical of Juglandaceae on surface of the nutlet in B, viewed by epifluorescence microscopy. Scale bars = 1 cm in A, B, 100 μ m in C.

face, and/or protrusions into the locule. Fossil endocarps and locule casts conforming in these features to the Phytocreneae, but not attributable to an extant genus, are assigned to *Palaeophytocrene* Reid & Chandler. Such fruits are common in the Eocene of England (Reid & Chandler, 1933) and western North America (Manchester, 1994b; Manchester & Tiffney, 1993).

The extant genus *Pyrenacantha*, which currently is disjunct between Asia and Africa, is recognized in the fossil record on the basis of endocarps with parallel-sided (not broadly conical), spine-like projections extending into the locule. This genus is known from the Eocene of Oregon (Manchester, 1994b), California, and Egypt (Manchester & Tiffney, 1993). These occurrences indicate that *Pyrenacantha* may be a remnant of the Eocene boreotropical forest with early biogeographic ties to Africa.

Illiciaceae. *Illicium* occurs today from India to eastern Asia and western Malesia, and in eastern North America, Mexico, and the Caribbean. It is known on the basis of fruits from the Miocene of Vermont (Tiffney & Barghoorn, 1979) and Germany (Mai, 1970).

Juglandaceae. Several genera of the Juglandaceae give clues to the biogeographic pathways. The identification of juglandaceous precursors such as the flowers and fruits of *Caryanthus* Friis in the late Cretaceous of the southeastern United States (Crane & Herendeen, 1996) and Europe (Friis, 1983) indicates an early connection across the North Atlantic. Modern genera of the family were not recognizable on the basis of fruits until the lower Paleocene (Manchester, 1989b). Since my earlier review of the biogeographic history of this family (Manchester, 1987a), an additional genus has been

recognized in the Eocene of western North America and Europe (*Cruciptera*: Manchester, 1991; Manchester et al., 1994), and a comprehensive review of the Russian fossil record of the family has been published (Budantsev, 1994b).

Carya, which occurs in eastern Asia and eastern North America today, is first confirmed by fruits in the late Eocene of Florissant, Colorado. The greatest diversity occurs in Europe, with many species recognized from the Oligocene to the Pliocene (Kirchheimer, 1957; Mai, 1981). Although *Carya*-like pollen occurs in the Paleocene, these grains are much smaller than those of most modern species and appear to be associated with fruits of *Juglandicarya simplicarpa* Manchester (1989b).

Cruciptera Manchester is an extinct genus with four wings radiating from the equator of a globose nutlet. It is known from the Middle Eocene to Oligocene of western North America (Fig. 6A; Manchester, 1991, 1994b; Wehr, 1995; Meyer & Manchester, 1997), and from the middle Eocene of England and Germany (Fig. 6B; Manchester et al., 1994). Peltate scales visible on the nutlet surface (Fig. 6C), together with the nutlet internal morphology, confirm affinities within the Juglandaceae. *Cruciptera* is absent from any of the known Tertiary deposits of Asia.

Cyclocarya, although native to southern and central China today, is recognizable based on distinctive fruits in the Paleocene of North America (Manchester & Dilcher, 1982; Manchester, 1987a). A Paleocene specimen from northeastern China was described as *Cyclocarya macroptera* Tao and interpreted to be a fruit by Tao and Xiong (1986). However, I have reexamined the specimen and exclude it from *Cyclocarya* because there is no nutlet impression at the axis of the radiating veins. It might

be the remains of a peltate leaf similar to *Nelumbo*. Similarly, *C. minuta* Krassilov (1976) may be dismissed from *Cyclocarya* because the "fruit" lacks a nut and the wing does not possess veins. A winged fruit illustrated as *Cyclocarya* from the Eocene of Hokkaido (Tanai, 1992b) appears likely to be that of the rhamnaceous genus *Paliurus*. The criteria that I find useful to distinguish these highly convergent fruits are presented later under the discussion of *Paliurus*. *Cyclocarya* ranges from the Oligocene to Upper Pliocene in Europe and Asia (Manchester, 1987a; Mai, 1995).

Engelhardieae. Most genera of this tribe are readily recognized by having wings formed by persistent trilobed bracts. They are unknown from the Paleocene but are widespread by the middle Eocene both in Europe and North America and in the Oligocene of Asia. Fruits with deeply trilobed bracts similar to those of extant *Engelhardia* (Asia) and *Oreomunnea* (Central America) are placed in the organ genus *Palaeocarya* Saporta. *Palaeocarya* is well represented in the Tertiary of Europe, North America, and Asia. In addition, two extinct genera are known from the Eocene of southeastern North America. *Paleoengelhardtia* Berry has a small nutlet and a shallowly trilobate bract. *Paleooreomunnea* Dilcher, Potter & Crepet has a large nut and a shallowly trilobate bract (Dilcher et al., 1976; Manchester, 1987a). This greater diversity in southeastern North America at the time when this tribe makes its first appearance in the fossil record suggests that the group may have actually diversified in North America prior to dispersing to Europe and Asia.

Platycarya, native to China and Japan today, provides good evidence for a late Paleocene/early Eocene North Atlantic crossing, followed by a much later Tertiary arrival in Asia. The genus is confirmed on the basis of infructescences and fruits from the early Eocene of England (Reid & Chandler, 1933; Manchester, 1987a), North Dakota (Wing & Hickey, 1984), and Wyoming (Dennison Cap; UF localities 18120, 18216). Although Mai (1987) described a specimen from the Paleocene of Gonna, Germany, as *Platycarya cordiformis*, the locule cast, lacking nutlet and wings, is more properly placed in *Juglandicarya*. The lack of dorsiventral compression, and presence of four, rather than two, basal lobes excludes it from *Platycarya* and indicates similarity with the locule casts of *Cruciptera* and *Cyclocarya*. The extinct genera *Paleoplatycarya* Manchester and *Hooleya* Reid & Chandler are also believed to have affinities with *Platycarya* (Wing & Hickey, 1984; Manchester, 1987a).

Pterocarya is no longer native to North America

but has one species in the Caucasus region and several in eastern Asia. It is known from fruits first from the lower Oligocene of the Lyons and Bridge Creek floras of Oregon (Meyer & Manchester, 1997), and additional fruit records indicate that the genus survived into the Miocene in the Pacific Northwestern states (Manchester, 1987a). Fruits reported as *Pterocarya* by MacGinitie (1969) from the Eocene Green River Flora are now thought to more accurately be assigned to the extinct genus *Hooleya* Reid & Chandler. *Pterocarya* has excellent fruit records from the Oligocene to Pliocene of Europe and Asia (Budantsev, 1994b).

Polyptera Manchester & Dilcher is a Paleocene fruit genus known from one locality in Montana and several in Wyoming (Manchester & Dilcher, 1982, 1997). The morphology and symmetry of the fruit are somewhat similar to *Cyclocarya*, but the wing is divided into 8 to 12 prominent lobes. The fruits are associated with pinnately compound leaves of *Juglandiphyllites glabra* (Brown) Manchester & Dilcher, and catkins containing an extinct type of juglandaceous pollen (*Maceopolipollenites anellus* (Nichols & Ott) Manchester & Dilcher). *Polyptera* fruits are unknown outside North America, but the occurrence of pollen resembling *Maceopolipollenites anellus* in the Paleocene of China (Zhuang, 1990) indicates that *Polyptera* may have been present in Asia, or that *Maceopolipollenites* pollen corresponded to more than one kind of fruit (Manchester & Dilcher, 1997).

Leitneriaceae. *Leitneria*, with a single living species confined to the southeastern United States, has drupes with reticulately ribbed, slightly asymmetrical, ellipsoid, and somewhat flattened endocarps. Although still unknown from the North American fossil record, these distinctive endocarps have been identified from the Oligocene of western Siberia and the Miocene to Pliocene of Germany (Dorofeev, 1963, 1994; Mai, 1980). Transverse sections of the endocarp reveal virtually identical anatomy in extant *Leitneria floridana* and in the fossil species (Dorofeev, 1994).

Lemnaceae. *Limnobiophyllum* Krassilov emend Kvaček (1995) was a floating aquatic plant with reniform to nearly orbicular laminae attached in small rosettes interconnected by stolons with simple adventitious roots. Recent work on specimens from the Paleocene of Alberta (Stockey et al., 1997) revealed attached stamens containing globose, monoulcerate, echinate pollen. The combined characters of this plant indicate affinities both with the Araceae and the Lemnaceae (Kvaček, 1995; Stockey et al., 1997). In North America, *Limnobiophyllum* occurs in the Paleocene of Alberta (Stock-

ey et al., 1997) and Saskatchewan (McIver & Basinger, 1993, as *Spirodela scutatum* Dawson) and in the Middle to Late Eocene of Colorado (Kvaček, 1995). In Asia, the same genus is known from the early Paleocene of Primorye (Krassilov, 1976: pl. 11, fig. 5 only). Other specimens illustrated under this name by Krassilov (1976) and Golovneva (1994) are actually an unrelated genus called *Porosia* Hickey (see below). In Europe, *Limnophyllum* is represented by a similar species in the Early Miocene of Bilina and Zelenky, western Czech Republic, the Middle Miocene of Oeningen and Kreuzau, Germany, and the Late Miocene of Sosnica, Poland (Kvaček, 1995).

Lythraceae. *Decodon* is endemic to swampy areas of southeastern North America today and has a good fossil record in Europe and Asia, as well as North America. Silicified fruits are known from the Eocene of Princeton, British Columbia (Cevallos-Ferriz & Stockey, 1988), and Oregon (Manchester, 1994b). The distinctive seeds are known from the Eocene to Pliocene in Europe (Mai & Walther, 1978; Friis, 1985) and from the Oligocene and Miocene of Asia (Dorofeev, 1977; Matsumoto et al., 1997a). The extinct *Microdiptera* Chandler occurs from the Middle Eocene to Miocene of Europe and also in the Miocene Brandon Lignite of Vermont (Tiffney, 1981a).

Magnoliaceae. The fossil record of Magnoliaceae includes some extinct genera that extend well into the Cretaceous (Friis et al., 1997), but extant genera are not confirmed by reproductive structures prior to the Tertiary. *Magnolia* seeds have a distinctive morphology that allows them to be easily identified in the fossil record (Reid & Chandler, 1933; Tiffney, 1977b). *Magnolia* seeds occur in the upper Paleocene of Wyoming (UF loc. 18132) and are well documented in the middle Eocene of Tennessee (Grote, 1989) and Oregon (three species; Manchester, 1994b). Miocene records include seeds from the Brandon Lignite of Vermont (Tiffney, 1977b) and a multifollicular fruit from the Clarkia beds of Idaho (Rember, 1991). The identification of leaves to this genus is more difficult because of the convergence with similar leaf architecture among many different dicotyledonous families. In Europe and Asia, the record of *Magnolia* extends from the Paleocene to Pliocene (Mai, 1995).

Liriodendron, which is disjunct between eastern North America and China today, is readily recognized by its distinctive, apically notched, bisymmetrical, lobed leaves, and by its elongate-winged fruitlets. Leaves of *Liriophyllum* Lesquereux from the mid-Cretaceous and *Liriodendrites* K. Johnson (1996) from the late Cretaceous are similar to *Lir-*

iodendron and are considered to represent Magnoliaceae, but can be distinguished by the depth of the apical sinus and the nature of the midvein as it nears the apical sinus. Although magnoliaceous infructescences and seeds sometimes occur together with these leaves, no samaroid fruitlets of the *Liriodendron* type have been found prior to the Tertiary (Friis et al., 1997). *Liriodendrites* Knobloch & Mai seeds from the Late Cretaceous are anatomically similar to the seeds of *Liriodendron* except that the fossil seeds are winged, rather than the fruitlets (Friis et al., 1997). Leaves and fruits that can be attributed unequivocally to the extant genus occur relatively late in North America, in the Miocene of Idaho (Baghai, 1988). The genus has an earlier record in the Oligocene of Markvartice (Bůžek et al., 1976), where it is noted to have a lower leaf cuticle that is smooth like that of the extant North American species *L. tulipifera*, in contrast to the finely papillate lower cuticle of the extant Chinese *L. chinense*. The last European records are upper Pliocene (Wilde et al., 1992). *Liriodendron* occurs in the middle and late Miocene of Japan (Uemura, 1988) based on leaves of *L. honshuensis* Endo and winged fruitlets of *L. fukushimaensis* Suzuki. The genus is absent from the Pliocene of Japan and is no longer native to the islands.

Malvales. Judd and Manchester (1997) proposed, based upon cladistic analyses, that the Tiliaceae, Sterculiaceae, Bombacaceae, and Malvaceae should be combined into one family, the Malvaceae s.l. To alleviate confusion prior to a general consensus on this matter, I refer to the group here simply as the order Malvales. The extant genus *Craigia*, traditionally placed in the Tiliaceae, has two species in southern China. It was widely distributed through the Tertiary, and its fruits were formerly thought to be an extinct genus, *Pteleacarpum* Weyland (Bůžek et al., 1989). With the recognition that the fossil fruits represent *Craigia* (Kvaček et al., 1991), it has been possible to document an extensive history of this genus in the Northern Hemisphere (Kvaček, 1994). The distinctive fruits are known from the Eocene of Spitzbergen and of John Day Gulch, Oregon, and Bonanza, Utah. In North America, the latest record of *Craigia* is early Oligocene (Meyer & Manchester, 1997), but in Europe the fruits extend from the Oligocene to the Pliocene, and in Asia they are known in the fossil record from the Eocene to the Miocene (Bůžek et al., 1989).

Tilia is a tree of North Temperate distribution that also extends south to Indochina and Mexico today. Bracts of *Tilia* suggest an interesting phylogeographic scenario (Manchester, 1994a). The ear-

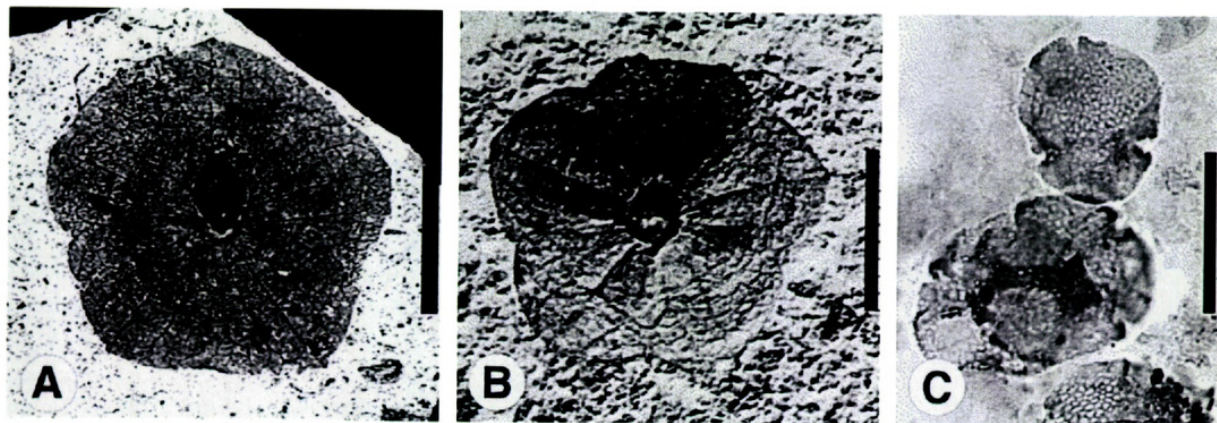


Figure 7. *Florissantia* (Malvales) calyces from the Eocene of western North America and Miocene of Asia. —A. *Florissantia quilchenensis* (Mathewes & Brooke) Manchester, from the Middle Eocene Republic flora of Washington, western North America, UWBM 57556. —B. *Florissantia sikhote-alinensis* (Kryshtofovich) Manchester comb. nov. from the Miocene Amgu flora of Sikhote Alin. Specimen missing, figure reproduced from Kryshtofovich (1921). —C. Malvacean pollen removed from the anther of a *Florissantia speirii* flower (Manchester, 1992). Scale bars = 1 cm in A, B, 30 μ m in C.

liest known *Tilia* bracts are from the late Eocene of North America. They are elongate and have the peduncle adnate only to the base of the bract ("type B" morphology), as seen in only a few Chinese species today. Also in the late Eocene of Idaho and early Oligocene of Oregon, an extinct type of bract with a circular, rather than elongate, outline became common ("type A" morphology). This kind of bract is not known from floras outside western North America. In Europe, *Tilia* bracts are unknown prior to the Oligocene, and they conform to type B, suggesting dispersal across the North Atlantic. By the Pliocene in Europe, a third type appeared that is elongate and has the peduncle adnate along the lower 1/4 to 1/3 of the bract. This "type C" morphology also extends from the Oligocene to the Pliocene in Asia and characterizes most extant species in North America, Europe, and Asia. Thus, the kind of bract that is widespread in the Northern Hemisphere today occurs only in Asia in the middle Tertiary and evidently arrived relatively late in the Tertiary of Europe and North America (Manchester, 1994a).

Florissantia Knowlton (Fig. 7) is an extinct genus with fruit, flower, and pollen morphology indicating malvacean affinity, common in the Eocene to Oligocene of western North America. At the time the record was summarized (Manchester, 1992), I overlooked its occurrence in the Miocene of eastern Asia. Kryshtofovich (1921) had earlier described a calyx that he considered similar to *Florissantia speirii* (then known under the name *Porana speirii* Lesq.) from the Miocene of Amgu, Sikhote-Alin. Although the specimen has not been relocated, the published description and photograph (Fig. 7B) leave little doubt that it represents the same genus.

The species that Kryshtofovich described now provides the basis for a new combination: *Florissantia sikhote-alinensis* (Krysh.) Manchester comb. nov. (see Appendix 1).

The stratigraphic ranges of *Florissantia* in Asia and North America do not overlap, so the fossil record is clearly insufficient to resolve the precise timing of the migration between continents. However, the complete absence of these fruits from European Tertiary indicates that the likely route was across Beringia in the early to mid Tertiary.

Menispermaceae. This family is diverse in the tropics today but has a few outliers in temperate areas, e.g., *Menispermum*, *Calycocarpum*. The family can be recognized by its leaves, although different genera can be difficult to discriminate because of very similar venation patterns. The tribes and genera are recognizable from the endocarps. Although apparently absent from the Tertiary of southeastern North America, the family has a rich record in western North America. The family is relatively rare in the Paleocene (Crane et al., 1990), but it becomes common in the Eocene, with more than 12 genera of Menispermaceae based upon endocarps in the Eocene Clarno Nut Beds (Manchester, 1994b). Of these, *Tinospora*, *Tinomiscoidea*, *Atriaecarpum*, *Daviscarpum*, *Diploclisia*, *Eohypserpa*, and *Palaeosinomenium* are shared with the Eocene London Clay flora. *Anamirta*, known both from leaves in the Kulthieth Formation of Alaska (Wolfe, 1977) and endocarps from the Clarno Formation (Manchester, 1994b), grows today from India to Indochina and throughout Malesia. In North America Menispermaceae diminished in diversity by the end of the Eocene, and the family is known only from cf. *Menispermum* in the Oligocene Bridge Creek flo-

ra (Meyer & Manchester, 1997). The numerous reports of *Cocculus* and *Menispermites* leaves were formerly thought to represent Menispermaceae (LaMotte, 1952; Hickey, 1977), but based on co-occurrence at numerous localities through the Northern Hemisphere, many of these are now considered to belong to the extinct trochodendraceous plant *Nordenskioldia* (Crane et al., 1991; Manchester et al., 1991).

Musaceae. The banana family is represented by *Ensete* on the basis of seeds (Manchester & Kress, 1993) and fruits (Manchester, 1994b) from the Eocene of Oregon, and by fruits from the Eocene of Republic, Washington (Wehr & Manchester, 1996). Today this genus is distributed in Asia and Africa.

Myricaceae. *Comptonia*, which today is restricted to eastern North America, has distinctive, pinnately lobed leaves (Fig. 8A) that are easily recognized in the fossil record. It was widespread in the Tertiary of the Northern Hemisphere. Eocene occurrences include the Clarno Formation of Oregon; Republic, Washington (Wolfe & Wehr, 1987); Alum Bay, England (Fig. 8D); and Messel and Eckfeld, Germany (Wilde, 1989; Wilde & Frankenhäuser, 1998). In western North America, the leaves are known as late as the Miocene (Fig. 8C; Boyd, 1985). In Europe, *Comptonia* extends into the upper Pliocene of Willershausen (Wilde et al., 1992). Leaves also occur in the Lower Oligocene of central Kazakhstan (Zhilin, 1989; Akhmetiev, 1991). In eastern Asia the genus is known, for example, from the Eocene of Fushun (WGCP, 1978) and Yilan (Fig. 8B), China, the Miocene of Sikhote-Alin (Fig. 8E) and is diverse in the Middle Miocene of Japan (Tanai, 1961; Huzioka & Uemura, 1979). In Europe and western Asia, the record also includes endocarps (Dorofeev, 1994).

Although *Myrica* is well represented in the extant flora of eastern North America, its fossil record in North America is poor or nonexistent (Chourey, 1974). *Myrica* is known based on leaves from the Late Eocene of western Kamchatka (Budantsev, 1983, 1997) and by well-preserved fruits from the mid to late Tertiary of Europe and Asia (Dorofeev in Budantsev, 1994b).

Myrtaceae. This family is represented by permineralized fruits from the Paleocene of North Dakota and the Eocene of British Columbia with distinctive seeds similar to those of the guava, referred to *Paleomyrtinaea* Pigg, Stockey & Maxwell (1992). An extinct myrtaceous genus, *Syzygioides* Manchester, Dilcher & Wing, was recently established based on leaves and fruits from the Eocene Green River Formation of Colorado and Utah (Manchester

et al., 1998). Leaves of *Syzygioides americana* (Lesquereux) Manchester, Dilcher & Wing were formerly attributed to extant *Eugenia* (MacGinitie, 1969), but they have been found attached to twigs with an extinct kind of fruit (Manchester et al., 1998). Budantsev (1994a: pl. 5, figs. 4–6) illustrated strikingly similar leaves from the Eocene of Cape Rebrow, northwest Kamchatka, which he also referred to *E. americana*. The close similarity of these leaves to those from North America suggests the possibility of a Beringian connection; however, there is considerable overlap in patterns of venation among different genera in the family even today, and it is possible that the similarities are due to parallelism or convergence. A comparison of associated fruits is needed to assess whether the Kamchatka and Rocky Mountain species are indeed conspecific.

Oleaceae. *Fraxinus*, which occurs around the Northern Hemisphere today and is easily identified based upon its distinctive fruits, is known from the Eocene of both western and eastern North America (Call & Dilcher, 1992) and has records continuing through the Oligocene (Meyer & Manchester, 1997) and Miocene of the Pacific Northwest (Chaney & Axelrod, 1959). In Europe, fruits of *Fraxinus* are known from the lower Oligocene to Pliocene (Kirchheimer, 1957; Kvaček & Walther, in press). Asian fruit records include *Fraxinus honshuensis* Tanai & Onoe from the Late Miocene to Pliocene of Hokkaido and Honshu, Japan (Tanai, 1961), *F. stenoptera* from the lower Miocene of Orzhilansay, Turgayan Plateau (Zhilin, 1991), and *F. dayana* and *F. microcarpa* from the Miocene Shanwang flora of China (WGCP, 1978).

Palmae. *Sabal* is distributed today in southeastern North America, Central America, and the Caribbean region. It has an ancient record in North America extending back to the Campanian stage of the Upper Cretaceous based upon seeds from Big Bend, Texas (T. Lehman, E. Wheeler & S. Manchester, unpublished obs.), as well as leaves. The genus is known from seeds and foliage from the Eocene of Oregon and from foliage with epidermal preservation in the Eocene of Tennessee, etc. (Daghlian, 1978). By the Eocene this genus had become widespread in the Northern Hemisphere. It is known from seeds in the early Eocene London Clay, the late Eocene/early Oligocene Bembridge beds (Reid & Chandler, 1926), and the middle Eocene Geiseltal of Germany, as well as by leaves from the Eocene of Europe (Paris Basin and Czech Republic; Knobloch et al., 1996) and Kamchatka (Budantsev, 1979, 1994a). Its range diminished after the terminal Eocene cooling, and the genus was

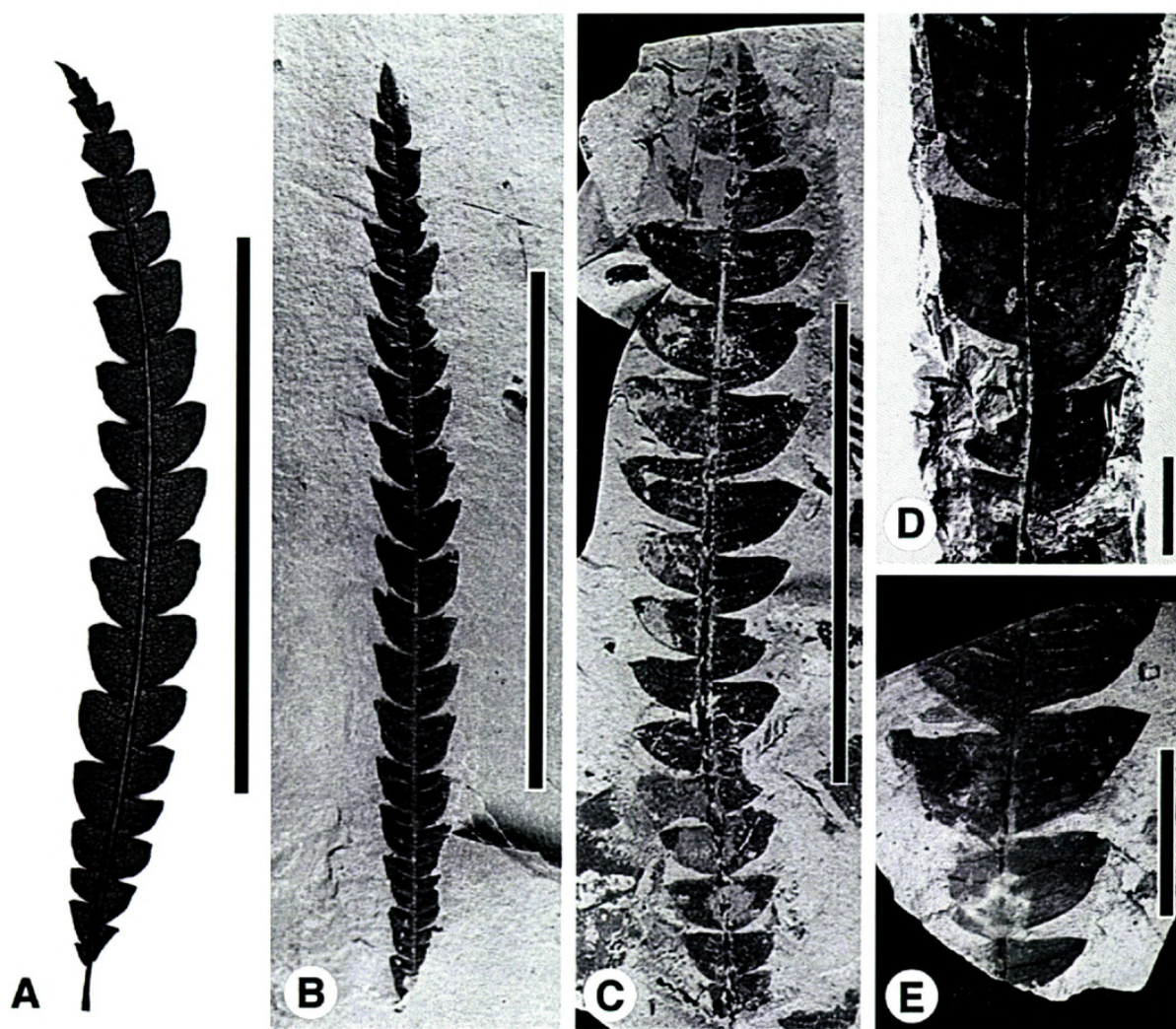


Figure 8. *Comptonia* (Myricaceae) from North America, Europe, and Asia. —A. Extant *Comptonia peregrina* (L.) Coulter from Baltimore, Maryland, FLAS 186865: *E Baltars* 1212. —B. *Comptonia* sp. from the Eocene of Yilan, China. Beijing Paleobotanical Coll. 9456. —C. *C. hesperia* Berry, Miocene of Oviatt Creek, Idaho, UF 18343–25433. —D. *Comptonia* sp. from the Eocene of Alum Bay, Gardner Coll., Natural History Museum, London, V46154. —E. *Comptonia* sp. from the Miocene of Velikaja Kema, Eastern Sikhote-Alin, Akhmetiev coll., Geol. Inst. Russ. Acad. Sci. no. 3820/801. Scale bars = 5 cm in A–C, 1 cm in D, E.

eradicated from Eurasia after the Miocene. It is known from the Miocene in Florida (Berry, 1916).

Platanaceae. The Platanaceae were already widespread in the Northern Hemisphere in the mid Cretaceous, represented mainly by palmately lobed simple leaves with palinactinodromous venation of a type that continued to be abundant during the Tertiary. Similar leaves occur today in extant *Platanus* sect. *Platanus*. Although the fruits were borne in globose infructescences, as today, the fruits of Cretaceous and some early Tertiary Platanaceae lacked dispersal hairs (Manchester, 1986; Friis et al., 1988). The occurrence of *Platanus*-like leaves in the Cenomanian of Bohemia and Kansas indicates that the Platanaceae had spread across the Northern Hemisphere long prior to the Tertiary. Leaves and infructescences attributable to modern *Platanus* occur in the Paleocene (Maslova, 1996).

Platanites is characterized by ternate leaves with a terminal leaflet that is indistinguishable from the simple leaf of extant *Platanus*, accompanied by a pair of smaller asymmetrical lateral leaflets. It occurs in the Paleocene of North America and Scotland (Crane et al., 1988; McIver & Basinger, 1993). This distribution, and its apparent absence in Asia, suggests a North Atlantic crossing during or perhaps prior to the Paleocene. Ternate-leaved Platanaceae were more common in the late Cretaceous as indicated by the occurrence of *Platanites marginatus* (Lesq.) Johnson in the Maastrichtian of Colorado, Montana, South Dakota, and North Dakota, and the segregate genus *Erlingdorfia* Johnson in the upper Maastrichtian of North Dakota, South Dakota, and Montana (Johnson, 1996). The latest known records for *Platanites* are in the Eocene of Wyoming (MacGinitie,

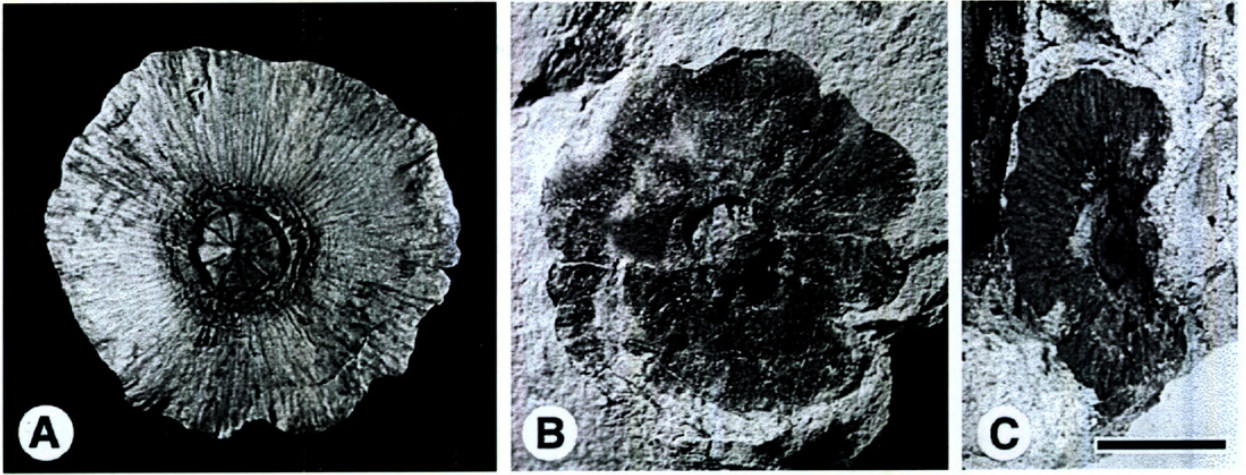


Figure 9. Fruits of extant and fossil *Paliurus* (Rhamnaceae). —A. Extant *Paliurus spina-christi* Gilan, Iran, MO 1983529; *M. L. Grant* 16425. —B. *Paliurus* sp. from the Early Eocene Wind River Formation, Wyoming, UCMP 168324. —C. *Paliurus* fruit impression, Middle or Upper Miocene Alum Bluff, Florida, UF 18048–26117. Bar = 1 cm, applies to A–C.

1974: pl. 14, fig. 1) and Oregon (John Day Gulch, UF 265–27869, 27870).

Macginitiea Wolfe & Wehr was a digitately lobed platanaceous leaf common at some localities in the upper Paleocene and Eocene of western North America (Manchester, 1986). Recently, *Macginitiea* has also been discovered in the Paleocene to Eocene of Kamchatka (Budantsev, 1996). Thus, it appears that *Macginitiea* dispersed across Beringia in the late Cretaceous and/or early Tertiary, perhaps at about the same time that *Platanites* spread across the North Atlantic bridge.

Rhamnaceae. *Paliurus*, which occurs today in southern Europe and eastern Asia, is readily recognized by its disk-winged nuts (Fig. 9A). There is remarkable convergence in general form and wing venation with fruits of the juglandaceous genus *Cyclocarya*, and this has led to some confusion in the assignment of paleobotanical specimens. However, the two genera can be readily distinguished if the fossils are well preserved. *Paliurus* fruits have a persistent perianth disk scar on the basal side of the ovary, which can be observed in fossils as a circular raised rim on the fruit body below the wing, surrounding the pedicel scar. Such a disk is lacking in *Cyclocarya*, which merely has four separate sepals near the apex. If the internal morphology is preserved, *Paliurus* can be distinguished by having two or three distinct locules. *Cyclocarya* fruits have a single locule with incomplete primary and secondary septa that frequently preserve in fossil specimens (Manchester & Dilcher, 1982; Manchester, 1987a).

Although *Paliurus* is no longer native in North America, the genus is documented by fruits as early as the early Eocene from the Wind River Formation

of Wyoming (Fig. 9B). In North America it persisted through the Miocene both in the West (Washington: Berry, 1928) and Southeast (Fig. 9C; Alum Bluff, Florida, from the locality of Berry, 1916). In Asia, the earliest fruit records are middle Eocene (e.g., Ube flora, Japan, Huzioka & Takahashi, 1970). Later records include those from the middle Miocene Shanwang flora of China (WGCPC, 1978), the late Miocene of northeast Honshu, Japan (Tsukagoshi & Suzuki, 1990), and the late Miocene of Kazakhstan (Zhilin, 1989: fig. 3b). In Europe, *Paliurus* is known from the Upper Oligocene and Miocene (Kirchheimer, 1957; Bůžek, 1971).

Rosaceae. Although Rosaceae are rare or absent in Paleocene floras, fossil foliage indicates that the family was becoming diverse in northwestern North America by the middle Eocene. Because of overlap in leaf architectural patterns among different extant genera, it is sometimes difficult to specify precise generic affinities without flowers and/or fruits. Extant *Prunus* is verified based on endocarps from the Middle Eocene of Princeton, British Columbia (Cevallos-Ferriz & Stockey, 1991), and the Clarno Formation of Oregon (Manchester, 1994b), and a diversity of rosaceous foliage is known from the Middle Eocene Republic flora of Washington (Wehr & Hopkins, 1994). *Rosa* itself is confirmed by rose hip fruits and compound leaves in the Early Oligocene of Oregon (Meyer & Manchester, 1997). The Rosaceae are well suited for a critical investigation of their phytogeographic history in the Northern Hemisphere, but such a study was not undertaken for this review.

Rubiaceae. *Emmenopterys*, endemic to China today, is represented by well-preserved infructescences, fruits, and seeds from the Eocene of Oregon

(Manchester, 1994b). *Pinckneya*, endemic to the southeastern United States today, is known from the Oligocene of Oregon based on seeds (Meyer & Manchester, 1997). An extinct genus, *Paleorubiaceophyllum* Roth & Dilcher, from the Eocene of Tennessee and Kentucky was a Rubiaceae, and showed similarities of cuticle and a distinctive adnate stipule indicating similarity with the Cinchonoidae. However, a more recently collected specimen from the Eocene of Mississippi (Bolden Clay Pit, UF 15738–27774) shows the leaves attached to a twig with alternate phyllotaxy. Extant Rubiaceae, including the genera cited as most similar to the fossil by Roth and Dilcher (1979) have opposite phyllotaxy. The significance of this discovery to the systematic position of *Paleorubiaceophyllum* requires further study.

Rutaceae. Seeds with morphology diagnostic of *Euodia*, a genus now found in tropical Africa, Asia, Australia, and the Pacific, have been recognized from the Upper Eocene of England and Miocene Brandon Lignite of Vermont (Tiffney, 1981b). Two additional genera recorded from the Brandon lignite are *Zanthoxylon* and *Phellodendron* (Tiffney, 1981a). Seeds assigned to the fossil genus *Rutaspermum* Chandler from the Eocene of Messel, Germany, share characters with extant *Zanthoxylon*, *Toddalia*, and *Euodia* (Collinson & Gregor, 1988).

Ptelea, which is endemic to North America today, appears to have been confined to this continent also during the Tertiary. Although it has been mistakenly reported in many instances of leaves and fruits in North America and Europe, the only unequivocal fruit records are a few specimens of *Ptelea enervosa* H. V. Smith from the Miocene of Idaho and Oregon (Call & Dilcher, 1995).

Sabiaceae. *Meliosma* occurs in tropical to warm temperate areas of Asia, North America, and South America today. Its distinctive endocarps are known from the late Cretaceous (Maastrichtian) of Walbeck, Germany (Knobloch & Mai, 1986), from the upper Paleocene of Gonna, Germany (Mai, 1987), from the Eocene of England (Reid & Chandler, 1933), and the Miocene to Pliocene of Germany, Poland, Italy (Martinetto, 1994, 1998), and Bulgaria (Mai & Palamarev, 1977). In North America the record of *Meliosma* endocarps extends from the latest Cretaceous and Paleocene to the Eocene (Manchester, 1994b). *Sabia* is recognized based on endocarps from the Maastrichtian of Germany (Knobloch & Mai, 1986) and from as late as the Pliocene in Alsace, France (Geissert & Gregor, 1981), and northwestern Italy (Martinetto, 1994, 1998) and from the Eocene of Oregon and Montana (Manchester, 1994b).

Sapindaceae (including Aceraceae). Schizocarpic samaras closely resembling those of extant *Acer* first occur in the late Paleocene (Crane et al., 1990), and the genus has an excellent record based on both fruits and leaves in the Eocene and later Tertiary of North America with at least 91 species (Wolfe & Tanai, 1987). The genus is also diverse in the Tertiary of eastern Asia (Tanai, 1972, 1983) and Europe (Walther, 1972; Procházka & Bůžek, 1975). Interpretations of the subgeneric ranking of fossil species are often provided in the paleobotanical literature, but usually without specifying the characters unique to the group to which the fossil species are assigned. Because *Acer* is an exceptionally diverse genus, often with more than one species occurring at a single location, it is difficult or impossible to link the isolated fruits with the isolated leaves as the same species, yet determination to extant section often requires both fruit and leaf characters. Because the fossil record of this genus is so abundant, there is potential to unravel details of the history of intercontinental exchanges through the Tertiary (Wolfe & Tanai, 1987; Kvaček, 1996); however, it is likely that only the most distinctive sections or species groups can realistically be traced. Also, the natural relationships of extant *Acer* species should be reevaluated with help from molecular studies. The early occurrences of *Acer* in North America, together with the related extinct Eocene fruit, *Deviacer* (Manchester, 1994b; Wehr, 1995), and the North American records of *Dipteronia* mentioned below, all point to North America as a possible center of origin for the “Aceraceae” clade of the Sapindaceae.

Dipteronia has one living species that is restricted to China that is readily recognized by its distinctive elliptical schizocarpic samaras (Fig. 10A). The genus has an excellent record of these fruits in North America, beginning in the late Paleocene (Hells Half Acre, Wyoming; UF 15740D–23086), and continuing through the Eocene (Fig. 10B) and early Oligocene (Meyer & Manchester, 1997). Several complete specimens from the middle Eocene of Republic, Washington, show that the fruits were borne in threes (a typical feature of Sapindaceae) rather than in pairs as in the modern species (e.g., pl. 3, fig. 8 in Wehr, 1995). Whether fruits from the other North American Tertiary occurrences were borne in threes or in pairs is unknown, but the morphology of the schizocarps leaves no question that they are closely related and belong to the same genus. The Republic specimens were sometimes placed in the sapindaceous leaf genus *Bohlenia* Wolfe & Wehr, but without attachment or repeated close association to prove the connection. A single

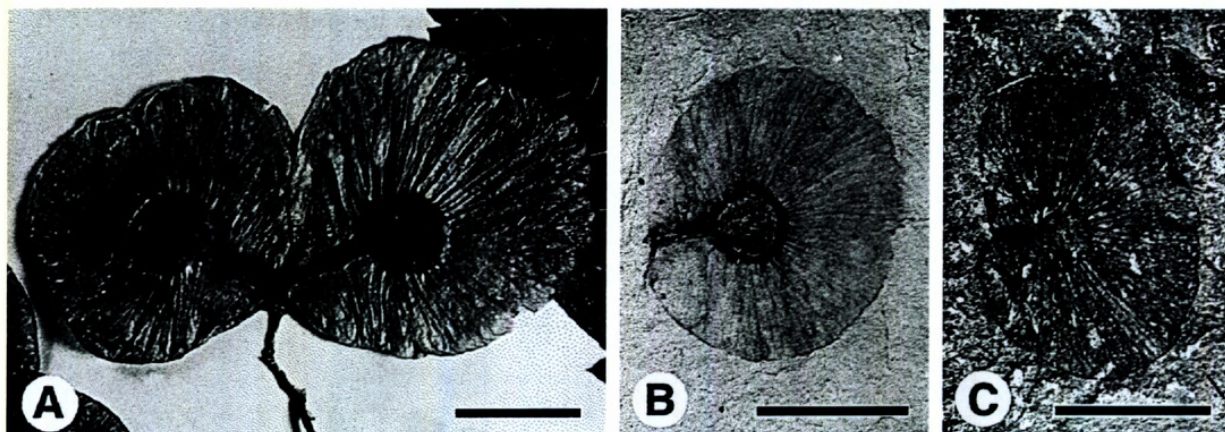


Figure 10. Fruits of *Dipteronia* (Sapindaceae/Aceraceae) from Asia and North America. —A. *Dipteronia sinensis* Oliv. from western Szechuan, China, A: E. H. Wilson 883. —B. *Dipteronia insignis* (Lesq.) Brown from the Oligocene Ruby flora, Montana, H. F. Becker Coll., YPM 35346 (orig. Becker, 1960: 393, fig. 11). —C. *Dipteronia* sp. from late Eocene Fushun flora, northeastern China, UCMP 168225. Scale bars = 1 cm.

Dipteronia fruit specimen was recovered from the late Eocene Fushun flora of northeastern China (Fig. 10C), but the genus has not been found in Europe.

Although Asian today, *Koelreuteria* is recognizable by its distinctive inflated winged capsules (Fig. 11B), which are first known in the Eocene of the Green River (Fig. 11A) and Florissant Formations of North America (Edwards, 1927; MacGinitie, 1953, 1969) and from the Oligocene (Weyland, 1937) to Miocene of Germany (Rüffle, 1963), Czech

Republic, and Hungary (Bůžek, 1971). In Asia the fruit valves are also known from the Miocene Shanwang flora of China (Hu & Chaney, 1940). In some instances fruit valves of *Craigia* (= *Pteleaecarpum*, Tiliaceae) have been mistaken for *Koelreuteria*, but they can be distinguished by the serial attachment of seeds and the complete septum. *Koelreuteria* has an incomplete septum with seeds borne at a single level within the pod.

Sargentodoxaceae. *Sargentodoxa*, which is native to China today, was recognized by Tiffney

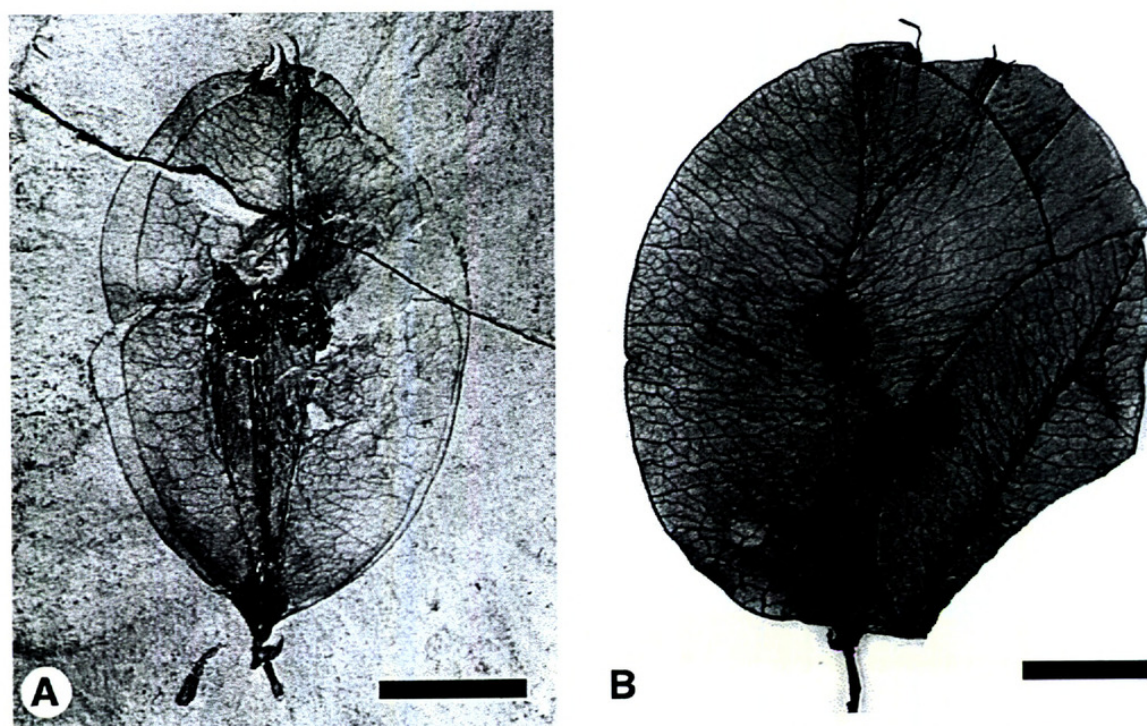


Figure 11. *Koelreuteria* (Sapindaceae) fruits. —A. *Koelreuteria nigricans* (Lesq.) Brown [*Staphylea viridifluminis* Hollick (1929, Bull. Torrey Bot. Club 56: pl 2, fig. 3)], Green River Formation, DeBeque, Colorado, YPM 20681. —B. Extant *Koelreuteria bipinnata* Franch. Cult., US National Arboretum, FLAS 186865; F. G. Meyer NA34048. Scale bars = 1 cm.

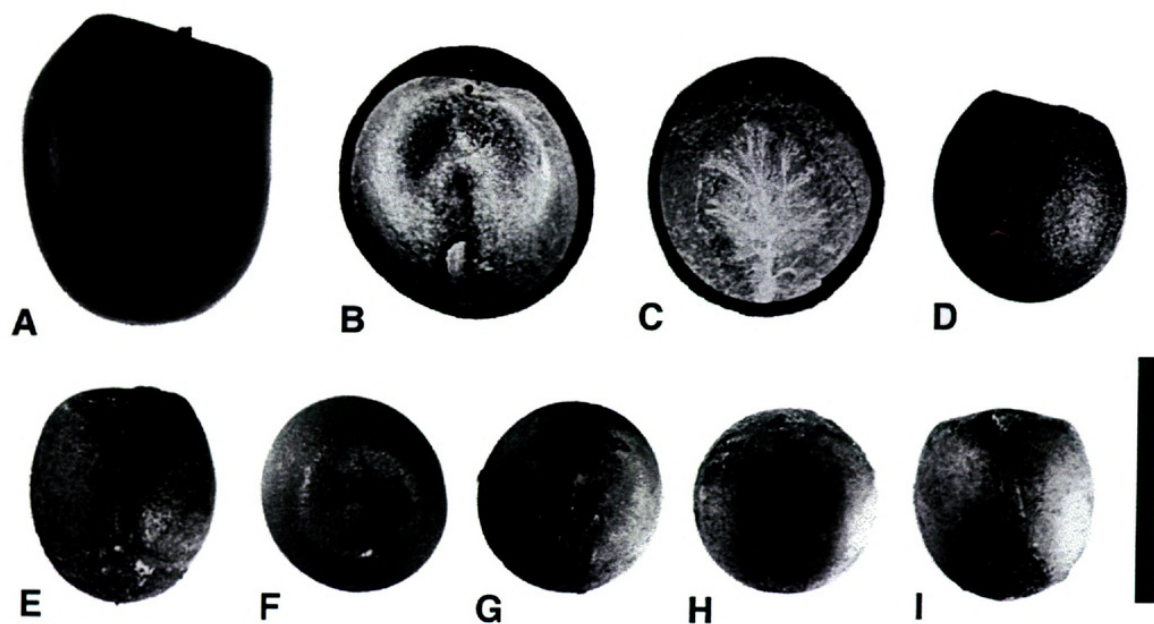


Figure 12. *Sargentodoxa* (Sargentodoxaceae) seeds from Asia and North America. A–C. Extant *Sargentodoxa cuneata* (Oliver) Rehder & Wilson from Anwei Prov., China, PE 1137193. —A. Lateral view of seed showing smooth shiny testa, hemispherical base, obliquely truncate apical surface. —B. Transversely fractured seed showing thin black seed coat at periphery. Endosperm removed, looking inside toward the apex to reveal the circular facet with micropyle at top, and raphe at bottom. —C. Looking into the basal half of the fractured seed coat, showing the radiating strands of chalaza. D–H. *Sargentodoxa globosa* (Manchester) Manchester comb. nov. from the Middle Eocene Clarno Nut Beds, Oregon. —D. Lateral view showing obliquely truncate apical surface, USNM 424663. —E. Holotype, face view, showing raphe leading between chalaza at base and hilar facet apically, USNM 424644. —F. Same as D, apical view. —G. Specimen in apical view, showing aperture through which raphe passed, USNM 424662; compare with B. —H. Basal view of a specimen showing radiating fibers of chalaza; compare with C. UF 8669. —I. Same specimen in face view, showing chalaza at base and apical facet. Scale bar = 5 mm.

(1993) from the Miocene Brandon Lignite. In addition, the seeds that I described as *Bumelia? globosa* from the middle Eocene of Oregon (Manchester, 1994b) are in reality internal seed molds of the seed coat of *Sargentodoxa*. Both *Bumelia* and *Sargentodoxa* have ovoid seeds with an oblique hilar facet and a thick seed coat; however, the distal end of *Bumelia* is pointed, whereas that of *Sargentodoxa* is more smoothly rounded. In addition, the fossil seeds match *Sargentodoxa* perfectly in the placement of the raphe, micropyle, and chalaza (Fig. 12). Accordingly, I now provide the following new combination, *Sargentodoxa globosa* (Manchester) Manchester comb. nov. (see Appendix 1).

Sargentodoxa also occurs in the uppermost Miocene-lower Pliocene Saugbagger flora of Alsace (Geissert et al., 1990), indicating that it was in Europe at least by the late Tertiary. Bruce Tiffney (pers. comm. 1997) brought to my attention that a seed identified as *Pulmonaria gossmannii* Geissert, Gregor & Mai (pl. 16, figs. 24, 25) is actually *Sargentodoxa*. However, the holotype of *Pulmonaria gossmannii* is not *Sargentodoxa*.

Schisandraceae. *Schisandra*, with 1 extant species in eastern North America and about 24 in Asia, is known from fossil seeds in the Eocene of

Oregon (Manchester, 1994b), Miocene of western Czech Republic (Bůžek et al., 1996), and Pliocene of Alsace, France (Gregor, 1981).

Simaroubaceae. *Ailanthus* has distinctive winged fruits that are both easily recognized (Fig. 13A) and readily preserved in lacustrine deposits where leaves are preserved. Although distributed from western China to Korea and in Australia today, the genus was widespread in the Tertiary of the Northern Hemisphere (Tralau, 1963). *Ailanthus* fruits are present in the Middle Eocene of Messel, Germany (Collinson, 1988), as well as the Oligocene of France, Hungary (Rásky, 1956), the Oligocene to early Miocene in the western Czech Republic (Knobloch & Kvaček, 1993; Kvaček, 1996), and the middle Miocene of the Randecker Crater (Rüffle, 1963). In Asia, the fruits occur in the early Oligocene of Kiin Kerish, Kazakhstan (Akhmetiev, 1991), from the Eocene/Oligocene of Fushun (WGCPC, 1978), and the Miocene of Shangwang, China (Hu & Chaney, 1940; WGCPC, 1978), Velika Kema, Sikhote Alin (Fig. 13C), and Shanabuchi, Northeastern Hokkaido, Japan (Tanai & Suzuki, 1965). In North America, *Ailanthus* samaras are known from the Eocene of Colorado, Wyoming (MacGinitie, 1969), Montana (Becker, 1961),

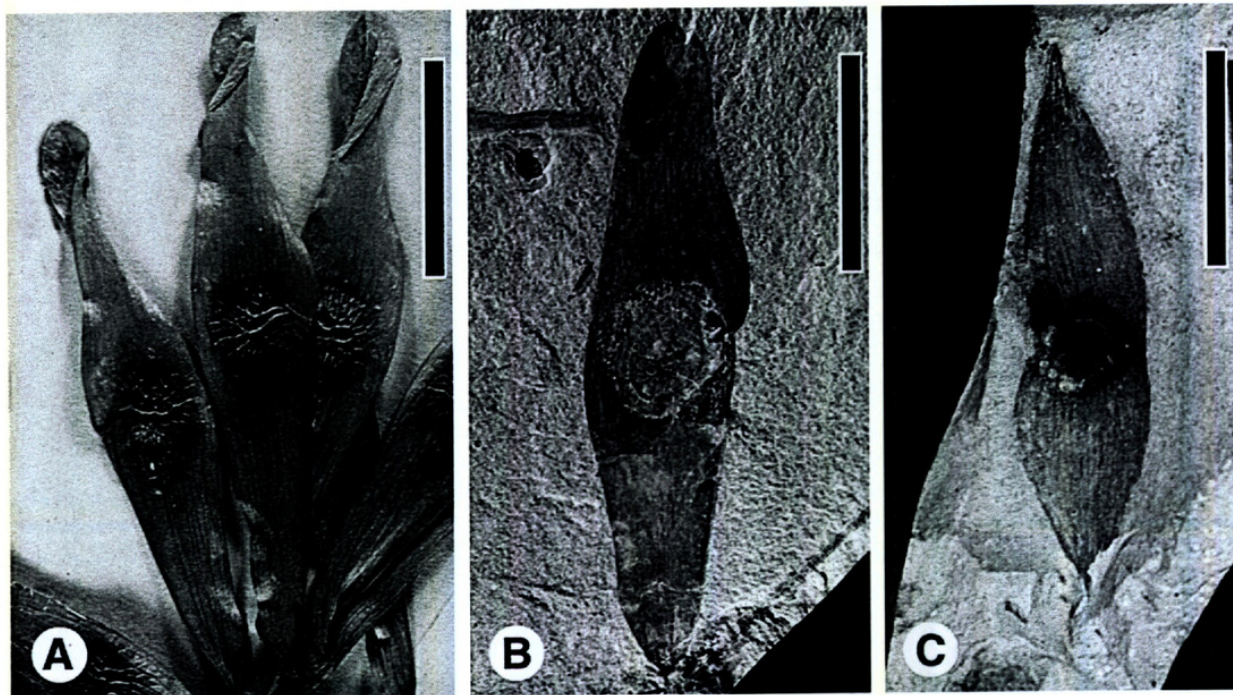


Figure 13. *Ailanthus* (Simaroubaceae) samaras from Asia and North America. —A. Extant *Ailanthus* sp. Chekiang, China, MO 1897584. —B. *Ailanthus* sp. from the late Eocene of Teater Road, Oregon. UF 256–20713. —C. *Ailanthus* sp. from the Miocene of Velikaja Kema, Eastern Sikhote-Alin, Akhmetiev Coll., Geol. Inst. Russ. Acad. Sci. no. 3820/594. Scale bars = 1 cm.

Oregon (Fig. 13B), and California (MacGinitie, 1941), and from the Miocene of Oregon and Idaho (Chaney & Axelrod, 1959; Fields, 1996).

Staphyleaceae. *Turpinia*, distributed today from Indomalesia to Japan and in tropical America, is known on the basis of seeds from the Miocene of Vermont (Tiffney, 1979) and central Europe (Mai, 1964). *Tapiscia*, which occurs today in the mixed mesophytic forests of China, has distinctive fruits and seeds (Fig. 14A, B) that are known as fossils from the Eocene of England (Fig. 14E, F), Germany (Mai, 1980), and Oregon (Fig. 14C, D; Manchester, 1988, 1994b). The extant Caribbean genus *Huerteia* has seeds similar to, but larger than those of *Tapiscia* (Manchester, 1988), and may be an indication of former exchange between the Caribbean and North America during the Tertiary.

Styracaceae. *Halesia* has extant five species in eastern China and eastern North America. The trees bear fruits with longitudinal wings (usually two or four) that radiate from a spindle-shaped fruit body. Fruits of this genus have been reported from the North American Tertiary (e.g., Brown, 1946a; Lakhanpal, 1958); however, those occurrences do not represent *Halesia* and are probably not even Styracaceae because they lack the diagnostic thick intramarginal vein seen on each of the fruit wings in this genus. Although no longer native to Europe, the genus is well represented by anatomically preserved endocarps in the European Tertiary (Kir-

chheimer, 1957). Tralau (1965) illustrated particularly well-preserved specimens from the upper Pliocene of Weilerswist, western Germany, with intact wings showing the characteristic intramarginal veins.

Symplocaceae. *Symplocos* is disjunct today between the Old World (excluding Africa) and tropical America. Characteristic fruits occur in the Eocene of Oregon (Manchester, 1994b), California (Tiffney & Haggard, 1996: 41), and Virginia (Tiffney, in press) and the Miocene of Vermont (Tiffney, 1977a). They are especially well represented in the Tertiary of Europe, ranging from the early Eocene (Reid & Chandler, 1933) through the Pliocene with several morphologically distinct species (Kirchheimer, 1950, 1957; Mai, 1995). Also in the European Tertiary are two extinct genera that fit in the Symplocaceae based on fruit morphology: *Palliopora* Kirchheimer and *Sphenotheca* Kirchheimer (Kirchheimer, 1957). In Japan, fruits are known from the upper Pliocene (fig. 9J in Miki, 1937). On the basis of paleopalynology, Krutzsch (1989) provided a summary of the fossil record of Symplocaceae, interpreted to show an upper Cretaceous origin in North America, followed by Paleocene spread across the North Atlantic into Europe, late Eocene arrival in Asia, survival of a European population into the Pliocene, and the southward extension of the genus into the Caribbean and South America, and to the South Pacific during the Pliocene.

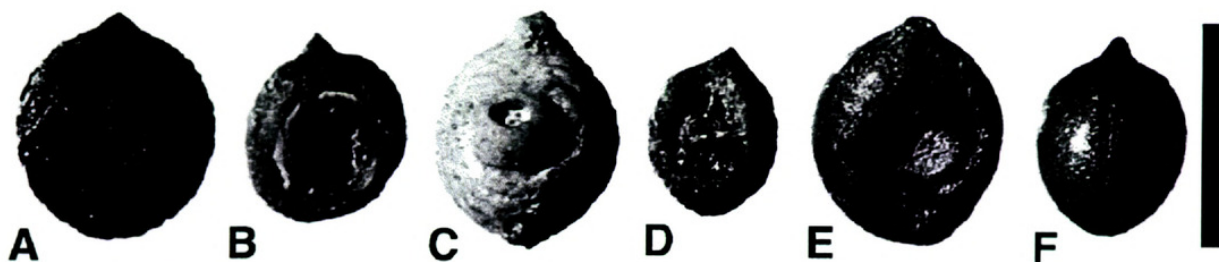


Figure 14. *Tapiscia* (Staphyleaceae) fruits and seeds. —A, B. Fruit and seed from extant *Tapiscia sinensis* Oliv. western Hupeh, China, A: E. H. Wilson 108. —C, D. *T. occidentalis* Manchester silica casts of fruit and seed, Middle Eocene Clarno Nut Beds, Oregon. UF 5201, 5205. —E, F. *T. pusilla* (Reid & Chandler) Mai pyrite seed casts, Early Eocene London Clay, England. Scale bar = 5 mm.

Theaceae. *Gordonia*, with about 30 species in tropical and subtropical Asia and one disjunct species in southeastern North America, has distinctive pentalocular, loculicidally dehiscent capsules and winged seeds. It is well represented in the Eocene of southeastern North America by fruits and seeds and in the Miocene of Idaho by seeds (Grote & Dilcher, 1992). *Gordonia* is also well represented in the Eocene to late Miocene of Europe, sometimes attributed to the segregate genus *Polyspora* (Gregor, 1978; Grote & Dilcher, 1992; Mai, 1995). Related extinct fruit genera, including *Andrewsiocarpus* Grote & Dilcher (1989) and *Gordoniopsis* Grote & Dilcher (1992) show that this family was diverse in the Eocene of Tennessee and Kentucky. Extant *Cleyera*, disjunct between Asia and tropical America, has fossil seed records in the Eocene of western North America (Manchester, 1994b) and in the Eocene to Miocene of Europe (Friis, 1985).

Trapaceae. *Trapa* is an aquatic plant with distinctive spiny fruits that grows today in central and southeastern Europe, temperate and tropical Asia, and Africa. Although absent from North America today, the genus is confirmed on the basis of fruits from the Late Oligocene/Early Miocene Weaverville flora of California (Tiffney, pers. comm. 1998), the Miocene of Idaho (Brown, 1937), and the Pliocene Red Bluff flora (Citronelle Formation) of Alabama (Berry, 1914). In Europe, fruits of *Trapa* first occur in the Middle Miocene and continue through the Neogene to the present day (Mai, 1985b, 1995; Wójcicki & Bajzáth, 1997).

Fruits remarkably similar in size and morphology to those of extant *Trapa* occur as early as the Late Cretaceous (Maastrichtian) in Far Eastern Russia (Golovneva, 1991). They differ from the modern species in being borne in a raceme rather than isolated and were therefore placed by Golovneva in the extinct genus *Palaeotrapa* Golovneva. If this may be taken as a direct predecessor of *Trapa*, then the lineage would appear to have its roots in Asia. Later records include fruits from the Pliocene of

Japan (Miki, 1952). Despite the apparent antiquity of *Trapa* in Asia, the genus apparently did not spread to Europe or North America until the Neogene (Mai, 1985b). Certainly in Europe it would be expected to be found earlier if it were present, because of the numerous lignitic deposits favorable for preservation of hard aquatic fruits. Although the genus has sometimes been reported on the basis of rosettes of aquatic leaves (e.g., Brown, 1962), these are only superficially similar to those of *Trapa* and are now placed in a fossil genus (*Quereuxia*; see incertae sedis discussion) of unknown familial affinity.

Trochodendraceae. This family includes the extant Asian vesselless genera *Trochodendron* and *Tetracentron*. *Trochodendron* is known based on fossil fruiting racemes from the Eocene of Washington (Wehr, 1995), the Miocene of Idaho and Oregon (Manchester et al., 1991; Fields, 1996: 304–307), and the Miocene of Kamchatka (Chelebaeva & Chigayeva, 1988) and Japan (Manchester et al., 1991). Wolfe (1989) illustrated and discussed leaves of an extinct trochodendraceous morphology from the middle Eocene of Republic, Washington. The leaves resemble those of extant *Trochodendron* in thick texture (probably evergreen) and small appressed teeth typically confined to the apical half of the lamina, but they differ from leaves of the single extant species of the genus by having palmate venation, a possible primitive feature shared with extant *Tetracentron* (Wolfe, 1989). The subsequent discovery of *Trochodendron* fruits and infructescences from the same locality (Wehr, 1995) leads to the hypothesis that these organs were produced by the same genus, namely *Trochodendron*, but by an extinct species that retained some primitive foliar characters.

Nordenskiöldia Heer is an extinct genus based on fruits and infructescences that were widespread in the Paleocene of the Northern Hemisphere. It is also known from the Upper Cretaceous in Asia and North America and from the Miocene of Idaho, in

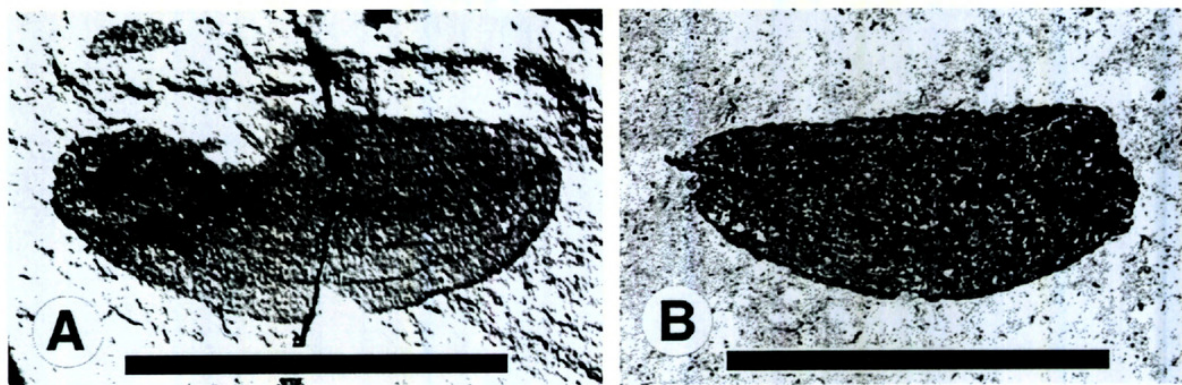


Figure 15. *Cedrelospermum* (Ulmaceae) fruits from North America and Europe. —A. *C. nervosum*, White Cliffs, Clarno Formation, Oregon, UF262–17733. —B. *C. leptospermum*, Messel, Germany, SM.B. Me 7274. Scale Bars = 5 mm.

each case associated with leaves of the “*Cocculus* type” assignable to *Ziziphoides* Seward & Conway (Crane et al., 1991). The trochodendraceous affinities of *Nordenskioldia*, first suggested by Kryzstofovich (1958), were corroborated by Crane et al. (1991), on the basis of anatomically preserved fruits and vesselless xylem of the fruiting axis and associated twigs. *Nordenskioldia* was already established in the Late Cretaceous of North America (Serbet, 1997) and Asia (Senonian of Velui River, Vakrameev, 1958) and had become widespread in northern latitudes of North America, Europe, and Asia by the Paleocene. It was evidently extinct in most areas by the Eocene, but it occurs in the middle Eocene of Washington (Wehr, 1995), and is abundant in the Miocene of Washington and Idaho (Manchester et al., 1991).

Ulmaceae. The Ulmaceae are well represented in the fossil record (Manchester, 1987b). This family is represented in the North American fossil record by both subfamilies: Ulmoideae (*Ulmus*, *Cedrelospermum*, maybe *Zelkova*) and Celtidoideae (*Aphananthe*, *Celtis*). The extant endemic of eastern North America, *Planera*, has been reported from time to time in the literature on fossil leaves of Europe and North America, but none of these are particularly convincing.

Ulmus occurs today in North Temperate areas. Leaves that compare favorably with this genus are common in the Paleocene of the Northern Hemisphere at sites in North America, Greenland, Spitzbergen, and Asia. However, the distinctive winged fruits of *Ulmus* have never been found in association. Although the Paleocene leaves certainly are correctly placed in Ulmaceae (short petioles, asymmetrical lamina, blunt teeth with submedial entry of principal vein), the lack of associated *Ulmus* fruits suggests that they belong to another, possibly extinct, genus of the family. I concur with Kvaček et al. (1994: 116) who noted in reference to spec-

imens from the Paleogene of Spitzbergen that “until associated fruits are recovered to help identify the generic affinity, we suggest that a fossil genus is used . . .” The name *Ulmites* Dawson is applied in this context (Kvaček et al., 1994). *Ulmites* was spread widely in the Northern Hemisphere by the Paleocene.

Ulmus itself makes its first appearance based on fruits during the Eocene with occurrences in the west-coastal part of North America including California, Oregon, Washington, and British Columbia (Manchester, 1989b). These oldest fruits have narrow wings similar to those of extant section *Chaetoptelea* (e.g., *Ulmus mexicana* and *U. alata*). A rare specimen from One Mile Creek, British Columbia, shows the fruits attached to a foliage-bearing twig (Manchester, 1989b).

Cedrelospermum is an extinct genus of Ulmaceae. Although first described based upon isolated fruits like those in Figure 15, the genus is now known from twigs with attached leaves, fruits, and flowers (Manchester, 1989a). The oldest known fruits and leaves are from the Middle Eocene both in western North America (Green River Formation, Clarno Formation) and Europe (Messel, Germany). In North America the genus persists until the Oligocene in Texas (Manchester, 1989a) and to the Oligocene or Miocene of southern Mexico (Magallón-Puebla & Cevallos-Ferriz, 1994c). But in Europe the genus survived to the middle Miocene. The absence of the distinctive fruits and leaves in any of the known Asian Tertiary floras indicates that it did not cross Beringia and did not penetrate eastward beyond the Urals.

It is interesting to note similarities and differences in apparent evolutionary trends between the European and North American populations of *Cedrelospermum*. Both in North America and in Europe, the smallest fruits (5–7 mm) occur in the oldest localities, and the largest ones occur in the

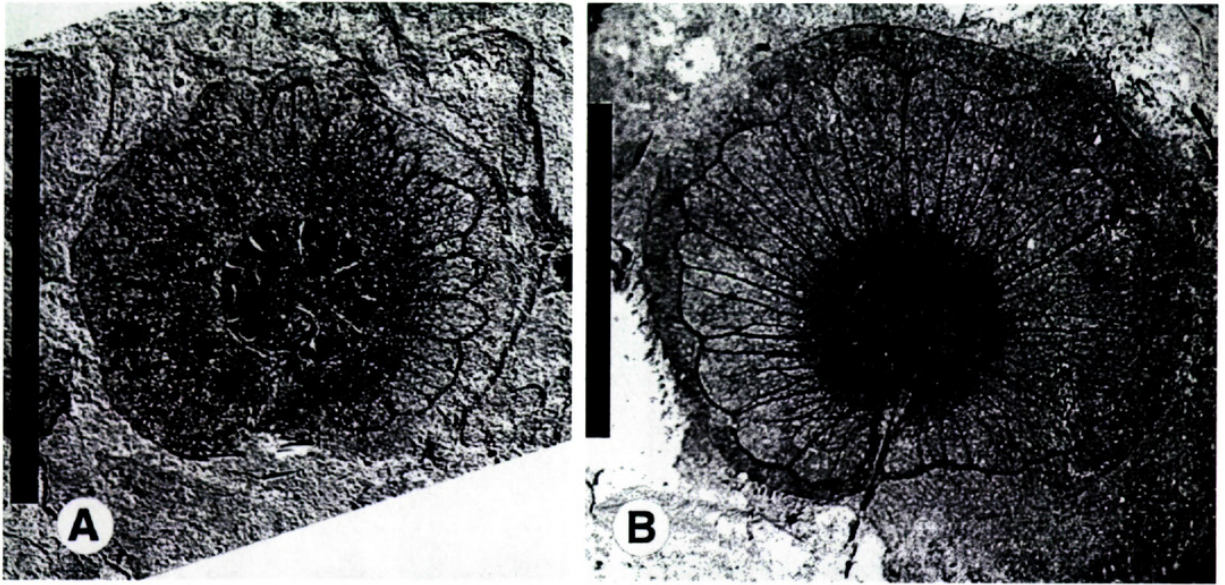


Figure 16. *Buzekia tertiaria* (Weyland) comb. nov. from the Tertiary of central Europe and western North America. —A. Specimen from the late Oligocene of Rott, Germany. Köln coll. Weyland no. 1773. —B. Specimen with identical morphology and venation from the middle Miocene of Oviatt Creek flora, Idaho, UF 18343. Scale bars = 1 cm.

youngest localities. In Europe, all observed specimens are consistent in having a single wing with a distal stigmatic notch. In the Oligocene to Miocene of North America the normal condition is to have two wings, one of them large and comparable in venation to the single wing of the European species, and a second, small vestigial wing (Manchester, 1987b). However, in the middle Eocene of North America there is variation from forms with a single wing resembling the European species, to those with two wings, of the type found later in North America. This greater variability in the North American Eocene forms may indicate that the original populations were more plastic, and that after separation of the two geographic areas, the European and American populations became canalized in different morphological patterns.

INCERTAE SEDIS

Buzekia gen. nov. (see Appendix 1 for generic diagnosis) is a distinctive winged fruit of uncertain affinities that was formerly placed provisionally in the extant legume genus *Pterocarpus* (Weyland, 1937; Bůžek, 1992). *Buzekia tertiaria* (Weyland) Manchester comb. nov. (see Appendix 1) is well known from the late Oligocene and early Miocene of central Europe (Fig. 16A) and has recently been recovered from the middle Miocene of Idaho (Fig. 16B).

A propeller-like fruit with an elongate body and six epigynous wings was named *Calycites ardtunensis* by Crane (1988). Occurrences in the Paleocene of Scotland (Crane, 1988; Boulter & Kvaček, 1989)

and Wyoming (Crane, 1988) indicate a likely North Atlantic crossing. In North America, the fruits persist into the middle Eocene of the Clarno Formation, Oregon, and Republic, Washington (Crane, 1988; Wehr, 1995: pl. 5, fig. 5).

Distinctive reniform, lenticular, sometimes paired, verrucate-walled objects known as *Porosia* Hickey (1977) are present in the late Cretaceous and Paleocene of the Rocky Mountains (Fig. 17B, C; Brown, 1962, as *Hydromystria*; Hickey, 1977; McIver & Basinger, 1993; Crane et al., 1990), and in the Paleocene of the Amur region, southeastern Russia (Fig. 17A; Krassilov, 1973: pl. 23, figs. 49–61; 1976: pl. 12, figs. 1–6, as *Limnobiophyllum*), the Koryak highland of northeastern Russia (Golovneva, 1994: pl. 27, figs. 4–6, as *Limnobiophyllum*), and eastern Kazakhstan (Akhmetiev & Chelebaeva, 1989: figs. 5, 6, as *Limnobiophyllum*). They are also known from the Paleocene or early Eocene Pilot Rock flora, Oregon (Fig. 17D; Gordon, 1985: fig. 3d). *Porosia* is unknown from Europe and thus seems to be a good example of a taxon that dispersed across Beringia during the Late Cretaceous or Paleocene.

When Krassilov (1976) erected the genus *Limnobiophyllum*, he illustrated it with specimens of *Porosia* (sensu Hickey, 1977), but he based the genus on *Lemna* (*Spiradela*) *scutata* Dawson, a species with thin, orbicular leaves now known to be an extinct genus of lemnaceous affinity (Kvaček, 1995; Stockey et al., 1997). The former hypothesis that *Porosia verrucosa* represented float leaves produced by the same plant as *Limnobiophyllum* (Krassilov,

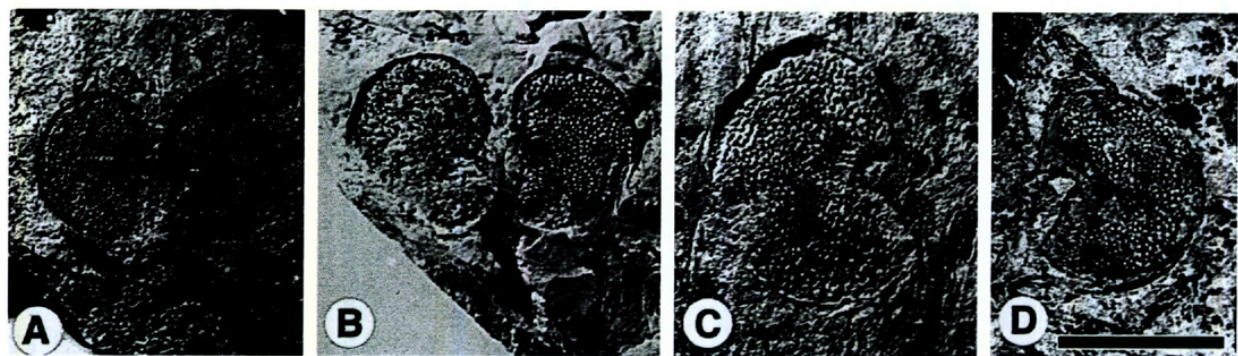


Figure 17. *Porosia verrucosa* (Lesquereux) Hickey from the Paleocene of eastern Asia and North America. —A. Pair of fruits from Belagory, Amur District, Russia, UF 18650–27771. —B. Pair of fruits on peduncle, East Fork, Razor Creek, Montana, UF 18163–25934. —C. Individual fruit showing verrucate texture, Linch, Wyoming, UF 18260–15023. —D. Similar specimen from Late Paleocene or Early Eocene Herron Formation, Pilot Rock (Denning Spring), Oregon, UF 271–27772. Scale bar = 1 cm, applies to A–D.

1976) resulted in use of the same name for two plants now considered to be unrelated. However, that hypothesis remains unsubstantiated, and the lack of *Porosia* in co-occurrence with the *Limnobiophyllum* at European localities casts doubt on their affiliation. Analysis of silicified *Porosia* specimens from the Maastrichtian of Alberta (Aulenback & Braman, 1991) has led some workers to the conclusion that these are fruits, rather than leaves (McIver & Basinger, 1993; Serbet, 1997), as Lesquereux (1878) originally supposed. Cuticularly preserved specimens from the lower Paleocene middle part of the Tsugayan Formation near the confluence of the Dermakon and Bureya Rivers of Amur District, southeastern Russia, provide useful epidermal information for *Porana* (Krassilov, 1973, 1976, as *Limnobiophyllum*). Krassilov (1973) described them as epistomatic leaf blades with rare stomata, the guard cells and lateral subsidiary cells thinly cutinized, sunken in a pit formed by polar subsidiary cells and encircling cells, and scattered simple short conical trichomes. Krassilov noted that this cuticular structure is distinct from that of Hydrocharitaceae, Nymphaeaceae, and Lemnaceae, and more comparable to the stomatal complexes present in several extant araceous genera.

Quereuxia Kryshstofovich ex Nevolina (syn. *Trapago* McIver & Basinger) is an extinct genus of floating aquatic plant with rosettes of simple and compound leaves with up to nine or eleven obovate serrated leaflets (Fig. 18). It occurs in the late Cretaceous and Paleocene of both North America and eastern Russia (Kryshstofovich, 1953). Some confusion has surrounded the name of this plant because *Quereuxia* was first published invalidly (Kryshstofovich, 1958, provided no diagnosis, hence creating a nomen nudum). Therefore, McIver and Basinger (1993) proposed a new name, *Trapago*, for the genus. However, in the intervening years, Nev-

olina (1977) had validated *Quereuxia* by providing a diagnosis and designating *Q. angulata* as the type species. I thank Leo Hickey for his help in unravelling the complex nomenclatural history of this taxon. The Russian occurrences were recently reviewed (Samilina, 1988; Golovneva, 1991), and a suite of relatively complete vegetative plants was described in detail from the Cretaceous of Alberta, Canada (Stockey & Rothwell, 1997). The North American representatives were sometimes misplaced in *Trapa* (Brown, 1962), but the affinities with that genus are only superficial (McIver & Basinger, 1993; Stockey & Rothwell, 1997). Although *Quereuxia* is shared between North America and Asia during the late Cretaceous and Paleocene, it is unknown from the European Tertiary and appears to have become extinct by the end of the Paleocene.

PATTERNS

The modern flora of North America is the result of evolution, immigration, and extinction of numerous taxa during a period when angiosperms had become dominant in all but the highest elevations and latitudes. Although some of the extant genera indigenous to North America have fossil records that can be traced to the Cretaceous, most have their first known records in the Tertiary.

During any given time interval, the genera found in North America can be classified into one of four main patterns of geographic distribution (Fig. 20): (1) Circumboreal, with species in Asia, North America, and Europe (usually also Greenland and Spitsbergen; Fig. 20A); (2) Euro-North American, with species found in North America and Europe (Fig. 20B); (3) Amer-Asian, with species shared between North America and Asia (Fig. 20C); and (4) North American endemics (Fig. 20D), those not known to be present in the other regions. All of

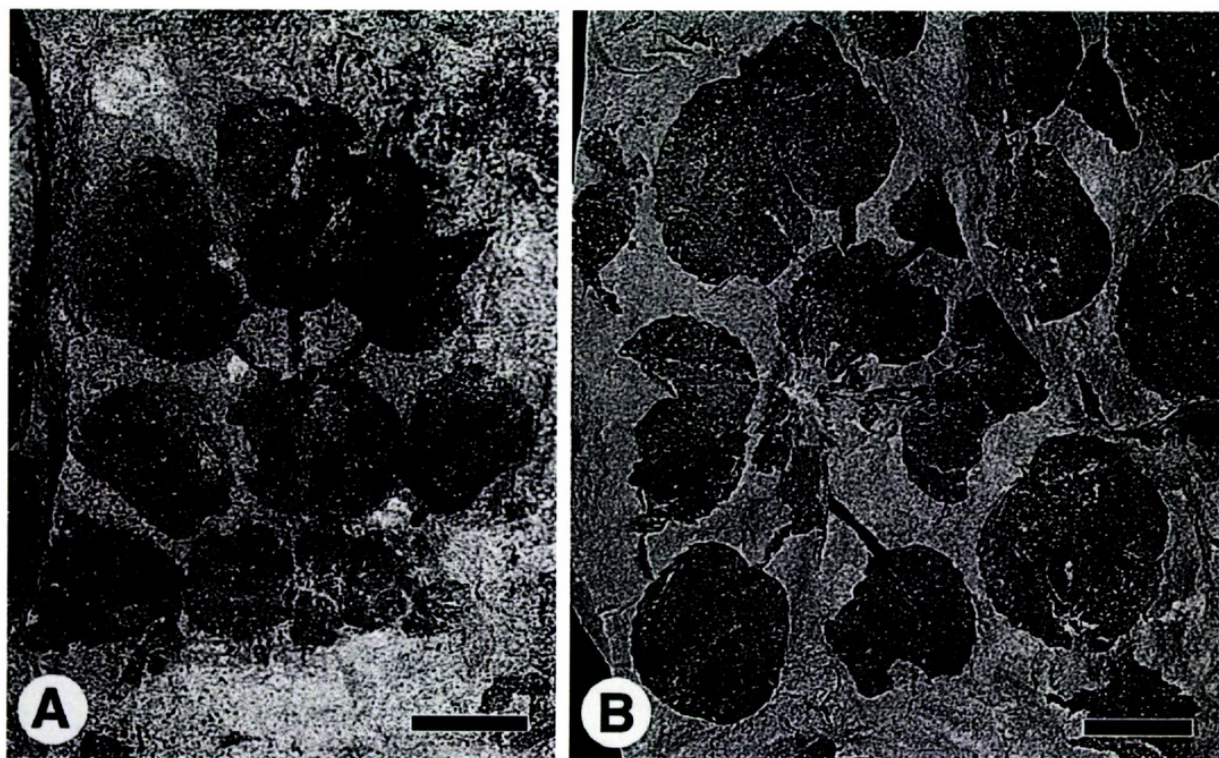


Figure 18. *Quereuxia angulata* (Newberry) Kryshstofovich from the Paleocene of Asia and North America. —A. Rosette of several leaves from Raritkin Series, Koryak Upland, northeastern Russia, Golovneva 90–642. —B. Similar specimen from the Fort Union Formation, Black Buttes, Wyoming, UF 15886–14176. Scale bars = 1 cm.

these patterns occur in each of the Tertiary epochs, but the proportion of taxa in each category differs from one epoch to the next. During the Eocene, for example, pattern 2 predominates, whereas in the Miocene, pattern 1 is the strongest. Other patterns exist that do not include North America (e.g., taxa shared between Europe and Asia, but not North America, and those endemic to Europe or Asia) but are outside the charge and scope of this article. For this overview, comparisons have been made at the generic level. Analysis at the species level is reasonable only in the case of those genera whose fossilized organs preserve characters sufficient to permit the morphological distinction of species using criteria comparable to those used to distinguish modern species in related extant genera.

The stratigraphic and modern distributions of selected genera are summarized graphically in the summary chart (Fig. 19) and in Figures 21–25. By comparing the stratigraphic ranges of genera within different landmasses, it is possible to infer likely routes and timing of intercontinental dispersals of different taxa. Caution must be exercised in evaluating the data, because the apparent absence of a taxon from a particular time interval and/or region may be due to absence of comparable fossiliferous strata or less thorough sampling. For example, Pliocene paleobotanical localities are rare in North America but common in Europe and Ja-

pan; thus the ranges of many North American taxa appear to end in the Miocene. However, in cases of genera with Miocene records in North America that are still living in North America today, I plot the range to include the intervening Plio-Pleistocene.

PALEOCENE

Paleocene floras of Wyoming, Montana, North Dakota, Alberta, and Saskatchewan are dominated by deciduous taxa of Taxodiaceae, Ginkgoaceae, Platanaceae, Cercidiphyllaceae, Trochodendraceae, Betulaceae, and Juglandaceae. Other common elements include Cupressaceae, Lauraceae, Zingiberaceae, and aquatic plants of the Araceae/Lemnaceae (Brown, 1962; Crane et al., 1990; McIver & Basinger, 1993; Stockey et al., 1997). Many of the genera are shared with other Paleocene floras of the Northern Hemisphere. Figure 21 shows three genera that were circumboreal during the Paleocene, with records in North America, Europe, Greenland, and Asia: *Nordenskioldia*, *Nyssidium*, and *Palaeocarpinus*. The first two were already present in North America and Asia by the Maastrichtian, so their distribution in the Paleocene may be simply a function of earlier history. A similar situation is apparent for *Metasequoia*, *Glyptostrobus*, and *Platanus*. The distribution of *Palaeocarpinus*, however,

suggests that overland passage was possible across Europe, North America, and Asia during the Paleocene. "Paleocene endemics" of North America (i.e., taxa not known from other continents at that time) include *Cranea*, *Cyclocarya*, and *Polyptera* Manchester & Dilcher (Fig. 22). *Cranea* and *Polyptera* apparently became extinct without spreading to other continents, whereas *Cyclocarya* subsequently appeared in Europe and Asia and remains today in China.

There is some evidence of provinciality during the Paleocene. Several genera of the North American Paleocene are shared with the Asian Paleocene, but apparently are lacking in the Paleocene of Greenland, Spitsbergen, and Europe (examples in Fig. 23): *Amersinia*, *Fokieniopsis*, *Limnobiophyllum*, *Macginitiea*, *Porosia*, and *Quereuxia*. This suggests probable continuity via Beringia. There are also some genera shared between North America and Europe during the Paleocene that are unknown in the Asian Paleocene (Figs. 24, 25): *Calycite ardtunensis*, *Fagopsiphyllum*, *Meliosma*, and *Platanites*.

Geophysical data have been interpreted to indicate that both the Beringial and North Atlantic corridors were present during the Paleocene (Tiffney, 1985b). However, Woodburne and Swisher (1995: 338) indicated that intracontinental overland interchange of mammals involving North America was minor during the Paleocene except in the latest part of the epoch. They inferred that the first important land mammal migration episode of the Tertiary occurred during the Clarkforkian, with the introduction of mammalian taxa of both European and Asian origin.

Paleobotanical evidence for late Paleocene/early Eocene exchange across the North Atlantic derives from the occurrence of fruit and seed taxa in the early Eocene London Clay flora (Reid & Chandler, 1933; Chandler, 1961; Collinson, 1983) that are also known from the late Paleocene (Clarkforkian) of the Rocky Mountain and Great Plains regions. Examples include *Cornus* (cornelian cherry group), *Juglandicarya cantia* Reid & Chandler (similar to *J. simplicarpa* of North America), *Langtonia* Reid & Chandler (Tiffney & Haggard, 1996), and *Meliosma* sect. *Kingsboroughia* (Van Beusekom, 1971; Crane et al., 1990). *Platycarya* may also conform to this pattern, being known from pollen in the Paleocene Reading Beds of England and some sites in the Rocky Mountain region (Wing, 1984) and confirmed on the basis of infructescences and fruits in the early Eocene of both regions.

EOCENE

The Eocene was the longest epoch of the Tertiary (ca. 21 million years), about twice as long as the Paleocene. This was an especially important interval in the history of the North American flora, during which climate reached the warmest conditions of the Tertiary. With the addition of genera suited to warmer climate, floras of the Eocene became more diverse than those of the Paleocene. All of the dicotyledonous families common in the North American Paleocene persisted into the Eocene, and many underwent further radiation producing both extinct and extant genera.

Woodburne and Swisher (1995) recognized three mammalian faunal interchange "events" during the Eocene. The first, in the Early Eocene (Wasatchian), is a major overland dispersal between North America and western Europe, with greater generic similarity between the faunas of North America and western Europe than any time in the Cenozoic before or since (McKenna, 1975; Woodburne & Swisher, 1995). The second, during the Middle Eocene (Late Uintan), records an influx of probable Asian immigrants (Woodburne & Swisher, 1995). The third interchange interval, during the Late Eocene (Chadronian), involves fewer taxa, but also appears to indicate exchange across Beringia. Through the early and middle Eocene, similarities between the flora of western North America and western to central Europe became very pronounced with numerous shared genera, including both thermophilic and mesophytic elements. Some taxa were also shared between the Eocene of North America and Asia, but most of these seem to be holdovers from the Paleocene, rather than new appearances (examples: *Fagopsiphyllum* gen. nov., *Ginkgo*, *Nordenskioldia* Heer, *Nyssidium* Heer, *Palaeocarpinus* Crane, and *Platanus*). A few newly appearing genera that were shared between the Eocene of Asia and North America include *Craigia*, *Eucommia*, and *Paliurus*. In general, the Asian Eocene flora appears to lack the diversity of thermophilic elements such as Icacinaceae and Menispermaceae observed in North America and Europe. It remains possible that the apparent dissimilarity of the floras results from fewer sampled sites in Asia and the lack of rich fruit and seed assemblages there for comparison with those in Europe and North America.

It is noteworthy that the Aceraceae, Betulaceae, Cercidiphyllaceae, Icacinaceae, Menispermaceae, Pinaceae, Taxodiaceae, and Vitaceae, which are common in western North American Eocene localities, are lacking from the Eocene of southeastern

Genus	Stratigraphic and Geographic Distribution							Comments
	K	PA	EO	OL	MI	PL	RE	
<i>Acer</i>		NA	NA AS	NA EU AS	NA EU AS	> EU AS	NA EU AS	Paleogene Beringial crossing; subsequent arrival in Europe.
<i>Actinidia</i>			NA	EU	EU	EU	AS	Asian endemic today with Euramerican Tertiary record.
<i>Ailanthus</i>			NA EU AS	EU AS	NA EU AS	EU AS	AS	Now native from Asia to Australia; formerly widespread in Northern Hemisphere.
<i>Alangium</i>			NA EU	EU	NA EU	EU AS	AS	Now native in Asia and Africa, once common in Europe and N Amer. Ignore leaf reports.
<i>Alnus</i>			NA EU AS	NA EU AS	NA EU AS	NA EU AS	NA EU AS	These ranges are plotted based on the diagnostic woody infructescences.
<i>Amentotaxus</i>	NA	NA EU	NA EU	> >	NA EU		AS	Paleogene North Atlantic crossing; subsequent arrival in Asia.
<i>Amersinia</i>		NA AS						Eocene Beringial crossing; absent from Europe.
<i>Anamirta</i>			NA				AS	Tertiary Beringial crossing.
<i>Betula</i>		AS	NA	NA EU AS	NA EU AS	NA EU AS	NA EU AS	Occurrences confirmed from diagnostic trilobate inflores- cence bracts.
<i>Buzekia</i>				EU	NA EU			Possible middle or late Tertiary Beringial crossing.
<i>Calycites ardtunensis</i>		NA EU	NA					North Atlantic crosser.
<i>Carya</i>			NA	NA EU	NA EU AS	NA EU AS	NA AS	Highly diverse in Miocene of Europe.
<i>Catalpa</i>				NA EU			NA AS	Plotted on the basis of winged seeds.

Figure 19. Chart showing the stratigraphic and geographic distribution of selected conifer and angiosperm genera in the Northern Hemisphere. K = Cretaceous; PA = Paleocene; EO = Eocene; OL = Oligocene; MI = Miocene; PL = Pliocene + Pleistocene; RE = Recent; NA = North America; EU = Europe; AS = Asia. The symbol > indicates fossils unknown from that interval but inferred because of related species in both older and younger intervals.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	P A	EO	OL	M I	PL	RE	
<i>Cedrelospermum</i>			NA EU	NA EU	EU			Eocene North Atlantic crossing; absent from Asia.
<i>Cercidiphyllum</i>				NA EU	NA EU	EU AS	AS	Fruits in clusters. Racemose fruit occurrences are treated here as <i>Nyssidium</i> .
<i>Comptonia</i>		AS	NA EU AS	NA EU AS	NA EU AS	> EU AS	NA	Eastern North American endemic today with circumboreal Tertiary distribution.
<i>Cornus</i>		NA	NA EU	NA EU AS	NA EU	> EU	NA EU AS	Also native today in South America and Africa.
<i>Corylopsis</i>			NA EU	EU	EU	EU	AS	Eocene North Atlantic crossing; subsequent arrival in Asia.
<i>Craigia</i>			NA SP AS	NA EU AS	EU AS	EU AS	AS	North America, Asia and Spitsbergen (SP) in Eocene; Oligocene appearance in central Europe.
<i>Cruciptera</i>			NA EU	NA				Eocene North Atlantic crossing; absent from Asia.
<i>Cyclocarya</i>		NA	NA	EU AS	EU AS	EU AS	AS	First appearance in N. America; survival in Europe through Pliocene and in Asia through Recent.
<i>Decodon</i>			NA EU	EU AS	EU AS	EU	NA	Eocene North Atlantic crossing, subsequent arrival in Asia.
<i>Dipteronia</i>		NA	NA AS	NA			AS	Tertiary Beringial crossing.
<i>Emmenopterys</i>			NA				AS	Possible Beringial crossing.
<i>Ensete</i>			NA				AS	Also extant in Africa.
<i>Eucommia</i>			NA AS	NA AS	EU AS	EU AS	AS	Paleogene Beringial crossing; subsequent arrival in Europe.

Figure. 19. Continued.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	P A	EO	OL	M I	PL	RE	
<i>Fagopsiphyllum</i>		NA EU	AS					Paleocene North Atlantic crossing, Eocene arrival in Asia.
<i>Fagus</i>				NA EU AS	NA EU AS	> EU AS	NA EU AS	Dispersed rapidly across Northern Hemisphere in early Oligocene.
<i>Florissantia</i>			NA	NA	AS			Tertiary Beringial crossing; absent from Europe.
<i>Fraxinus</i>			NA	NA EU	NA EU AS	> > AS	NA EU AS	Ignore leaf reports in favor of samaras.
<i>Gordonia</i>			NA EU	> EU	NA EU	>	NA AS	Eocene North Atlantic crossing, subsequent arrival in Asia.
<i>Glyptostrobus</i>		NA EU AS	NA EU AS	EU AS	NA EU AS	EU AS	AS	Asian endemic today with former circumboreal distribution.
<i>Halesia</i>					EU	EU	NA AS	Winged fruits with prominent intramarginal veins.
<i>Hydrangea</i>			NA EU	NA EU	NA EU AS	> EU >	NA AS	Occurrences confirmed from calyces.
<i>Illicium</i>			EU		NA	>	NA AS	North American fossil occurrence based on fruit; European based on seeds.
<i>Iodes</i>			NA EU	EU			AS	Plotted distribution includes <i>Palaeohosiea</i> . Also occurs in Africa today.
<i>Juglans</i>			NA	NA EU AS	NA EU AS	NA EU AS	NA EU AS	Sec. <i>Rhysocaryon</i> confined to N America. Sec. <i>Cardiocaryon</i> circumboreal in Oligocene.
<i>Koelreuteria</i>			NA	EU	EU AS		AS	Eo-Oligocene North Atlantic crossing, subsequent appearance in Asia.
<i>Langtonia</i>		NA	NA EU					Late Paleocene or Eocene North Atlantic crossing.

Figure. 19. Continued.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	P A	EO	OL	M I	PL	RE	
<i>Leitneria</i>				AS	EU AS	EU	NA	North American endemic with Eurasian fossil record.
<i>Limnobiophyllum</i>		NA AS	NA		EU			Paleocene Beringial crossing; subsequent arrival in Europe.
<i>Liquidambar</i>			NA AS	NA EU AS	NA EU AS	EU AS	NA AS	Distinctive leaves and infructescences.
<i>Liriodendron</i>				EU	NA EU AS	EU >	NA AS	Good Tertiary record in Europe despite absence there today.
<i>Macginitiea</i>		NA AS	NA AS					Paleocene Beringial crossing.
<i>Mahonia</i>			NA	NA EU	NA EU	>	NA AS	Initial North Atlantic crossing; subsequent arrival in Asia.
<i>Mastixia</i>			NA EU	EU	EU	EU	AS	Initial North Atlantic crossing; subsequent arrival in Asia.
<i>Meliosma</i>	NA EU	NA EU	NA EU	EU	EU	EU	NA AS	Initial North Atlantic crossing; subsequent arrival in Asia.
<i>Metasequoia</i>	NA AS	NA EU AS	NA AS	NA AS	NA AS	AS	AS	Classic example of Chinese living fossil.
<i>Nordenskioldia</i>	NA NA	NA EU AS	NA AS		NA			Circumboreal in Paleocene, North American endemic in Miocene.
<i>Nyssa</i>		NA	NA EU	NA EU AS	NA EU AS	NA EU AS	NA AS	Classic Amer-Asian disjunct modern distribution with former European distribution.
<i>Nyssidium</i>	NA AS	NA EU AS	NA EU AS					Circumboreal Paleocene to Eocene; precursor of <i>Cercidiphyllum</i> .
<i>Palaeocarpinus</i>		NA EU AS	NA AS					Paleocene circumboreal.

Figure. 19. Continued.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	P A	EO	OL	M I	PL	RE	
<i>Palaeophytocrene</i>		NA	NA EU	NA				Eocene North Atlantic crossing.
<i>Paliurus</i>			NA AS	NA EU AS	NA EU AS	> AS	EU AS	Eocene Beringial crossing; Late Oligocene appearance in Europe.
<i>Pentoperculum</i>			NA EU					Eocene North Atlantic crossing.
<i>Platanites</i>	NA	NA EU	NA					Maastrichtian or Paleocene North Atlantic crossing.
<i>Platycarya</i>			NA EU				AS	Early Eocene North Atlantic crossing; Late Tertiary arrival in Asia.
<i>Porosia</i>	NA ?	NA AS	NA ?					Paleocene Beringial crossing.
<i>Pterocarya</i>				NA EU	NA EU AS	EU AS	EU AS	Distribution plotted on the basis of diagnostic biwinged fruits.
<i>Pyrenacantha</i>			NA EU				AS	Also in Oligocene Fayum flora, Egypt. Disjunct between Asia and Africa today.
<i>Quereuxia</i>	NA AS	NA AS						Maastrichtian Beringial crossing.
<i>Sabal</i>	NA	NA EU	NA EU AS	NA EU AS	NA EU AS	> EU	NA	Distribution plotted on the basis of distinctive seeds and costapalmate leaves.
<i>Sargentodoxa</i>			NA		NA	EU	AS	Chinese endemic with Eur-American history.
<i>Schisandra</i>			NA			EU	NA AS	Classic Amer-Asian disjunct distribution with former European distribution.
<i>Symplocos</i>			NA EU	EU	NA EU	EU	NA AS	Eocene North Atlantic crossing.
<i>Tapiscia</i>			NA EU				AS	Eocene North Atlantic crossing; subsequently in Asia. Sister genus <i>Huertea</i> extant in Cuba.

Figure. 19. Continued.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	PA	EO	OL	MI	PL	RE	
<i>Tetraclinis</i>			EU	NA EU	EU	EU	EU	Eo-Oligocene North Atlantic crossing.
<i>Tilia</i>			NA	NA EU AS	NA EU AS	> EU AS	NA EU AS	Bract characters indicate initial North Atlantic crossing with subsequent arrival in Asia.
<i>Toricellia</i>			NA EU		EU		AS	Eocene North Atlantic crossing with subsequent arrival in Asia.
<i>Trapa</i>	AS				NA EU AS	EU	EU AS	Earliest known occurrence is <i>Palaeotrappa</i> from Maastrichtian of Koryak Upland.
<i>Trochodendron</i>			NA		NA AS		AS	Miocene or prior connection across Beringia.

Figure 19. Continued.

North American localities in Tennessee, Kentucky, and Mississippi. The Eocene Mississippi Embayment floras have a diversity of legumes and Theaceae not observed in the western North American Tertiary. These floristic differences may indicate barriers to dispersal as well as environmental dissimilarity due to the differences in latitude and physiographic relief.

Some components of the Middle Eocene Claiborne flora in Tennessee and Kentucky, although assigned to extinct genera, seem to show closest affinities to taxa living in South America today (Roth & Dilcher, 1979; Taylor & Crepet, 1987).

Investigating the diversity of legumes in the Eocene of southeastern North America, Herendeen (1992) recognized three genera of tropical South American affinity, two of tropical Asia and Africa, two of pan-tropical distribution, and two of temperate North America and Asia. Noting that many legumes are tolerant of saline conditions and can be dispersed across ocean barriers, Herendeen (1992) proposed that there may have been exchange between the Mississippi Embayment and South America by way of ocean currents. This scenario would also explain the occurrence of *Crepetocarpon* Dilcher & Manchester, a close relative of *Hippomane* (Euphorbi-

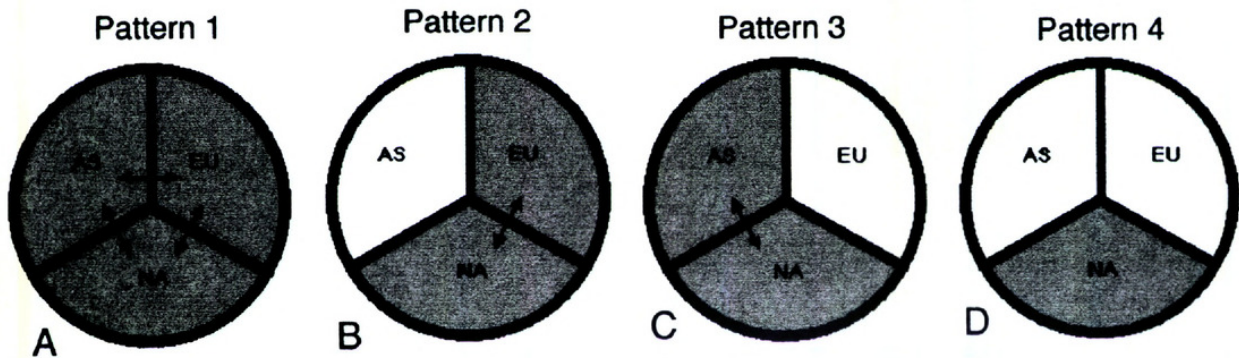


Figure 20. Four main patterns of geographic distribution of taxa in the Northern Hemisphere, emphasizing the possible ties between North America and adjoining northern landmasses. —A. Circumboreal. —B. Euro-American, indicating interchange between Europe and North America, usually inferred to have occurred via land bridge(s) in the North Atlantic. —C. Amer-Asian, indicating interchange between North America and Asia, probably via Beringia. —D. Endemic, taxa that are not known outside North America during a particular time interval. NA = North America; AS = Asia; EU = Europe.

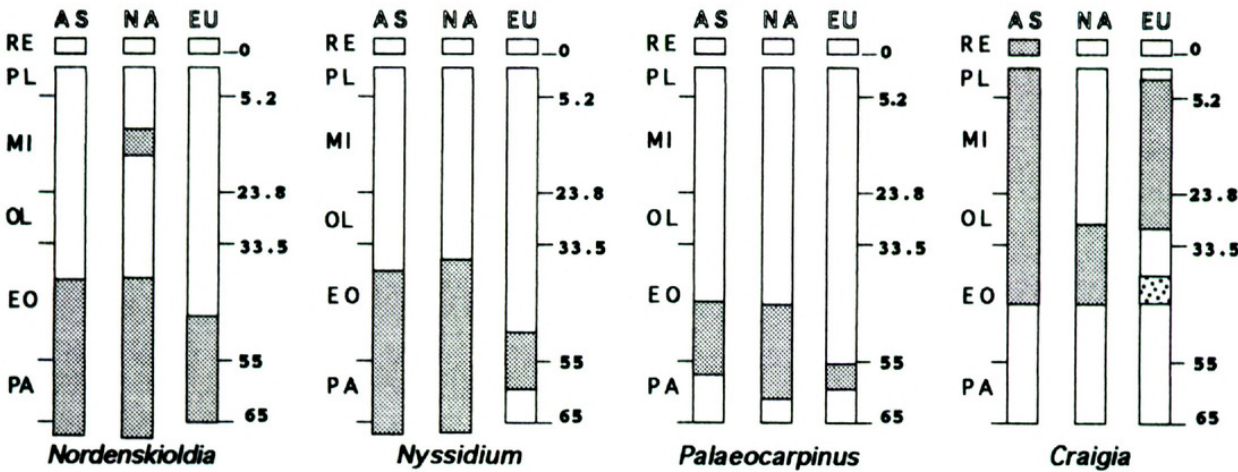


Figure 21. Examples of genera with circumboreal distribution patterns during the Paleocene (*Nordenskioldia*, *Nyssidium*, *Palaeocarpinus*) and Eocene (*Craigia*). Spitsbergen occurrence stippled in the column for Europe.

aceae), in the Eocene of the Mississippi embayment area (Dilcher & Manchester, 1988).

OLIGOCENE

Climatic cooling near the end of the Eocene resulted in the reduction in range of numerous thermophilic taxa in North America and Europe. Few North American Oligocene floras have been studied in detail, but an overview of assemblages that are available for study reveals that the diversity of broad-leaved evergreen taxa such as Icacinaceae, Lauraceae, Menispermaceae, and others had declined considerably since the middle Eocene. Temperate genera, many of which were already established by the late Eocene, become dominant elements. Still, approximately 13% of genera from the early Oligocene Bridge Creek flora, Oregon, are extinct (Meyer & Manchester, 1997).

Comparison of early Oligocene floras in North

America and central Europe reveals high levels of generic similarity, indicating either that these plants were still able to migrate across the North Atlantic or that they had already spread across both continents prior to the Oligocene and maintained their similarity through evolutionary stasis on either side of the Atlantic Ocean. Studies at the species level are needed to determine the extent of taxonomic similarity between these floras.

MIOCENE

The maximum expansion of mixed mesophytic forest across the Northern Hemisphere was reached by the Middle Miocene. Useful overviews of Miocene floras are presented in Chaney and Axelrod (1959), Rember (1991), Graham (1993), Fields (1996), and Tiffney (1977a–1994a). A large proportion of the arborescent genera known from the Miocene of North America are also seen in the Mio-

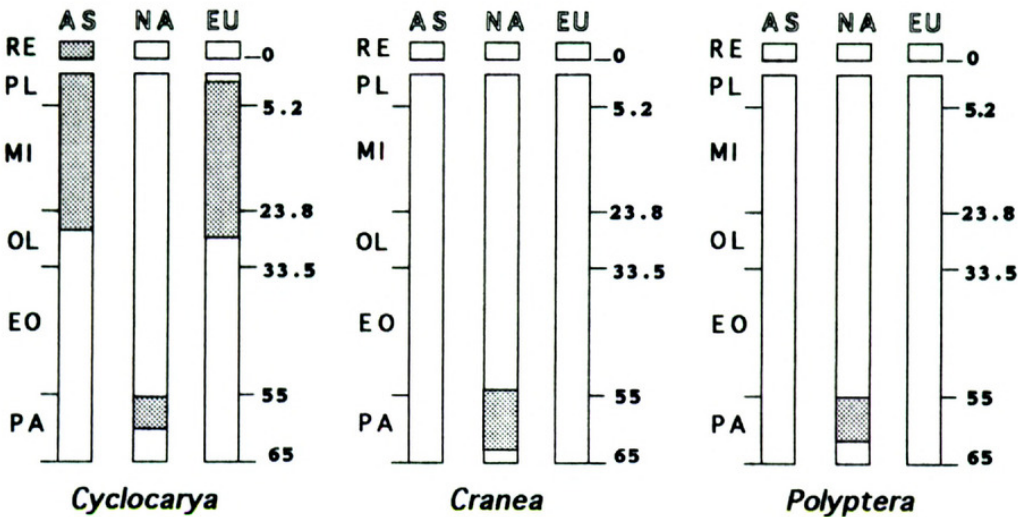


Figure 22. Examples of North American Paleocene endemic genera.

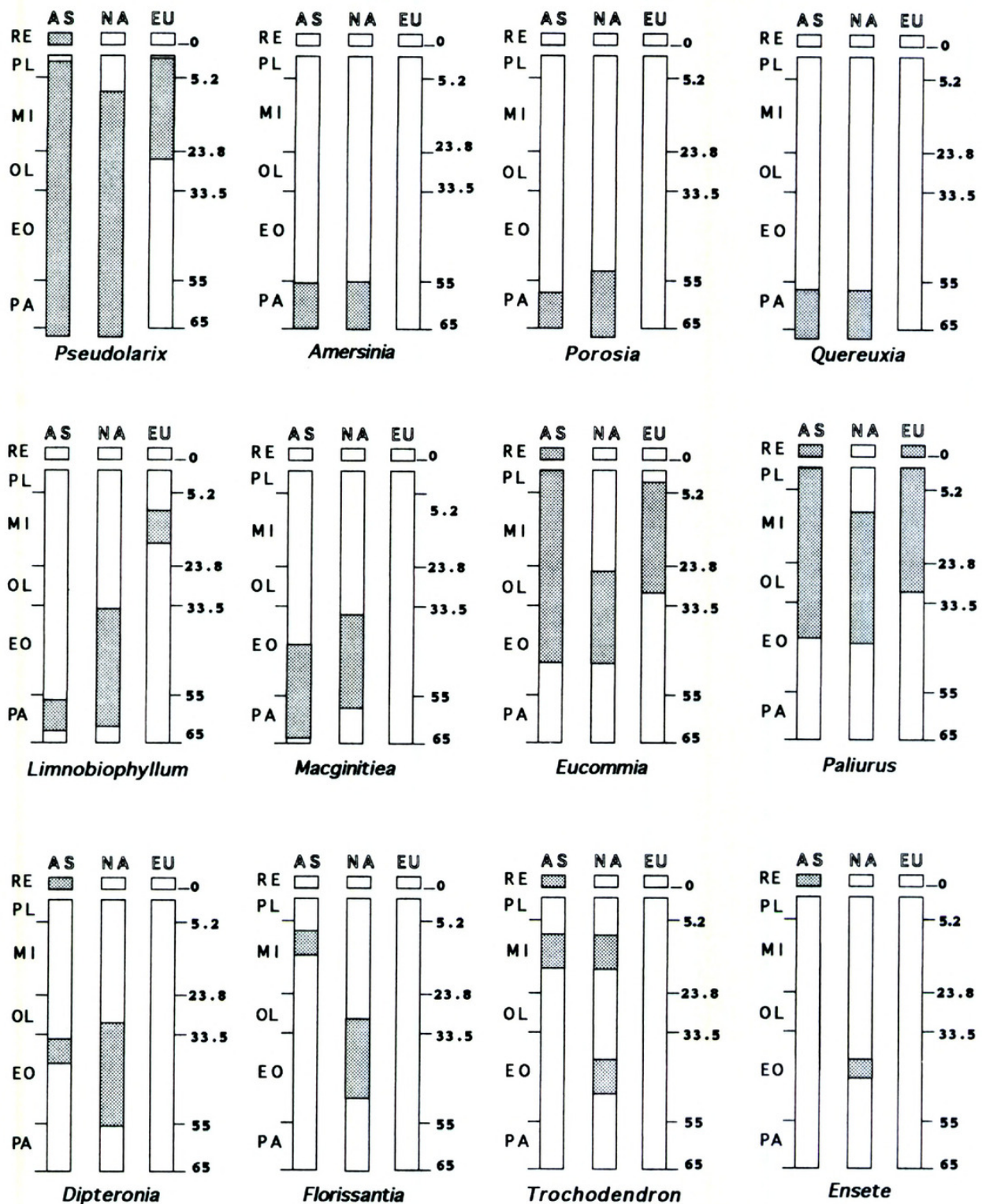


Figure 23. "Beringia crossers." The first six examples suggest direct interchange between Asia and North America during the Paleocene. The other examples appear to indicate a later, perhaps Eocene, interval of interchange between the two continents. In three instances (*Eucommia*, *Paliurus*, *Pseudolarix*), the genera subsequently colonized Europe.

cene of Europe and Asia, indicating that by this time the Euro-American flora had spread into Asia. At the same time we may expect that Asian elements were invading Europe and North America, such as *Trapa*. The first North American record of

Liriodendron occurs at this time; either it was "hiding out" prior to the Miocene, or it arrived relatively late from another continent. The arrival of Euro-American elements in Asia may have been by both routes, Beringia and Turgai. Presumably, however,

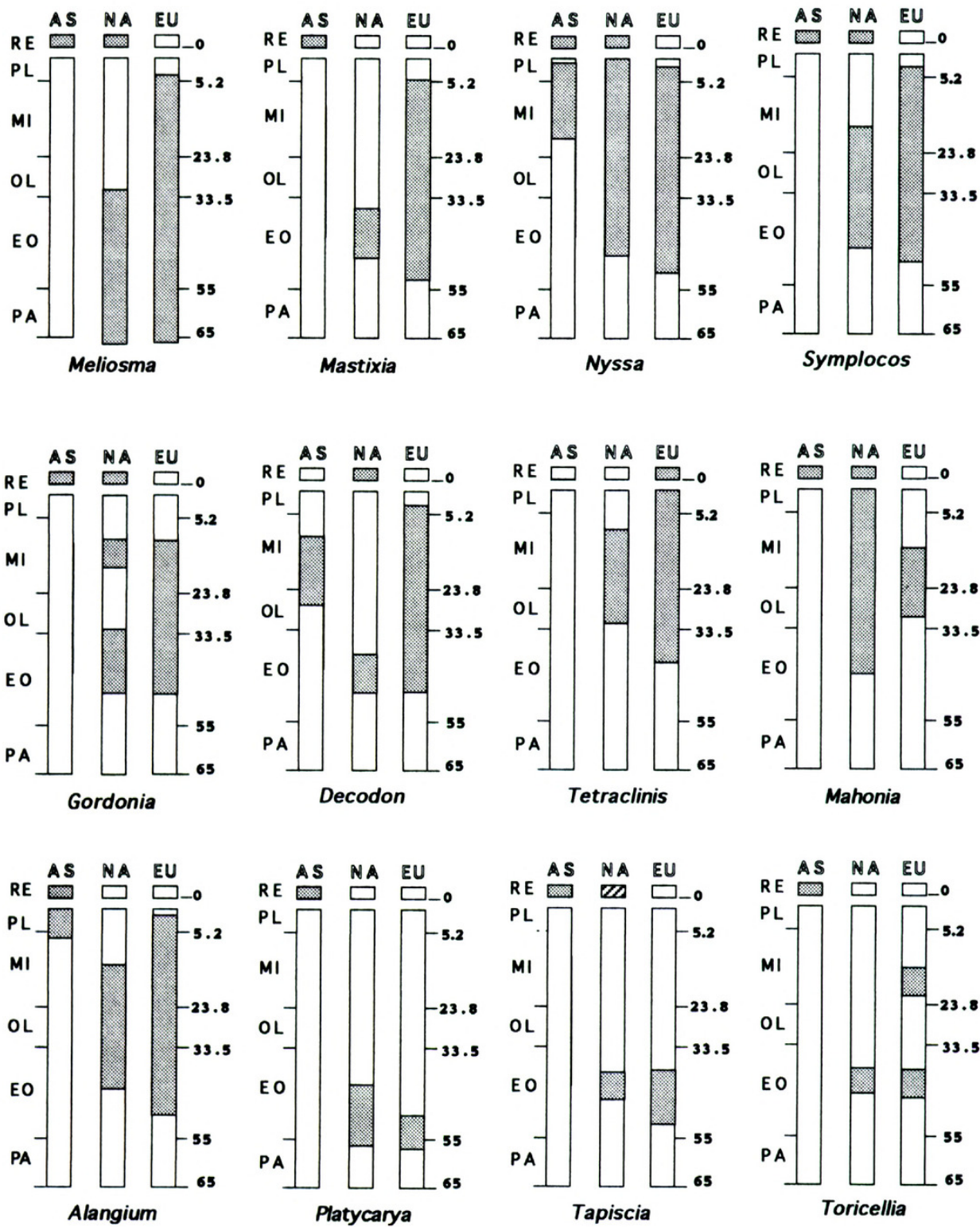


Figure 24. Extant genera of initial Euramerican distribution, in some cases with subsequent arrival in Asia. Diagonally stippled box represents *Huertea*, the extant Cuban sister genus to *Tapiscia*.

the more thermophilic elements would have come by way of Europe and the Turgai crossing, because the relatively high latitude of the Beringial connection would have been inhospitable for tropical species (Tiffney, 1994b).

The majority of North American Miocene genera

are still living in the Northern Hemisphere today. Even in the Middle Miocene, however, there are some conspicuous extinct genera remaining, including *Diplodipelta* Manchester & Donoghue, *Nordenskioldia* (Fig. 21), and *Pseudofagus* Smiley & Huggins.

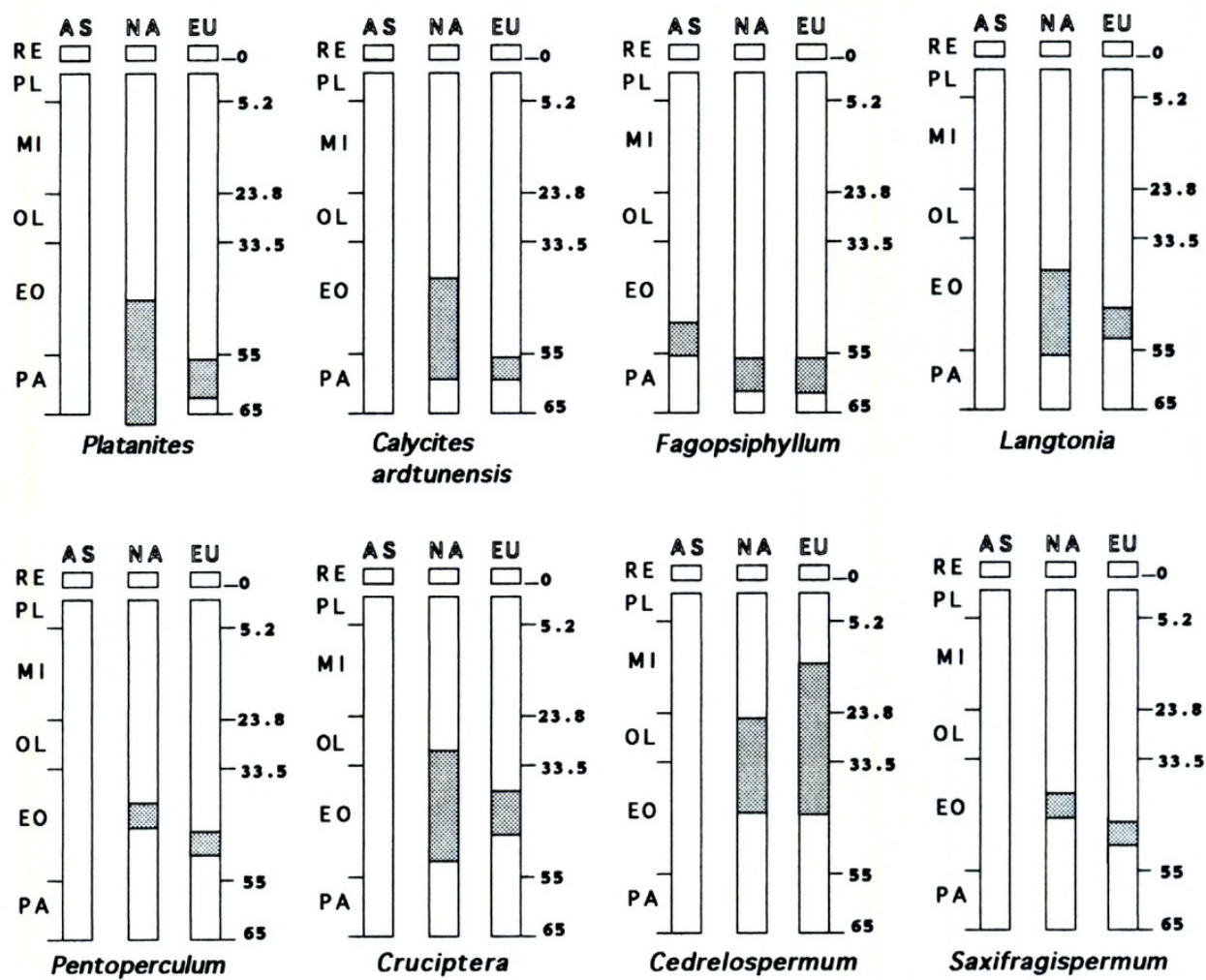


Figure 25. Extinct genera that apparently crossed the North Atlantic. The first four examples appear to indicate interchange between Europe and North America during or prior to the Paleocene, whereas the other examples appear to indicate Eocene interchange.

GENERAL OBSERVATIONS

Extinct genera have commonly been overlooked or ignored in phytogeographic studies, possibly because of the lack of modern analogs for direct environmental interpretations. Nevertheless, extinct genera are useful to illustrate important paleogeographic patterns. Figure 25 shows the ranges of extinct genera that appear to have crossed the North Atlantic: *Cedrelospermum* Saporta, *Cruciptera* Manchester, *Fagopsiphyllum* gen. nov., *Langtonia* Reid & Chandler, *Pentoperculum* Manchester, *Platanites* Forbes, and *Saxifragispermum* Reid & Chandler. *Platanites* was established in North America already in the Maastrichtian, and it is possible that the passage between Europe and North America occurred prior to the Paleocene. From the other examples we may infer passage across the North Atlantic during the late Paleocene (*Fagopsiphyllum*, *Langtonia*) or later. Most of these genera became extinct by the end of the Eocene, but *Cruciptera* persisted into the early Oligocene in North

America, and *Cedrelospermum* made it into the late Miocene of Europe. Of these genera, only *Fagopsiphyllum* arrived later in Asia. The others are unknown from the Asian record. The absence of most of these genera from the Asian fossil record cannot be attributed solely to lack of adequate sampling in Asia. The winged fruits *Cedrelospermum* and *Cruciptera* are distinctive, easily recognized taxa that commonly preserve in lacustrine localities. Thus, if they were present near areas of deposition, we would expect to find them among the numerous Asian shale deposits from which leaves have been collected over the past century.

Figure 24 shows the distribution of selected modern genera with records indicating early Tertiary exchange between North America and Europe. A common pattern observed in these data is that of taxa shared between the Eocene of Europe and North America that are indigenous to Asia today. In many instances the genera have become extinct both in North America and Europe but survive only

in Asia today. Examples include *Actinidia*, *Ailanthus*, *Amentotaxus*, *Cercidiphyllum*, *Corylopsis*, *Diplopanax*, *Mastixia*, *Toricellia*, and *Platycarya*. These genera, including both thermophilic and mesophytic taxa, evidently were able to cross between North America and Europe, but were blocked from entering Asia until later in the Tertiary. The paucity or lack of *Mahonia* in the Asian fossil record is striking because this leaf type would easily be recognized if present. It is also worth noting that *Platycarya* has very distinctive pollen that could easily be recognized if present in the Tertiary of Asia. Some other taxa shared between the Eocene of Europe and North America are found both in Asia and tropical America today (*Meliosma*, *Symplocos*). *Tapiscia* is native to Asia today, and its sister genus *Huertea* of the Caribbean region suggests a fragmentation of a more continuous ancestral range (Manchester, 1988). Some genera found in the Eocene of North America that now occur both in Africa and Asia include *Ensete*, *Iodes*, and *Pyrenacantha*.

Figure 23 shows some taxa that appear to have dispersed directly between North America and Asia, i.e., across Beringia. These include *Amersinia* Manchester, Crane & Golovneva, *Dipteronia*, *Eucommia*, *Florissantia* Knowlton, *Quereuxia* Krysh-tofovich ex Nevolina, *Limnobiophyllum* Krassilov emend. Kvaček, *Macginitiea* Wolfe & Wehr, *Paliurus*, *Porosia*, and *Trochodendron*. These taxa suggest crossings of Beringia during the Paleocene (*Macginitiea*, *Amersinia*, *Porosia*), Eocene (*Eucommia*), and later, *Florissantia*, distributed from the Eocene to Oligocene in western North America, is known only in the Miocene of eastern Asia, suggesting a post-middle Eocene, pre-middle Miocene crossing. Thus, it appears that crossings were possible at various times during the Tertiary. Indeed, it has been suggested that a land connection existed, and that the only barrier was climate. Three of the genera shown in Figure 23 succeeded in colonizing Europe later in the Tertiary, after the initial dispersal between Asia and North America.

Some of the genera endemic today to North America, such as *Sequoia*, *Sabal*, *Comptonia*, and *Decodon*, have fossil records showing former widespread distribution in the Northern Hemisphere (examples in Fig. 19). *Decodon*, which survives today only in eastern North America, has a good fossil record in both North America and Europe. *Pinckneya* is limited to the southeastern United States today, but is known from the Oligocene of western North America. Although endemic to the southeastern United States, *Leitneria* has no con-

firmed North American fossil record, but it is well documented in central Europe to western Siberia.

Extant genera that have attracted special attention because of their modern disjunct distribution between North America and Asia and/or the Caucasus region include *Carya*, *Catalpa*, *Gordonia*, *Halesia*, *Liquidambar*, *Liriodendron*, *Magnolia*, *Nyssa*, *Platanus*, *Pterocarya*, and *Schisandra*. Each of these has reliable fossil records throughout the northern continents (examples in Fig. 19). Others are found today in all three northern continents, but have their earliest known megafossil records in North America, e.g., *Fagus*, *Ostrya*, and *Tilia*. Still others occur in both Europe and Asia today but are absent from the extant flora of North America despite their presence in the Tertiary, e.g., *Trapa*, *Paliurus*. Additional examples are provided by Tiffney (1994b).

Many of the genera found as fossils in the western part of North America are no longer native to that region today, but survive in eastern North America or in Asia. The extirpation of these taxa in western North America may have been brought on by increasing summer drought in the late Tertiary (Axelrod & Schorn, 1994).

Those taxa that are found first in Europe and North America and subsequently in Asia (Fig. 24, except *Tetraclinis*) are likely to have crossed the North Atlantic prior to arriving in Asia. However, it is difficult to determine the more parsimonious route to explain their arrival in Asia. They could have arrived from Europe as the Turgai seaway receded, or they could have arrived from North America via Beringia. Indeed, it is likely that both directions were involved and that different taxa followed independent courses.

In instances where the primary crossing was between North America and Asia, the subsequent arrival in Europe could be attributed either to a North Atlantic crossing or to a Turgai crossing. Comparative phylogenetic analyses at the species level may be required to unravel the probable sequences and directions of migration. It is likely, for example, that *Acer* first crossed between North America and Asia, and then from Asia into Europe. This conclusion derives from the observation that several Tertiary species belong to sections that are shared between the Eocene and Oligocene of North America and Asia (and not Europe), and that *Acer* arrived later in Europe with some species corresponding to the Asian, rather than American, sections. The occurrences of *Dipteronia* and the extinct genus, *Deviacer* Manchester (1994b; Wehr, 1995), in the North American early Tertiary suggest an initial radiation

of "Aceraceae" in North America followed by successive emigration to Asia and to Europe.

How late was migration between North America and Europe possible? It is considered likely that separation of landmasses in the North Atlantic severed biogeographic ties between Europe and North America by the late Eocene (Tiffney, 1985a, b; Woodburne & Swisher, 1995). In this context, it is interesting that *Buzekia* samaras are found both in the late Oligocene and early Miocene of central Europe (Fig. 16A), and in the middle Miocene of Idaho (Fig. 16B). This might be an indication that plants could still disperse between the two continents in the Oligocene or Neogene. Alternatively, it may be that the known fossil occurrences reflect an earlier, perhaps Eocene, dispersal of a species that remained morphologically unchanged for millions of years following isolation of the two populations.

Although the main sources of North American vegetation appear to be Laurasian, Dilcher (1973), Taylor (1990), and Herendeen (1992) have called attention to apparent ties with South America and/or Africa. Particularly in the Eocene of southeastern North America, there appear to be some affinities with the flora of South America. In most of these instances it is not known whether the taxa were already in South America during the early Tertiary, but their presence there in the modern-day flora indicates that floristic exchange did occur at some times in the past. *Juglans* appears to have had a North American origin, with first occurrences in the Eocene (Manchester, 1987a). Black walnuts from the late Miocene or early Pliocene Punta Gorda Formation of Ecuador (Brown, 1946b) indicate that *Juglans* sect. *Rhysocaryon* entered South America by the Pliocene. Today the black walnuts are also distributed in the Caribbean, suggesting that a route through the Caribbean area may have facilitated its colonization of South America.

Although there seems to be some support for limited floristic exchange between the floras of southeastern North America and South America, there is very little evidence for the introduction of southern elements into western North America during the Tertiary. Although MacGinitie (1953) reported some extant South American elements in the Florissant flora (e.g., *Astronium*, *Lomatia*, *Petrea*), none of these have withstood more detailed comparative analyses (Manchester, in press). Clearly, there was some interchange with Mexico, as indicated by the correspondence of *Populus wilmattae* of the Green River formation with extant *P. mexicana* Wesm. (Eckenwalder, 1980; Manchester et al., 1986), the occurrence of several "arctotertiary elements" in

the mountains of Mexico, and by the occurrence of *Cedrelospermum* and *Eucommia* as far south as Puebla Province during the late Tertiary (Magallón & Cevallos, 1994a-c).

The Arctotertiary concept, that many of the Northern Hemisphere temperate taxa evolved at high latitudes and moved southward across North America, Europe, and Asia as the climate cooled, is neither confirmed nor disproved by this review. Clearly, land connections at high latitude were important to the intercontinental dispersal of plants during the Tertiary, and it is plausible that the high latitudes may have served as a "cradle" for some species. However, few if any of the taxa reviewed in this study show identical patterns of geographic dispersal, and it is unlikely that any single mechanism can account for the separate histories of so many different taxa. Although some temperate elements may have descended from the North, many others may have evolved at high elevations in the early Tertiary and spread across lower elevations subsequently as climate cooled near the end of the Eocene.

As paleobotanical work continues, and carefully determined stratigraphic and geographic occurrences of particular taxa are added to computer databases, it is becoming possible to study the distribution patterns of particular species, and the vegetation that they comprise, through the Tertiary in some regions (Kovar-Eder et al., 1996). Eventually such studies can be expanded to allow direct comparison of the patterns in different continents with higher taxonomic, geographic, and temporal resolution than I have been able to provide here. In addition, molecular and morphological phylogenetic investigations of extant genera disjunct between two or more of the refugial regions can be compared with the paleobotanical data to provide improved resolution of the times and places of divergence between extant species (Wen, 1998, in press).

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APPENDIX 1

In the process of preparing this review, several nomenclatural revisions became necessary, including new generic names and new combinations. Information required to validate these names is provided below in alphabetical sequence.

Buzekia Manchester, gen. nov.

DIAGNOSIS (from species diagnosis of Bůžek, 1992: 20): “Fruits small, winged, indehiscent, with one central locule and a single seed. The wing surrounds the seed locule (fruit body) and has a small incision at the base. Stipe short, narrow, tapering. The fruit body is circular or sub-circular and 0.3–0.4 cm in diameter. The wing is up to 0.6 cm wide. The width of the entire fruit is 0.7–1.3 cm (in vertical direction up to 1.5 cm). The fruit body and wing are covered with a prominent, single venation system. The venation pattern of the fruit body consists of an irregular network of polygonal meshes and is connected with the wing venation which consists of radially oriented



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